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GROUND VEGETATION CARBON AND ITS RELATION TO CLIMATE AND SPECIES RICHNESS

ABSTRACT. Ten pine forest sites located along the transect between 50°28' and 70°09' N were studied. The purposes of the present paper are: 1) to determine the volume of the organic carbon pool in selected layers of the analysed forest ecosystems (shrubs, herb layer, mosses and lichens, litter, and the humus horizon of the soil); and 2) to elaborate the correlation-based prediction models relating the organic carbon pools in these layers with the selected variables characterising the climate and the species richness of the pine forests. The results indicate a clear horizontal heterogeneity of the ground layer in the pine forests considered. This is reflected, in particular, through the differentiation of the carbon pool in particular places within the ecosystem. There is a distinct geographical variability in the carbon pool among the sites in particular layers, with the average annual and January temperatures having the largest influence on this variability. However, in different cases there are different combinations of the factors describing these relations in the best way. The relations between the carbon pool and the species richness of the sites along the transect show that either the minimal carbon pool occurs at sites of an average species richness, or there is no relation between these variables. The analysis implies that there are two points of the transect at which various characteristics of the system undergo an abrupt shift. The first of them is equivalent to the passage of the annual +1°C isotherm, while the second at approximately 5–6°C. There is the possibility that these regularities occur within the entire range of the pine forests.

KEY WORDS: carbon pool, biomass, species richness, dwarfshrubs, mosses, lichens, climate factors, geographical variability.

1. INTRODUCTION

Geographical location, temperature, water, availability of nutrients, and the land use type are the primary factors influencing the processes taking place in the forest ecosystem, including production and vertical, as well as horizontal distribution of the organic matter (Stephenson, 1990; Neilson *et al.*, 1992). In case of climate change (expected to occur as the consequences of global warming caused by humans) many of the plant formations would change their spatial ranges. There are numerous models describing the forecasted changes. One can mention here the correlation-based models (Holdridge, 1947), the process-based models (Box, 1981; Shugart, 1984; Woodward, 1987), and the ones taking into account the ecosystem constraints (Neilson, 1995). Most of them refer to the changes in plant formations, the dominating species, or the dynamics of stands, neglecting the more detailed issues, such as the changes in species composition, species diversity and the productivity of the ground layer.

Modelling of these changes will be possible when the necessary information is gathered on the connections between the main structural features of the forest communities, including the carbon pool in the particular layers of the ecosystem, and the driving variables, including geographical position, climate characteristics, and species richness.

It is worth to emphasize that the distinct latitudinal changes of the carbon pool of the herb layer in the pine forests is associated first of all with the radiation balance, that is the amount of light received, conditioning the efficiency and the duration of photosynthesis (Hari *et al.,* 1996).

Different studies proved that the relation between the productivity and the pool of carbon on the one hand, and the species richness on the other is not quite unambiguous. These quantities may not be correlated at all (Haskell *et al.,* 2001), or the increase of the species diversity corresponds to the increase of production (Brown and Gibson, 1983; Currie and Paquin, 1987; Currie, 1991), or, conversely, to the decrease of production (Huston, 1980). Most often, though, the relation between the number of species, or diversity, and the carbon pool is described by a unimodal, hump-shaped curve, meaning that the maximum of the carbon pool occurs for the average species richness (Grime, 1973; Al-Mufti *et al.,* 1977; Tilman, 1982, Wheeler and Giller, 1982; Moore and Keddy, 1989; Gough, 1998; Guo, 1998; Cox *et al.,* 2001) and for average diversity, irrespective of the nature of indicator used (Zobel and Liira, 1997).

Other studies imply that the nature of interrelation carbon pool-species richness depends upon the size of the area analysed. In case of very small and uniform habitats the correlation may be positive or negative, but when larger areas are considered, encompassing differentiated micro-habitats, one obtains ultimately the unimodal curve (Guo, 1998). It is assumed that the mechanism responsible for the differentiation of the relations between the carbon pool and the number of species is most often constituted by the *competitive exclusion principle* with respect to species and by the disturbance (Moore and Keddy, 1989; Abrams, 1995; Rosenzweig, 1995; Guo, 1998).

The present paper shows the results obtained during the long-term and comprehensive team study, which general objective is to determine the influence exerted by geographical and climatic differentiation on the basic structural properties and ecological processes, taking place within the ecosystems of the pine forests (see Breymeyer, 2003a, b, in this volume). The purpose of the paper is first of all a) to determine the size of the organic carbon pool in definite layers of the analysed forest ecosystems (shrubs, herb layer, mosses and lichens, litter, humus horizon of the soil); b) elaboration of the correlation-based prediction models, linking the carbon pool in these layers with the selected climate variables and the species richness of the forest communities.

The subject of the analysis is constituted by ten forest study sites, located along the transect stretching from 50°28' N to 70°09' N. The research was carried out in the years 1997–2000. The phytosociological and floristic characteristics of the study sites are provided in a separate paper (Solon, 2003a, in this volume). The study sites are coded as follows: NO1 – North Norway, FN1, FN2, FN3 – North, Central and South Finland, ES1 – Estonia, LV1 – Latvia, LI1 – Lithuania, PL1, PL2, PL3 – North-Eastern, Eastern and South-Eastern Poland.

2. METHODS

2.1. DETERMINATION OF THE BIOMASS POOL

The biomass of the shrubs was determined in an indirect manner. In September of 2001 the dimensions of the brushes were measured at each site on two plots, 100 m^2 each. The individuals were accounted for, which diameter at the ground level exceeded 4 mm (the smaller ones were treated as the components of the herb layer). The quantity of dry biomass was determined on the basis of the regression equations contained in the BIOPAK database (Means *et al.*, 1996). In case of lack of dependence for a given shrub species, the equations were used corresponding to the species closest in morphological terms (Table 1). The average from two repetitions was then used in further considerations and tables.

For determination of the biomass of the herb layer and humus square plots of dimensions 11 m × 11 m were designated at each of the study sites. Within these surfaces 12 locations were selected for taking samples ac-

Table 1. Species measured in the field, and species which characteristics were taken from BIOPAK database (Means *et al.*, 1996) used for biomass calculation.

