BIOLOGIA PLANTARUM (PRAHA)

30 (4) : 285–293, 1988

Comparative Study of Growth and Carbon Uptake in *Fagus sylvatica* L. Trees Growing under Different Light Conditions

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Abstract. Growth, carbon uptake and carbon utilization in leaves of various growing phase shoots (GPS) on beech trees (*Fagus sylvatica* L.) growing under different light conditions were compared. The values of photosynthetic capacity (maximum daily net photosynthetic rate, $P_{N\ max}$) were used as comparable parameters.

Daily time and irradiance (I, PhAR), when $P_{N\ max}$ was attained, were investigated similarly. Statistically significant differences were found in growth, $P_{N\ max}$ and SLM (specific leaf mass) between different GPS and within the same stand, as well as within the same GPS and different stands. $P_{N\ max}$ and SLM increased in the leaves of GPS I (spring – plagiotropic shoots) on trees from a sun stand from May till September. At the end of the growing season, the spring leaves exhibited, in comparison with the summer ones, intensive senescence, but leaves of the GPS II and III (summer – orthotropic shoots) evidently attained higher values of $P_{N\ max}$ and SLM at higher I (PhAR).

The correlation of growth, $P_{N\ max}$ and SLM in relation to environmental conditions, as well as the importance of transport, distribution and utilization of assimilates for annual carbon gain and biomass production are discussed in detail.

Understanding of how natural conditions control the processes of tree biomass production in a forest stand is mainly based on experimental work performed on seedlings or young trees growing under natural external conditions (*e.g.* KOZLOWSKI 1982). Very few reports are available on the CO_2-exchange (photosynthesis and respiration) of broadleaf forest trees with polycyclic shoot growth (*cf.* pioneering work of ROY *et al.* 1986). All work related to the study of photosynthesis or respiration in broadleaf forest trees has hitherto been pursued with spring leaves (first growing phase) only.

The aim of our experiment was to find the differences in leaf carbon uptake and carbon utilization of shoots in individual growing phases of beech trees growing under different light conditions. Photosynthetic capacity (defined as net photosynthetic rate expressed per unit leaf area at some standardized climate, *cf.* SCHULZE 1982) expressed as daily maximum net photosynthetic rate under optimum (water non-limiting) conditions was used.

Received October 13, 1987; accepted November 12, 1987

MATERIAL AND METHODS

Gas exchange measurements were performed in 11-year old trees of *Fagus sylvatica* L. growing in a natural environment under different light conditions:

sun stand (100 % irradiance)
partially shaded stand (13 % of full irradiance)
shaded stand (4 % of full irradiance)

The trees were regularly and sufficiently irrigated. Detailed descriptions of the stand and site are given by MASAROVIČOVÁ and MINARČIC (1984).

The studies of CO_2-exchange within the stand were carried out using an open gas exchange system with a simple assimilation chamber for short time exposure (approximately 10 min). Carbon dioxide concentration was measured by IRGA (Infralyt 4, VEB Dessau, GDR). The measurements and equipments used were described in detail by MASAROVIČOVÁ and ELIÁŠ (1986). Gas exchange was measured on the same leaf during the day, namely in shoots of various growing phases and under different light conditions, as well. Samples were taken from the middle part of the tree crown.

Values of $P_{N\ max}$ were obtained from daily curves of CO_2-exchange. The time of day and irradiance at which $P_{N\ max}$ value was attained were also determined. Standard *t*-test has been used in the subsequent statistical evaluation of results.

RESULTS

Growth of Shoots and Leaves

Terminal buds of plagiotropic shoots (spring shoots, GPS I) laid out in autumn 1984, started developing in trees of the sun stand on April 19. At this period the weather was sunny and warm (Table 1). The development of terminal buds in trees of partially shaded and shaded stands lagged behind by one week. Only as late as on May 12 the intensive growth of leaves and GPS I was observed. At the end of May the growth of spring shoots finished and terminal buds appeared at all sites (Fig. 1). In June the leaves of the spring shoots which were as much as 50 cm long attained photosynthetic maturity. In the preceding two growing seasons up to three growth phases occurred with a large assimilation area, which was a precondition for a very intensive growth of shoots in spring 1985.

