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BEECH COARSE WOODY DEBRIS CHARACTERISTICS IN TWO VIRGIN FOREST RESERVES IN SOUTHERN SLOVENIA

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Abstract

Beech (*Fagus sylvatica* L.) coarse woody debris (CWD) was studied in two forest reserves in southern Slovenia: Krokar and Rajhenavski Rog. Each tree (from over 100 trees per reserve) (including snag if remaining, log and crown parts) was enumerated, described (decay phase (1=least decomposed to 6=most decomposed), diameters at different lengths (cm), length (m), contact with soil, bark, herbs, moss coverage (all in %), exposure (sun, shaded)) and mapped and volume (m^3) calculated. For CWD of decay phases 1 to 3 (4) age-since-death was studied using dendrochrolonogy and comparisons to a standard dendrochronological sequence for the area. Sixty dead trees (82 logs and snags altogether) in Rajhenavski Rog from the 113 fallen trees were selected for C, N, S, P, K, pH, moisture and wood density analysis. The total volume of beech CWD in the sampled area in Rajhenavski Rog was 100 m^3/ha and 192 m^3/ha of silver fir CWD; for the sampled area in Krokar the total beech CWD volume was 57 m^3/ha and silver fir CWD 88 m^3/ha. N, S and P concentrations increased with decay phase, while C:N ratio declined. Age dependent decay curves were produced for 44 dated trees. The expected time for decay beyond decay phase 4 was over 32 years.

Key words: coarse woody debris, beech, *Fagus sylvatica* L., nutrients, moisture, age decay functions, forest reserves, Rajhenavski Rog, Krokar, Slovenia

ZNAČILNOSTI ODMRLIH VELIKIH LESNIH OSTANKOV BUKVE V DVEH GOZDNIH REZERVATIH V JUŽNI SLOVENIJI

Izvleček

V dveh gozdnih rezervatih v južni Sloveniji smo raziskovali velike odmrle lesne ostanke (CWD) bukve (Fagus sylvatica L.). Vsako drevo (od preko 100 na rezervat) (panj, če je obstajal; deblo in deli krošnje) smo oštevilčili in zanje podrobno opisali zunanje značilnosti: fazo razkroja; premere (cm) na različni dolžini in dolžino (m); stik s tlemi; pokritost s skorjo, mahovi ter zelišči (vse v %). Položaj lesnih ostankov smo vrisali v karto; izračunali smo jim prostornino (m^3). Za manj razkrojene CWD (faze razkroja 1 do 3 (4)) smo starost določili z dendrokronološko analizo in s primerjavo s standardizirano dendrokronologijo bukve iz tega območja. Šestdeset CWD (skupno 82 debel in panjev) smo vzorčili za analize C, N, S, P, K, pH, vlažnosti in gostote lesa. V rezervatu Rajhenavski Rog je bila skupna prostornina bukovih CWD na vzorčeni ploskvi 100 m^3/ha, jelovih CWD pa 192 m^3/ha; v rezervatu Krokar je bila prostornina bukovih CWD na vzorčeni ploskvi 57 m^3/ha, jelovih pa 88 m^3/ha. Vsebnosti N, S in P so z večanjem razkroja naraščale, C/N razmerje pa padalo. Na osnovi 44 datiranih dreves smo določili časovne funkcije razkroja; čas za razkroj do 4. faze je daljši od 32 let.

Ključne besede: lesni ostanek, bukev, Fagus sylvatica L., pragozd, razkroj drevesa, odmrlo drevo, hranila v lesu, dendrokronologija, Krokar, Rajhenavski Rog

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1 INTRODUCTION
UVOD

The continuing flow of energy through any ecosystem depends upon maintenance of nutrient supplies to primary producers and since there is only a limited input of nutrients from outside, a balanced cycle within the ecosystem is essential (DIGHTON / BODDY 1989). Three main types of cycles provide nutrients to the primary producer: the external hydro-geological cycle, the biological cycle and the internal cycle within subsystems (soil, plant, herbivores, carnivores, decomposers) and within individual organisms (*ibid.*).

Decomposition is the process whereby the complex organic structure of biological material, such as wood, is reduced to its mineral form (MACKENSEN / BAUHUS 1999). Decomposition of organic substrates results from a variety of interacting biotic and abiotic factors: non-enzymatic chemical reactions (sunlight, temperature etc.), leaching (due to water and climatic conditions) and volatilisation (loss of oils, waxes and resins), comminution (reduction in particle size) and catabolism (biologically mediated), in which the main mediators are fungi (DIGHTON / BODDY 1989). Fungi are the major decomposers of organic substrates in terrestrial ecosystems and are consequently responsible for the return of nutrients immobilized in dead plants, animals and microbial tissues to the soil pool (*ibid.*).

Coarse woody debris (CWD) can be defined as dead woody material located above the soil. It includes standing dead trees (snags), fallen boles (logs), but may include also large branches, stumps and roots (CLARK *et al.* 1998). In our study, fallen dead trees (including snags if remaining, log and crown parts) were defined as studied individual CWD.

The functional importance of CWD depends not only on the amount but also on its distribution in terms of size, stem densities, decay states, tree species, position and spatial arrangement (HARMON *et al.* 1986, cit. in CLARK *et al.* 1998). CWD provides a substrate or host for a wide range of organisms, particularly fungi and invertebrates; cavities formed by rot are used as nesting sites or shelter by many vertebrates; decaying logs may act as safe sites for seed germination or growth of bryophytes away from the competition of woodland ground flora. Fallen logs may create bare soil patches and crush or shade out the ground vegetation; they may slow soil and water movement on slopes or through the ground; soil nutrient levels are likely to be higher around or under dead wood and thus affect the ground flora at that point (FALINSKI 1986, cit. in KIRBY *et al.* 1998). The spatial and temporal scale of CWD of different sizes are hypothesized as playing an important role as i) substrates and sources of nutrients for the organisms occurring on CWD, as ii) long-term sources of nutrients for organisms influenced by CWD and iii) for the processes in forest ecosystems. Therefore, the overall goals of the studies of CWD would be to assess the importance of CWD for biodiversity and for nutrient storage, leading to possible future directives for management of similar forests in the studied regions with respect to conservation of biodiversity and sustainable management of forest ecosystems. Such studies should also provide the basic data for future models of the influence on nutrient cycling of different organisms living on CWD.

In our study, which was part of the European 5FW project NAT-MAN (QLRT1-CT99-1349), we have selected and described beech (*Fagus sylvatica* L.) CWD in two virgin forest reserves in southern Slovenia. The CWD described were applied in parallel studies of diversity of vegetation, mosses and fungi (KUTNAR *et al.* 2002, ODOR / van DORT 2002, PILTAVER *et al.* 2002). In this paper, we present the results of physical-chemical characteristics of CWD in the virgin forest reserves. For this, a selected number of CWD from one forest reserve, Rajhenavski Rog, was characterised regarding nutrients, moisture and wood density. Additionally, the age since death for the less-decayed CWD was analysed on both study sites for estimation of the time needed for total decomposition, i.e. for recycling the nutrients from CWD in the ecosystem.

The objectives of physical-chemical studies of CWD were:

- to identify the role of beech CWD in nutrient storage,
- to determine the relationships between beech-CWD dimensions, age, decay state and physical-chemical characteristics.

Standard age-decay functions were generated. The role and importance of CWD for nutrient storage was analysed for further development of modelling.

2 MATERIAL AND METHODS
MATERIAL IN METODE

2.1 SITE DESCRIPTION
OPIS RAZISKOVALNIH PLOSKEV

Two sites were chosen for CWD studies, both in the northern part of Dinaric Mountains, near Kočevje in southern Slovenia. The first one, named Rajhenavski Rog, lies in the middle of a largest forest area, the second, named Krokar, at the border of Croatia. As secondary virgin forests (as defined by HARTMAN 1999), they are important parts of the forest reserve network in the country (MLINŠEK *et al.* 1980) (Figure 1).