Evaluated species	Measurements	Species from BIOPAK
Betula pendula	DBA, HT	*Betula papyrifera*
Betula pubescens ssp. czerepanovii	DBA, HT	*Betula papyrifera*
Frangula alnus	DBA	*Alnus sinuata*
Juniperus communis	DBA	*Juniperus communis*
Picea excelsa	DBH, HT	*Picea engelmannii*
Pinus sylvestris	DBA, HT	*Pinus ponderosa*
Populus tremula	DBH, HT	*Populus tremuloides*
Quercus robur	DBA	*Quercus kelloggii*
Sorbus aucuparia	DBA	*Sorbus scopulina*

DBA – stem basal diameter (cm); DBH – diameter at breast height (cm); HT – height (cm).

cording to the scheme of Fig. 1. The samples were taken at the centre of the one-metre squares with the help of the sampler having the form of a cylinder open on both ends. The area of the cross section of the cylinder is equal to 200 cm^2. The sampler was driven into the ground so as to make it reaches the depth of 25 cm from the surface of the AO horizon of the soil. The obtained plant-and-soil mass was packed in paper and plastic bags.

This mass was divided in the laboratory into the following six fractions:

- the dwarfshrubs biomass,
- the biomass of the remaining vascular plants,
- the moss biomass,
- the lichen biomass (only on the site NO1 the mosses and the lichens were treated together),
- the mass of the litter,
- the mass of the cap humus (encompassing not only the proper humus, but also the roots and other underground parts of plants, found in this layer).

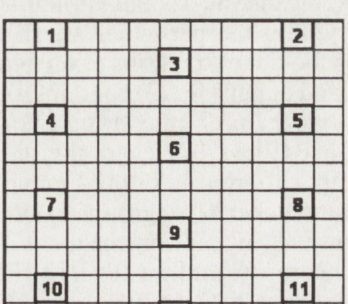

Fig. 1. The biomass sampling scheme for the study sites. 1–12: locations of 1 m^2 quadrats for sampling biomass within the 11 m × 11 m observation plot.

Altogether 719 samples were obtained (10 study sites × 12 one-metre square plots × 6 (5) fractions).

The classification of the aboveground phytomass into so many fractions resulted from the following prerequisites: a) significant horizontal heterogeneity of the herb layer, b) differentiated percentage content of carbon in particular groups of plants, c) various persistence of the definite forms of biomass, and therefore, their different roles in the cycling of elements.

The purified fractions were dried to a constant weight in the temperature of 90°C and then weighted with accuracy of 0.01 g. The results were converted to the values in grams per m^2.

2.2. DETERMINATION OF THE CARBON POOL

A detailed carbon content in dry biomass was established for the three Finnish sites (FN1, FN2, FN3), the Lithuanian one (LT1), and one of the Polish sites (PL3). For this purpose a mixed sample was prepared from three basic square plots for each of the fractions. Carbon content was determined with the Alten's method (Dziadowiec and Gonet, 1999). The analyses were carried out at the Department of Soil Science of the Nicolaus Copernicus University in Toruń. The results were expressed as the percentage share of carbon in the biomass. For the remaining sample plots carbon content in the biomass was estimated on the basis of values from two closest sites. For the shrubs the carbon content in dry biomass equal 47.5% was assumed (Schlesinger, 1991).

2.3. STATISTICAL ANALYSIS

The significance of the differences between the mean values of biomass for particular sites was determined with the *t*-Student test.

In the assessment of the influence of climate on the pool of carbon on the study sites the following independent variables were assumed: latitude, long-term mean annual temperature, long-term mean temperature of January, long-term mean temperature of July, long-term mean of precipitation, and two additional indicators: a) the Lang indicator (Lang, 1915), expressed as: "Lang" = precipitation/annual temperature, b) the Martonne indicator (Martonne, 1926), expressed as: "Marton" = precipitation/(annual temperature +10).

For the analysis of relation between carbon pool and the species richness, the data from the paper of Solon (2003b, in this volume) were used, especially the number of the herb layer species per 400 m^2, as well as the parameters *a* and *b* of the allometric equations $y = ax^b$, where y – number of species, x – surface area of measurement (Table 6 in Solon, 2003b, in this volume).

In order to present the general character of interdependencies between the features analysed and to reduce the number of variables the Principal Component Analysis was applied. The detailed relations between the dependent variables (carbon pool in particular layers) and the independent variables (geographical location, climatic characteristics, species richness) were established on the basis of the correlation and regression analysis. In the course of analysis the stepwise variable selection procedure was, in particular, used in the selection of the independent variables influencing the most the value of the carbon pool.

3. RESULTS

3.1. PLANT, LITTER AND HUMUS BIOMASS

The summarized results of the biomass differentiation are presented in Table 2. It is visible that the study sites are distinctly differentiated with respect to the observed biomass of the shrubs. The maximum values exceed 470 g m^{-2} (site NO1), while the smallest one amount to only roughly 3.3 g m^{-2} (site FN3). Hence, the differences in the biomass of shrubs among the pine forest sites along the transect amount to more than factor of 140. The study sites can be classified into three groups in terms of magnitude of the biomass of shrubs. Two Finnish sites (FN2, FN3), the Estonian one (ES1), the Latvian (LT1) and one of the Polish sites (PL3) are characterised by very low biomass of shrubs (less than 60 g m^{-2}), then the sites FN1, LI1 and PL2 (average shrub biomass between 130 and 180 g m^{-2}), while on the Norwegian site (NO1) and the remaining Polish one (PL1) the biomass of shrubs ranges between 260 and 480 g m^{-2}.

The biomass of the vascular plants is differentiated both in terms of various sites and within these sites. The FN1 site has, on the average, five times as much of the herb layer vascular plant biomass as the poorest site (LT1). The differences between the mean values of the herb layer biomass at individual sites are very weakly pronounced. Somewhat different from the remaining ones are the sites LT1 and PL1, displaying significantly lower average biomass and the sites FN1 and PL2, having significantly higher biomass than the majority of the remaining sites.

