POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	52	1	35–45	2004

Regular research paper

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ADAPTATION OF EUROPEAN BEECH (*FAGUS SYLVATICA* L.) TO DIFFERENT ECOLOGICAL CONDITIONS: LEAF SIZE VARIATION

ABSTRACT: This paper focuses on the issue related to the response of beech leaves to the opening of stand canopy resulting from a shelterwood cut of various intensity. Four research plots each with a different stand density provided different conditions for the development of foliage. The research was conducted on dominant, codominant and subdominant sample trees representing the mean stand diameter of all plots. The data were compared for the upper, middle and lower layer of tree crowns (each equals to one third of crown length). As for dominant and codominant trees, mean leaf area showed a tendency to increase towards the lower crown layer. As for subdominant trees, relation between the location of leaves in the crown and leaf area was similar to dominant and codominant trees but this trend was observed only on the plot most open. Only in the case of codominant trees the leaf area was decreasing with a decreasing stand density. Greater stand opening results in a proportionally smaller leaf area. Growing conditions for subdominant tree leaves were completely different when compared to conditions for upper tree classes. On the plots with harvest cutting we observed that a decreasing stand density resulted in a general increase of leaf size. The only exception to the rule was the control plot where the parameters recorded were higher and inconsistent with the above described trend.

KEY WORDS: leaf size, light adaptation, *Fagus sylvatica* L., shelterwood cutting, stand density, mature stand

1. INTRODUCTION

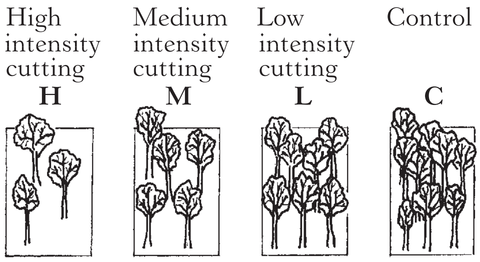
Leaves are highly important organs of a tree, responding very sensitively to growth conditions in a stand, especially during a leaf expansion phase (Roloff 1987, Mašarovicová 1988). Consequently, they can be expected to effectively adapt to the habitat conditions (primarily the water regime – Bussotti *et al.* 1995, Tognetti *et al.* 1995, light regime – Niinemets 1995, Garzía-Plazaola and Becerril 2000, Wittmann *et al.* 2001) through appropriate changes in their morphology (Castro-Diez *et al.* 1997, Gravano *et al.* 1999, Bussotti *et al.* 2000), structure (Kull *et al.* 1999) and metabolism (Marchetti *et al.* 1995). Vertical distribution of a stand's leaf area has been put in relation with relative light conditions in the stand (Johanson 1996, Čermák 1999), connected also with various canopy closure (Frazer *et al.* 2000) and stand density (Jack and Long 1991). During the regeneration period, ecological conditions in the stand change by shelterwood cut from a full canopy to a clear area (Korpel' *et al.* 1991). It induces the changes in leaf light conditions, reflected in changes in leaf morphology and a leaf area because beech leaves can adapt to the local light climate (Burschel and Schmaltz 1965, Peters 1992). The key factor in this process is the amount of radiation in the period of initiation and differentiation of the assimilatory organs. In this period, morphological characteristics of the leaves are created. The plants adapted to shade create large leaf surface. Unlike these, the plants exposed to light with higher intensity create leaves with a smaller area, several mesophyll layers, thicker epidermis and cuticle and several other characteristic properties (Lichtenthaler *et al.* 1981, Nobel and Hartsock 1981, Larcher 1988). These morphological changes are partially orientated in such a way as to control the photosynthetic rate (Begon *et al.* 1997). The absorbed radiation does not contribute to the photosynthesis without accessible carbon dioxide, which primarily inputs through open stomas. The problem consists of the fact that open stomas enable water to evaporate from plant bodies.

In this paper, we study changes in the leaf surface area of beech trees, resulting from the changes in ecological conditions induced with shelterwood cut of various intensity. The research was conducted for the whole crown area of the mature stand in connection with the sociological status in the stand and position within the tree crown (divided vertically into the three thirds).