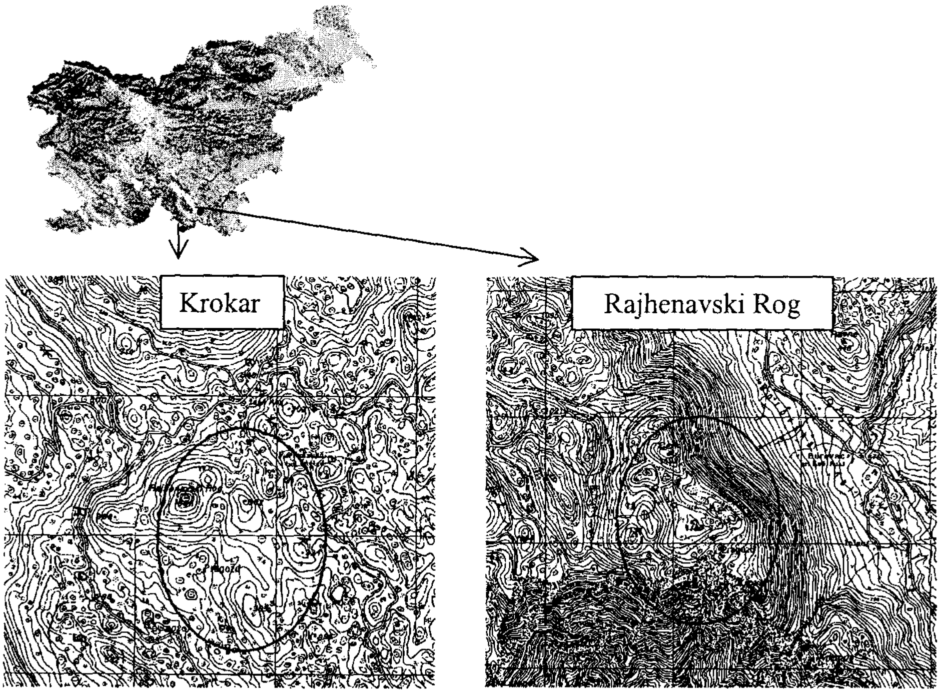

Figure 1: The locations of the two forest reserves in southern Slovenia
Slika 1: Položaj dveh gozdnih rezervatov v južni Sloveniji

The climate of these regions is montane Dinaric with an annual precipitation of about 1.500 mm. Stand structure, regeneration, and spatial distribution of forest developmental phases have been studied in these reserves in detail, mainly in Rajhenavski Rog (BONČINA 1999, 2000a, 2000b). Phyto-sociological relations of ground flora of both reserves have also been studied (PUNCER / ZUPANČIČ 1970, PUNCER *et al.* 1974, PUNCER 1980, HOČEVAR *et al.* 1985, 1995, ZUPANČIČ / PUNCER 1995, ACCETTO 2002).

2.1.1 Rajhenavski Rog Forest Reserve

Gozdni rezervat Rajhenavski Rog

Table 1: Physical and ecological characteristics of the site Rajhenavski Rog (BONČINA 1997, MEKINDA-MAJARON 1995, ZUPANČIČ 1995)

Preglednica 1: Krajinske in ekološke značilnosti ploskve Rajhenavski Rog (BONČINA 1997, MEKINDA-MAJARON 1995, ZUPANČIČ 1995)

Physical characteristics / *Značilnosti terena*		Ecological characteristics / *Ekološke značilnosti*	
Area / *Površina rezervata*	51,3 ha		
Sampled area / *Površina vzorčne ploskve*	3,20 ha	Annual average temperature / *Povp. letna temp.*	7,7 °C
Longitude / *Geogr. dolž.*	E 15° 01′	Coldest month (January) / *Najhladnejši mes. (januar)*	-1,9 °C
Latitude / *Geogr. šir.*	N 45° 40′	Warmest month (July) / *Najtoplejši mes. (julij)*	16,9 °C
Altitude / *Nadm. viš.*	852-905 m (865 m)	Average annual precipitation / *Povp. kol. letnih padavin*	1.579 mm

Parent material: limestone (cretaceous period)

Soil type (FAO 1988): eutric cambisols and rendzic leptosols

Continuity (HARTMAN 1999): Rajhenavski Rog was treated as a forest reserve and taken out of use in the year 1894, when the first management plan was made. Before that, it was virgin forest. There were only minor fellings about hundred years ago and in 1948 at the border zone of reserve, when 7 % of growing stock was cut. In the 1980's it was officially declared to be a forest reserve.

The investigated part of Rajhenavski Rog belongs to the Dinaric fir-beech forest (*Omphalodo-Fagetum* (Treg. 1957, corr. Puncer 1980) Mar. *et al.* 1993) (PUNCER / ZUPANČIČ 1970, PUNCER *et al.* 1974, PUNCER 1980), which can be divided to different sub-associations (e.g. *-galietosum odorati, -festucetosum altissimae, -mercurialetosum perennis, -aceretosum*).

The site conditions are relatively uniform and mesophilic species predominate.
Actual stand composition: Composed of silver fir (*Abies alba* Mill.) and beech (60 %: 40 % of growing stock, respectively). There is less than 1 % of other tree species: spruce (*Picea abies* (L.) Karst.), maple (*Acer pseudoplatanus* L.), elm (*Ulmus glabra* Huds.) and lime (*Tillia cordata* Mill.). Growing stock is 800 m^3/ha and total basal area 52 m^2/ha.

CWD-quantity (HARTMAN 1999): In the total area of the forest reserve the average number of all (beech and fir) dead trees per hectare is 125 (52 standing and 73 fallen). Dead biomass amounts to 284 m^3/ha with 28 % share of beech.

2.1.2 Krokar Forest Reserve
Gozdni rezervat Krokar

Table 2: Physical and ecological characteristics of the site Krokar (BONČINA 1997, MEKINDA-MAJARON 1995, ZUPANČIČ 1995)

Preglednica 2: Krajinske in ekološke značilnosti ploskve Krokar (BONČINA 1997, MEKINDA-MAJARON 1995, ZUPANČIČ 1995)

Physical characteristics / *Značilnosti terena*		Ecological characteristics / *Ekološke značilnosti*	
Area / *Površina rezervata*	72,8 ha		
Sampled area / *Površina vzorčne ploskve*	2,88 ha	Annual average temperature / *Povp. letna temp.*	8,4 °C
Longitude / *Geogr. dolž.*	E 14° 46′	Coldest month (January) / *Najhladnejši mes. (januar)*	-1,6 °C
Latitude / *Geogr. šir.*	N 45° 33′	Warmest month (July) / *Najtoplejši mes. (julij)*	17,8 °C
Altitude / *Nadm. viš.*	840-1.170 m (1.120 m)	Average annual precipitation / *Povp. kol. letnih padavin*	1.526 mm

Parent material: dolomite, limestone
Soil type (FAO 1988): eutric cambisols and rendzic leptosols
Continuity: In the earliest forest management plan in the year 1894, the forest reserve Krokar was taken out of use and treated as a forest reserve. Before 1894, it was virgin forest. It was closed to public until 1990 due to protective military use. The Krokar Reserve has already been described by HOČEVAR *et al.* (1985, 1995). Based on this study and the fact that the only floristic element differentiating between mountain beech forest and Dinaric fir-beech forest is *Abies alba* (MARINČEK et al. 1983), we could describe the selected site as a transition zone between Pre-Dinaric mountain beech forest and Dinaric fir-beech forest.

According to further studies (SURINA 2001, 2002, ACCETTO 2002) the fir-beech forest was classified as *Omphalodo-Fagetum* (Treg. 1957, corr. Puncer 1980, Mar. et al. 1993) var. geogr. *Calamintha grandiflora* Surina 2001, subvar. geogr. *Campanula justiniana* Accetto 2002, forma *Adenostyles glabra* Accetto 2002. In this part, different sub-associations of this geographical sub-variant are present (ACCETTO 2002). In this part of the Krokar Reserve, the beech forest in a narrow zone behind the rock faces above the Kolpa valley was classified as *Allio victorialis-Fagetum* (Tomažič 1958) Accetto 2002 *caricetosum pilosae* (Tomažič 1958 nom. nud.) Accetto 2002 var. *Erythronium dens-canis*. In a deeper sinkhole, phytocoenoses of the association *Stellario montanae-Fagetum* (Zupančič 1969 Mar. et al. 1992) *lunarietosum redivivae* Accetto 2002 are present.

Actual stand composition: The forest is composed of silver fir (*Abies alba* Mill., 9 %), beech (87 %) and maple (*Acer pseudoplatanus* L., 4 % of growing stock). Growing stock in 1995 was 672 m^3/ha and total basal area about 56 m^2/ha.

CWD-quantity (HARTMAN 1999): In total area of the forest reserve the average number of all (beech and fir) dead trees per hectare is 284 (137 standing and 92 fallen). Dead biomass amounts to 153 m^3/ha with 51 % share of beech.

2.2 METHODS
METODE DELA

For all activities in the virgin forest reserves a written permission had to be obtained from the Regional Unit of the Slovenian State Forest Service as the nature-conservation office responsible for the area.

2.2.1 Selection of the CWD
Izbor velikih lesnih ostankov

The selection of the CWD was carried out according to the agreed upon protocol (van HEES 2003, in prep.), based on similar studies in the northern Europe (SIPPOLA / RENVALL 1999, HEILMANN-CLAUSEN 2001 and others). Only fallen dead trees (the remaining log was the first selection criteria) in the area were taken into consideration. All parts (snag (if remaining), log and crown parts) of CWD belonging to the same tree were marked as one reference tree. Selection was continued until the adequate number of trees was attained. Altogether 214 trees were selected in two sites - 101 trees in the Krokar forest reserve and 113 trees in the Rajhenavski Rog forest reserve. It was intended to attain an even distribution of trees over decay phase classes and diameter classes. For further inventories and studies in Rajhenavski Rog, sketches of all selected trees and their position were mapped and geo-referenced by GPS. In order to calculate the contribution of beech CWD to total dead biomass and nutrient storage in the analysed areas of the two forest reserves, all non-numerated beech and all silver fir CWD was also measured (as by November 2001).