The differences of the biomass values within one site may attain almost 900 g m^{-2} (FN1 site), although they are most often contained in the interval between 180 and 390 g m^{-2}. As the consequence of the horizontal differentiation of the herb layer within the same phytocoenosis the most abundant places are characterised most often by the biomass 10–30 times higher than the locally poorest places.

The joint biomass of the aboveground mosses and lichens is differentiated. One can observe both the differences between the sites and the distinct spatial variability of this feature within the particular sites. The site, which is the richest in terms of the biomass of mosses and lichens (FN2) contains, on the average, more than 2.7 times as much of it as the poorest one (PL3). In view of the statistically significant differences in the biomass of the mosses and lichens two groups of sites can be distinguished in a clear manner. The first group encompasses the sites LI1, PL1, PL2 and PL3, that is the sites situated in the southern part of the transect, and, in addition, the site FN1. They are characterised by a relatively smaller mean biomass, smaller standard deviation from the mean and a distinctly

Table 2. Dry weight (in g m^{-2}) of different fractions of biomass on study sites

	site	NO1	FN1	FN2	FN3	ES1	LT1	LI1	PL1	PL2	PL3
Shrub Layer	mean[x]	**473.35**	**168.74**	**27.26**	**3.36**	**6.2**	**53.96**	**138.4**	**266.19**	**153.01**	**13.3**
Dwarfshrubs	mean[x]	135.65	365.83	272.54	142.38	214.58	67.25	109.88	81.29	258,00	176,00
	SD[xx]	77.84	265.92	201.24	89.31	103.69	55.8	107.9	83.1	107.6	135.78
Herbs & grasses	mean[x]	1.92	0,00	0,00	0,00	2.67	1.54	42.25	18.58	6.46	0.46
	SD[xx]	6.36	0,00	0,00	0,00	7.11	2.8	106.96	27.39	21.42	1.52
Herb layer total	mean[x]	**137.57**	**365.83**	**272.54**	**142.38**	**217.25**	**68.79**	**152.13**	**99.88**	**264.46**	**176.46**
	SD[xx]	**76.92**	**265.92**	**201.24**	**89.31**	**106.13**	**55.43**	**128.89**	**95.39**	**115.14**	**136.26**
	differences[xxx]	FN1,FN2, LT1,PL2	NO1,FN3,LT1, LI1,PL1,PL3	NO1,LT1, PL1	FN1,LT1, PL2	LT1,PL1	NO1,FN1,FN2, FN3,ES1,PL2, PL3	FN1,PL2	FN1,FN2, ES1,PL2	NO1,FN3,LT1, LI1,PL1	FN1,LT1
Mosses	mean[x]	no data	178.53	498.25	463.58	508.54	414.5	218.67	242.33	213.67	222.96
	SD[xx]		189.48	243.36	257.37	191.35	186,00	116.82	60.56	80.19	108.39
Lichens	mean[x]	no data	82.59	103.67	71.63	0,00	32.96	35.79	0,00	27.25	0,00
	SD[xx]		51.99	167.22	107.62	0,00	87.99	70.6	0,00	90.38	0,00
Moss layer total	mean[x]	**413.63**	**261.12**	**601.92**	**535.21**	**508.54**	**447.46**	**254.46**	**242.33**	**240.92**	**222.96**
	SD[xx]	**169.98**	**190.75**	**165.6**	**209.18**	**191.35**	**185.35**	**113.71**	**60.56**	**91.97**	**108.39**
	differences[xxx]	FN2,LI1,PL1, PL2,PL3	FN2,FN3, ES1,LT1	NO1,FN1,LI1, PL1,PL2,PL3	FN1,LI1,PL1, PL2,PL3	FN1,LI1,PL1, PL2,PL3	FN1,LI1,PL1, PL2,PL3	NO1,FN2,FN3, ES1,LT1	NO1,FN2,FN3, ES1,LT1	NO1,FN2, FN3,ES1,LT1	NO1,FN2,FN3, ES1,LT1
Litter	mean[x]	**817.56**	**866.63**	**578.75**	**713.38**	**720.42**	**655,00**	**1021.54**	**632.63**	**843.46**	**849.00**
	SD[xx]	**399.09**	**306.75**	**175.38**	**315.17**	**272.5**	**161.27**	**276.94**	**219.1**	**275.59**	**301.38**
	differences[xxx]		FN2	FN1,LI1, PL2,PL3	LI1	LI1	LI1	FN2,FN3,ES1, LT1,PL1	LI1	FN2	FN2
Humus	mean[x]	**6041.04**	**4307.13**	**2352.71**	**3560.58**	**9262.08**	**7747.88**	**4594.96**	**4843.04**	**6490.13**	**7732.33**
	SD[xx]	**3167.25**	**2604.16**	**738.92**	**1050.98**	**2486.74**	**2150.31**	**1010.33**	**2694.48**	**1456.62**	**1005.55**
	differences[xxx]	FN2,FN3,ES1	FN2,FN3, ES1,LT1, PL2,PL3	NO1,FN1, FN3,ES1, LT1,LI1,PL1, PL2,PL3	NO1,FN2, ES1,LT1,LI1, PL2,PL3	NO1,FN1, FN2,FN3,LI1, PL1,PL2	FN1,FN2, FN3,LI1,PL1	FN2,FN3, ES1,LT1, PL2,PL3	FN2,ES1, LT1,PL3	FN1,FN2, FN3,ES1, LI1,PL3	FN1,FN2, FN3,LI1, PL1,PL2

[x]mean - mean of 12 replications (only for shrubs - 2 replications)

[xx]SD - standard deviation of the mean

[xxx]differences - sites with the means significantly different (for $p<0.05$) in comparison to a given mean (on the basis of t-Student's test)

lower horizontal variability of the moss and lichen layer than the second group, encompassing the remaining sites (NO1, FN2, FN3, ES1, LT1).

The differentiation of the joint biomass pool of the mosses and lichens is also quite pronounced within the particular sites, although it is significantly smaller than in the case of the herb layer biomass. The differences between the biomass values within one site may amount to roughly 700 g m^{-2} (at the Norwegian site NO1), although they are mostly contained between 300 and 600 g m^{-2}. It means that due to the horizontal differentiation of the biomass pool of the mosses and lichens the richest places contain most often 2–12 times as much biomass as the locally poorest places within the confines of the same phytocoenosis.