2. STUDY AREA

The research was conducted in a beech stand at the Ecological Experimental Station (EES) the Western Carpathians, Central Slovakia (48°38'N, 19°04'E). The beech stand in the EES is 100 years old and is situated on a 12–20° western slope at 470 m above sea level. The mean annual temperature (1978–1997) was 8.2°C (during the vegetation period 14.9°C), and the mean annual precipitation was 664 mm (370 mm in the vegetation period). The leading stand-forming association is *Dentario*

A. Sampling plots:



B. Tree crown layers and tree social status:

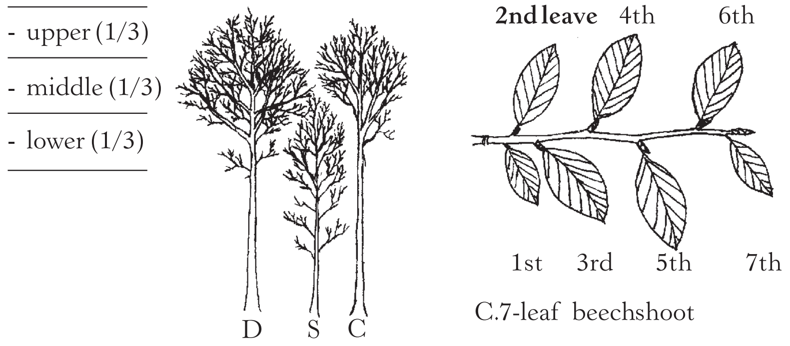


Fig. 1. Scheme A. Sampling beech plots (H, M, L, C) with different stand densities. B. Crown layers for dominant tree (upper, middle, lower) and social status classes of sampling trees (D – dominant, C – codominant, S – subdominant). C. Beech shoot – second leaf taken for as a sample.

bulbiferae-Fagetum Zlatnik 1935, with locally admixed *Carici pilosae-Fagetum* Oberd 1958. For both associations, to the permanent constituents (at different dominances and abundances) belong: *Carex pilosa, Carex sylvatica, Carex digitata, Galium odoratum, Dentaria bulbifera, Anthyrium filix-femina, Dryopteris filix-mas* (Kontriš *et al.* 1993). Before the research, the stand had been managed according to the common forestry practice. Over 30 years preceding the research (1986) the stand was three times subjected to silvicultural measures. At present, the plots formerly treated with stronger cutting (H, M; see explanations below) begin to create second storeys consisting of natural regeneration. The dominant tree species at the locality is beech (80–95%); fir, oak and hornbeam are the associated species. More details on the EES can be found in Kodrík (1993), Kellerová *et al.* (1997) and Barna (2000).

The influence of stand opening intensity was studied at the EES, on four sampling plots with different densities (Fig. 1A) which resulted after shelterwood cut interventions of various intensity (according to volume of large wood) executed in February 1989: plot **C** – 90% stand density of full stocking (control plot – no cutting), **L** – 70% (low intensity cutting), **M** – 50% (medium intensity cutting) and **H** – 30% (high intensity cutting). The data on variable trends on the individual plots after the cut (1989) compared with the corresponding data from 1996 (sampling) are given in Table 1.

Table 1. Main characteristics of beech stands in sampling plots (C – Control and L – Low, M – Medium, H – High intensity cutting).

Plot	Year	Density stems (ha^{-1})	Height (m)	DBH[a] (cm)	Volume[b] (m^{3}ha^{-1})	Stand density
C	1989	700	23.6	25.3	571.2	0.90
	1996	633	26.3	26.6	619.8	0.87
L	1989	397	25.4	29.4	398.9	0.70
	1996	363	28.2	32.7	497.1	0.78
M	1989	243	26.9	31.3	256.8	0.50
	1996	229	28.6	35.4	353.4	0.62
H	1989	160	27.7	32.0	193.7	0.30
	1996	160	29.3	37.5	280.2	0.40

[a] the mean diameter at breast height,

[b] volume of large wood (>7 cm d.o.b.)