2.2.2 Description of the selected CWD
Opis izbranih velikih lesnih ostankov

The unit of research was a fallen dead beech tree with its parts revealed in the field (snag, bole, branches, all together representing a single instance of CWD). Single pieces of selected dead trees were tagged (with a unique CWD number), measured (diameter of a tree at breast height when it was alive, lower and upper diameter of all pieces, length) and described (assessments of % coverage with bark, % of moss, % of herb, % of soil contact, notes on solar exposure (shaded, sunlit) and position (on the ground, partly in the soil, in the air). The tree or its thinnest piece was measured down to the diameter of 10 cm. Parts of dead trees (snag, log, crown) were additionally described as an average (decay phase and also the span of decay phases of the part, % bark, % moss, % herb, % soil contact). The branches down to the diameter of 10 cm at the point of attachment to the bole were counted and their mean diameter and total length were measured. Volumes of single pieces were calculated as cylinders using average diameter (average of maximum and minimum diameter) and length and then summed to get volumes of tree parts and whole trees. Volumes of pieces in decay phases 1 to 4 were obtained from measured diameters. For decay phases 5 and 6 diameters and lengths of pieces were assessed twice: first, the actual diameters (dbh real) and lengths were measured; second, the diameters and lengths of remaining parts of the tree were estimated (after traces on the ground) as the probable diameters (the lengths were equal) before the decay had started (dbh hypothetical). Consequently two volumes were obtained: i) the decayed volume (real volume) and ii) the estimated volume of the CWD parts as if they had retained their dimensions without decaying (volume hypothetical).

For the decay status of CWD, the common descriptions were agreed upon (van HEES 2003, in preparation, based on SIPPOLA / RENVALL 1999 and HEILMANN-CLAUSEN 2001) as presented in Table 3. The decay phase was assessed as an average and as a span of decay phases for the whole tree and all tree parts that were measured.

The position of selected trees in the forest reserve was determined by the use of GPS. The exact locations and orientations of fallen CWD in the research plot of Rajhenavski Rog are schematically presented in App. 1.

All the data was written in a field form in which was also drawn a sketch of the CWD (all its parts) and a route from the nearest CWD (using the compass direction and distance). Additionally, all CWD of other tree species (mainly silver fir) were measured for calculation of total CWD volume per the sampled area.

Table 3: Description of decay phases (DP) (modified after van HEES 2003, in prep.)

Preglednica 3: Opis faz razkroja (DP) (prirejeno po van HEES 2003, in prep.)

Decay phases / *Faze razkroja*	Bark / *Skorja*	Twigs and branches / *Veje in poganjki*	Softness / *Trdota lesa*	Surface / *Površina*	Shape / *Oblika*
1	intact or missing only in small patches, more than 50% / *manjka največ 50%*	present / *prisotni*	hard or knife penetration 1-2 mm / *trd, nož se zapiči največ 2 mm globoko*	covered by bark, outline intact / *prekrita s skorjo, površina nedotaknjena*	circular / *krožna*
2	missing or less than 50% / *manjka več kot 50%*	only branches (>3 cm) present / *samo veje nad 3 cm prisotne*	hard or knife penetration less than 1 cm / *trd, nož največ 1 cm globoko*	smooth, outline intact / *gladka, površina nedotaknjena*	circular / *krožna*
3	missing / *manjka*	missing / *manjkajo*	begin to be soft, knife penetration 1-5 cm / *postaja mehak, nož 1 – 5 cm globoko*	smooth or crevices present, outline intact / *gladka ali razpokana, površina nedotaknjena*	circular / *krožna*
4	missing / *manjka*	missing / *manjkajo*	soft, knife penetration more than 5 cm / *mehak, nož čez 5 cm globoko*	large crevices, small pieces missing, outline intact / *razpokana, manjši deli manjkajo, površina nedotaknjena*	circlular or elliptic / *krožna ali ovalna*
5	missing / *manjka*	missing / *manjkajo*	soft, knife penetration more than 5 cm / *mehak, nož čez 5 cm globoko*	large pieces missing, outline partly deformed / *veliki deli manjkajo, površina spremenjena*	flat elliptic / *plosko ovalna*
6	missing / *manjka*	missing / *manjka*	soft, partly reduced to mould, only core of wood / *mehak, samo ostanki lesa*	outline hard to define / *površina težko določljiva*	flat elliptic covered by soil / *plosko ovalna, prekrita z zemljo*

2.2.3 Selection, sampling and laboratory analyses of CWD
Izbor, vzorčenje in analize velikih lesnih ostankov v laboratoriju

2.2.3.1 Selection and sampling of CWD
Izbor in vzorčenje velikih lesnih ostankov na terenu

A common protocol has been agreed upon for sampling and chemical analyses of CWD. In Slovenia, 60 CWD sites were selected for nutrient analyses in the Rajhenavski Rog virgin forest reserve. An equal distribution of all decay phases and diameter classes has been searched for in both forest reserves and also in CWD sites for nutrient studies. However, in order to allow fast mapping of organisms on CWD for the parallel study, all CWD needed to be distributed within a relatively small area, easily reachable for different specialists. Also, several studies were linked to the same forest reserves that were impacted by numerous visits of researchers during field studies. Therefore, a limited area of both reserves has been chosen resulting in an unequal distribution of CWD in the decay phases and diameter classes.

Due to the methodology agreed upon for biodiversity studies, all trees were enumerated, all parts of trees were sketched and numbered on the field forms and all approaches to CWD were assigned on the maps with compass directions. Furthermore, for possible estimation of the age of CWD since falling, exact positions of snags were mapped with GPS.

Protocols for field sampling for nutrients, density and moisture determination were developed for the needs of this study. For all analyses, samples were taken from the surface (bark included if present) to (if possible) the centre of the log. The minimum quantity of sampled material for nutrients was 100 g of air-dried sample. The quantity of all sub-samples had to be similar; the minimum number of sub-samples was six from a log and six from a snag (when present). Sub-samples were taken systematically at equal distances in a spiral (if possible) from 0 to 6 m of logs and at DBH (if snag remained). The position on the log was determined from the thickest end of the log. Sub-samples were taken either with a cordless drill (Mod. 6343DWBE Makita), woodborer or a chisel. Each sub-sample was stored and treated separately. Additional sub-samples were taken in the same manner for wood moisture analyses. Similarly, six additional sub-samples for logs and three for snags, each made of 3 to 4 pieces, were taken with a core borer (decay phases 1-3) or a chisel for wood density determination.

The age since death of CWD could be estimated by eye and experience, tree ring analyses, rings of released trees, aero-photo or by historical data. In Slovenia, the age of decay phases 1 – 3 was determined by tree-ring analyses. For all of the more-decayed CWD, the age since death was extrapolated from the model based on measured ages (see part 2.2.4).

At the time of sampling, weather conditions were noted; the actual decay phase of the sampled part of tree and several characteristics were also noted (KRAIGHER 2003, in prep.).

2.2.3.2 ***Laboratory analyses of CWD***
Laboratorijske analize velikih lesnih ostankov

Nutrient and pH analyses:
All sub-samples were dried at 40° C, ground (FRITSCH) and stored. A combined sample was formed for nutrient analyses from the stored sub-samples (for logs and for snags separately).

Moisture
In the field, 10-15 g of fresh wood sample was stored into a weighing vessel of known mass. In the laboratory, samples were weighed, then dried over night at 105°C, cooled down to room temperature in a desicator and again weighed. Moisture content was calculated from sample weight loss.

Preparation of composite samples
For pH and nutrient analysis, all sub-samples were dried at 40° C and ground to a particle size of approximately 1 mm. For each CWD, 10 ml of wood powder by sub-sample was blended into the composite sample. Only composite samples were analysed for pH and nutrients.

pH analysis
A suspension of ground composite sample (2 g) and 20 ml purified water was prepared for pH determination. The suspension was shaken for 5 min. After 15 min pH was measured with a combined glass pH electrode (TORELLI / ČUFAR 1995).

C, N and S analysis
The carbon, nitrogen and sulphur concentrations were determined with the LECO CNS-2000 element analyser. Wood composite samples (100-200 mg) were oxidized to carbon dioxide (CO_2), nitrogen oxides (NO_x) and molecular nitrogen (N_2) and sulphur dioxide (SO_2) at 1350°C. The amount of CO_2 and SO_2 was measured using an infrared detection method. After transforming of all nitrogen forms into N_2 by passing the combustion gasses over a Cu-catalysator, the content of N_2 was measured using thermal conductivity detection (http://www.icp-forests.org/pdf/manual4.pdf).

P and K analysis
For determination of P and K, composite samples were first digested in a microwave oven (Milestone, Ethos) in a HNO_3 and $HClO_4$ (5:1) mixture. Phosphorus (P) was determined spectro-photometrically using ammonium heptamolybdate as colour reagent. Potassium (K) was measured by AAS (Thermo Jarrel Ash, Scan 1). (http://www.icp-forests.org/pdf/manual4.pdf).

