

THE INFLUENCE OF RECOVERY FROM VIRUS DISEASES ON THE RATE OF PHOTOSYNTHESIS AND NETT ENERGY CONTENT OF HOP PLANTS (*HUMULUS LUPULUS* L.)*

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The influence of recovery from the complex of virus diseases on photosynthetic characteristics of Saaz semi-early red bine hop (Osvald clone No. 72) was investigated in the hop gardens of the Hop Research Institute in Žatec. The plants were monitored in the years 2001 and 2002. The photosynthetic rate and the pigment content in leaves and the energy content in the above-ground parts of the hop plants were determined. Recovered plants showed higher photosynthetic rate in comparison with non-recovered plants. During the vegetation season, the recovered hop plants had an average photosynthetic rate of $8.44 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ and non-recovered $5.78 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$. Plant recovery didn't influence the changes in pigment amount in the leaf tissues. These changes were caused by the weather conditions during the investigation period. During both experimental years higher nett energy values for recovered plants were found in comparison with non-recovered plants. In 2001 the average nett energy content was 16.33 kJ g^{-1} in recovered plants and 16.00 kJ g^{-1} in non-recovered plants. In 2002 the average nett energy content was 16.25 kJ g^{-1} in recovered plants and 16.11 kJ g^{-1} in non-recovered plants. The highest average values of nett energy content were determined for the generative organs (hop cones), the smallest nett energy contents were located in the hop bine.

Humulus lupulus L.; hop plants; virus diseases; recovery; rate of photosynthesis; pigments; nett energy content

INTRODUCTION

The long term hop cultivation and the mostly traditional technology of hop growing caused a significant increase of pathogens, largely viruses and viroids, in the hop gardens. The yield of affected hop plants decreases and they do not make use of their potential yield even when effective agricultural engineering is applied. Modern *in vitro* cultivation methods allow healthy clones to grow free of viruses and viroids after the use of apical meristem. The photosynthesis of hop plants was studied mainly in the 1970's. Currently there are no publications studying the photosynthetic differences between the recovered and non-recovered hop clones.

The whole above-ground part of the hop plants, except fruits (hop stones), is adapted to intensive photosynthesis. However, leaves of bines and leaves of shoots are the main organs of photosynthesis (Rybáček, 1980). In cases where the hop plant is contaminated by a viral infection the leaves are the most damaged part of the plant which results in a decrease in the photosynthetic efficiency of an individual. The decrease in the rate of photosynthesis, caused by the decrease of chlorophyll content, in *Eupatorium makinoi* L. infected by tobacco leaf curl virus was proved by Funayama-Noguchi and Terashima (2006). Similar results were published by Guo et al. (2005) who recorded the decrease in the rate of photosyn-

thesis, the rate of transpiration, the chlorophyll content and the increase in CO_2 extracellular concentration on white mustard infected by the turnip mosaic virus. The viral leaf-roll in the experiments of Bertamini et al. (2004) caused a significant decrease in the rate of photosynthesis and the rate of transpiration and stomatal conductance in *Vitis vinifera* L. plants.

The gross calorific value calorimetrical assessment of the plant tissues' dry matter and the subsequent calculation of nett energy in the dry matter unit proved to be a suitable method for photosynthetic rate measurements. The calorific value of the individual plant parts depends upon the chemicals present in these organs. Sugars have the lowest energy content (glucose 15.4 kJ g^{-1} , sucrose 16.5 kJ g^{-1}). Starch contains about 17.4 kJ g^{-1} , cellulose 17.6 kJ g^{-1} , lignin 26.3 kJ g^{-1} . In general, carbohydrates contain 17.2 kJ g^{-1} , proteins 23.7 kJ g^{-1} , lipids 39.6 kJ g^{-1} (Larcher, 2003).