3. PLANT MATERIAL AND STATISTICAL ANALYSIS

Svoboda (1972), studying variability in morphology of beech (*Fagus sylvatica* L.) leaves in relation to their position on shoots, revealed that there were considerable differences between the leaf sizes. By comparing the leaf area variability of leaves taken from different points of the compass of the crown with the vertical variability and the variability within one shoot, Svoboda (1972) concluded that variability related to the position of leaves within one shoot was the greatest. Size of leaves on individual annual shoots is variable, but they have similar shape and development. Leaf size increases from the shoot base up to the third, sometimes the fourth leaf but then decreasing trend is observed. On the basis of this fact, additionally being supported by the knowledge that the third leaf of a short shoot is the least variable, the author chose the third leaf as an ideal average leaf. Cicák (1998), who conducted research not only on short shoots but also on long ones, found out that average leaf area of one shoot is approximating the area of the second leaf of this shoot, taking from its basis. After evaluation of a set of shoots with various leaf numbers sampled from young and adult beech trees, another regularity was found – unlike the other leaves, the second leaf from the base has a tendency to maintain approximately the same area.

On the research result basis, leaf sampling methodology was prepared. This methodology is used for the identification of average leaf area as a response to the canopy opening via shelterwood cut. Cicák (1998) representative leaf method recommends always to take the second leaf from three and more-leaved shoots (Fig. 1C). This approach allowed to eliminate significant factors leading to a great variability of leaf area in relation to the leaf branch position. This way, a higher accuracy of the results could be secured. Other criteria were the position of the individual leaves within tree crowns (according to the crown layers) and tree social status (Kraft 1884) within the particular forest stand (Fig. 1B). In order to assess the influence of a various level of canopy opening on the leaf area, there were trees representing average stand diameter of individual sampling plots chosen into the sample tree group. This way, 12 sample trees were selected for the research; three sample trees (dominant – with very well developed and strong crowns, codominant – with well developed crowns; forming the general level of canopy, subdominant – with irregularly developed, crowns suppressed on one or several sides) for each plot (4 plots in total – C, L, M, H, each of them with a different intervention intensity). From these sample trees, 100 leaves from each crown layer (upper, middle, lower) – 3.600 leaves in total were analysed. Leaf area was measured by a photo-planimeter Li-Cor LI-3000 A (USA).

The influence of different stand densities on the changes in leaf morphological parameters was evaluated using the analysis of variance (ANOVA). The sample sets were preliminary subjected to Kolmogorov-Smirnov test for goodness of fit. In the relevant cases the values were transformed: $x' = x^{-2}$. The sample homogeneity was tested using Cochran test. The significance of differences between the mean values of leaf area was determined by multiple comparisons between the individual mean values using the LSD test ($P \leq 0.05$). The analyses were performed using the Statistica Software, Inc. Tulsa OK (USA).

4. RESULTS

Table 2A summarises the results obtained with the one-way ANOVA evaluating the influence of one factor (stand density) on the observed variable (leaf area). With all the analyses a significant influence of the stand density degree has been confirmed. Based on the calculated results we can conclude with 99.9% confidence that the differences in the leaf size between the sampling plots are statistically significant (Fig. 2). The only exception was the case of lower layers of crowns in dominant trees where the confidence did not reach 95.0% ($P = 0.053$). In the case of dominant and codominant trees the greatest differences in leaf area were recorded in upper and middle, the smallest in the lower layers of crowns. That means that the influence of stand density on leaf area size decreases with decreasing position within the crown. An opposite trend was observed with subdominant trees (Table 2A).

Statistically significant differences in leaf size in the upper layers of crowns of dominant trees were detected only between the control (plot C) and the other plots (Fig. 2). The same trend was maintained also in the middle layer of crown, however,

