Estimation of tree biomass of Norway spruce forest in the Plešné Lake catchment, the Bohemian Forest

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Abstract: This paper evaluates the total biomass and pools of major nutrients and ecologically important metals of the tree layer in the catchment of Plešné jezero (PL) in the Bohemian Forest (Šumava, Czech Republic), and compares them to analogous data on understory vegetation and soils. The results are based on field measurements and semi-automatic image analyses of aerial orthophotographs. The tree layer was relatively sparse with open canopy in some parts of the catchment. Stand density varied between 44 and 328 individuals per hectare. The catchment weighted mean total biomass of trees was 134 t ha^{-1} dry weight, of which needles, branches, roots, and stems represented 5%, 10%, 14%, and 71%, respectively. The stem wood and bark represented 67% and 4%, respectively, of the total tree biomass. The catchment weighted mean element pools were 568 and 3.0 mol m^{-2} (i.e., 68 and 0.42 t ha^{-1}) for C and N, respectively. The other pools were 76 mmol P m^{-2}, 602 mmol Ca m^{-2}, 133 mmol Mg m^{-2}, 39 mmol Na m^{-2}, 347 mmol K m^{-2}, 19 mmol Al m^{-2}, 6.2 mmol Fe m^{-2}, and 35 mmol Mn m^{-2}. The element pools accumulated in the tree biomass represented from $< 1\%$ (Al, Fe) to 37% (C) of their total pools (soil + tree layer + understory vegetation) in the catchment. Pools of Ca and Mg in the tree biomass were similar to their exchangeable pools in the catchment soils, while those of K were 3 times higher. Nutrient (N, P, Ca, Mg, and K) and C pools in the tree biomass were 2–11 times higher than those in the understory vegetation, with the minimum for P and maximum for C.

Key words: Aerial photos, canopy, element pools, *Picea abies.*

Introduction

Determining the role of forest ecosystems in biogeochemical cycles has been the aim of many studies for a long time (BINKLEY & VALENTINE, 1991; HEDIN et al., 1995; SCHLEPPI et al., 1998). Carbon and nitrogen cycles in forests are among the most studied processes, because of their key practical implications for global wood biomass production and biological CO_2 fixation (DIETER & ELSASSER, 2002; JOOSTEN & SCHULTE, 2002; FINÉR et al., 2003). The process of soil acidification followed by nutrient deficiency and decline of some forest ecosystems called for research on biogeochemical cycles of other elements such as calcium and magnesium (WATMOUGH et al., 2005). The biogeochemical cycles of mineral nutrients in forests are intimately related because the foliage nutrient content strongly controls carbon assimilation and therefore ecosystem productivity. Forest production is controlled by ecological gradients of nutrient availability, soil properties, and climatic conditions (SCARASCIA-MUGNOZZA et al., 2000). Significant differences in production and element concentrations were found in a recent study on tree biomass and nutrient pools of spruce forests along a European ecological transect (SCARASCIA-MUGNOZZA et al., 2000). Therefore, any particular ecosystem study dealing with biogeochemical cycles should not simply rely on the data published from other ecosystems.

The aim of this paper is to determine tree layer biomass, its distribution within the catchment under varying environmental conditions (terrain morphology), and the associated element pools in the catchment of glacial lake Plešné jezero (Plešné Lake), situated in the Bohemian Forest (Šumava, Böhmerwald). The chemistry and element fluxes of the Plešné catchment-lake ecosystem have been intensively studied since the 1990s (VRBA et al., 2003). The catchment has been exposed to high deposition of S and N compounds during the last six decades, but has been partly recovering from the acid stress since the late 1980s (MAJER et al., 2003). Many results on the element fluxes within this catchment and its biological recovery were already published (KAŇA & KOPÁČEK, 2006; KOPÁČEK et al., 2001, 2002a, 2006a, b), but they did not address element pools associated with individual catchment parts. An important part of the catchment element pools, the tree layer, was omitted, because of the lack of reliable data. This study should fill a gap in the present knowledge on the role of the tree layer on the elements cycling within this ecosystem. Here we evaluate: (1) the amount of biomass of the tree layer and the associated pools of major nutrients (C, N, P, Ca, Mg, K) and ecologically important metals (Al, Fe, Mn) in the Plešné Lake catchment, (2) spatial variability of the studied characteristics (biomass and element pools) within the catchment, and (3) a comparison of the element pools stored in the tree layer with those in the soil and understory vegetation.

Study site

The research was carried out in the catchment of Plešné Lake (48°46′35″ N, 13°52′0″ E; elevations = 1087–1378 m a.s.l.; catchment area = 63.9 ha (including lake = 7.4 ha)) in the Bohemian Forest, Czech Republic; all morphological data were updated according to a new digital elevation model and orthophotographs. The catchment is located in the spruce forest (8^{th}) altitudinal zone according to the Czech site typological system (Viewegh et al., 2003). This area is represented by an anemo-orographic system of glacial cirque (Jeník, 1961; Sofron & Štěpán, 1971). The catchment area is marginally covered by the beech-spruce (7^{th}) altitudinal zone (Viewegh et al., 2003). Forest covers almost the whole catchment. It is on average 160 years old and dominated (99%) by Norway spruce (*Picea abies* L.), with minor contributions of mountain-ash (*Sorbus aucuparia* L.) and beech (*Fagus sylvatica* L.). Timber biomass ranges between 15 and 720 m^3 ha^{-1} (catchment mean of 230 m^3 ha^{-1}) according to the Stožec (1995–2004) and Plešný (1996–2005) forest management plans (I. Vicena – pers. commun.). Few data are available in the literature on the history of land-use in the Plešné catchment, summarized by Veselý (1994). Disturbances occasionally affecting the surroundings of the Plešné catchment (logging, pasturing, or fires) were probably negligible within the catchment during the last ~250 years (I. Vicena – pers. commun.). Details on forest development in the study area are given by Jankovská (2006). *Vaccinium myrtillus* L. is the dominant species of the understory vegetation; more details on the understory vegetation are given by Svoboda et al. (2006a).