The methods of combustion calorimetry were used in the experiments of Hniličková (1999) where the differences of photosynthetic rate between irrigated and non-irrigated hops were observed. Also the translocation of assimilates between individual parts of the above-ground organs of the hop plants during the vegetation period was observed. The maximum energy in the individual organs of the hop plant was concentrated into the period of the intensive growth of leaves.

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Nett energy was decreasing in the next stages of vegetation development with the exception of hop bines where an increase of nett energy during the harvesting period was measured. In comparing individual organs, the greatest amount of nett energy was accumulated in the leaves of bines, which ranged from 16.80 to 17.77 kJ g⁻¹.

The percentage of energy in the individual parts of the hop plants of the Osvald's clone was studied by K a f k a (1983). The amount of energy stored in the above-ground shoots part of the plant was in the range of 23–41% in the hop cones. However, the most common range was between 25–35 %. After the harvest of the hop cones (the agriculturally usable part) 65–75% of energy still remains in the plant. Depending on the year, there is 52–57% of energy utilised in bines and 43–48% in leaves on bines and leaves on shoots.

A caloric value of different parts (a root, a trunk, branches, leaves) of *Tectona grandis* L. was measured by P a n d i t and J a n a (2001). The smallest energy value of the dry matter was found in branches – 20.05 kJ g⁻¹ – during the winter period. The highest energy value was also noted in the branches – 24.25 kJ g⁻¹ – during the summer period. The energy value in the mangrove trunks in a reserve of the Hainan province was measured by L i n et al. (2000). The netto energy values ranged from 17.70 to 20.10 kJ g⁻¹. V o o k o v á (1985) established the average caloric value of the individual parts of eighteen common woody species in Malé Karpaty. The average energy content in the leaves was 19.38 kJ g⁻¹, in the tree rings 19.19 kJ g⁻¹, in the wooden parts 19.73 kJ g⁻¹ and in a tree bark 19.30 kJ g⁻¹.

MATERIAL AND METHOD

Monitored plants of the Saaz semi-early red bine hop (Osvald clone No. 72) were planted out and grown in the hop garden of the Hop Research Institute in the Žatec. The experiment was carried out using two variants of the hops. The first group was planted with the use of cutting transplants of the hop field clones of mother plants. The second group of individuals was obtained from recovered meristematised *in vitro* cultures. The plants were observed in the years 2001 and 2002. On the beginning of observing were plants 6 years old.

Health condition was done by evaluation of visual symptoms and of immunoenzymatic method DAS – ELISA. It was monitored agricultural most significant viruses that are – Apple mosaic virus (ApMV), Hop mosaic virus (HMV) (S v o b o d a, 1993) and viruses scheduled in EPPO for hop plants (PNRSV, CLRV, TNV, SLRV, CMC, ArMV and PMMV) (EPPO 2001). There were applied antidotes by comp. Bioreba and Löewe. From fifty plants were taken leave samples on high 2 m. The plants were analyzed on the occurrence of viruses separately. Plants for following physiological parameters were selected from that collection.

The dates of plant sampling and measuring were chosen to represent the main growth periods of the hop plant.

First sampling was in the period of establishment, second sampling in the period of shoots and shooting, third sampling in the catkins stage, fourth sampling in the flowering period and fifth sampling in the period of hop cones formation.

One in 50 plants from the field was chosen for sampling in each data collection time; every variant had five repetitions. Thirds of the above-ground parts of the hop stems were separately evaluated due to a high heterogeneity of the plant physiological processes (K a f k a, 1972; H n i l i č k o v á, 1999).

The photosynthesis rate was identified in the intact leaves by means of a commercial portable gasometric infrared analyser LCA-4 (ADC Bio Scientific Ltd., Hoddesdon, UK) with a leaf chamber LC4/PLC4BT-1/E in 2001 only.