Wood density:
The samples were (whenever possible) cut into 3 x 2 x 2 cm cubes, dried at 105° C for 24 h and cooled to room temperature in exiccator, weighed (accuracy of the balance: 0,0001 g) and dipped into the mercury volume-meter (according to Breuil, accuracy $\pm$ 0,001 cm^3). Larger cubes (up to 7 x 5 x 5 cm) were dipped into water (accuracy $\pm$ 0,1 cm^3). The absolute density was calculated as g of dry wood per cm^3 of dry wood.

Quality control
For all nutrients, in each batch of samples one measurement of plant sample ALVA Probe 2/1999 (from circular laboratory testing programme) was carried out to control quality of analysis. Measurements were done in replicates.

2.2.4 Age determination of CWD
Določanje starosti velikih lesnih ostankov

For CWD age analysis, a single sample was taken with a core borer, or a pie reaching towards the centre of the snag / log was chain-sawed from the dead wood. The samples were dried at room temperature, cut and their faces were ground with sandpaper of different grit. Tree rings were analysed on the measuring table LINTAB using the TSAP/x and PAST-32 programmes. Mostly, the last 50 to 60 tree rings below bark or from periphery to the inner parts of CWD were measured.

A standard chronology for beech from the broader regional area was prepared and the CWD samples were cross-matched to it. The tree-ring widths of the sample were visually and statistically synchronised to the standard chronology for beech. If visual cross-match, the t-value according to Baillie-Pilcher (tBP) and the time correlation coefficient (Gleichlaeufigkeit, GLK) between the standard and measured sample chronology were above the limit (tBP>2,50, BAILLIE / PILCHER 1973 and GLK%>65%, ECKSTEIN / BAUCH 1969) the sample was dated and the date of death could be estimated.

Predominantly, CWD of decay phases 1 to 3 from all 113 CWD in Rajhenavski Rog and 101 CWD in Krokar were used for dendrochronological analysis, while for the more decayed CWD the age was calculated by extrapolation. Outliers were removed from the database used for the AGE-DECAY model. In total, 93 samples were taken; however, due to degradation of wood properties, only 58 could be dated. Due to outliers, which were not used for the model, 44 samples were used for production of age-decay phase curves.

2.2.5 Database organization and statistics
Oblikovanje baz podatkov in statistične analize

Several databases were made from CWD property data and chemical and physical characteristics of CWD. All databases (including those form the parallel studies, mapping of fungi and vegetation on CWD) can be linked by a unique label.

The databases were organized using EXCEL and Visual FoxPro; nutrient storage data was further analysed using the Basic Statistics and Multiple regression module in the STATISTICA programme. The regression analyses of physical and chemical characteristics were primarily aimed at the identification of trends in the variables studied in relation to decay of beech CWD (as described by the classification in decay phases). The average (absolute) wood density was applied for the calculation of biomass of CWD per ha, which was then used for further calculations of individual nutrient contents in CWD per ha. Nutrient release from CWD per ha per year was calculated using the shortest calculated period for CWD to be totally decomposed (i.e. 35 years).

For the age-decay model, the average decay phase (DP) was used as an independent variable (because this was estimated as an entry into the analysis of CWD) and the age since death (AGE) as the dependent variable (because not all CWD were dated and we needed to calculate the AGE for majority of CWD). To estimate the missing values for AGE we used a simple exponential regression ($y=a*e^{bx}$). For the final presentation the curves were reversed, so that the age since death (AGE) was presented as an independent variable, while the average decay phase (DP) was presented as the dependent one (after log-transformations applied).

3 RESULTS
REZULTATI

3.1 PHYSICAL QUALITY AND QUANTITY OF CWD
KOLIČINA IN ZUNANJE ZNAČILNOSTI VELIKIH LESNIH OSTANKOV

In order to be able to estimate the role of CWD in nutrient cycling in the studied forest reserves, their total volume in the forest reserves was needed. Also, CWD from both sites were used for age determination of CWD. Their distribution in decay phases and diameter classes is presented in Tables 4 and 5.

Table 4: Number of all selected trees in decay phase classes

Preglednica 4: Število vseh odmrlih dreves v posameznih stopnjah razkroja

Site / *Ploskev*	No. of trees in decay phase / *Število dreves v fazi razkroja*						
Decay phase / *Faza razkroja*	1	2	3	4	5	6	Total
Krokar	8	16	15	28	24	10	101
Rajhenavski Rog	20	29	13	17	23	11	113
Total / *Skupaj*	28	45	28	45	47	21	214

Table 5: Distribution of all selected dead trees in diameter classes and decay phase classes

Preglednica 5: Porazdelitev vseh odmrlih dreves v debelinskih razredih in stopnjah razkroja

Decay phase / *Faza razkroja*	Diameter class / *Debelinski razred* (cm)					Total / *Skupaj*
	< 31	31-45	46-60	61-75	> 75	
1	3	7	7	8	3	28
2	8	12	9	10	6	45
3	6	9	5	8	0	28
4	24	6	7	5	3	45
5	21	15	6	3	2	47
6	4	7	7	2	1	21
Total	66	56	41	36	15	214

Rajhenavski Rog

In the sampled area (3,2 ha), there were 22 snags and 35 logs of beech per hectare (uprooted trees are considered as logs). The volume of dead biomass of beech in the sampled area was 100 m^3/ha (34 %) and 192 m^3/ha (66 %) of silver fir (situation in November 2001). All data is calculated with respect to the beech CWD in the sampled area, not in the whole forest reserve (as described in part 2.1.1). CWD quantity is presented in Table 6 and Figures 2-3.

Table 6: Volume distribution of dead biomass of beech (in m^3/ha) as to decay phase and CWD parts in Rajhenavski Rog

Preglednica 6: Porazdelitev prostornine odmrlih bukev (v m^3/ha) v stopnjah razkroja za posamezne dele dreves v Rajhenavskem Rogu

CWD parts / *deli CWD*	Volume of CWD per decay phase / *Prostornina CWD v fazi razkroja* (m^3/ha)						Total / *Skupaj* (m^3/ha)
Decay phases / *faza razkroja*	1	2	3	4	5	6	
Snag / *panj*	9,0	12,5	2,5	2,3	1,1	0,2	27,6
Log / *deblo*	17,9	21,3	7,9	11,0	4,3	1,4	63,8
Crown / *krošnja*	3,9	2,9	0,8	0,5	0,2	0,0	8,3
Total / *skupaj*	30,8	36,8	11,1	13,8	5,6	1,5	99,7
Share / *delež* (%)	31	37	11	14	6	1	100

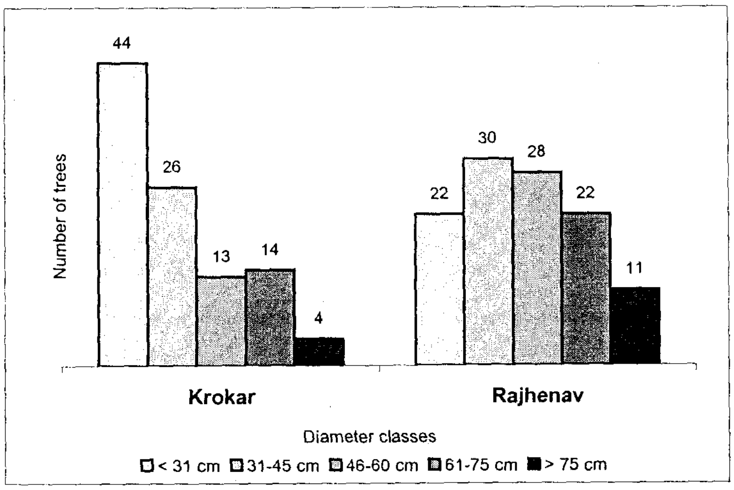

Figure 2: Number of dead trees in the 5 diameter classes (cm) in Krokar and in Rajhenavski Rog

Slika 2: Število dreves v 5 debelinskih razredih (cm) v rezervatih Krokar in Rajhenavski Rog

Krokar

In the sampled area (2,88 ha), there were 19 snags and 35 logs of beech per hectare (uprooted trees are considered as logs). The volumes of dead biomass of beech and silver fir in the sampled area were 57 m^3/ha (40 %) and 88 m^3/ha (60 %), respectively. CWD-quantity is presented in Table 7 and in Figures 2-3 for both sites.