Terminal buds of GPS II (summer or orthotropic shoots) started developing on trees from sun and partially shaded stands at the beginning of June (June 3); on trees of shaded stands the onset of summer shoot growth was delayed by one week. Until the end of June the leaves of the GPS II were observed to be growing intensively on trees of the first two habitats. On trees of the shaded stand the leaves of the GPS II started developing as late as the beginning of July (July 5). At the end of July the growth of the GPS II finished and leaves attained photosynthetic maturity (Fig. 1). On August 11, the growth of GPS III set in intensively from the terminal buds on trees from a sun stand. At the end of August (August 25) the shoots had terminal

Abbreviations used: GPS = growing phase of shoots; I = irradiance; IRGA = infrared gas analysis; PhAR = photosynthetic active radiation; $P_{N\ max}$ = maximal net photosynthetic rate; SLM = specific leaf mass.

TABLE 1
Climatic characteristics of the months and days in which measurements were made. (According to the data of the Slovak Institute of Hydrometeorology in Bratislava — Koliba, 1985)

Months Days		Air temperature [°C]			Relative air humidity [%]			Global radiation [J cm^{-2} d^{-1}]	Precipitation [mm]	Sunlight duration [h]	Number of tropical days
		$\bar{x}$	max.	min.	$\bar{x}$	max.	min.	Total	Total	Total	Total
April	$\bar{x}^+$	10.1	15.5	5.5	59	69	45	45 481	19.0	196.5	
May	$\bar{x}^+$	15.8	21.1	11.3	70	78	58	56 640	81.8	216.6	
20		16.8	20.1	12.0	69	78	55	1 703		6.6	
23		15.8	21.2	8.4	60	74	34	2 771		12.5	
28		21.4	27.3	15.9	56	63	43	2 636		12.3	
June	$\bar{x}^+$	15.1	20.1	11.1	74	80	64	55 037	87.5	204.7	
5		21.4	28.0	13.9	63	72	49	2 622		11.7	
25		14.2	20.4	11.8	77	77	75	2 325		10.5	
July	$\bar{x}^+$	20.4	26.1	15.1	67	73	50	67 662	44.4	288.4	6
5		20.0	25.2	13.5	53	66	42	2 521		10.5	
15		22.9	31.2	16.9	65	79	45	2 410		10.6	
22		18.3	24.3	11.2	55	66	35	2 690		12.9	
29		26.1	33.0	19.0	62	73	50	2 309		11.4	
August	$\bar{x}^+$	19.0	24.5	14.3	74	83	62	52 541	139.6	231.6	5
September	$\bar{x}^+$	15.8	21.1	11.3	69	81	54	41 517	26.3	231.1	
12		13.4	19.4	11.3	63	81	47	1 887		11.4	
13		13.5	19.4	8.0	65	80	48	1 796		11.0	
18		17.9	22.0	15.4	70	78	57	1 623		10.4	
23		19.2	25.3	16.5	72	85	63	1 408		7.5	

$\bar{x}^+$ mean per month

buds so that in the first half of September the leaves of the GPS III reached photosynthetic maturity (Fig. 1). GPS III was not observed on trees of partially shaded and of shaded stands.

The weather was sunny and warm throughout September. In this period, the senescence of all leaves of spring shoots was observed. Leaves of summer shoots did not yet exhibit these symptoms. Only in October did they quickly start yellowing (Fig. 1).