The energy content (kJ g⁻¹ dry matter) in the samples of dry matter (approximately 0.5 g) of all measured organs from all three parts of the plant was determined using the Laget MS 10 A automatic adiabatic combustion calorimeter. The method is based upon combusting a sample of the dry matter and calculating the combustion heat from the thermal leap ascertained. After converting to dry matter mass the gross energy is determined. After allowing for the amount of ash the net energy is given.

The chlorophyll and carotenoid content was determined by the method of measuring the absorbance from the acetone solution of the photosynthetic pigments with a spectrophotometer Spekol 11. The amount of pigments in the leaf tissues was calculated with the use of a formula by A r n o n (1949).

The statistical evaluation was carried out by using the variance analysis with $\alpha = 0.05$ in the computer software Statistica, ANOVA module.

RESULTS AND DISCUSSION

In visual evaluation there was not observed any visible symptoms (eg. leave colour, shape defects). Recovered plants had more vigorous, overgrowth, stately habitus in comparison with non-recovered plants. The non-recovered hop plants were fully infected by Apple mosaic virus (ApMV) and Hop mosaic virus (HMV). These viruses were not identified on recovered plants. The others tested viruses were not detected on both variants.

The recovery of the hop plants statistically proved to have a highly positive influence on the leaf photosynthetic rate. In our experiments, the recovered hop plants had an average photosynthetic rate of 8.44 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and non-recovered 5.78 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. The photosynthetic rate of the recovered hop plants ranged from 2.42 to 15.41 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and from 1.90 till 11.78 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in non-recovered plants (Fig. 1). Higher values of photosynthetic rate of hop plants in the fields trials were published by K e n n y (2005). Forty hop genotypes had a photosynthetic rate ranging between 9.00 and 22.30 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and the average value from the whole experiment was 16.20 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Lower values of photo-

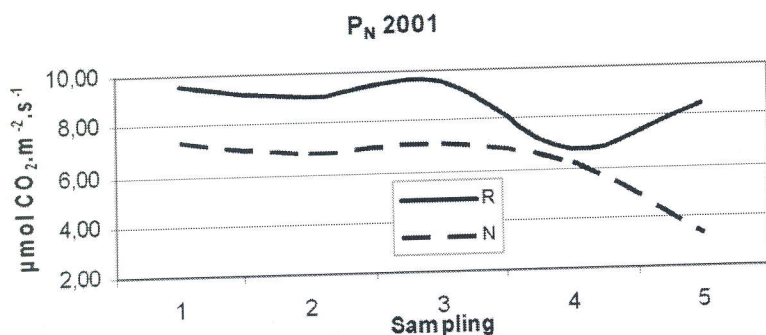


Fig. 1. The photosynthetic rate of recovered (R) and non-recovered (N) hop plants during the growth season

Table 1. Statistical evaluation of chlorophylls' and carotenoids' content – analysis of variance between 2001 and 2002

Tukey HSD test		Variable Ch <i>a+b</i> Variance = 0.02542 Degree of freedom = 98.000		Variable Carotenoids Variance = 0.00353 Degree of freedom = 98.000	
	Year	{1}	{2}	{1}	{2}
	2001	1.0213	0.89052	0.35115	0.27715
1	2001		0.000191		0.000110
2	2002	0.000191		0.000110	

photosynthetic rate for a spring barley were measured by Hejnák (2003). The photosynthetic rate in his experiments ranged between 5.72 and 15.14 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ with the average photosynthetic rate of 10.83 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ from the whole crop. These results correspond with the report on sugar cane by GLAZ et al. (2004) where the average photosynthetic rate was 8.60 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

During the vegetation season the photosynthetic rate decreased (Fig. 1). In the first date of measuring, the average photosynthetic rate was the highest for both variants. It was 9.59 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for recovered plants and 7.30 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for non-recovered plants. In the second half of the vegetation period the photosynthetic rate decreased in the recovered treatment to an average of 6.74 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at the fourth date of measuring. The decrease of photosynthetic rate in non-recovered plants was deeper and more permanent. The lowest average value of 3.29 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ was recorded for the last date of measuring. There were no statistically significant differences between individual thirds of the plants, the data collection time, bine and shoot leaves.