The catchment of Plešné Lake is steep. Up to 10% of the total area has slopes up to 5°. Approximately 50% of the total area represents sites on slopes up to 20°. Slopes up to 48° and 63° are present in 95% and 99% of the total area, respectively. The bedrock is formed by granite (Veselý, 1994). The catchment is covered with ~0.2 m deep leptosols (38%), and ~0.45 m deep podsols (29%) or dystric cambisols (27%); the rest is bare rocks (5%) and wetland (~1%). Soil is sandy (~75%), low in clay (~2%), and its catchment weighted mean pool is 92 kg m^{-2} (< 2 mm dry weight soil fraction). Soil pH_{CaCl2} is low, with minimum values of 2.5–3.1 in the A-horizons and maximum values of 3.2–4.4 in deeper mineral horizons. The mean effective cation exchange capacity of the soils is 0.13 cmol kg^{-1} (NH_4Cl and KCl extractable) and is dominated by exchangeable Al^{3+} (57%) and protons (28%), while base saturation represents 15% (Kopáček et al., 2002b).

Material and methods

Remote sensing

Colour aerial photographs were prepared by Argus Geo System Ltd. (Hradec Králové, Czech Republic) on the 18 June 2000 (scale of 1 : 7000). A digital orthophotograph, 0.2 m in pixel size, together with a digital elevation model (DEM) and topographical/hydrographical GIS data, was processed by GEOREAL Ltd. (Plzeň, Czech Republic) and the Institute of System Biology and Ecology AS CR (České Budějovice, Czech Republic).

Biomass estimation

Estimation of the biomass on the catchment scale was done in the following steps. (1) The set of sample trees was selected in the field. Regression analysis was used to determine the relationships between the parameters of the sample trees. (2) Total catchment area was then divided into a regular 50 × 50 m grid (Fig. 1). Forty-two randomly distributed cells of the grid were selected for further evaluation. The stand density in the cell and the relative crown diameter of each tree in the cell were determined. The tree parameters in the cells were estimated based on the data from the sample trees. (3) Total catchment area was divided into 7 altitudinal zones by 50 m intervals, using DEM (Fig. 1). The area of each zone was measured in GIS. (4) The stand parameters in each altitudinal zone were estimated using regression analysis. (5) The biomass of the forest stand was calculated using selected equations valid for the Czech Republic.

Tree sampling procedure

Tree selection was done to represent all objectively selected partial plots, stratified according to elevation and forest-site conditions (Fig. 1). Groups of the sample trees (identifiable in the orthophotograph) were selected in the field in 2004. Each plot was represented by a group of 7 to 13 trees. Both the tree height (H) and diameter at breast height (DBH) were measured together on 158 sample trees. Altitude and terrain inclination of each tree site was obtained from DEM.

Estimation of tree crown diameter

Diameters of the tree crowns were estimated using colour aerial photographs (transformed into the orthophotographs, pixel size 0.2 m). The centre of each tree crown was determined visually on the orthophotographs. This method has been implemented as a software module in the program PlotOA (www.infodatasys.cz). The procedure seeks a homogenous circular area around a determined point. Mean diameter of the homogenous area is reported as tree crown diameter (D). The homogeneity measure is calculated as a three dimensional variance (it is the sum of the variances for three colours – red, green, and blue; the square root of this variable for an area of a determined size is referred to as LIMITVAL) after a specific transformation of the colours for each pixel. This transformation equilibrates pixels with different illuminations. Manually determined centres of all tree crowns represent an auxiliary set of input data.

Each of 158 sample trees was described by a set of parameters: H, DBH, altitude, D, LIMITVAL, and means of transformed values for the red, green and blue components