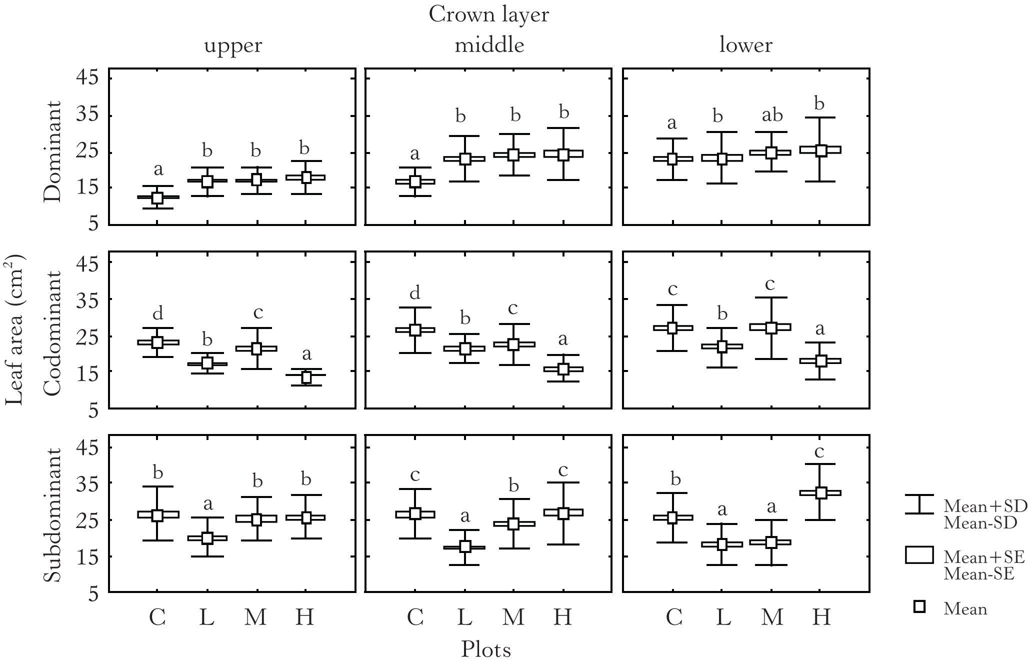


Fig. 2. Leaf area of beech sample trees (dominant, codominant and subdominant – see Fig. 1) for individual sampling plots (C, L, M, H see Table 1) with various stand density. Different letters indicate statistically significant differences between means; LSD test applied ($P \leq 0.05$).

Table 2. Results of ANOVA analysis of the influence of: A. beech stand density on the leaf area size by social status and leaf position within crown (upper, middle and lower layer are succesive thirds of the living crown height); B. leaf position within the crown on the leaf area size split by social status and stand density on plots (C, L, M, H see Table 1).

Source of variation		df	F	*P*
A. Social status	Crown layers			
Dominant	Upper	3	43.31	<0.0001
Dominant	Middle[a]	3	41.90	<0.0001
Dominant	Lower	3	2.58	0.0530
Codominant	Upper[a]	3	122.01	<0.0001
Codominant	Middle	3	83.02	<0.0001
Codominant	Lower	3	48.26	<0.0001
Subdominant	Upper	3	22.20	<0.0001
Subdominant	Middle	3	40.36	<0.0001
Subdominant	Lower[a]	3	103.59	<0.0001
B. Social status	Plot			
Dominant	C[a]	2	174.60	<0.0001
Dominant	L[a]	2	38.94	<0.0001
Dominant	M	2	73.91	<0.0001
Dominant	H[a]	2	33.63	<0.0001
Codominant	C	2	14.31	<0.0001
Codominant	L	2	35.37	<0.0001
Codominant	M	2	20.06	<0.0001
Codominant	H	2	30.11	<0.0001
Subdominant	C	2	0.70	0.4975
Subdominant	L[a]	2	7.20	<0.0009
Subdominant	M	2	31.00	<0.0001
Subdominant	H	2	23.49	<0.0001

[a] for correct use ANOVA data was transformed ($x' = x^{-2}$)
A.(B.) Error df = 396(297); total df = 399(299)

with larger leaf area mean values. In lower layers of crowns the differences in mean leaf area between all the individual plots were small. That means that in this case the influence of stand density was the smallest (Table 2A, F-value 43.31, 41.90, 2.58). With codominant trees (Fig. 2) the leaf area decreased in all the layers of crowns with decreasing stand density. The more intense radiation resulted in a smaller leaf area. In controversy with this trend were only the data from plot M, which were greater than the corresponding data from plot L. In the case of subdominant trees the growth conditions are totally different compared with the previous tree classes. Comparing the data from plots L, M and H it is obvious that the leaf size increases with a decreasing stand density (Fig. 2). Additionally we can say that the significance of stand density influence on a leaf area increases towards the lower tree crown layers (Table 2A).