The influence of the year on the amount of leaf pigments was highly significant for both chlorophylls and carotenoids (Table 1). Both pigments were presented in higher amounts in 2001. The average chlorophyll content was 1.0213 mg g^{-1} in 2001 and 0.8905 mg g^{-1} in 2002.

Table 2. The pigment content in leaves of recovered and non-recovered hop plants (mg g^{-1})

Year		Ch <i>a</i>	Ch <i>b</i>	Ch <i>a/b</i>	C
2001	R	0.496	0.512	0.969	0.331
	N	0.518	0.543	0.954	0.366
2002	R	0.423	0.480	0.881	0.281
	N	0.400	0.479	0.835	0.273

Legend: R – recovery, N – non-recovery, Ch *a*, *b* – chlorophyll *a*, *b*, C – carotenoids, Ch *a/b* – chlorophyll ratio

There were statistically no significant differences in the chlorophyll and carotenoid content between recovered and non-recovered plants in either year. In 2001 the average chlorophyll *a + b* and carotenoid content was higher in non-recovered plants (Ch *a,b* = 1.0438 mg g^{-1} , C = 0.3669 mg g^{-1}) in comparison with recovered plants (Ch *a,b* = 0.9988 mg g^{-1} , C = 0.3354 mg g^{-1}). In 2002 the chlorophyll content was higher in recovered plants (Ch *a,b* = 0.9025 mg g^{-1} , C = 0.2814 mg g^{-1}) compared to non-recovered clones (Ch *a,b* = 0.8785 mg g^{-1} , C = 0.2729 mg g^{-1}). Recovered plants had a higher Ch *a/Ch b* ratio than non-recovered plants in both years (Table 2).

No differences between chlorophyll content can be caused by the long-term plants' adaptation to the complex of viruses found in their organisms. Closer examination shows no apparent difference in pigmentation of the leaf blades. Bertamini et al. (2004) showed the decrease in chlorophyll and carotenoid content in grapevine due to viral leafroll infection. Steddom et al. (2003) in their sugarbeet experiment differentiated between healthy individuals, individuals infected by a beet necrotic yellow vein virus (rhizomania agent) with symptoms and infected individuals without symptoms. Their results show that infected plants without symptoms can have higher pigment amounts than healthy plants. The author explains this fact by emphasising the higher nitrogen content in the leaves without symptoms. The differences between healthy and infected plants can probably be reduced by the influence of favourable meteorological conditions.

The energy value of the dry matter of plants ranged between 14.43 and 17.68 kJ g^{-1} in 2001 (Table 3). The average was 16.17 kJ g^{-1} . In 2002 the nett energy of the plants' dry matter ranged between 14.14 kJ g^{-1} to 18.05 kJ g^{-1} (Table 4). The average for the whole vegetation period reached 16.15 kJ g^{-1} . There were not found any statistically significant differences between the years. This fact doesn't correspond with the results of Hnilíčková

Table 3. The nett energy content (kJ g⁻¹ dry matter) in organs of individual thirds of the above-ground part of the hop stems of the recovered and non-recovered hop plants – experimental year 2001