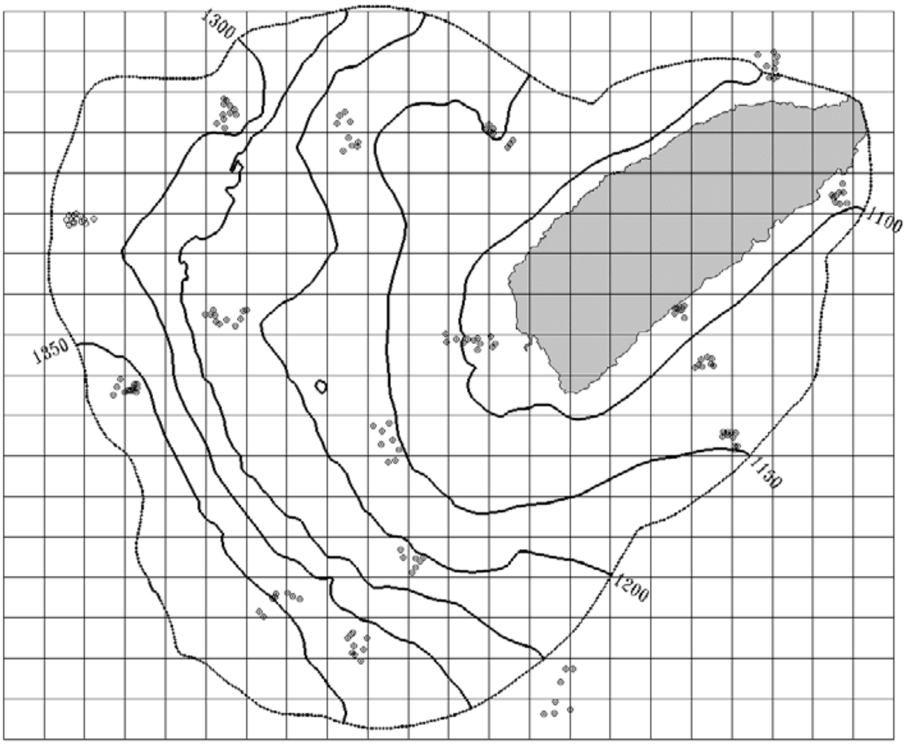

Fig. 1. The catchment of Plešné Lake with altitude contour lines and location of sample trees (points) in a 50 × 50 m grid.

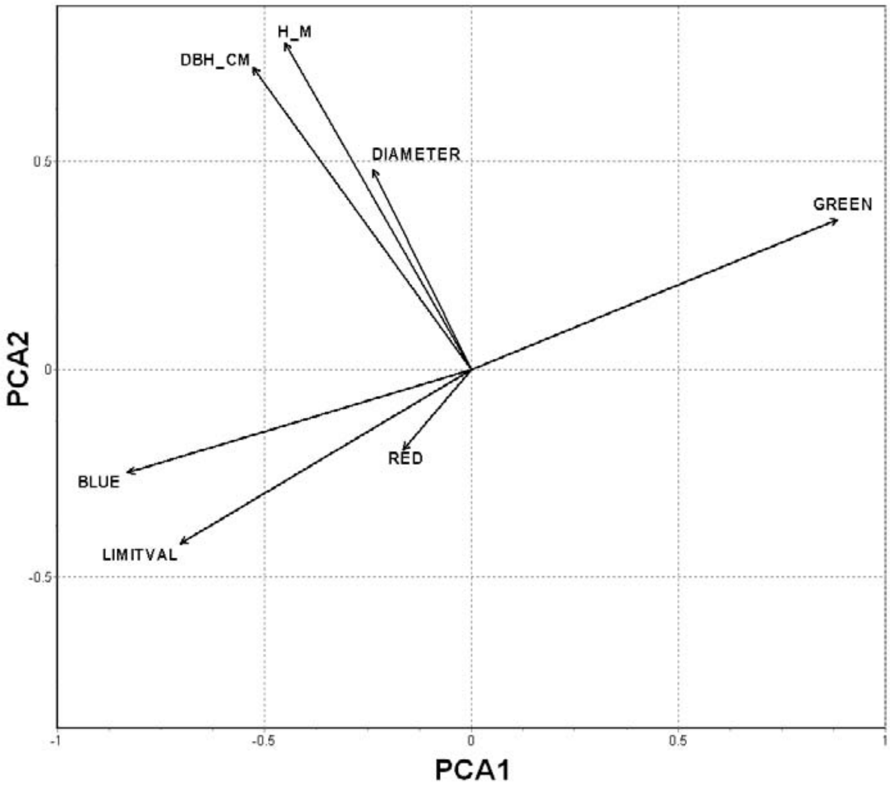

Fig. 2. Principal component analysis for 7 variables obtained during determination of crown projection diameters (DIAMETER) in a set of 158 sample trees. RED, GREEN and BLUE are the means of three transformed colour components for the whole tree-crown. LIMITVAL was determined as the colour variance of a circular area representing the tree crown. DBH_CM is tree diameter at breast height and H_M is tree height.

Table 1. Mean element concentrations in selected compartments of Norway spruce in the Plešné Lake catchment (data source Svoboda et al., 2006b).

Biomass compartments	C mol kg^{-1}	N	P	Ca	Mg	Na mmol kg^{-1}	K	Al	Fe	Mn
Stem wood	42.3	126	0.7	19	4.6	2.7	13	0.3	0.1	1.6
Stem bark	42.8	392	16	205	33	3.6	62	1.7	0.6	8.5
Foliage – 1st year	42.8	1198	60	64	40	1.8	158	2.2	0.9	7.3
Foliage – 2nd year	43.1	1116	50	97	41	2.1	125	2.8	1.1	11
Foliage – 2nd year or older	43.2	1005	37	108	24	2.9	97	5.8	2.0	9.6
Branches	42.7	580	24	111	27	3.7	60	7.4	2.4	5.4
Roots	43.0	222	5.4	31	7.5	3.1	31	2.6	0.5	1.6

over all pixels representing the crown circle. Variable relationships were studied using principal component analysis (PCA). The tree size parameters (as measured in the field or calculated on the base of orthophotograph) have no significant correlation with colour features of pixels over tree crown, shown by PCA (Fig. 2). It points out that there is no possibility to get more precise crown size on the base of orthophotographs. Red colour was empirically down weighted in the procedure, because the red colour component of the pixel, set over tree crown circular area, had a minimal influence on the constitution of the ordination. The crown diameter of all the trees within selected cells of the grid was determined by the same method as that used for the sample trees.