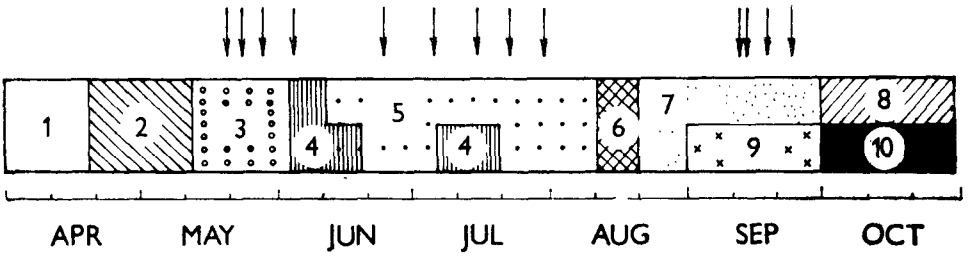

Fig. 1. Phenological phases of various growing phase shoots and their leaves in beech trees growing under different light conditions (April—October 1985).
1 — dormancy; 2 — beginning of GPS I growth; 3 — finishing of GPS I growth (maturing of the leaves); 4 — beginning of GPS II growth; 5 — finishing of GPS II growth (maturing of the leaves); 6 — beginning of GPS III growth; 7 — finishing of GPS III growth (maturing of the leaves); 8 — formation of leaf primordia in the buds (for the year 1986); 9 — senescence of GPS I leaves; 10 — yellowing of all the leaves; ↓ date of the gas exchange measurements.

Seasonal Changes of $P_{N\ max}$ and SLM

The leaves of all three growth phases of trees of sun and partially shaded stands attained $P_{N\ max}$ in the forenoon hours and at rather high irradiance (I), in trees of shaded stands this occurred later and under lower I (Table 2). In the predominant part of the growing season a statistically significant higher $P_{N\ max}$ in leaves of the GPS I and II in trees of sun stands in comparison with shaded stands was found. These differences were evidently greater in the case of GPS II leaves (Table 2).

The leaves of the GPS I exhibited higher $P_{N\ max}$ at all sites than in other GPS (except values in trees of the sun stand in September, when leaves of spring shoots were already in the stage of senescence). On the whole, the highest $P_{N\ max}$ was found in July in leaves of the GPS I of trees from the sun stand (0.984 mg CO_2 m^{-2} s^{-1}). This is assumed to have been due to the high I and to the optimum air temperature, as well as to the intensive growth of leaves of GPS II (Table 1, Fig. 1).

It is also believed that the considerable variability of $P_{N\ max}$ and SLM in leaves of the GPS I in the partially shaded stands was caused by the presence of frequent and pronounced sunflecks (Table 2).

Leaves of the GPS II attained the highest $P_{N\ max}$ at the first two sites in September (0.812 and 0.650 mg $CO_2 m^{-2} s^{-1}$, respectively). High $P_{N\ max}$ values in September were also found in leaves of the GPS III (0.719 mg CO_2 m^{-2} s^{-1}) (Table 2).

On the basis of these findings the leaves of the summer shoots (GPS II and III) are assumed to be significant for annual carbon gain only at the end

TABLE 2
Seasonal changes of $P_{N\ max}$ and SLM in the leaves of GPS I, II and III in the beech trees growing under different light conditions (May 20 to September 23, 1985)