Table 7: Volume distribution of dead biomass of beech (in m^3/ha) as to decay phase and CWD parts

Preglednica 7: Porazdelitev prostornine odmrlih bukev (v m^3/ha) v stopnjah razkroja za posamezne dele dreves v Krokarju

CWD parts / *deli CWD*	Volume of CWD per decay phase / *Prostornina CWD v fazi razkroja* (m^3/ha)						Total / *Skupaj* (m^3/ha)
Decay phases / *faza razkroja*	1	2	3	4	5	6	
Snag / *panj*	2,0	7,6	4,9	1,4	1,2	0,1	17,1
Log / *deblo*	5,8	10,5	4,4	6,5	3,7	3,1	34,0
Crown / *krošnja*	0,9	3,8	0,4	0,3	0,1	0,0	5,6
Total / *skupaj*	8,7	22,0	9,7	8,2	5,0	3,2	56,6
Share / *delež* (%)	15	39	17	14	9	6	100

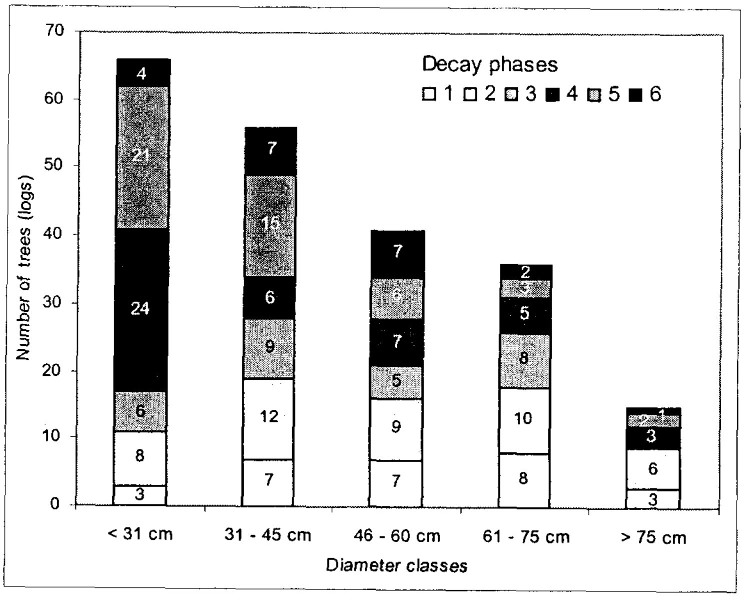

Figure 3: Amount of CWD of different decay phase classes (1 to 6) in different diameter classes (diameter classes are equal as in Figure 2)

Slika 3: Število odmrlih lesnih ostankov v različnih stopnjah razkroja (1 do 6) in debelinskih razredih (uporabljeni so isti debelinski razredi kot v sliki 2).

3.2 AGE CHARACTERISTICS OF BEECH CWD IN THE STUDIED FOREST RESERVES
STAROST ODMRLIH VELIKIH LESNIH OSTANKOV V DVEH GOZDNIH REZERVATIH

Based on the dendro-chronologically determined age of CWD since death in decay phases 1, 2, 3 and partially 4, we have developed a model of the time for decay. The model is based on two functions:

1. a multiple (exponential) regression using the decay phase (DP) as an independent variable and the dendro-chronologically dated age of CWD as a dependent variable (measured for 44 samples); the function (formula [1]) obtained was:

[1] $AGE = 5.451 \, . \, e^{0.374 * DP}$ (Figure 4a) equal to [2]:

[2] $\ln(AGE) = 1.6957 + 0{,}374 * DP$ ($r=0{,}48$; $r^2=0.22$; $F\{1, 42\} = 12.750$; $p<0{,}00091$)

2. the obtained exponential function (formula [1]) was then modified, so that the age since death of CWD (AGE) was presented as independent variable and the average decay phase (DP) was dependent; for this, a logarithmic transformation was done using the following formulas:

[3] $DP = 1.258 * e^{0{,}023*AGE}$ (Figure 4b) equal to [4]:

[4] $\ln(DP) = 1{,}258 + 0{,}023 * AGE$ ($r=0{,}46$; $r^2=0.21$; $F\{1, 42\} = 11.088$; $p<0{,}00182$)

The above formula [1] was used for calculation of an expected age since death for CWD of different decay phases (Table 8).

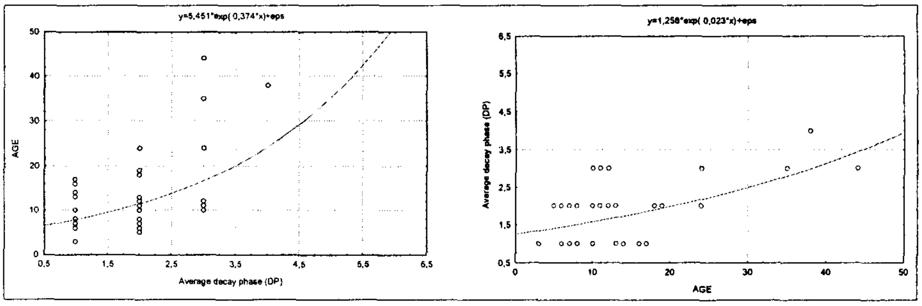

Figure 4: The age-decay functions. Figure 4a: Average decay phase as an independent variable. Figure 4b: Age since death of CWD as an independent variable.

Slika 4: Odvisnost stopnje razkroja in starosti. Slika 4a: Povprečna stopnja razkroja kot neodvisne spremenljivka. Slika 4b: Starost odmrlih lesnih ostankov kot neodvisna spremenljivka.

Table 8: Model age classes for different decay phases

Preglednica 8: Modelni razredi starosti odmrlih debel v različnih stopnjah razkroja

Decay phase / *Faza razkroja*	Model age class (years) / *Izračunan čas od odmrtja (leta)*	Dendrochronologically dated age classes (years) / *Dendrokronološko ugotovljen čas od odmrtja (leta)*		
		Min	Aver. / *povp.*	Max / *maks.*
1	8	1	14	17
2	12	2	15 – 22	52
3	17	6	23 – 32	66
4	24	-	>32	-
5	35	-	-	-
6	51	-	-	-

3.3 CHEMICAL CHARACTERISTICS OF BEECH CWD IN RAJHENAVSKI ROG

REZULTATI LABORATORIJSKIH ANALIZ VELIKIH LESNIH OSTANKOV

In the 60 trees sampled for nutrient, moisture and density analyses in Rajhenavski Rog, 23 of them contained also snags, therefore the total number of combined samples per analysis were 83. Their volume was 152 m^3, the average volume per tree was 1,8 m^3.

The distribution of this CWD of different diameters and decay classes is presented in Figure 5, the physical characteristics in Figure 6, chemical in Figure 7 and the averages for both in different decay phase classes in Table 9. The total nutrient and moisture storage capacity per hectare of the sampled area is presented in Table 10.

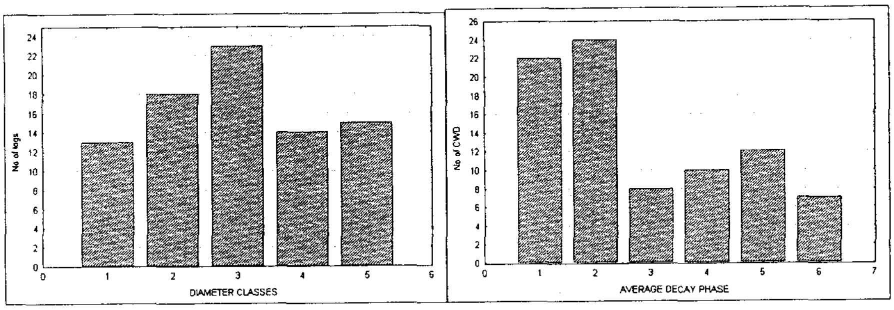

Figure 5: The distribution of CWD, used for nutrient studies, in diameter (left) and decay classes (right) (diameter classes are equal as in Figure 2).

Slika 5: Porazdelitev odmrlih lesnih ostankov, v katerih smo analizirali hranila, v debelinske razrede (levo) in stopnje razkroja (desno) (uporabljeni so isti debelinski razredi kot v sliki 2).

With respect to Figure 6, the real measured volume of the first 6 m of logs tends to fall with increasing decay phase. The absolute density tends to fall with increasing decay phases. There is a large variability of density, especially in decay phases 2 and 3. The pH value falls and moisture rises with increasing decay phase. Furthermore, moisture tends to increase exponentially after the second decay phase.

In Figure 7, basic nutrient relationships with decay phases of CWD are presented. The concentration of C in different decay phases is best fitted with a polynomial curve; N, S and P with an exponential function, while the concentrations of K tend to decrease (the best fitted curve is smoothed least squares). C to N ratio tend to decrease negatively exponentially.