Sampling	Third	LB		LS		HB		HC	
		R	N	R	N	R	N	R	N
1	1/3	17.02	17.15	x	x	15.87	16.13	x	x
	2/3	x	x	x	x	x	x	x	x
	3/3	x	x	x	x	x	x	x	x
2	1/3	16.12	16.12	17.21	16.18	15.90	14.96	x	x
	2/3	16.27	16.60	17.68	17.17	15.67	15.38	x	x
	3/3	17.29	17.04	x	x	15.98	16.09	x	x
3	1/3	15.16	14.88	17.02	16.10	15.47	15.37	x	x
	2/3	16.45	16.17	16.77	16.28	16.14	15.52	17.09	16.02
	3/3	16.19	16.77	16.53	16.16	16.01	15.68	16.80	17.18
4	1/3	15.19	14.54	15.89	14.96	15.11	14.94	16.84	15.27
	2/3	16.18	15.52	16.06	14.97	16.02	15.86	17.39	16.23
	3/3	16.43	16.41	16.67	15.55	15.94	15.65	16.54	15.83
5	1/3	15.23	14.43	15.24	16.33	15.64	15.87	17.46	16.52
	2/3	16.05	16.65	16.87	16.82	15.66	15.25	17.59	17.61
	3/3	16.60	16.13	16.56	16.75	15.98	15.65	16.93	17.43

Legend: HB – hop bine, HC – hop cones, LB – leaves of bines, LS – leaves of shoots, N – non-recovery, R – recovery, 1/3 – base of plant, 2/3 – mid-dle of plant, 3/3 – apex of plant

(1999) where the energy accumulated in plants depended on the year, i.e. the course of the weather conditions. Similar results were concluded by H n i l i č k a and N o v á k (1998) in their experiments with winter wheat. Significant nett energy differences between the individual years were also showed by H e j n á k (2003) where the average nett energy in dry matter of the three barley varieties was 13.29 kJ g⁻¹ in 2000 and 14.62 kJ g⁻¹ in 2001. The reason

why there were no significant differences in our experiment with hop plants lies probably in the course of the weather conditions during 2001 and 2002 when the vegetation periods were evaluated as thermally above normal.

During both experimental years the higher nett energy values for recovered plants were found in comparison with non-recovered plants. However, this difference was statis-

Table 4. The nett energy content (kJ g⁻¹ dry matter) in organs of individual thirds of the above-ground part of the hop stems of the recovered and non-recovered hop plants – experimental year 2002

Sampling	Third	LB		LS		HB		HC	
		R	N	R	N	R	N	R	N
1	1/3	16.56	16.44	x	x	16.21	16.10	x	x
	2/3	x	x	x	x	x	x	x	x
	3/3	x	x	x	x	x	x	x	x
2	1/3	15.07	14.14	15.99	15.76	15.39	15.03	x	x
	2/3	15.53	15.93	18.05	16.78	16.62	15.30	x	x
	3/3	16.51	16.30	14.87	14.49	15.59	16.59	x	x
3	1/3	15.09	14.88	14.78	15.79	16.22	15.79	x	x
	2/3	15.81	15.97	15.79	16.46	15.23	15.80	16.24	16.79
	3/3	16.64	16.36	16.82	16.86	16.95	16.70	17.01	17.34
4	1/3	16.78	15.49	17.36	16.44	15.35	15.39	16.46	16.71
	2/3	17.77	17.17	16.87	17.37	15.47	15.75	16.44	15.98
	3/3	17.17	17.57	17.42	17.31	15.52	16.06	16.15	16.89
5	1/3	15.26	15.14	16.29	16.44	15.94	15.08	16.01	16.91
	2/3	16.40	16.67	16.22	17.08	16.01	16.80	16.04	17.98
	3/3	16.61	16.11	16.56	16.62	15.60	16.94	17.52	17.72

Legend: HB – hop bine, HC – hop cones, LB – leaves of bines, LS – leaves of shoots, N – non-recovery, R – recovery, 1/3 – base of plant, 2/3 – mid-dle of plant, 3/3 – apex of plant