GPS	Date		Sun stand			Partially shaded stand			Shaded stand		
			$P_{N\ max}$ [mg $CO_2 m^{-2} s^{-1}$]	SLM [g m^{-2}]	I(PhAR) [W m^{-2}]	$P_{N\ max}$ [mg $CO_2 m^{-2} s^{-1}$]	SLM [g m^{-2}]	I(PhAR) [W m^{-2}]	$P_{N\ max}$ [mg $CO_2 m^{-2} s^{-1}$]	SLM [g m^{-2}]	I(PhAR) [W m^{-2}]
I	May 20, 22, 28	$\bar{x}$	0.5977	60.44	342	0.7160	60.04	200	0.6601	53.06	125
		$s_{\bar{x}}$	0.0431	3.83		0.0587	4.59		0.1518	11.91	
		C_v	12.48	10.97		14.19	13.24		39.84	38.88	
	June 5, 25	$\bar{x}$	0.7881	60.62	293	0.5387	67.32	75	0.3696	39.94	18
	July 5, 15, 22, 29	$\bar{x}$	0.9839	66.05	288	0.7130	64.46	179	0.3112	53.67	80
		$s_{\bar{x}}$	0.0758	2.27		0.0703	2.53		0.0514	2.80	
		C_v	15.40	6.87		19.7195	7.85		33.03	10.45	
	September 13, 18, 23	$\bar{x}$	0.6380	68.46	188	0.6077	66.56	198	0.3090	48.83	17
		$s_{\bar{x}}$	0.0685	5.81		0.0091	0.51		0.0359	1.59	
		C_v	18.58	14.71		2.60	1.32		20.12	5.66	
II	June 25	$\bar{x}$	0.5283	44.78	80	0.3419	54.37	35	—	—	—
	July 5, 15, 22, 29	$\bar{x}$	0.7656	68.12	299	0.4099	67.07	184	0.2963	45.27	100
		$s_{\bar{x}}$	0.0370	3.99		0.0734	0.96		0.0855	5.55	
		C_v	9.66	11.71		35.83	2.87		57.74	24.52	
	September 12, 13, 18, 23	$\bar{x}$	0.8120	86.36	267	0.6495	76.14	245	0.2634	53.96	21
		$s_{\bar{x}}$	0.0569	7.44		0.0931	2.39		0.0487	3.29	
		C_v	14.01	17.22		28.66	6.29		37.01	12.19	
III	September 12, 13, 18, 23	$\bar{x}$	0.7189	89.09	271	—	—	—	—	—	—
		$s_{\bar{x}}$	0.0662	9.00							
		C_v	18.41	20.21							

$\bar{x}$ — mean, $s_{\bar{x}}$ — standard error, C_v — coefficient of variation.

of the growing season (September) when leaves of the spring shoots (GPS I) already start aging and their photosynthetic capacity declines markedly.

In leaves of GPS I and II trees of a sun stand, the SLM values exhibit a rising trend during the growing season. In the case of trees from shaded stands, the SLM differences were least pronounced. Comparing the SLM values of various growing phases in the same period, then leaves of the GPS I of trees from the first two sites are found to have higher SLM only in June (60.62 and 67.32 g m^{-2}, respectively), and from the shaded stand in July (53.68 g m^{-2}). The overall highest SLM values were found in leaves of the GPS II and III in September (86.36 and 89.09 g m^{-2}, respectively). Lower values of this parameter in leaves of the GPS I in September were due to the lower $P_{N\ max}$ as a result of their senescence (Table 2).

As in the case of $P_{N\ max}$, the most pronounced seasonal dynamics and inter-habitat differences in SLM were also found in leaves of GPS II (Table 2).

A positive correlation between $P_{N\ max}$ and SLM was found in leaves of the GPS II of trees from the first two sites. Also in leaves of the GPS I this correlation was detected (except September).

DISCUSSION

Polycyclic growth is accompanied by a loss of plagiotropism at the shoot level (2nd cycle shoots are orthotropic with alternate leaves), and sometimes by a loss of apical dominance at the plant level (development of "forks"). Thus, polycyclism seems to be an adaptation to high irradiance (Roy *et al.* 1986). Similarly, Barnola *et al.* (1986) proposed a new hypothesis for the determination of rhythmical (polycyclic) growth in *Quercus pedunculata*. This he thought to be connected with regular and short variations of potential exchange rates between the apical bud and the underlying tissues of the stem. Shoot differentiation in *Fagus sylvatica* into exploitation and exploration shoots, was suggested by Dupré *et al.* (1986). Only exploration shoots may be polycyclic, *i.e.* have several growth periods in one growing season. Higher I increases the number of exploration shoots as well as the total height of trees. Of course, the growth of shoots from terminal buds must be distinguished from lateral types of branching, like prolepsis and syllepsis (*cf.* Remphrey and Powell 1985, von Wühlisch and Muhs 1985).

In the distribution of photosynthates into the particular organs of the overground (shoots and leaves) and underground parts (roots), internal factors (like source-sink relations and phytohormones) are of basic importance, too (Masarovičová 1985).