The biomass of the litter is very poorly differentiated, both between the sites and within them. The Lithuanian site (LI1), which is the richest in terms of litter, contains on the average only 1.8 time more of this biomass than the poorest Finnish site (FN2). It was not possible to distinguish any consistent group of sites, for which the average biomass pool would differ significantly from that of the other sites (except for the already mentioned LI1, which is characterised by the distinctly highest biomass of the litter). The differences between the values within one site may amount to as much as 1500 g m^{-2} (NO1), although they are most often contained in the range 700–1100 g m^{-2}. It means that due to the horizontal differentiation in the distribution of litter the richest places contain on the average most often 2–3 times more mass than the locally poorest places within the same phytocoenosis.

Contrary to the little diversified pool of the litter the mass of humus is clearly differentiated. One can observe both the differences between the sites and the variability within the individual site. The Estonian site (ES1), which is the richest one, contains on the average approximately four times more humus than the poorest Finnish one (FN2).

Two not very distinct groups of study sites can be defined on the basis of the statistically significant differences in the humus mass. The first of them encompasses LT1, PL3 and ES1, to which also the sites NO1 and PL2 are in a way similar. The second group, characterised by a lower humus reserve, is composed of the sites FN3, FN1, PL1, LI1. Finally, the site FN2, featuring the lowest humus mass, is distinctly different from the remaining ones.

The differences between the values within one site range from approximately 2.7 kg m^{-2} to approximately 11 kg m^{-2}. It means that due to the horizontal differentiation of the pool of humus within the same phytocoenosis, the places richest in it contain most often 2–7 times more of it than the locally poorest places.

3.2. CARBON CONTENT IN THE BIOMASS

The percentage share of carbon in the biomass of the particular fractions varies only slightly, while it is more differentiated among the fractions (Table 3). Within the fraction of the living plants the relatively highest carbon

Table 3. Content (in %) of carbon in dry mass of different fractions.

Study site	Dwarfshrubs	Other vascular	Mosses	Lichens	Litter	Humus
NO1[(a)]	55.2	45.5	43.5		53.8	51.8
FN1	55.2	np.	42.6	44.5	53.8	51.8
FN2	49.9	np.	44.9	42.6	52.5	50.9
FN3	51.3	np.	45.2	42.4	51.3	49.4
ES1[(a)]	51.3	45.5	45.2	np.	51.3	49.4
LT1[(a)]	50.1	45.5	43.6	42.4	48.2	36.9
LI1	50.1	45.5	43.6	42.4	48.2	36.9
PL1[(a)]	50.5	45.5	44.4	np.	50.3	40.4
PL2[(a)]	50.5	45.5	44.4	42.4	50.3	40.4
PL3	50.9	45.5	45.2	np.	52.4	43.8

[(a)] estimated.

np. – fraction not present in collected biomass.

content characterises the dwarfshrubs (between 50 and 55%), while the lowest content is noted in the lichens (42–44%). Higher variability is observed within the fraction of the dead biomass, which is associated with the presence of the mineral parts of soil in the sample.

The summary image of the carbon pool in the analysed layers of the forest ecosystems is presented in Table 4. In comparison with the biomass of the particular fractions the pool of carbon analysed for all the fractions together is much less variable, both among the sites and within them. The richest Norwegian site (NO1) contains on the average roughly 2.5 times more of it than the poorest Polish one (PL3).

that there are two primary factors of variability of the features (Fig. 2, Table 5). The first one corresponds to the geographical-climatic differentiation of the study sites. This factor is first of all composed of latitude, annual mean of air temperature, and mean annual precipitation, as well as the species richness of the vascular plants of the herb layer, and the carbon pool in the herb layer. The second factor consists mainly of the carbon pool in the litter and in the moss-and-lichen layer, which corresponds to the differentiation of the local conditions. It is indirectly associated with the structure of the tree stands and the amount of room available for the vascular plants. These two factors explain together more than 66% of variability in the data.

Table 4. Carbon pool (in g m^{-2}) in different fractions of biomass on study sites

Site	NO1	FN1	FN2	FN3	ES1	LT1	LI1	PL1	PL2	PL3
Shrub Layer (B)	236.68	84.37	13.63	1.8	3.1	26.98	69.2	133.1	76.51	6.65
Dwarfshrubs	74.89	201.98	136.11	73.00	110.02	33.67	55.00	41.04	130.26	89.6
Herbs & grasses	0.87	0.00	0.00	0.00	1.21	0.7	19.24	8.45	2.94	0.21
Herb layer (C) total	**75.76**	**201.98**	**136.11**	**73.00**	**111.23**	**34.37**	**74.24**	**49.49**	**133.2**	**89.81**
Mosses	180.05	75.96	223.47	209.35	229.66	180.64	95.29	107.6	94.87	100.8
Lichens		36.76	44.12	30.38	0.00	13.98	15.18	0.00	11.56	0.00
Moss layer (D) total	**180.05**	**112.72**	**267.59**	**239.73**	**229.66**	**194.62**	**110.47**	**107.6**	**106.43**	**100.8**
B,. C and D layers	***492.49***	***399.07***	***417.33***	***314.53***	***343.99***	***255.97***	***253.91***	***290.19***	***316.14***	***197.26***
Litter	**439.93**	**466.33**	**303.79**	**366.18**	**369.79**	**315.38**	**491.87**	**318.08**	**424.09**	**444.88**
Humus	**3131.07**	**2232.38**	**1198.00**	**1759.28**	**4576.4**	**2859.74**	**1696.00**	**1954.17**	**2618.77**	**3385.22**

On the basis of the statistically significant differences in the mass of carbon several groups of sites can be distinguished. The first of them is equivalent to just one Polish site (PL3). The second is composed of the Lithuanian (LI1), Latvian (LT1), one Polish (PL1) and one Finnish (FN3) site. The last group, characterised by a higher carbon content, consists of the following sites: the remaining Polish one (PL2), the Estonian (ES1), two Finnish sites (FN1 and FN2), and the Norwegian one.