Data processing

Relationships between variables were quantified using standard linear or quadratic regression analysis. Sum of least squares was used to calculate the regression equations. Biomass of the compartments of a single tree was calculated using the following general allometric equation:

$$W = a(DBH^2 \times H)^b, \tag{1}$$

where W is weight of any particular tree compartment (stem wood, stem bark, live branches, and foliage in kg of dry matter), DBH (cm), H (m), and values a and b are empirical constants, specific for dry matter of tree biomass in Norway spruce forests of the Czech Republic (Černý, 1990). Total stem dry matter was calculated as the sum of W_{sw} (stem wood), W_{sb} (stem bark), W_{b} (branches), and W_{f} (foliage), which were calculated using the respective a and b constants (Černý, 1990), and root biomass. Root (belowground) biomass of Norway spruce trees (W_{r}) was related to the stem and branch biomass using the empirical relationship derived from data published by Vyskot (1981):

$$W_{\mathrm{r}} = 0.173(W_{\mathrm{b}} + W_{\mathrm{s}}), \tag{2}$$

where W_{b} and W_{s} are the weight of branch and stem biomass, respectively. Values of W_{r} include the coarse roots only.

Tree biomass in the whole catchment was calculated using the following steps: (1) Regression analysis was used to determine the relationships between the sample tree parameters (H – height, DBH – diameter, D – diameter of the tree crown) and altitude (A). (2) Total catchment area was divided into a regular 50 × 50 m grid (Fig. 1). Forty-two randomly distributed cells of the grid were selected for further evaluation. The position of all trees in each selected cell was determined using an orthophotograph. Only trees of the main canopy that were identified in the digital aerial photo were counted. Understory trees were not included. The relative crown diameter was determined for each tree using the method described above. The trees identified on the aerial photo were counted and their mean altitude was assigned to the centre of the square. The measured tree parameters (number of trees per unit area and mean tree crown diameter) were related to mean altitude. (3) Total catchment area was divided into 7 altitudinal zones by 50 m intervals, using DEM (Fig. 1). The area of each zone was measured in GIS. (4) The stand parameters (stand density, mean H and mean DBH) in each altitudinal zone were estimated using regression analysis (see points 1 and 2). (5) The analyzed trees were divided into the following classes, based on the crown diameter related to mean crown diameter at the respective altitude. The classes A, B, and C contain trees of a relative size up to 50%, 51–75%, and 75–100% of the mean, respectively. Class D contains all larger trees. Mean percentage of these classes was calculated for the whole catchment. (6) Total number of trees per 1 ha in each altitudinal zone was divided into the size classes A to D. Catchment weighted mean (CWM) tree biomass was calculated using the following equation:

$$W_{\mathrm{T}} = \Sigma P_z N_{zi} s_{zi} W_{zi} / \Sigma P_z \tag{3}$$

where, W_{T} is the CWM tree biomass, P_z is area of the altitudinal zone (z is an index of the altitudinal zone), N_z is number of trees of the i-th size class (A to D) in the z-th altitudinal zone, s_{zi} is the proportion of trees of the i-th size class in the z-th altitudinal zone, and W_{zi} is the biomass of the mean tree in each tree class, estimated using the allometric model.

Catchments weighted mean (CWM) pools of elements stored in the tree layer were estimated as the product of CWM biomass pools and mean element concentration in the tree biomass. The mean element concentrations in the tree biomass, derived from Svoboda et al. (2006b), are summarized in Table 1.

Estimated tree and stand parameters

The semi-automatic image processing applied to trees in the selected 50 m grid cells gave the following results: (1) Mean tree crown diameter varied between 3.3 and 6.0 m according to grid cell (mean of 4.6 m). This crown diameter was related to altitude (correlation $r = -0.49$) (Fig. 3) and DBH (correlation $r = 0.27$) (Tab. 1). The mean ratio of D to DBH was equal to 10 ± 4 (± standard deviation) and was independent of altitude and inclination. (2) For DBH

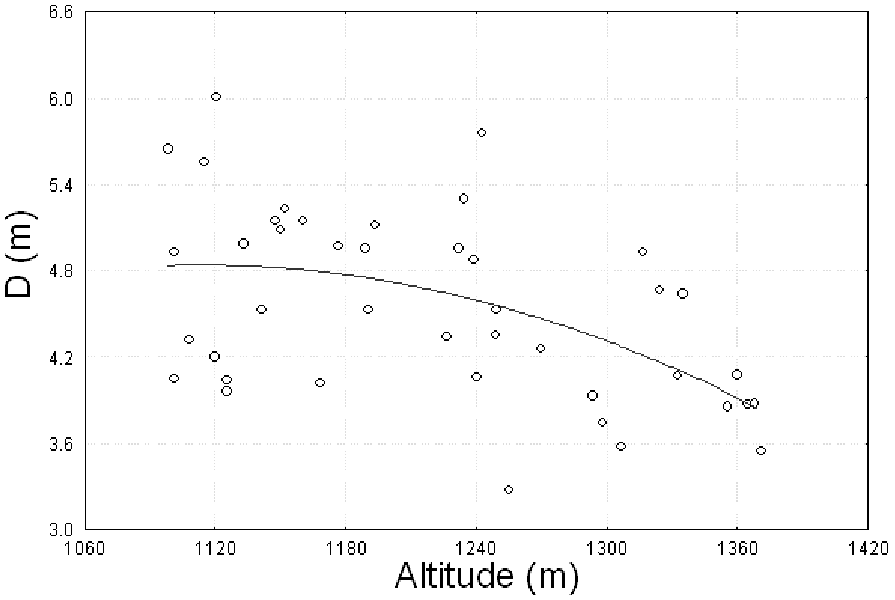

Fig. 3. Relationship of mean crown diameter (D) and altitude in the dataset of analyzed 50 m squares. Fitted regression curve $y = 14 + 0.034x - 1.510^{-5}x^2$ ($n = 42$, $r^2 = 0.26$).