Based on the results obtained with ANOVA and summarised in Table 2B, it is possible to evaluate the significance of the influence of leaf position within crown on leaf size on the plots with various stand density. All the analyses proved the significant influence of leaf position within the crown on the leaf area. The single exception was the subdominant sample tree on the control plot where the position within the crown had no significant influence on the leaf area size. This can be explained by a compact stand where light conditions in the whole subdominant tree crowns are the same in whole crowns.

The mean leaf area of dominant trees increased from the upper layer to the lower layer crown on all the sampling plots (Fig. 3). The most remarkable influence of leaf position within the crown was observed on the control plot (C), the least remarkable on plot H (Table 2B). It follows that the greatest differences in leaf size according to position within the crown were noted on plot C and the smallest ones – on plot H. It is because after the cutting the area around the crowns was opened and all the crowns were released, primarily in their middle and lower layers. The wider stand opening, the more homogeneous light conditions created for the whole crown. On the other hand, on the control plot that was not subjected to any cut, the differences in growth conditions according to the leaf position within the crown and differences of mean leaf area are the most remarkable (Fig. 3). There are no statistically significant differences between middle and lower layers of crowns on the plots subjected to the cutting.

Also in the case of codominant trees the mean leaf area increased from the upper layers of crown to the lower ones (Fig. 3). The influence of the position within the crown on the leaf size was the least remarkable on the sample tree from the control plot (Table 2B). It is because the upper layer is not exposed to as much light as upper ones of dominant trees and, consequently, within the whole crown the differences in leaf area size were the smallest – 3.9 cm^2 (100%). On the other plots treated with cut, the upper layer of crown is more open, and, as a result, also the leaf area values are smaller (Fig. 2). Within crowns the differences between the layer of crown are bigger: L – 5.7 cm^2 (146%), M – 5.6 cm^2 (144%), H – 4.3 cm^2 (110%).

With subdominant trees (Fig. 3) the influence of position within the crown on leaf area was similar to higher tree classes only in the case of plot H (the most intense cut). On plots M and L the leaf size decreased with decreasing position within the crown. On the control plot no influence of the position within crown on the leaf size could be confirmed. The leaf area of this sample tree according to the position within the crown is the least variable and the differences have no statistical significance ($P > 0.05$). With decreasing stand opening also the influence of the position within crown on the leaf size decreases (Table 2B).

The results of the two-way ANOVA on the influence of stand density and position within the crown on dominant tree leaf area are summarised in Table 3A. In the case of these trees, all variability in leaf size was significantly dependent on both the factors as well as on their interaction. This conclusion has been confirmed also by high F-ratio values, by higher table quantiles of the F-distribution according to the given degrees of freedom as well as by low values of significance level in the performed variance analyses. The position within the crown has the greatest share of the explained variability. That means that in this tree class leaf size formation is influenced most by its position within the crown. Figure 2 shows that in the case of dominant trees the leaf area size in the individual crown layers decreases non-significantly with increasing stand density on all the plots with exception of the control plot. As for the differences between the leaf position within crown, there are unambiguous and significant differences between the upper and the other two lower crown layers (Fig. 3).

The results obtained with two-way ANOVA of codominant tree leaf area are summarised in Table 3B. The data show that in the case of these trees the stand density and the position of leaves within the crown significantly influence the leaf area size. Unlike in the dominant trees, a greater influence of stand density compared with the influence of leaf position within-crown can be observed. Figure 2 shows that the mean leaf area of the sample trees decreases with decreasing stand density. The only exception is the sample tree from plot M. The same is valid also for the leaf position within crown (Fig. 3).