3.3. CARBON POOL AGAINST THE CLIMATE FACTORS

The analysis of interrelations between the main geographical variables and the carbon pool in the selected layers of the pine forest ecosystems, carried out with the help of the Principal Component Analysis, indicates

A more detailed assessment of the relations between the variables was done on the basis of the linear correlation coefficients. Out of 224 potential correlation associations (28 dependent variables × 8 independent variables) in only 66 cases (roughly 30%) correlation was statistically significant at $p<0.1$. Most frequent are the statistically significant correlations between the carbon pool and the mean annual temperature, the mean temperature of January and the latitude. In only 20 cases the correlation coefficients are higher than 0.75, but they concern mostly the standard deviation of the carbon content, and not its average content in particular fractions. Taking into account the strength of the correlation dependencies and the mutual associations between the independent variables, we can state that there is a general regularity of decreasing carbon pool contained in the biomass along with the increase of the mean an-

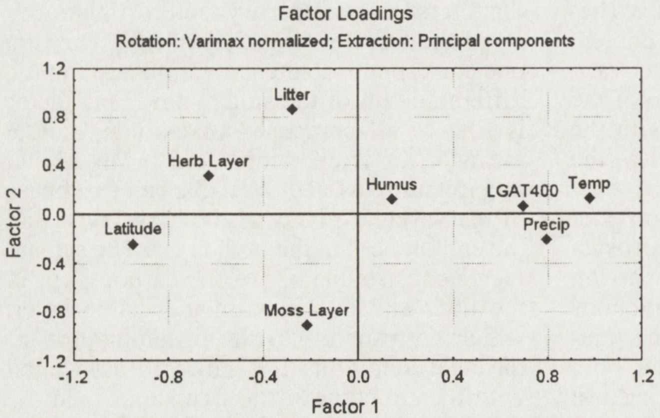

Fig. 2. The results of Principal Component Analysis for carbon pool and geographic variables. Variables description – see Table 5.

Table 5. Relationship between ground vegetation C biomass and selected climatic variables according to Principal Component Analysis (rotation: Varimax normalized). Most important factor loadings marked in bold.

Variable name	Factor loadings	
	Factor 1	Factor 2
Temp	**0.98**	0.13
Precip	**0.79**	-0.21
Latitude	**-0.95**	-0.24
LGAT400	**0.7**	0.06
Herb Layer	**-0.63**	0.31
Moss Layer	-0.22	**-0.91**
Litter	-0.28	**0.86**
Humus	0.14	0.12
Eigenvalue	3.51	1.8
% of total variance	43.9	22.5

Variable descriptions:
Temp – mean annual temperature (°C).
Precip – mean annual precipitation (mm).
Latitude – geographical latitude (°N).
LGAT400 – number of a herb layer vascular species per 400 m^2.
Herb Layer – carbon pool in a herb layer (g m^{-2}).
Moss Layer – carbon pool in a moss and lichen layer (g m^{-2}).
Litter – carbon pool in litter (g m^{-2}).
Humus – carbon pool in humus (g m^{-2}).

nual temperature towards the South. Within the above regularity the influence of winter temperatures is bigger than of the summer temperatures. At the same time, there is a similar regularity with respect to the decrease of the horizontal distribution of carbon within particular study sites (Table 6).

Linear correlation sufficiently well defines the relations between the carbon pool in the biomass and the geographical characteristics in the majority of cases. In only three cases the results of multiple regression, with application of the stepwise variable selection procedure, yield associations that are distinctly stronger than obtained from the simple linear correlation (Table 7). Thus, it turns out that the joint carbon pool of the herb layer and the moss-and-lichen layer can best be described with the help of the climatic variables, i.e. temperature and precipitation.

The decisive part of the herb layer carbon pool is contained in the dwarfshrubs, while in the moss-and-lichen ground layer – in the mosses (Table 4). The carbon pool in these fractions displays a clear relationship with the mean annual temperature, which is best described by the model $y = a + bx + cx^2$ (Fig. 3, 4). According to this model, in case of the carbon pool accumulated in the dwarfshrubs the minimum values occur in conditions of the mean annual temperature ranging between 3 and 6°C (Fig. 3). On the other hand, in the mosses, the maximum values of carbon pool are observed when mean annual temperature ranges between 1 and 5°C (Fig. 4).

The joint carbon pool in the mosses and lichens does not display any significant association neither with individual climatic factors, nor with their linear combination. It turns out, though, that these relations can be described with a non-linear model, accounting jointly for the influence of mean annual precipitation and the average temperature in January (Fig. 5). The correlation between the actual data and the values obtained from the model equals to 95%.

The association of the carbon pool in the humus with the climatic variables is described with sufficient reilability by the model $y = a + bx + cx^2$, in which the independent variable is the mean annual precipitation (Fig. 6). Conform to this model the minimum values of the carbon pool in the humus occur in the conditions of annual precipitation contained in the range 450–600 mm.

Table 6. Linear correlation coefficients between carbon pool and selected geographic variables.

	Variables	Mean annual tempe-rature	Mean annual preci-pitation	Mean temperature of January	Mean tempe-rature of July	Lang index	Marton index	Latitude	Vascular species richness (per 400 m^2)
Carbon pool (g m^{-2})	Dwarfshrubs	-0.58*		-0.63*					
	Herb layer	-0.56*		-0.60*					
	Mosses					0.57*			
	Lichens	-0.59*		-0.67**			0.57*		
	Herb layer and moss and lichen layer	-0.59*		-0.74**			0.60*	0.62*	
	Herb layer, moss and lichen layer and litter	-0.64**		-0.66**				0.61*	-0.57*
	Shrubs, herb layer and moss and lichen layer	-0.80***	-0.71**	-0.76**	-0.87***			0.89***	
	Shrubs, herb layer, moss and lichen layer and litter	-0.73**	-0.76**	-0.62*	-0.81***			0.76**	
(Carbon in humus) to (carbon in shrubs, herb and moss and lichen layers and litter) ratio			0.56*						
Standard deviation of carbon pool	Dwarfshrubs	-0.65**		-0.67**					
	Mosses	-0.57*		-0.71**			0.60*	0.61*	
	Herb layer and moss and lichen layer	-0.88***		-0.93****	-0.77**		0.68**	0.83***	-0.65**
	Litter		-0.610*						
	Herb layer, moss and lichen layer and litter	-0.78***	-0.64**	-0.77***	-0.67**			0.65**	-0.59*
	Humus				-0.74**			0.56*	
	All fractions together (without shrubs)	-0.56*			-0.77**			0.59*	
	Shrubs, herb layer, moss and lichen layer	-0.88***		-0.93****	-0.77**		0.68**	0.83***	-0.65**
	Shrubs, herb layer, moss and lichen layer and litter	-0.78***	-0.64**	-0.77***	-0.67**			0.65**	-0.59*
	All fractions together (with shrubs)	-0.56*			-0.77**			0.59*	

*$p<0.1$; **$p<0.05$; *** $p<0.01$; **** $p<0.1001$.