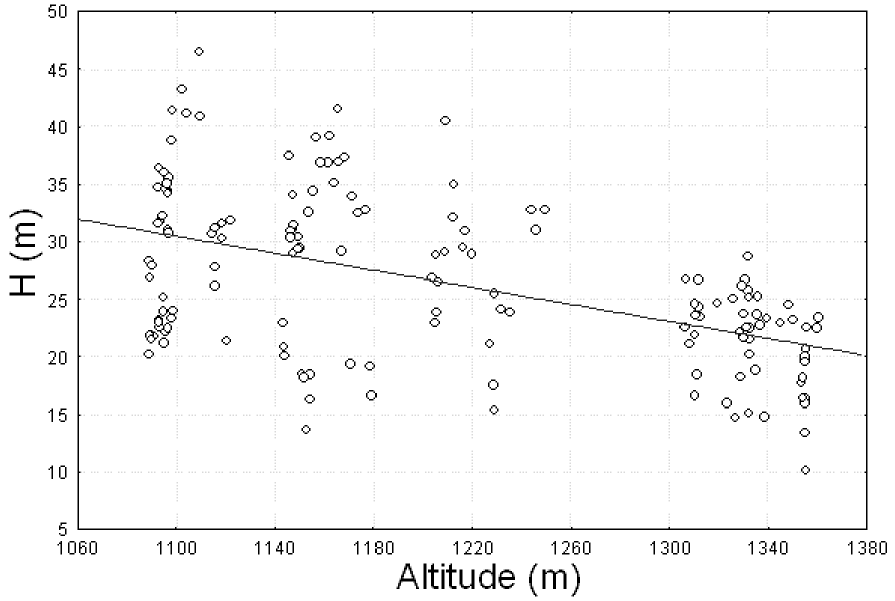

Fig. 4. Relationship of tree height (H) and altitude for the sampled trees. Fitted regression line $y = 71 - 0.037x$ ($n = 154$, $r = -0.51$).

(cm), the following model was derived from the regression between D and altitude (A, m) (Fig. 3) and the mean D to DBH ratio of 10:

$$DBH = (-13.9 + 0.034A - 0.0000151A^2)/10 \qquad (4)$$

The following model for tree height (H in m) was calculated on the basis of sample tree data (multiple $r = 0.87$):

$$H = 47.4 - 0.031A + 0.301DBH, \qquad (5)$$

where A is in m a.s.l., and DBH in cm. The mean tree height decreased by ~3 m per each 100 m of elevation increase (or by 4 m, without DBH as a co-variable; Fig. 4).

There was a significant ($P < 0.001$) correlation between inclination and stand density ($r = -0.50$). A relationship between altitude and terrain inclination can be a reason for the non-linear dependency of stand density (N; number of trees per 1 ha) on altitude (A in m) (Fig. 5):

$$N = 4 \times (1418.9 - 2.26A + 0.000924A^2) \qquad (6)$$

Results and discussion

Stand biomass

The stand density varied between 44 and 328 trees per hectare in 2000. The relatively low mean stand den-

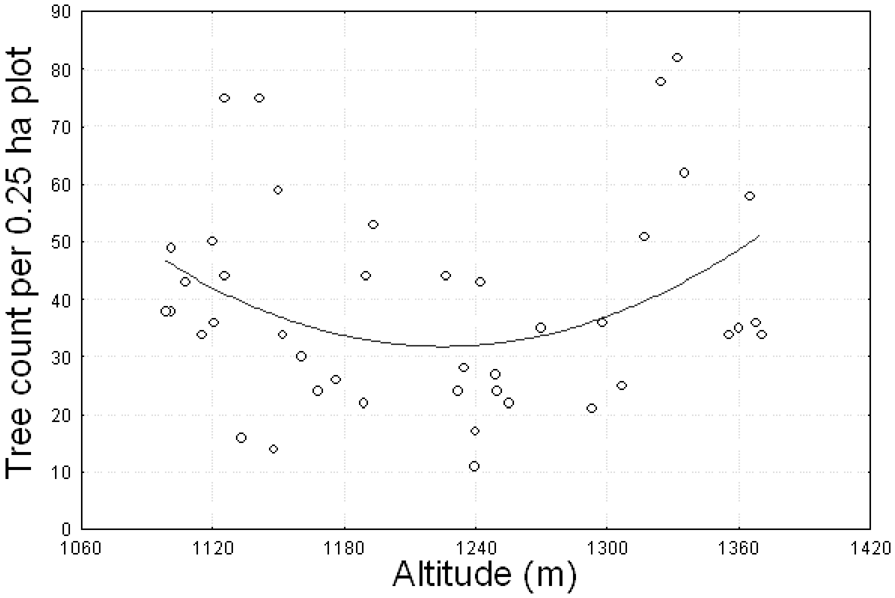

Fig. 5. Relationship of stand density and altitude in the dataset of analyzed 50 m squares. Fitted regression curve $y = 1419 - 2.3x - 9.210^{-4}x^2$ ($n = 42$, $r^2 = 0.12$).

Table 2. Correlation coefficients of the relationships between the measured parameters of the sample trees in the Plešné Lake catchment.