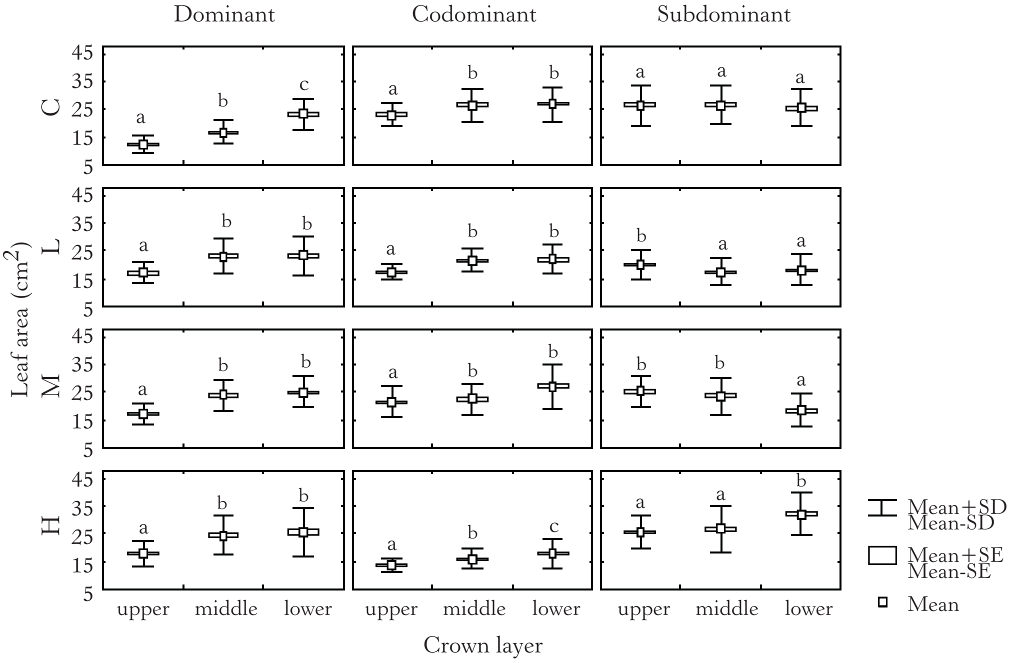


Fig. 3. Leaf area for individual crown layers (upper, middle, lower) of sample trees on plots with various stand density (C, L, M, H see Table 1). Different letters indicate statistically significant differences between means; LSD test applied ($P \leq 0.05$).

Table 3 (A–C). Results of two-way ANOVA[a] analysis of the influence of beech stand density (C, L, M, H plots – see Table 1) and the leaf position within the crown layer (upper, middle, lower) on the leaf area size by social status (A – dominant, B – codominant, C – subdominant) of sample trees in stand. D. Three-way ANOVA[b] analysis of the influence of stand density, the leaf position within the crown and social status on the leaf area size.

Source of variation	df	F	*P*
A. Dominant trees			
1: Stand density	3	57.97	<0.0001
2: Crown layer	2	241.80	<0.0001
Interaction 1×2	6	9.10	<0.0001
B. Codominant trees			
1: Stand density	3	221.73	<0.0001
2: Crown layer	2	78.13	<0.0001
Interaction 1×2	6	3.48	0.0021
C. Subdominant trees			
1: Stand density	3	135.79	<0.0001
2: Crown layer	2	3.19	0.0415
Interaction 1×2	6	20.58	<0.0001
D. Three-way ANOVA			
1: Stand density	3	52.47	<0.0001
2: Crown layer	2	143.84	<0.0001
3: Social status	2	91.44	<0.0001
Interaction 1×2	6	7.29	<0.0001
Interaction 1×3	6	157.71	<0.0001
Interaction 2×3	4	63.87	<0.0001
Interaction 1×2×3	12	14.35	<0.0001

[a] (b) Error df = 1188(3564); total df = 1199(3599)

The less remarkable the shading (the higher situated are the leaves within a crown), the smaller is the corresponding leaf area.

In the case of subdominant trees (Table 3C, Fig. 2) a significant influence of stand density on leaf area size was detected (*P* <0.0001). The influence of the position of leaves within the crown is lower (*P* = 0.0415). Comparing the results from each tree class we can see that the influence of the position of leaves within the crown decreases with decreasing tree class – from the dominant to subdominant trees.

Table 3D summarizes the results of the three-way ANOVA, which evaluates the influences of the stand density, leaf position within the crown and tree social status in the stand as well as their mutual interactions on leaf area size. The data shows that the variability in leaf area size "between" the sample groups is statistically more significant than the variability "inside" the groups. It follows that all the studied factors have very significant influences on the leaf area size in all the crowns of the mature stand.