Table 7. The strongest relationships between the carbon pool and multiple climatic variables. Selected results of the Multiple Regression with Stepwise Variable Selection.

Live = –2459.30 + 368.75 temp – 8.42 prec + 1.36 lang + 142.01 marton

Parameter	Estimate	Std. Error	T Statistic	P-Value
CONSTANT	–2459.3	635.81	–3.87	0.012
temp	368.75	99.18	3.72	0.014
prec	–8.42	2.22	–3.79	0.013
lang	1.36	0.32	4.26	0.008
marton	142.01	35.28	4.02	0.01

adjusted R^2 =0.82

Sdwarf = –88.20 + 33.70 temp – 0.97 prec + 13.76 marton

Parameter	Estimate	Std. Error	T Statistic	P-Value
CONSTANT	–88.2	56.35	–1.57	0.169
temp	33.7	10.76	3.13	0.02
prec	–0.97	0.25	–3.79	0.009
marton	13.76	3.45	3.99	0.007

adjusted R^2 =0.84

Sratio = 8.59 + 0.30 temp + 0.004 prec – 0.67 july

Parameter	Estimate	Std. Error	T Statistic	P-Value
CONSTANT	8.59	1.41	6.11	0.001
temp	0.3	0.07	4.5	0.004
prec	0.004	0.001	4.23	0.006
july	–0.67	0.11	–5.9	0.001

adjusted R^2 = 0.86

Live – carbon stored in herb and moss-lichen layers (g m^{-2}).
Sdwarf – standard deviation of the carbon stored in dwarfshrubs.
Sratio – standard deviation of the (Carbon in humus) to (carbon in shrubs, herb and moss and lichen layers and litter) ratio.
temp – mean annual temperature (°C).
prec – mean annual precipitation (mm).
lang – Lang index=(mean annual precipitation/mean annual temperature)
marton – Marton index=(mean annual precipitation/(10+mean annual temperature)).

3.4. THE RELATION BETWEEN THE CARBON POOL AND SPECIES RICHNESS

The analysis of relationship between the species richness of a study site and the carbon pool in the selected layers of the forest, conducted with the help of the Principal Component Analysis, showed that there exist two main factors describing the general variability of the features considered (Fig. 7, Table 8). The first of them corresponds to the local variability within the sites. It is composed first of all of the carbon pool in the litter and the number of species of the vascular plants appearing on the area of 20 m^2, that is, in the locations of sampling of the biomass. It is also related to the value of the parameter "*a*" from the allometric equation, representing the relation between the number of species and the area. The second factor characterising the geographical variability of the sites is mainly dependent upon the latitude, the

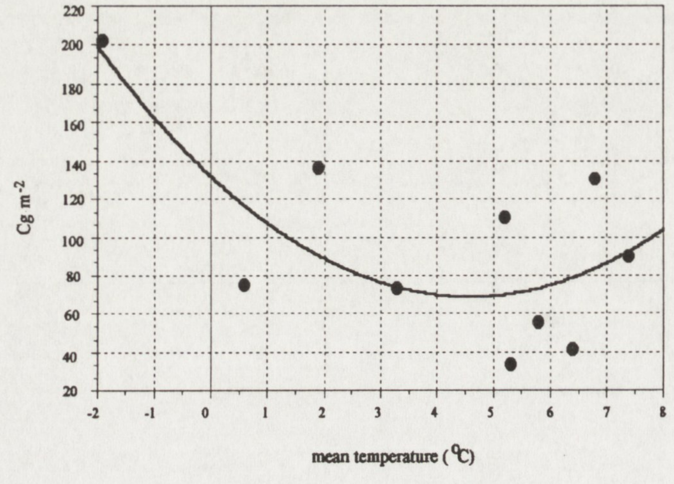

Fig. 3. Relationship between carbon pool in dwarfshrubs (dependent variable) and mean annual temperature (independent variable) according to the model $y = a + bx + cx^2$. Parameters: a = 131.90; b = –27.57; c = 3.01; correlation coefficient = 0.74.

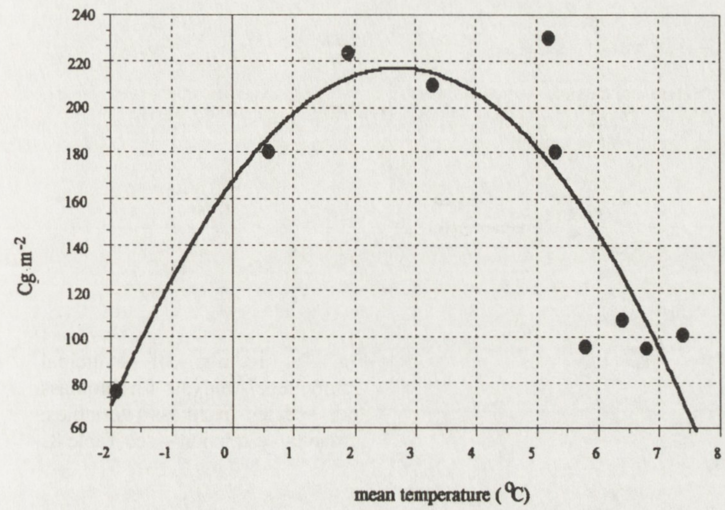

Fig. 4. Relationship between carbon pool in mosses (dependent variable) and mean annual temperature (independent variable) according to the equation $y = 168.36 + 35.98x + (-6.64)x^2$. Parameters: a = 168.36; b = 35.98; c = –6.64; correlation coefficient = 0.87.