	Altitude	H	DBH	H:DBH	D	D:DBH
Altitude	1.00	−0.51 *	−0.12	−0.50 *	−0.13	−0.06
H		1.00	0.76 *	0.18 *	0.28 *	−0.35 *
DBH			1.00	−0.47 *	0.27 *	−0.55 *
H:DBH				1.00	−0.03	0.40 *
D					1.00	0.58 *
D:DBH						1.00

Explanations: * $P < 0.05$.

sity (155 ± 10.9 ha^{-1}) was related to the extreme morphological conditions of the site (glacial cirque). Some extreme parts of the catchment were covered with only sparse forest stands, especially at middle elevations (1200–1250 m a.s.l.). Total sum of the tree crown area was between 774 and 5806 m^2 ha^{-1} according to stand density. The model (equations 4–6) estimated the CWM total biomass of the tree layer at 134 t ha^{-1} dry weight (Tab. 2). Needle biomass represented 5% (7 t ha^{-1}), while branches represented 10% (13 t ha^{-1}) of the total biomass, respectively. Stems represented most of the total tree biomass (71%, 94 t ha^{-1}), of which the wood was 67% and bark ~4%. Total root biomass represented 14% (19 t ha^{-1}).

Generally, total forest biomass is a function of several factors, such as age, soil fertility, geographic position, etc (Scarascia-Mugnozza et al., 2000). The total mean biomass of Norway spruce stands varied from 154 to 317 t ha^{-1} along the European ecological transect, with a mean of 237 t ha^{-1}, (Scarascia-Mugnozza et al., 2000). The total biomass of stands in geographical positions similar to those in our study site were 215 and 317 t ha^{-1} in the Czech Republic and Germany, respectively (Scarascia-Mugnozza et al., 2000). However, the Czech stand was relatively young (58 years), while the German stand was about 140 years old. The lower CWM biomass of the spruce forest in the Plešné Lake catchment probably resulted from the following factors: (1) The Plešné catchment is less fertile, situated at a higher altitude, and has extreme morphology and strongly acidic soils (Kopáček et al., 2002b). (2) The structure of the Plešné forest stands differs from the other Czech and German sites. The site conditions in the Plešné Lake catchment are rather extreme, with steep slopes (up to 60 degrees) and stony undeveloped soils (Kopáček et al., 2002b). Therefore, in some parts of the catchment (up to 50% of the total catchment area), the forest stands have a relatively open canopy structure with low density. This is probably the reason why the total biomass of our study site is even lower than the total biomass of an old-growth forest stand with similar structure in northern Sweden (198 t ha^{-1}; Scarascia-Mugnozza et al., 2000). (3) The approach (remote sensing) used in this study to analyze stand parameters of the tree layer can underestimate some parameters, like density and crown size, leading to underestimation of the total tree biomass. Our method of tree biomass estimation has several critical points, which can bias the results. We do not expect any important error associated with tree counting because the trees were detected in an orthophotograph (compare with automated methods used by Šumbera & Žídek, 2002; Erikson & Olofsson, 2005; Pouliot et al., 2005). However, sample trees measured in the field created a sample set, with some features different from the set of all trees in the studied stand, because only trees

Table 3. Estimated stand parameters, stand biomass and catchment total biomass in the catchment of Plešné Lake.

	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	Zone 6	Zone 7	Total
Mean altitude (m)	1075	1125	1175	1225	1275	1325	1360	
Area (ha)	4.8	13.9	10.2	9.1	5.4	8.6	4.5	56.5
Tree crown diameter class A (1.0% of all trees in the zone) – single tree parameters								
DBH (cm)	23.7	23.8	23.7	23.1	22.2	21.0	19.9	
H (m)	21.1	19.6	18.0	16.3	14.5	12.5	11.1	
Stem wood (kg)	193	184	170	151	129	106	88.4	
Stem bark (kg)	11.2	10.6	9.8	8.8	7.5	6.1	5.2	
Foliage (kg)	15.1	14.4	13.3	11.8	10.0	8.1	6.8	
Live branches (kg)	17.6	16.4	14.6	12.4	10.0	7.4	5.8	
Roots (kg)	38.4	36.5	33.6	29.8	25.4	20.6	17.2	
Tree crown diameter class B (15.9% of all trees in the zone) – single tree parameters								
DBH (cm)	34.1	34.3	34.1	33.3	32.0	30.2	28.7	
H (m)	24.3	22.8	21.1	19.4	17.4	15.3	13.8	
Stem wood (kg)	384	369	343	309	267	220	186	
Stem bark (kg)	22.0	21.2	19.7	17.8	15.4	12.7	10.8	
Foliage (kg)	30.8	29.5	27.4	24.6	21.1	17.4	14.6	
Live branches (kg)	46.7	44.2	39.9	34.3	27.9	21.2	16.7	
Roots (kg)	78.3	75.2	69.7	62.4	53.7	44.0	37.0	
Tree crown diameter class C (38.4% of all trees in the zone) – single tree parameters								
DBH (cm)	45.2	45.5	45.2	44.1	42.4	40.1	38.0	
H (m)	27.6	26.2	24.5	22.6	20.6	18.3	16.6	
Stem wood (kg)	664	643	603	546	476	396	337	
Stem bark (kg)	37.9	36.7	34.4	31.2	27.2	22.7	19.4	
Foliage (kg)	54.2	52.4	49.0	44.2	38.4	31.8	26.9	
Live branches (kg)	102	97.4	88.8	77.1	63.4	48.9	38.9	
Roots (kg)	139	135	126	113	98.0	81.0	68.5	
Tree crown diameter class D (44.7% of all trees in the zone) – single tree parameters								
DBH (cm)	51.4	51.8	51.4	50.2	48.3	45.6	43.3	
H (m)	29.5	28.0	26.4	24.5	22.3	20.0	18.2	
Stem wood (kg)	858	833	783	712	622	520	444	
Stem bark (kg)	48.8	47.4	44.6	40.6	35.5	29.8	25.5	
Foliage (kg)	70.5	68.4	64.2	58.2	50.7	42.1	35.8	
Live branches (kg)	147	141	129	113	93.0	72.0	57.6	
Roots (kg)	182	177	166	150	130	108	91.3	
Catchment total biomass (t)								
Stem wood	701	1540	880	659	366	586	311	5043
Stem bark	40	88	50	38	21	34	18	288
Foliage	57	126	72	54	30	47	25	410
Live branches	112	244	136	97	51	76	38	753
Roots	148	324	185	137	76	120	64	1053