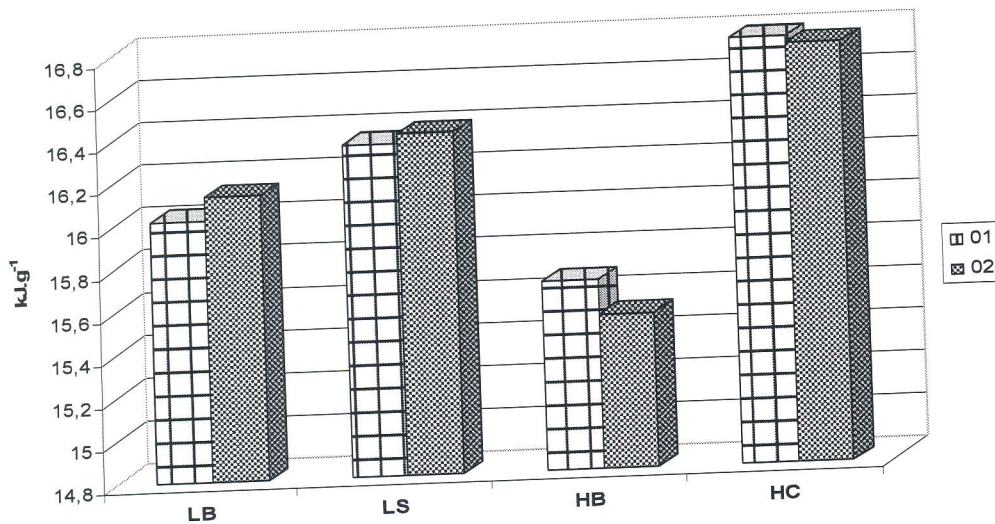


Fig. 2. Nett energy content of individual organs of hop plants in the years 2001 and 2002
 Legend: HB – hop bine, HC – hop cones, LB – leaves of bines, LS – leaves of shoots

tically evident only in 2001. In recovered plants the average nett energy was 16.33 kJ g^{-1} and non-recovered plants 16.00 kJ g^{-1} in 2001. In 2002 this energy value was 16.25 kJ g^{-1} in recovered plants and 16.11 kJ g^{-1} in non-recovered plants. Observing the energy value of the plants' dry matter generates information about its photosynthetic efficiency. Plants exposed to stress factors, in our case the viral presence, respond by a decrease in photosynthetic processes. This causes a decrease in the production of energy-rich asimilates which results in a decrease in the caloric value of dry matter in stressed plants. A negative influence of a viral infection on the photosynthetic performance was shown by Friess, Mailliet (1996) and Ryšlavá et al. (2003).

The energy value of individual organs of the hop plants was observed in 2001 and 2002 (Fig. 2). The highest average values of nett energy content were calculated for the generative organs (hop cones), 16.80 kJ g^{-1} in 2001 and 16.76 kJ g^{-1} in 2002. This result corresponds with many authors' observations studying energy values of the plant organs. Kumar (1994) in his experiments with spring barley proved significantly higher average netto energy content in the dry matter of generative organs. Similar results presenting energy values of spring barley organs were published by Hejnák (2003). Hniličková (1999) in her hop experiments came to different conclusions. The energy value of the hop cones was of decreasing character during the ontogenesis, the lowest values were reported before harvesting when the netto energy of leaves of bines, leaves of shoots and hop bine was of higher values than that of hop cones.

Leaves of shoots had the second highest average nett energy during both experimental years (Fig. 2). In 2001 their average energy was 16.35 kJ g^{-1} and in 2002 16.40 kJ g^{-1} . Leaves of bines average energetic was lower in comparison with leaves of shoots in both 2001 and 2002. This difference can be explained by the ageing of the leaves of bines, their decrease in photosynthetic activity and the

redistribution of asimilates from the gradually aging leaves to other organs. Different conclusions were drawn in experiments of Hniličková (1999) where leaves of bines of the hop plants in the test treatment had a higher average nett energy 16.18 kJ g^{-1} in comparison with leaves of shoots 16.14 kJ g^{-1} . Hop bine had the lowest netto energy values per one gram in both 2001 (15.68 kJ g^{-1}) and 2002 (15.52 kJ g^{-1}) (Fig. 2).