Roy *et al.* (1986) analysed the physiological and anatomical variability of leaves of a 6-years old beech (*Fagus sylvatica* L.) that resulted due to changes in light conditions during different periods of the shoot growth. Growth of GPS I started at the end of April (leaf primordia development of GPS II started, too), the growth of GPS II set in at the beginning of July. In spring, plagiotropic shoot with shade leaves (GPS I) developed. Leaf features depended on light conditions in autumn when the leaf primordia in buds are formed, rather than on I at the time of leafing-out. In summer the orthotropic shoots with sun leaves developed (GPS II). Leaf features depended on light conditions occurring in the "current" growing season. Sun leaves of GPS II (measured in August at I = 190 W m^{-2}, 25 °C, 330 μmol CO_2 mol^{-1})

had higher P_N (14.2 μmol CO_2 m^{-2} s^{-1} = 0.625 mg CO_2 m^{-2} s^{-1}) than sun leaves of GPS I (11.8 μmol CO_2 m^{-2} s^{-1} = 0.519 mg CO_2 m^{-2} s^{-1}, measured in June under the same environmental conditions). However, shade leaves of GPS II had lower P_N (5.9 μmol CO_2 m^{-2} s^{-1} = 0.259 mg CO_2 m^{-2} s^{-1}) than shade leaves of GPS I (10 μmol CO_2 m^{-2} s^{-1} = 0.440 mg CO_2 m^{-2} s^{-1}). The sun leaves of both growing phase shoots had higher P_N than shade leaves but greater differences occurred evidently in leaves of the GPS II. Higher photosynthetic activity in leaves of GPS II was also confirmed for *Quercus cerris* and *Quercus petraea* by VIRÁGH and PRÉCSÉNYI (1985).

On the basis of our previous results (MASAROVIČOVÁ and MINARČIC 1985) the growth of leaves of GPS I is believed to depend on sufficient quantities of supply substances in the root system that were formed in the preceding photosynthetic period with positive carbon balance. Therefore the role of the photosynthetic activity not only of GPS I leaves but also of leaves of GPS II and III, namely at the end of the growing season is significant. NILSSON and ERICSSON (1986) came to the same conclusion in a willow stand (*Salix viminalis*).

A certain analogy in the significance and partitioning of current and one-year old needles (also developing under various light conditions) for annual carbon gain, may also be seen in coniferous trees. It is generally considered that the photosynthetic activity of current needles is higher than that of one-year old needles as soon as the current foliage has reached maturity and that thereafter the capacity will decrease with age (*cf.* TROENG and LINDER 1982). The translocation of photosynthates from one-year old foliage to the current shoot ceased when current needles had reached about 50 % of their final length (ERICSSON 1978). Seasonal change in the source-sink relationship between shoots of different age could then also influence the annual carbon gain.

NILSSON and ERICSSON (1986) found maximum leaf dry mass of *Salix viminalis* between early August and early September in older shoots, and in late September in younger shoots. Leaf and stem growth in spring was markedly higher in 2-years old shoots than in the 1-year shoots. The considerably higher spring growth observed in the 2-years old willow shoots was probably a consequence of the older shoots having higher initial assimilate and nutrient stores and buds ready to sprout. Thus, a larger fraction of I was utilized by older shoots during the period of higher I.

The final increment of wood biomass does not depend only on the P_N of leaves of the individual growing phase shoots, but it is a result of carbon balance during the whole growing season, including the above-mentioned transport and distribution of assimilates into the individual parts of the plant. MCDONALD (1984) suggested that dry mass partitioning or respiration rates are at least as important as (and probably much more important than) variations in photosynthetic capacity for the differences in harvest yield. Photosynthetic rate at rate-limiting I as well as growth might be the highest for the trees growing under low I because of a lower (about three times) respiration rate. Leaves of the beech (as a shade-tolerant forest woody tree), having higher P_N values, also exhibited higher values of photorespiration rate and dark respiration rate, and *vice versa* (ROY et al. 1986). READ and HILL (1985) came to the same conclusion for seedlings of 5 species of the *Nothofagus* genus. This also follows from the comparison of gas exchange

results presented in this paper with the results for beech trees published earlier (MASAROVIČOVÁ and MINARČIC 1984).