Table 9: Average density, moisture, pH, nutrient contents and ratios, volume and diameters of CWD of different decay phase classes

Preglednica 9: Povprečne vrednosti gostote (DENS), vlažnosti (MOIS), pH, vsebnosti hranil in razmerij med hranili, volumna in premera (DBH) odmrlih lesnih ostankov različnih fazah razkroja (DP)

DP	DENS (g/cm^3)	MOIS (%)	pH	C (g/kg)	N (g/kg)	S (g/kg)	P (g/kg)	K (g/kg)	C:N	C:S	N:P	VOL (m^3)	DBH (cm)
1	0,77	70,59	5,40	464,09	1,57	0,22	0,05	2,02	318	2.799	2,95	2,563	62
2	0,72	96,74	5,09	464,00	1,63	0,36	0,05	1,71	309	2.122	3,50	2,156	52
3	0,57	255,94	5,08	461,88	2,67	0,34	0,08	2,17	208	1.703	3,44	1,430	47
4	0,31	362,29	4,93	470,40	3,82	0,36	0,12	1,38	142	1.701	3,58	2,051	54
5	0,26	400,27	4,66	476,92	5,67	0,53	0,17	0,83	93	1.033	3,35	0,722	52
6	0,25	449,43	4,58	469,29	6,81	0,63	0,23	0,63	71	815	2,94	0,468	49
Mean / *povp.*	0,56	208,93	5,05	466,90	3,00	0,37	0,10	1,58	230	1.943	3,29	1,832	54

Table 10: Beech CWD biomass, moisture content, pH and average nutrient storage per hectare in Rajhenavski Rog

Preglednica 10: Skupna biomasa odmrlih lesnih ostankov, vlažnost, pH in povprečna vsebnost hranil na ha v rezervatu Rajhenavski Rog

	Average per CWD / *Povp. na CWD*	Total per hectare*/ *Količina na ha*	Calculated annual release** / *Izračunano letno sproščanje*
Biomass / *biomasa*	1,01 Mg	46,646 Mg/ha	-
Moisture (water) / *vlažnost (voda)*	209 %	209 m^3/ha	-
pH	5,5	-	-
C	466,90g/kg	21.779,02kg/ha	427 kg/ha
N	3,00g/kg	139,94 kg/ha	2,74 kg/ha
S	0,37g/kg	17,26 kg/ha	0,34 kg/ha
P	0,10 g/kg	4,66 kg/ha	0,09 kg/ha
K	1,58 g/kg	73,70 kg/ha	1,45 kg/ha

*Biomass and nutrient content was calculated with respect to the absolute density of dry wood. **The annual release of nutrients was calculated per 51 years decay (see Table 8). / * *Biomaso in vsebnost hranil smo izračunali glede na povprečno absolutno gostoto lesa.* ***Letno sproščanje hranil smo izračunali ob upoštevanju izračunanega predvidenega časa za popoln razkroj lesa 51 let.*

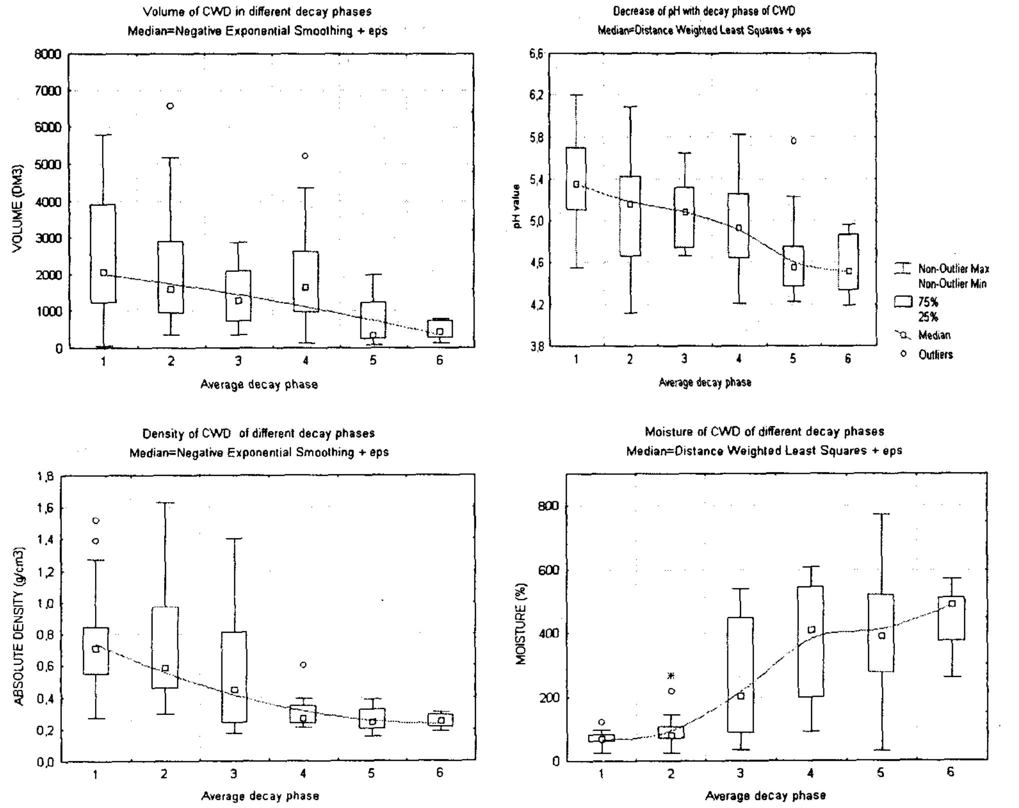

Figure 6: Volume, absolute density, pH, moisture, in different decay phase classes

Slika 6: Pregled in medsebojna odvisnost pojavljanja prostornine, absolutne gostote, pH, vlažnosti, v različnih fazah razkroja

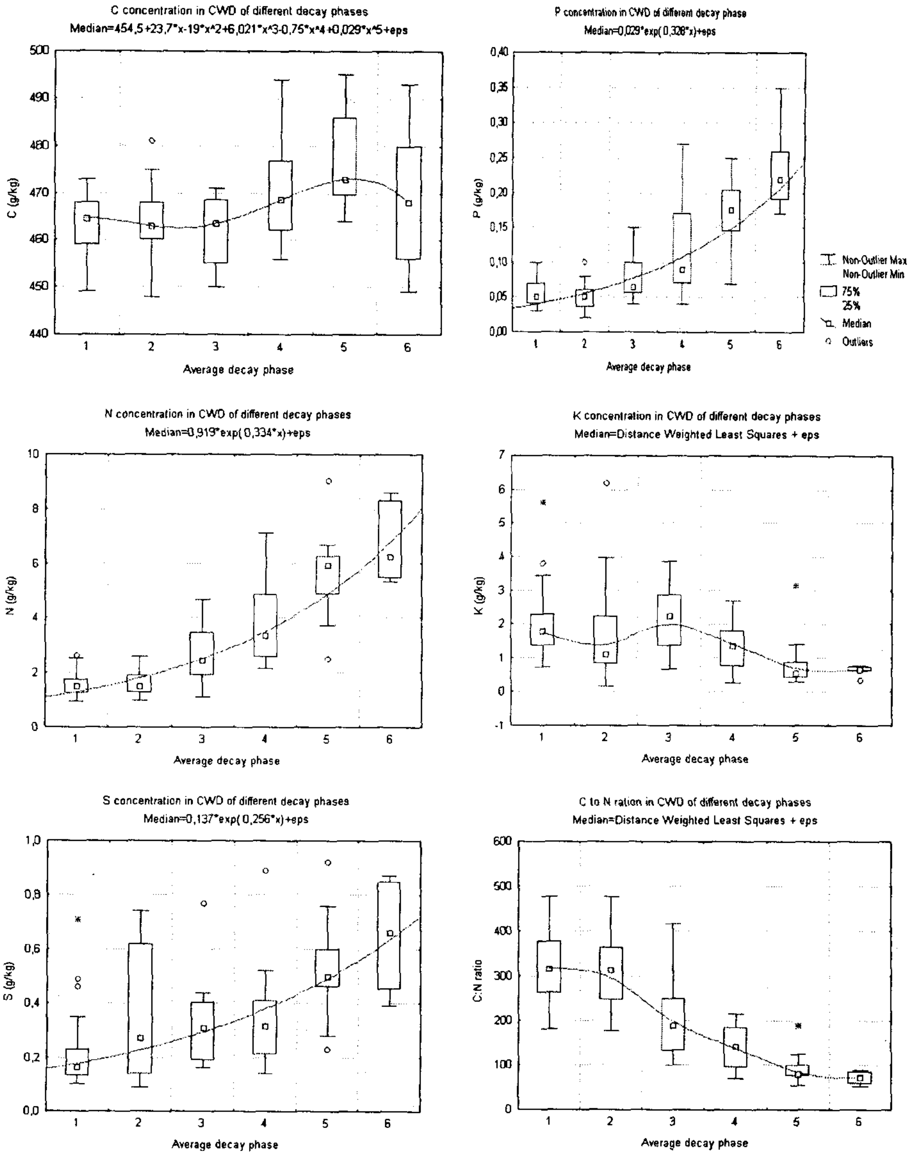

Figure 7: Contents of C, N, S, P, K (in g/kg) and C:N ratio in different decay phases

Slika 7: Vsebnost in odvisnost C, N, S, P, K (v g/kg) in C:N razmerje v različnih fazah razkroja

4 DISCUSSION
RAZPRAVA

4.1 FORMATION OF COMPOSITE SAMPLES AND VARIABILITY IN WOOD CHEMISTRY
PRIPRAVA SESTAVLJENIH VZORCEV ZA ANALIZE HRANIL IN NJIHOVA VARIABILNOST

Nutrients in CWD have been studied as part of stem nutrient content (COMERFORD / LEAF 1982). In the stem, they represent the total nutrient drain under conventional harvesting systems, while as CWD they are part of mineralization and immobilisation processes within the ecosystem. In stem nutrient studies (i.e. in non-decomposed wood) at least five disks were suggested to be taken in order to meet a 10 % allowable nutrient content error criterion *(ibid.)*. However, due to the heterogeneity of wood decay classes within hardwood logs (PYLE / BROWN 1999) and between the inner and outer wood (IDOL *et al.* 2001) the variability in nutrient concentrations might be larger, especially in the middle decay classes ((I) II to III (IV)). However, ALLEN *et al.* (2000) reported higher variability in more decayed logs of mountain beech in New Zealand. In order to minimise variability, we have analysed nutrients in composite samples made from 6 samples taken from different parts along the log or from the snag.