identified in the orthophotograph were counted, while most of the understory young trees were omitted. The correlation between DBH and crown diameter is weak ($r = 0.27$), but the standard error of the estimated mean D to DBH ratio is relatively small (~3%). The orthophotograph was divided into a grid, from which sample cells were selected randomly. Error caused by this selection is unsystematic. Standard error of the mean trees per grid cell was ~7%. The pixel size used (20 cm) increased the level of uncertainty. A high-resolution aerial image, with a pixel size of 3 to 10 cm, produces precision results of crown size (ERIKSON, 2004). There is, however, a question if more precise image analysis could give an adequately more precise result on tree biomass under conditions of the heterogeneous environmental parameters (wide range of altitude and inclination), reflected by the stand density and individual tree parameters. Consequently, we assume that the most serious error in our estimation was associated with determination of D and DBH from the orthophotograph. Despite the higher uncertainty in our results than in those by ERIKSON (2004), due to the higher pixel size we used, our results represent a reasonable estimate of tree biomass on the catchment scale, enabling us to compare it to analogous data on understory vegetation and soil in the study area.

Element pools

The CWM element pools associated with tree biomass, calculated using mean element concentrations in individual tree components (Tab. 3), and the associated CWM biomass pools are summarized in Table 4. The

Table 4. Estimated catchment weighted mean biomass and element pools in the tree layer of the Plešné Lake catchment in 2000.

Biomass parts	Biomass (t ha^{-1})	Biomass fraction (%)	C mol m^{-2}	N	P	Ca	Mg	Na	K	Al	Fe	Mn
				mmol m^{-2}								
Stem wood	89.3	66.8	378	1123	6	169	41	24	116	2.4	1.2	15
Stem bark	5.1	3.8	22	200	8	105	17	1.8	32	0.9	0.3	4.3
Foliage	7.3	5.4	31	452	20	122	25	2.3	62	1.4	0.5	6.3
Live branches	13.3	10.0	57	773	32	148	36	4.9	80	9.9	3.2	7.3
Roots	18.6	14.0	80	415	10	58	14	5.8	58	4.9	1.0	3.0
Total	133.6	100.0	568	2963	76	602	133	38.8	347	19.4	6.2	35

CWM element pools in tree biomass varied between 6 mmol m^{-2} for Fe and 568 mol m^{-2} for C. Similarly to total biomass, the element pools recorded in our study sites were lower compared to those of spruce forests along the European ecological transect (Scarascia-Mugnozza et al., 2000). Generally, the differences in element pools follow the same pattern as the differences in total biomass except for N. The mean nitrogen pool in the spruce stands across Europe was 560 kg ha^{-1}, being 745, 666, and 424 kg ha^{-1} at the German, Czech, and Swedish sites, respectively. The mean N pool in the Plešné tree biomass was 415 t ha^{-1} (3 mol m^{-2}), being similar to that in the Swedish site. Boreal forests are generally N limited (Finér et al., 2003), and therefore the pool of N stored in the tree layer is likely to be lower.

The Ca pools in the European spruce stands were 737, 447, and 424 kg ha^{-1} at the German, Czech, and Swedish sites, respectively, while 245 kg ha^{-1} in the Plešné catchment. The respective P and Mg pools ranged from 55–82 and 51–76 kg ha^{-1} in the European sites and were significantly lower in the Plešné catchment (24 and 32 kg ha^{-1}). The proportions of total pools of macronutrients (i.e., Ca and Mg) to the total biomass of the Plešné tree layer were similar to those in the sites along the European transect.

The element pools stored in different parts of the forest ecosystem (soil, understory vegetation and tree layers) provide important information about the element distribution among individual compartments of the catchment. Surprisingly, there are not many studies reporting these types of data across spruce forests in Europe. The element pools stored in the tree layer of Plešné catchment with those stored in the understory vegetation (Svoboda et al., 2006a) and soils (Kopáček et al., 2002b) are compared in Table 5. The highest fraction of most of the elements was stored in the soil. Significant fractions of C, Ca, and Mn (37%, 17%, and 18% of their total pools, respectively) were, however, associated with the tree layer. There was a large difference between C and N distribution among the individual ecosystem compartments. The respective CWM element pools stored in the soil, trees, and understory vegetation were 933, 566, and 51 mol m^{-2} (112, 68, and 6 t ha^{-1}) for C and 39, 3, and 1 mol m^{-2} (5.5, 0.42, and 0.14 t ha^{-1}) for N. Consequently, the respective C and N fractions stored in the tree layer represented 37% and 7% of their total catchment pools, and the most important N pool was associated with soils. The fraction of C and N stored in the Plešné tree layer was lower than in an old-growth spruce forest in Finland (60% and 15% of their total pools; 176 and 2.8 t ha^{-1}, respectively; Finér et al., 2003). The lower forest biomass in the Plešné catchment was a probable reason for this difference. The mean C to N ratio was similar in the tree layer of both sites. The results confirm the assumption that the tree layer of spruce forest ecosystems represents an important pool of total ecosystem C, while most of N is stored in the soil (Finér et al., 2003).