The study of polycyclic growth is also very important from the practical silviculture point of view. Under normal conditions, adult trees show only the spring cycle, but the growth of GPS II and III starts when climatic (soil water stress, high temperature, nutrient deficit, *etc.*), herbivory or pollution damages occur (*cf.* JAKUCS 1985).

Generally, it is apparent that much more information is needed before we may predict the dynamics of primary production of trees growing under natural conditions. Of primary importance is a better understanding of the carbon balance during the growing season. Data on carbon uptake, carbon utilization and growth of shoots in beech trees presented in this paper may also serve as input for the architectural model developed by ROY *et al.* (1986) for this economically important woody plant species.

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BOOK REVIEW

WILCOX, J. R. (ed.): SOYBEAN: IMPROVEMENT, PRODUCTION, AND USES. Second Edition. Number 16 in the series Agronomy. — American Society of Agronomy, Inc., Crop Science Society of America, Inc., Soil Science Society of America, Inc., Publishers, Madison 1987. XXXII + 888 pp., US $ 44.75 (incl. foreign postage).

Soybeans, originally and till the beginning of this century a major agricultural crop merely in Eastern Asia, is only from this time, and especially in the last two decades, introduced into other parts of the world, mainly into the USA, Brazil and Argentina. The reason of the increasing demands for soybeans, which would need the soybean planting area to be extended, is the nutritive value of this crop — high contents of edible vegetable oils and proteins. Research works increasing simultaneously with the production were focussed on production practices, protection of the crop from losses due to pathogens, insects and weeds and had an immediate effect on increasing soybean supplies. Increased research was also directed towards better knowledge of physiological processes, genetics and breeding that would open the way for future improvements in soybean production efficiency and in the quality of soybean products. The rapid increase in the breadth and depth of knowledge of this auspicious crop provoked ASA, CSSA and ASSA to replace the first edition of this book published in 1973 by a new, reworked and supplemented issue.

The first chapter (K. J. Smith and W. Huysen) documents recent changes in the world production of soybean, growing trends, economical and political reasons of these changes. The second chapter (T. Hymowitz and R. J. Singh) deals with taxonomic history, cytotaxonomic, morphological and chemosystematic topics. The next two chapters on vegetative (N. R. Lersten and J. B. Carlson) and reproductive morphology (J. B. Carlson and N. R. Lersten) were supplemented to this edition for better understanding the following chapters. Results of quantitative genetics and cytogenetics (R. G. Palmer and T. C. Kilen), quantitative genetics study relevant to soybean breeding (J. W. Burton), breeding methods and cultivar development (W. R. Fehr) are reviewed in three following chapters. Chapter on the seed production and technology (D. M. TeKrony *et al.*) inserted first in this edition is succeeded by four chapters on various aspects of soybeans production *i.e.* crop management (R. R. Johnson), tillage and irrigation (D. M. Van Doren, Jr. and D. C. Reicosky), weed control (T. N. Jordan *et al.*), soil fertility and liming (D. B. Mengel *et al.*). Special chapters are devoted to nitrogen metabolism (J. E. Harper), carbon assimilation and metabolism (R. Shibles *et al.*), stress physiology (C. D. Raper, Jr. and P. J. Kramer) and seed metabolism (R. F. Wilson). The subsequent group of four chapters present current knowledge of fungal (K. L. Athow), viral and bacterial (J. P. Ross) diseasses, nematodes (R. D. Riggs and D. P. Schmitt) and integrated control of insect pests (S. G. Turnipseed and M. Kogan). The final chapter (T. L. Mounts *et al.*) describes in detail how soybean crops are processed, utilized and points out the requirements of special handling.

The book is complemented by the subject index containing scientific and common plant, diseases and pest as well as cultivar names, list of contributors and, in this series regularly included table "Conversions Factors for SI and non-SI Units", although the SI units are used throughout the text. The book is an asset for all agronomists specializing in plant productivity, especially in countries where soybeans is not a traditional crop, and a significant volume to those interested in plant physiology and crop production.

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