These results bare witness to the fact that hop bines serve as a link for the transport of energy-rich asimilates from the leaves to the hop cones and to the root system. The root is an important sink for plant survival during dormancy. Hniličková et al. (1999) noted an increase of energy content in the hop bine just before harvesting. The same findings were reported by Křátek et al. (1981) in the experiments on the asimilates' distribution using radioactive ^{14}C .

The energy content in the individual levels (thirds) of the above-ground parts of the hop plants is thought to be constant (Hniličková et al., 1999). In our experiment, the average energy value was increasing from the first level and the highest values were reached in the third level of the hop plants during both experimental years (Tables 3 and 4). In the first year, there were highly statistically significant differences between the first and second level and between the first and third level. In the second year, statistically significant differences only existed between the first and third level. This gradation of dry matter energetic value with the increasing plant height is caused by the age of organs in the individual level of hop plants and also by the different substitution of energy-richer generative organs. Rybáček (1967) found that the vegetative organs, i.e. stem parts and leaves, absolutely dominate in the first level. In the second level, the hop cones reach about a half the weight of the vegetative organs. In the third level, where the top of the plant belongs, the weight of the hop cones and vegetative organs is almost the same.

CONCLUSION

The recovery of the hop plants from the complex of virus diseases had a positive influence on the leaf photosynthetic rate. However, this increase is not caused by the content changes of photosynthetic pigments in leaves. The chlorophylls and carotenoids content in the leaf tissues was significantly influenced by the year of growing. The photosynthetic rate was of decreasing character during the vegetation period. The accumulation of nett energy in the dry matter of the plants was not influenced by the weather conditions during the investigating years. A higher amount of nett energy was found in recovered plants in comparison with non-recovered plants. Generative organs (hop cones) had the highest amount of nett energy in the dry matter unit, followed by the leaves of shoots, the leaves of bines and the hop bines.

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Vliv ozdravení rostlin chmele (*Humulus lupulus* L.) od virových chorob na intenzitu fotosyntézy a obsah netto energie.

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U chmele Žatecký poloraný červeňák, Osvaldův klon č. 72, byl sledován vliv ozdravení rostlin od virových chorob na jejich fotosyntetické charakteristiky. Pokus se uskutečnil v letech 2001 a 2002 na chmelnicích Chmelařského institutu v Žatci. Byly hodnoceny intenzita fotosyntézy a množství pigmentů v listech a obsah netto energie v jednotlivých orgánech nadzemních částí rostlin (v révových a pazochoových listech, v révě a v hlávkách). Ozdravené rostliny měly vyšší intenzitu fotosyntézy oproti rostlinám neozdraveným. Průměrná intenzita fotosyntézy stanovená z hodnot naměřených v průběhu vegetace byla u ozdravených rostlin $8,44 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ a u neozdravených rostlin pouze $5,78 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Ozdravení nemělo vliv na obsah fotosyntetických pigmentů. Změny jejich obsahu v listových pletivech byly způsobeny průběhem počasí konkrétních let. V obou pokusných letech byl vyšší obsah netto energie zjištěn u ozdravených rostlin než u rostlin neozdravených. V roce 2001 byl v ozdravených rostlinách stanoven průměrný obsah netto energie $16,33 \text{ kJ g}^{-1}$ sušiny a v neozdravených rostlinách $16,00 \text{ kJ g}^{-1}$ sušiny. V roce 2002 byla průměrná hodnota obsahu energie v ozdravených rostlinách $16,25 \text{ kJ g}^{-1}$ sušiny a v neozdravených $16,11 \text{ kJ g}^{-1}$ sušiny. Nejvyšší průměrná hodnota obsahu netto energie byla zjištěna v sušině generativních orgánů, tj. ve chmelových hlávkách, nejnižší průměrný obsah netto energie byl naměřen ve chmelové révě.

Humulus lupulus L.; chmelové rostliny; virové choroby; ozdravení; rychlost fotosyntézy; pigmenty; obsah netto energie

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