In contrast to the other elements, the Al fraction stored in the understory vegetation was higher than that of the tree layer (11% vs. 5%). The relatively high concentrations of Al in the biomass of the fine roots of the understory vegetation and the higher proportion of belowground biomass in the total biomass for understory vegetation (Svoboda et al., 2006a) were probably the reasons for this pattern. The belowground biomass was only ∼14% of the total biomass of the tree layer, while it was comparable to the above ground biomass of understory vegetation (Svoboda et al., 2006a). It is not known to what extent the high Al concentrations in fine roots are associated with elevated Al mobility in soil solutions of the studied catchment due to atmospheric acidification (Majer et al., 2003). But, because only the biomass of the coarse roots of the tree layer was estimated in this study, detailed estimation of the fine roots biomass is needed, before any final conclusion can be made.

The most significant fractions of base cations (Ca, Mg, Na, and K) were stored in the soils. Soil pools of Na and K were about 10–25 times higher than those of Ca and Mg, which were comparable. In contrast, the Ca pool in trees was one order of magnitude higher than that of Mg (Tab. 5). The respective mean Ca pools stored in soil, trees, and understory vegetation were 1164, 245, and 46 kg ha^{-1} and those of Mg were 1185, 32, and 10 kg ha^{-1}, respectively. If we consider pools of exchangeable base cations ($\mathrm{Ca}^{2+}_{\mathrm{Ex}}$, $\mathrm{Mg}^{2+}_{\mathrm{Ex}}$, $\mathrm{Na}^{2+}_{\mathrm{Ex}}$, and $\mathrm{K}^{2+}_{\mathrm{Ex}}$), which more reliably describe the availability of cations to plants, the fractions of the elements stored in the tree layer are much higher. Then, the Ca, Mg, Na, and K pools in the tree layer represent 49%, 43%, 22%, and 61%, respectively, of the total exchangeable pools

Table 5. Element pools in the Norway spruce forest ecosystem of the Plešné Lake catchment in 2000.

	C t ha^{-1}	N	P	Ca	Mg	Na kg ha^{-1}	K	Al	Fe	Mn
Soil (total)$^{1)}$	112	5480	584	1128	1178	10175	26546	55200	8327	82
Soil (exchangeable)$^{2)}$	ND	ND	199	210	33	60	90	610	ND	ND
Trees (total)$^{3)}$	68	415	24	245	32	9	136	5	3	19
Understory vegetation (total)$^{4)}$	6	140	11	46	10	1	43	11	4	5
Total pool$^{5)}$	186	6035	619	1419	1220	10185	26725	55216	8334	106
Trees (% of total pool)$^{6)}$	37	7	4	17	3	0.1	1	0.01	0.04	18

Explanations: $^{1)}$ Element pools in the fine (< 2 mm) soil fraction (Kopáček et al., 2002); $^{2)}$ pools of exchangeable element fractions in the fine soil; i.e. NH_4Cl extractable Ca, Mg, Na, K, and Al; and oxalate extractable phosphate as P (Kopáček et al., 2002); $^{3)}$ total tree biomass: data were recalculated from Table 4; $^{4)}$ total herb biomass, including above- and belowground pools (Svoboda et al., 2006a); $^{5)}$ total pool is calculated as the sum of total soil, tree, and understory vegetation pools; $^{6)}$ the percentage of the element pools stored in the tree biomass from the total element pools in the catchment; ND – not determined.

in the ecosystem. The fraction of base cations stored in the tree layer might be even higher in spruce forest stands in less steep parts of the Bohemian Forest. The total tree biomass in the Plešné Lake catchment was relatively low, because of the extremity of the site conditions. Stands with higher stem and canopy densities would have higher total tree biomass. In contrast, the understory vegetation biomass (and associated nutrient pools) of these denser forest stands would be lower than in the catchment studied (Svoboda et al., 2006a).

The results found in this study have implications for forest management and are especially important in connection with recent data on soil acidification processes and soil base cation leaching in the study area (Majer et al., 2003; Kopáček et al., 2006b). Soil acidification, accompanied by elevated leaching of base cations (especially Ca and Mg), is of primary concern in many impacted regions and can represent a significant threat to the stability of numerous, nutrient-poor forest ecosystems (Watmough et al., 2005; Hruška & Cienciala, 2001; Matzner et al., 2004). Considering our data, as well as those from other studies (e.g., Jonsson et al., 2003; Majer et al., 2003; Matzner et al., 2004; Watmough et al., 2003, 2005), the integrated research, evaluating together the element pools and fluxes (deposition, leaching, and weathering), seems to be necessary to better assess sustainability of forest ecosystems in mountainous areas.

Conclusions

Our data represent the first estimation of the biomass and related element pools of the tree layer on a catchment scale in the Bohemian Forest. The tree layer biomass was relatively low compared to sites with similar character along the European transect. The relatively extreme morphological conditions of the Plešné catchment were probably the main reason for the relatively low tree biomass, low stand density, and open canopy.

The pools of some elements stored in the tree layer represented a significant fraction of the total element pools stored in the catchment. Especially, the pools of Ca and Mg stored in the tree biomass were similar to their exchangeable pools in the soils. Soil acidification, leaching of base cations and tree nutrient deficiencies can present a threat to the stability and sustainability of nutrient poor forest ecosystems in the area. For this reason, further research focused on the detail role of the tree layer in element storage and cycling, and assessing the impacts of possible management practices on element cycling, is needed.

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