IDOL *et al.* (2001) reported significant differences among inner and outer woody tissues in decay classes II and III (simplified but comparable to the decay phases used in our study). They suggested that the substrate quality of these two components most likely translates into different decomposition rates and nutrient dynamics. In our study, we have tried to sample the wood from the outer part to the centre of the logs / snags. However, in the timescale allowed this was not always possible to attain. Therefore the main part of the composite samples, used for nutrient analyses, was formed from the outer woody tissues. This might have an influence on the content of nutrients, on their variability and on total nutrient storage and release from CWD as calculated for Rajhenavski Rog (Figure 6, Table 8). Rates of litter decomposition have been correlated with initial nutrient concentrations and their ratios to carbon compounds. Element concentrations are higher in bark than in other components (RAYNER / BODDY 1988), which might also have an influence on mineral nutrient contents of the less decayed CWD in our study.

However, since bark is important for organisms living on CWD, we have decided to include it also in nutrient analyses.

4.2 AGE-DECAY FUNCTIONS OF CWD
ČASOVNA ODVISNOST RAZKROJA VELIKIH LESNIH OSTANKOV

Several methods can be applied for determination of the time of death of logs and snags in the forest ecosystems. The most reliable methods for calculation of decay constants can be done with historical studies where reliable data is available (STONE *et al.* 1998). Other methods include tree ring width chronology of the CWD, tree ring width of the released trees after CWD has disappeared from the crown area, studies of reaction wood or wounds healing on surrounding trees, aerial photographs of tree crown disappearance, establishment of seedlings on CWD, C-isotope studies (DANIELS *et al.* 1997, STORAUNET / ROLSTAND 2002). Due to restrictions of devastation in our virgin forest reserves, preciseness of the aerial photographs and the lack of the historical data, our study was done with comparisons of CWD dendro-chronology with a standardised beech dendro-chronology from the area.

Dendro-chronological analysis of CWD samples is a method for determination of the time of death of the studied trees. Dendro-chronological analysis is limited by four main factors:

- tree rings must be visible and the tree must form tree rings,
- the sample must be in compact form (too soft and too decayed samples are not usable) in order to prepare the surface properly for analysis,
- there must be a sufficient number of visible tree rings (min. 40),
- the periphery of the sample should be more or less intact or the date of death is hard to determine.

The AGE – DECAY PHASE model is based on the assumption that the tree stops growing at the moment it dies. This assumption is a very basic one, as we know that in the period before the tree actually dies, it grows very slowly and can already be colonised by fungi. It is also known that the tree rings that are formed in that period are very narrow and sometimes even partially (or completely) absent. A recent study on downed Norway spruce has shown that a tree could remain standing and withstand decay before falling for 70 or 90 years (STORAUNET / ROLSTAND 2002).

To build an AGE - DECAY PHASE model in such circumstances, we are faced with a problem of model reliability. A basic AGE-DECAY PHASE model is a relationship between decay phase (DP) and years since the death of the trees. The basic assumption is that decay increases with time since death of the tree. However, in practice we, have observed that position of the dead tree (snag / log) and the diameter (thin / thick) plays a crucial role for the development of decay. These correlations need further studies of a greater amount of CWD.

From the dendrochronological point of view, it is sometimes hard to date dying trees since their growth pattern does not correspond to the normal growth patterns of the surrounding trees and it is, therefore, hard to establish the year in which the tree died. To make the problem worse, a heavily degraded periphery is usually not suitable for measuring as it can fall apart during sample preparation, and dating the death of the tree is not accurate - errors could be high.

To base an AGE - DECAY PHASE model on such data is questionable and must be avoided. In our case, we did not take into account samples with "abnormal" death dates (like 50 years ago for DP 2).

Several statistical relationships might fit the model. When decomposition is measured by the remaining fraction of the original quantity of wood density, mass or volume, exponential models appear to give best explanations, even though exponential, logarithmic and linear models have all been found to describe the decay rate data equally well (STORAUNET / ROLSTAND 2002). However, the decay classes are visual descriptions of the logs. Therefore, the trend in decomposition over time simply depends on how these classes are defined. In the Norwegian study (*ibid.),* the relationship between time since fall and decay class showed the best fit in a linear model. The time since death and time since fall were however highly variable, ranging from 0 to 90 years difference.

Annual decomposition rate and turnover time for beech branches in UK has been reported as 15-32 % mass loss per year while the 95 % turnover time was 9 – 20 years

(RAYNER / BODDY 1988). There has been a great variation in reports on time for decomposition, in large due to resource quality, such as size, presence or absence of bark, nutrient status, as well as climate and site conditions and CWD exposition. Decay rate is greatly influenced by diameter, contact with soil, exposition to the sun etc. Also, existing heterotroph community structure has a considerable effect on decomposition rates (*ibid.).*

Our AGE-DECAY model was based only on dating of time since death for 44 trees from decay phase classes 1, 2, some 3, some from 4. Nevertheless, the applied regressions (formula [1] in section 3.2) have shown an acceptable correlation. The modelled age since death for complete decomposition was 51 years, although individual dated ages, considered as outliers, have shown that a dead tree might remain in decay phase class 2 for as much as 50 years. The modelled time for decomposition (51 years) was also used for calculations of nutrient storage and release from CWD in Rajhenavski Rog. This data should be compared to beech CWD decomposition in other EU countries collaborating in the 5FW EU project.

4.3 PHYSICAL AND CHEMICAL CHARACTERISTICS OF CWD
FIZIKALNE IN KEMIJSKE ZNAČILNOSTI ODMRLIH LESNIH OSTANKOV

Volume and biomass

From measured diameters of CWD (for more decayed CWD also from estimated initial diameter; data not shown) volume was calculated (Tables 6 and 7, Figure 6). The average density was used for calculation of biomass of CWD per hectare in Rajhenavski Rog (Table 9). The volume of CWD in different decay phases and diameter classes was found to have a differential effect on biodiversity (i.e. by KRUYS / JONSSON 1999), as the diameter influences the surface-to-volume ratios. It is also interesting to note that remains of snags were found and included into decay phase classes 5 or even 6. Biomass gives additional information on the quantity and quality of the decomposing substrate for in-wood growing organisms as well as for carbon and mineral nutrients storage capacity of CWD in the studied site.

Moisture

The moisture content of living beech trees was reported at approximately 72 % for sapwood and 55% for heartwood (RAYNED / BODDY 1988), while free water tends to increase in the outer rings of fresh wood and in bark (*ibid.*). In wood products, beech wood is considered dry at approximately 10 % (PHYLLIS 2002) and its fibre saturation point (which is defined as the moisture content at which the cell walls are saturated with no free water in the lumens and pits) is at 32 – 35 % moisture (TORELLI 2000). The average moisture content of CWD of decay phase class 1 was at approximately 71 ($\pm$21) %, which is close to the reported moisture of (living) sapwood. This might also indicate that most samples for moisture analysis from this decay phase were taken from outer wood tissue.

As the wood structure decays, moisture tends to increase, which was also shown in our study (Fig. 6). A sharp differentiation is recognisable between decay phases 1 and 2 and the more decayed CWD. In the latter, moisture content on average is very high (up to 700 % dry weight), but the variability is also very high. The variability might be partly due to the following reasons: i) the average decay phase was not necessarily always also the decay phase of the part of the CWD taken for moisture analysis; ii) wood is a highly heterogeneous material, while decaying wood is exponentially more heterogeneous, considering the potential of organisms, their succession and communities, involved in the processes of decay, and of their different impacts on decay; iii) samples for moisture analyses were taken in different weather conditions.

The general trend, as well as the high water content of CWD, indicates one of the most important roles of CWD in the forest ecosystem, i.e. its water retention capacity and therefore source of humidity, necessary for establishment and functioning of micro-organisms, fungi and plants in / on CWD. This is especially important in dry sites and in sites where water tends to disappear below ground rapidly, such as is the case for the Dinaric Alps and other Karst regions in Slovenia.

Density

Three densities (kg/m^3, g/cm^3) can be measured in wood analyses:

- absolute density (ρ_o) is calculated as oven dry mass per oven dry wood volume,
- basic density (R) is calculated as oven dry mass per volume of fresh wood,

- green density (ρ_{green}) is calculated as fresh mass per fresh volume (water saturated volume of dead wood remains equal at moisture over 30%).