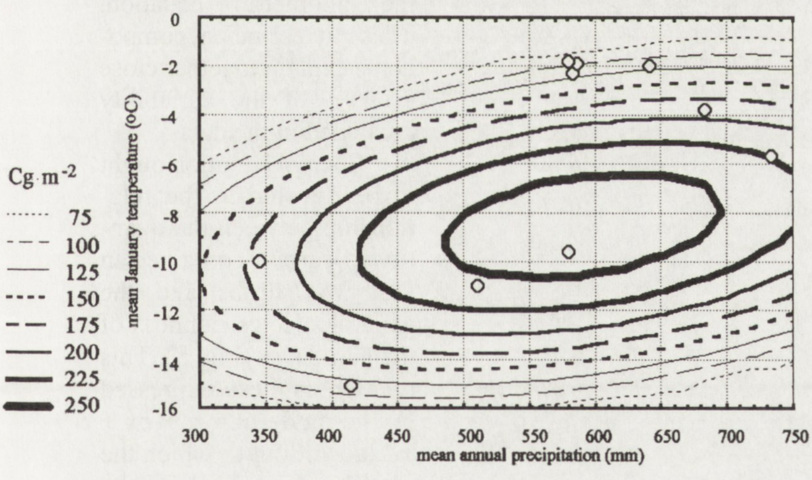

Fig. 5. Relationship between carbon pool in moss and lichen layer (dependent z variable) and mean annual precipitation (x) and mean January temperature (y):
$z = -803.099 + 2.263x - 93.730y - 0.002x^2 + 0.051xy - 3.732y^2$.
Small circles – location of study sites.

Fig. 6. Relation between carbon pool in humus (dependent variable) and mean annual precipitation (independet variable) according to the model $y = a + bx + cx^2$. Parameters: a = 14253.18; b = –48.86; c = 0.05; correlation coefficient = 0.76.

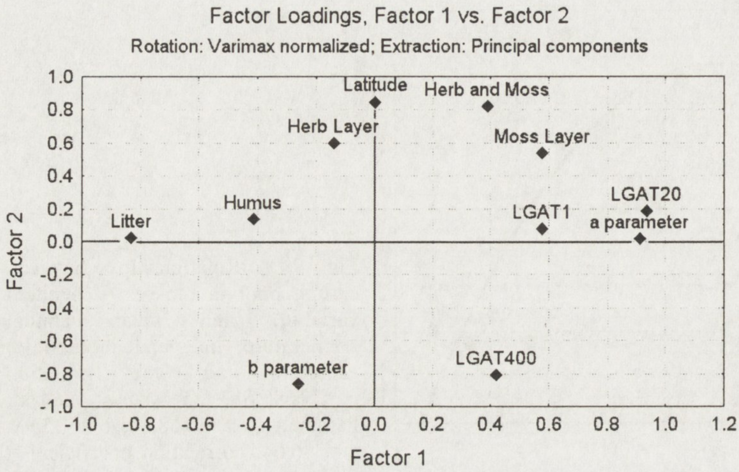

Fig. 7. Results of Principal Component Analysis for biomass and species richness variables. Variables description – see Table 8.

Table 8. Relationship between biomass and selected species diversity variables according to Principal Component Analysis (rotation: Varimax normalized). Most important factor loadings marked in bold.

Variable name	Factor loadings	
	Factor 1	Factor 2
a parameter	**0.91**	0.02
LGAT20	**0.93**	0.19
Litter	**-0.83**	0.03
b parameter	-0.26	**-0.86**
Latitude	0.01	**0.85**
LGAT400	0.42	**-0.81**
Herb and Moss	0.39	**0.82**
LGAT1	0.58	0.08
Herb Layer	-0.14	0.6
Moss Layer	0.58	0.54
Humus	-0.41	0.14
Eigenvalue	3.64	3.5
% of total variance	33.08	31.85

Variable descriptions:

a parameter – parameter from allometric model y = axb (see Solon 2003b, this volume).

LGAT20 – number of herb layer vascular species per 20 m^2.

Litter – carbon pool in litter (g m^{-2}).

b parameter – parameter from allometric model y = axb (see Solon 2003b, this volume).

Latitude – geographical latitude (°N).

LGAT400 – number of herb layer vascular species per 400 m^2.

Herb and Moss – carbon pool in herb and moss and lichen layers (g m^{-2}).

LGAT1 – number of herb layer vascular species per 1 m^2.

Herb Layer – carbon pool in a herb layer (g m^{-2}).

Moss Layer – carbon pool in a moss and lichen layer (g m^{-2}).

Humus – carbon pool in humus (g m^{-2}).

general species richness, and the parameter "*b*" from the allometric equation. These two principal components explain together close to 65% of the variability contained in the data.

Special attention ought to be devoted to the relationship between the quantity of carbon contained in the dwarfshrubs and the general species richness of the herb layer (Fig. 8). This relation is best expressed by the model $y = a + bx + cx^2$, according to which the small carbon pool in the dwarfshrubs corresponds to the intermediate species richness (15–21 species).

A similar unimodal distribution characterises the relations between, on the one hand, the carbon pool in the herb layer and summarized pool of the herb and the moss-and-lichen layers, and, on the other hand, the value of the parameter "*b*" from the allometric equation (Figs 9, 10). In both cases the minimal values of carbon pool occur for the intermediate values of the parameter "*b*" (between 0.20 and 0.27).