5. DISCUSSION

Solar radiation penetrating through several tree crown layers is absorbed and partially utilised (Eliáš *et al.* 1989). Radiation intensity decreases almost exponentially with increasing plant cover density (Larcher 1988). Shade-bearing leaves compensate lack of light by the greater leaf area. If we tried to explain the changes in the leaf area only on the basis of tree adaptability to different radiation intensity it is necessary to note that this rule can apply only to codominant and dominant trees. These observations neither depend on the leaf position within the crown (Fig. 3), nor they depend on the stand density (Fig. 2). This serves as an example of the morphological adaptation to variable light conditions in which leaves of mature beech trees developed and grew (Masarovičová and Štefančík 1990, Niinemets and Kull 1994).

Subdominant trees responded this way only on a plot H where the felling was of the greatest intensity. This intervention has led to a substantial opening of the site resulting in more favourable light conditions mainly for the subdominant trees, which are here only slightly shaded and suppressed by the canopy. Therefore, the relation between leaf area and leaf position within the crown was similar as between the dominant and codominant trees. Control plot (C) showed proportionally only small differences – 1.1 cm^2 (100%) of leaf area between different crown layers. These differences are statistically unimportant. It means that stand canopy on the control plot was almost totally closed and whole crown of subdominant trees there had approximately identical light conditions. Therefore, leaf area parameters are equally homogenous. Differences between various crown layers of subdominant trees recorded on the plots L and M, where low to medium canopy opening was realised, were more significant, L 2.7 cm^2 (246%), M 6.6 cm^2 (600%). However, in this case we could observe a noteworthy phenomenon: leaf size was not growing towards the lower crown layers like it was recorded in the case of dominant and codominant trees, but quite on contrary, it was decreasing (Fig. 3). It seems as if the light conditions were not worsening but improving towards the lower crown layers. At the same time it is, however, necessary to note that leaves from the lower crown layers had not only smaller leaf area than the leaves of the upper or middle layers but were also lighter and thinner than well-lit leaves of dominant and codominant trees. Specific leaf mass values (SLM, the ratio between dry leaf biomass and leaf area) were also lower (Table 4). This fact proves that these leaves were subjected to different growing conditions not only as for light conditions.

Table 4. Specific leaf mass (SLM) in g.m^{-2} by social status (dominant, codominant, subdominant) of a beech sample trees (C, L, M, H plots see Table 1).

Plot	Crown layer	Dominant	Codominant	Subdominant
C	Upper	71.05	80.68	32.26
	Middle	62.46	42.39	28.88
	Lower	31.95	35.14	26.75
L	Upper	62.55	75.14	28.72
	Middle	40.13	45.75	25.03
	Lower	30.78	34.46	22.56
M	Upper	77.68	55.30	39.07
	Middle	51.87	37.16	33.26
	Lower	47.50	36.06	28.57
H	Upper	69.55	79.66	52.22
	Middle	53.45	63.80	35.77
	Lower	44.49	51.81	34.23

Differentiation of mesophyll into palisade and sponge parenchyma represents one of the most important and characteristic differences in the anatomy of leaves growing in sun and shade conditions (Fahn 1967, Eschrich *et al.* 1989). Plants adapt not only to different light intensity (Smith 1974, Jakucs and Virágh 1975) and its different spectral distribution (Larcher 1988) but also to different soil and air humidity, which significantly affects the degree of mesophyll differentiation (Cunningham and Strain 1969). Increased canopy opening following the shelterwood cut application is linked to soil scorching, overheating of ground air masses, late ground frosts, weed overgrowth, etc. According to Innes (1993), the trees subjected frequently to stress produce smaller leaves because of lower nutrient uptake before or during foliage development. Lack of water is also a very important stressing factor because the beech is very sensitive to prolonged periods of drought (Aranda *et al.* 2000).

6. CONCLUSIONS

The morphological changes in the leaf area resulting from a regeneration cutting of various intensity were evaluated using a new method – the method of a representative leaf, elaborated by Cicák (1998). From the results of the evaluation we can draw the following conclusions:

- Leaf area of the dominant trees was decreasing towards the upper crown layers.
- Leaf area of the codominant trees was decreasing with reduced stand density and towards upper crown layers.
- Influence of stand density on the leaf area of dominant and codominant trees was decreasing towards lower crown layers (most significant influence on upper crown layers; lowest on lower crown layers) and was increasing in subdominant trees.
- Influence of a particular position of leaves within crown layers recognised on the leaf area of dominant trees was increasing with growing stand density (gradual leaf area increase from plot with the most intense cut – H to control plot – C); as for subdominant trees, it was decreasing with growing stand density.
- Most significant influence of stand density on the leaf area was recorded for the codominant trees; the smallest influence was recorded for the dominant trees.
- Influence of crown layers recognised on the leaf area was decreasing with a decreasing "social status" of the particular tree in the stand (influence showing decreasing tendency from the dominant trees towards the subdominant ones).
- From the factors compared we can say that the leaf area of beech stands was mainly determined by leaf position within the crown recognised; equally important was the position of individual trees within a particular stand ("social status"). Stand density was identified to be a less important factor. To sum it up, according to our results it is possible to conclude that all the above mentioned factors and their mutual interactions have statistically very significant influence ($P < 0.0001$) on the leaf area.

ACKNOWLEDGEMENTS: This research was financially supported by the Slovak Grant Agency for Sciences–VEGA (Grant No. 2/4158, 2/4168)

7. SUMMARY

In beech trees, both leaf morphology and leaf area show considerable adaptation capabilities to the local radiation climate. The plants adapting to shade conditions create large leaf area with high chlorophyll concentration and high water content in the living tissues. On the other hand, the leaves of plants exposed to radiation of higher intensity have smaller area, several layers of mesophyll, thick epidermis and cuticle, higher dry weight, higher energy potential of the dry mass and several other characteristic properties. After a cutting the trees in the residual stand respond by adjustment of photosynthesis and respiration, primarily according to the level of the radiation accessible during the initiation and differentiation of their assimilatory organs. This is the period of formation of significant morphological features of plants, their cellular and subcellular structures, and also biochemical processes determining characteristic properties of the exchange of CO_2 in light-demanding and shade-loving forms. The research was performed using a new method – the method of a representative leaf (Cicák 1998) separately on dominant, codominant and subdominant trees for upper, middle and lower crown layer. The sample trees represented mean stand diameter values on four sampling plots (Fig. 1, Table 1) with various stand densities corresponding to the intensity of the performed shelterwood cutting (H – high, M – medium, L – low intensity cutting and C – control plot).

The influence of stand density on the leaf size (Table 2A) was confirmed statistically significant ($P < 0.0001$) for all the classes (dominant, codominant, subdominant) and for all the crown layers (upper, middle, lower). The only exception were the lower crown layers of dominant trees in which the significance of influence of the cutting treatment was lower than 95.0% ($P = 0.053$). In this tree class the leaf area increased with decreasing density of the stand. In codominant trees the tendency was opposite and the subdominant tress were found creating their leaf area such sensitively also to other growth factors that there was not possible to indicate any obvious trend (Fig. 2). The largest differences in leaf area in dominant and codominant trees were observed in upper and middle crown layers, the smallest in the lower layers. That means that the influence of the stand density on leaf area decreased with decreasing crown layer. The opposite trend was in subdominant trees where the influence of stand density on leaf area size increased with decreasing layer of crown (Table 2A). Examining the influence of leaf position in crown (crown layer) on leaf size, we found significant dependence in all the cases, with the exception of the subdominant sample tree on control plot. The highest influence of crown layer on leaf area was found on control, the smallest on plot H with the strongest cutting intensity; that means, the influence decreased with the stand opening. In the dominant and subdominant trees we observed an opposite trend (Table 2B) – the mean leaf area increased with decreasing leaf position within tree crown (Fig. 3). As we have just mentioned, the subdominant trees, primarily owing to the competitions, showed higher sensitivity also to other growth factors, and, consequently, they did not show the same dependence on all plots, in spite of the fact that the SLM values (Table 4) had the same trend. Comparing the influence of the two studied factors – stand density and crown layer – on the size leaf area, in dominant trees there was observed higher influence of crown layer, in codominant and subdominant trees, determinative was the stand density (Table 3A, B, C). The influence of crown layer decreased with decreasing tree class, the most evident it was in dominant and codominant trees, the slightest in subdominant trees. The three-way ANOVA (the third factor was the tree social status) revealed statistically high influences of all the three factors as well as of their interactions (Table 3D) on leaf size in all the crown area of the examined beech stand. In 12 selected sample trees the highest influence on leaf area was found in leaf position in crown (crown layer).

8. REFERENCES

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(Received after revising July 2003)