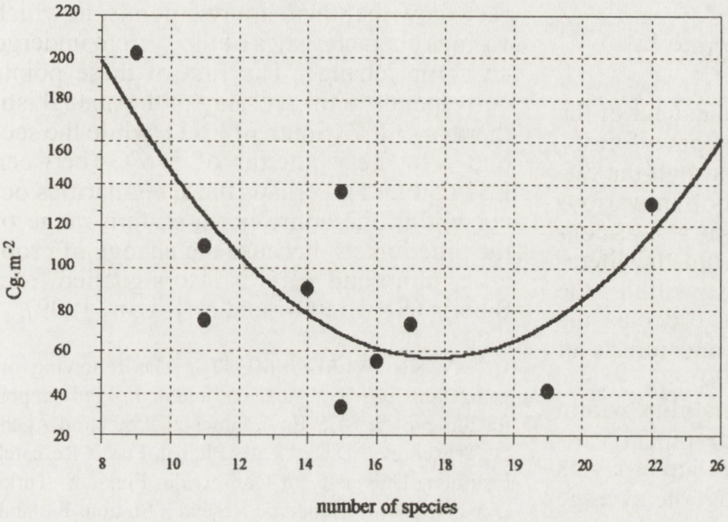

Fig. 8. Relationship between carbon pool in dwarfshrubs (dependent variable) and number of herb layer vascular plant species per 400m^2 (independent variable) according to the model $y = a + bx + cx^2$. Parameters: a = 528.49; b = –53.29; c = 1.51; correlation coefficient = 0.73.

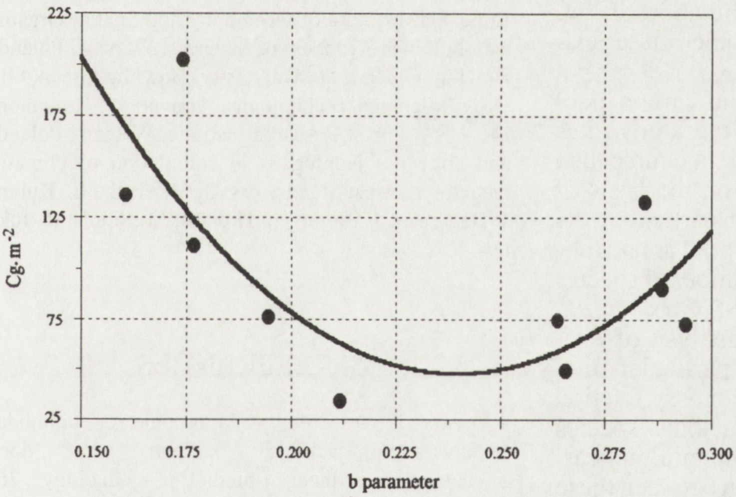

Fig. 9. Relationship between carbon pool in herb layer (dependent variable) and value of „b" parameter from allometric model $y = ax^b$ (indepenent variable) according to the model $y = a + bx + cx^2$. Parameters: a = 1158.92; b = –9275.15; c = 19359.06; correlation coefficient = 0.71. (Values of "b" parameter are taken from Table 6 in Solon, 2003b, this volume).

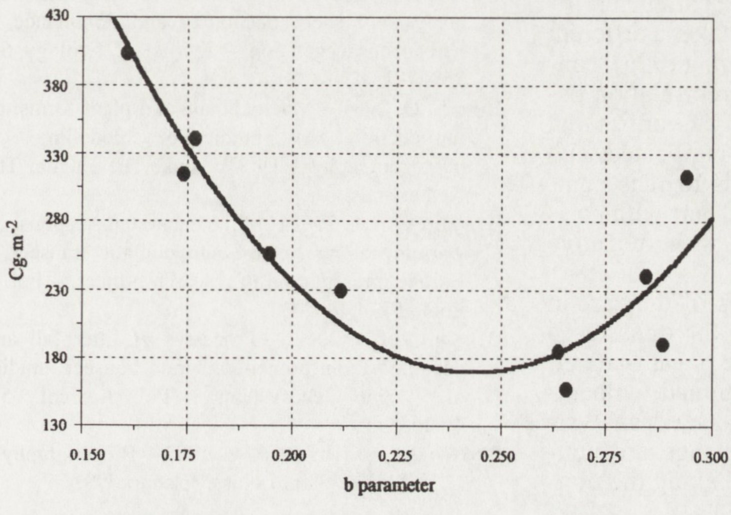

Fig. 10. Relationship between the summarized carbon pools of herb and moss and lichen layers (dependent variable) and value of „b" parameter from allometric model $y = ax^b$ (indepenent variable) according to the model $y = a + bx + cx^2$. Parameters: a = 2248.41; b = –17087.47; c = 35115.02; correlation coefficient = 0.93.

4. DISCUSSION AND CONCLUSIONS

A distinctly mosaic-like character of the herb layer is observed in the pine forests, which is seen, in particular, through the differentiation of the carbon pool in various places within the ecosystem. The results confirm appropriately the data from the literature, when the variability within the phytocoenosis is of the same order as the variability described for the pine forests of western Siberia (Gabeev, 1990).

Side by side with the variability within the ecosystem a distinct geographical variability of the carbon pool in particular layers is observed. Generally speaking, the average annual temperatures and the temperatures of January have the biggest influence on the changes in the carbon pool, although in cases of various fractions the combination of factors describing in the best manner these relations is different.

The relations between the carbon pool and the species richness of the study sites along the transect take a different course than it could have been expected on the basis of the most common models. In particular, the maximal values of the carbon pool are not observed for the intermediate number of species (Gough, 1998; Guo, 1998; Cox *et al.*, 2001). On the other hand the analysis of variability of the carbon pool in particular fractions of the herb layer and the mossy fraction shows that either the intermediate species richness is accompanied by the minimal carbon pool, or there is no relation between these variables.

Likewise, the relation between the carbon pool and the value of the parameter "*b*" from the allometric equation, takes a different shape as well. Pastor *et al.* (1996) concluded that there is negative correlation between these variables. Our study implies that the relation is much more complicated, and the curve, which corresponds to it is composed of three segments – the part with positive correlation, the one with negative correlation, and the flat part.

Numerous characteristics of the carbon pool on the study sites along the transect do change at a first glance in the linear manner, proportionally to the mean annual temperature and latitude. A more detailed analysis shows that the trends of change are nonlinear. The studies conducted along the transect show that there are two points, at which various characteristics of the system undergo an abrupt change. The first of these points corresponds to the crossing of the annual isotherm of +1°C (South of FN1), while the second – to the isotherms of 5–6°C (between ES1 and LT1). Perhaps these regularities occur within the entire north-eastern range of the pine forests, because the change of properties at around +1°C is also signalled from Siberia (Stolbovoi and Nilsson, 1999).

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