No statistical relationship can link the three densities. For beech wood, the following densities have been reported (WAGENFÜHR 1996):

ρ_o 490...680...880 kg/m^3,
R 540...720...910 kg/m^3,
ρ_{green} 820...1070...1270 kg/m^3.

In Slovenia, ρ_0 was measured in order for the procedure to be validated according to the tested protocols in the lab, which were standardised for dry wood analyses. Its mean value for all decay phases (566 kg/m^3) was within the reported range for beech wood. However, if the method permitted, the basic density would be more useful for the purposes of our study. Since absolute density was also used for biomass and nutrient calculations per hectare and their yearly release, these results are supposedly overestimated.

The average wood density was diminishing with higher decay phase classes (Figure 6) and could well represent the decay phase of CWD, which has also been shown in previous studies (i.e. PYLE / BROWN 1999). In our study, the variability in decay phases 1 to 3 was high. Also other authors (*ibid.*) have justified that the middle decay phases (esp. 2 and 3) may show high variability with respect to several characteristics (which should be also considered in nutrient storage, see below) since they are often represented as the average decay phases of the CWD, parts of which can be decayed from phase I to IV.

Within the decay phase classes 1 to 3, the absolute density could reach values above 1 (Figure 6). This characteristic could be explained in the biodiversity context since some of the fungi are known to be capable of altering their moisture environment (RAYNER / BODDY 1988). They alter the chemical composition of storage compounds, structural cell wall components and extractives, while in some of these, fungial pseudosclerotial plates can appear *(ibid.)*. All of these can involve an encrustation of the wood in lower decay phases, which might explain the high density (especially in decay phases 1 and 2) and the relationship of density and moisture.

pH value

The pH value in water for beech was reported at 5,4 for bark and 5,5 (FENGER / WEGENER 1989) or 5,1 to 5,4 (WAGENFÜHR 1996) for wood. In the measured CWD in Rajhenavski Rog the average pH in decay phase 1 was 5,4 (ranging from 4,5 to 6,2). It was decreasing towards decay phase 6 to the average value of 4,6 (range from 4,2 to 5,0). We expected such a decreasing trend since the fungal mycelium gradually colonised all the wood. pH values between 4 and 5 are required by many fungi for their growth and metabolism and they can be achieved by extrusion of protons, degradation products and differences in O_2 to CO_2 ratios inside the wood (RAYNER / BODDY 1988).

Carbon and mineral nutrients in CWD

In the studied CWD, the mean carbon concentration for beech CWD was 46,7 % (46,4 % for the decay phase 1), which is within the limits for average beech wood (43 to 48 %, PHYLLIS 2002). The concentrations of other nutrients in CWD of different decay phases (Table 9, Figure 7) are lower than reported for dry beech wood (for N 0,92 to 1,02 %, PHYLLIS 2002) and also lower than concentrations in whole plants. Potted beech plants were reported to contain 1,34 % N $\pm$ 0,22 in litter, 1,08 $\pm$ 0,15 in stems, 1,27 $\pm$ 0,29 in buds, 1,29 $\pm$ 0,80 in roots, in total 1.22 $\pm$ 0,05 % N in whole potted beech plants (EL KOHEN *et al.* 1992, cit. in MOUSSEAU *et al.* 1996). However, the analysed concentrations were comparable to previously reported concentrations of C, N, S, P and K in dead trees (Scots pine, Norway spruce, birch) from NW Russia (KRANKINA / HARMON / GRIAZKIN 1999) and in woody litter from Vancouver Island (KEENAN / PRESCOTT / KIMMINS 1993).

Carbon concentrations have shown a slight decline from decay phase 1 to 3, after which an increase was measured. However, the variability was high and increasing towards more decayed wood. Carbon-to-mineral nutrient ratios were reported for un-decayed and differently decayed wood, as represented by decrease in density and in percentage of weight loss (RAYNER / BODDY 1988). C to N ratios were calculated at approximately 250 : 1 in un-decayed wood, reducing to 89 : 1 and 44 : 1 in heavily decayed wood (at 0,2 and 0,1 g cm^{-3} or 64 and 82 % loss of weight respectively) (*ibid.)*. In our analyses C : N ratios were 318 : 1 for decay phase 1, 93 : 1 for decay phase 5 and 71 : 1 for decay phase 6 (absolute density in these two categories was 0,26 or 0,25 g cm^{-3} respectively). With respect to the density (similar to the heavily decayed wood in the cited reference), the C to N ratio in decay phase classes 5 and 6 corresponded to the heavily decayed wood (64 % loss of weight).

Rates of decomposition have been correlated with initial nutrient concentrations and their ratios to carbon compounds. Element concentrations are higher in bark than in other components. As bark is the first component lost during decay, the increasing N concentration with stage of decay and decreasing C/N ratio are unlikely to represent a differential loss of log components. The increased N concentration in logs has been reported elsewhere (e.g. KEENAN / PRESCOTT / KIMMINS 1992, ALLEN *et al.* 2000 and others).

At least three factors were named as possible causes for the decline in C : N ratio: i) C can be lost due to respiration as CO_2 while N remains fixed in microbial biomass; ii) N can be imported by contact with soil, mobilisation through mycelium and invasion by animals; iii) N fixation may occur (RAYNER / BODDY 1988). Since C content did not change substantially in the different decay classes, C loss through respiration might be considered as being of minor importance. Mycelial N translocation from other sources might primarily be directed into formation of sporophores, therefore most N in the decaying wood should result from N fixation. Our data (Figure 7) has shown an exponential increase in N concentration from decay phase 1 to 5 while in decay phase 6 the concentration was more variable and the median number was below the exponential curve. Therefore some export of nitrogen might have already occurred. This might happen through production of mycelial cords, rhizomorphs or sporophores or emigration of animals (*ibid.).*

An exponential increase of concentration of nutrients with higher decay classes was also found for sulphur and phosphorus. The N : P ratio (Table 9) increased from decay phase 1 to 2, remained stable to decay phase 5 and decreased again at decay phase 6. Since this decrease occurred with pH reaching the lower limit of 4,5 this could be linked to the ligninolytic activity, whereby ligninase has a pH optimum at 4,5. At the same time, this activity begins especially when certain essential elements for fungal growth become growth limiting; there was evidence that carbohydrate, sulphur and especially nitrogen, but not phosphorus, can activate the system (RAYNER / BODDY 1988). For K, however, the concentrations in the three lower decay phase classes were variable and did not show any trends, while in decay phases 4 to 6 less variability and a steady decrease in concentration was detected. K is a mobile ion, therefore its leaking have already started from more-decayed wood.

Nutrient contents and their release from CWD depend on their availability and on processes in different forest ecosystems. Mineral nutrients (N, S, P, K) released through the decomposition processes are assimilated in the microbial biomass, while C, which serves as an energy source for heterotrophs, is converted to CO_2 through respiration. A simplified model (CAMPBELL / GOWER 2000) can be based on the processes in which gross N mineralization occurs when older generation microbe cells excrete excess N in inorganic forms. Gross N immobilisation occurs when younger generation microbe cells, that require supplementary N, assimilate N from the inorganic pool. Therefore, the supply of readily consumable C drives the turnover of microbial biomass which functions to increase both gross N mineralization and immobilisation.

From the above model, we can conclude that nutrient mineralization or immobilisation depends on the availability of nutrients within the ecosystem and on the ratios between them. The patterns of nutrient contents during the processes of decay, therefore, depend on the initial nutrient concentrations in the CWD (LAIHO / PRESCOTT 1999), i.e. on the site and species characteristics.

The importance of CWD for nutrient cycles in the forest site
From nutrient concentration in CWD, its biomass per ha and time for decay as well as its role in nutrient cycling in the studied sites could be extrapolated.

In Slovenia, studies of nutrient contents in the soils and soil solution and annual litter fall were done in a comparable permanent forest research plot (PFRP) of the Slovenian Forestry Institute Preža near Kočevska Reka. The calculated annual input with precipitation into the PRFP Preža was 14,5 kg/ha N, and 14,2 kg/ha per year of S. The total litter mass shed per year was 473 g/m^2, from this 378 g/m^2 of foliar litter (i.e. woody litter was ca. 20%). For foliar litter, the calculated nutrient input was for N: 60,6 kg/ha per year, S: 4,3 kg/ha per year, P: 2,6 kg/ha per year, K: 15,8 kg/ha per year (all calculated from SIMONČIČ / KALAN / RUPEL 2000 and SIMONČIČ 2002; the calculations provided by Dr. Simončič). Therefore, the yearly release from CWD (Table

10) would represent up to 4 %, 7 %, 3 % and 8 % of these nutrients release, respectively, from foliar litter and wood decomposition.

Our data (Table 10) from a Dinaric silver fir - beech forest has shown similar contents of C as the analysed beech wood, but lower storage and yearly release of C, N, S, P and K from beech CWD in comparison to studies of conifers (KEENAN *et al.* 1993). All the woody material in and above the forest floor contained 51-59 % N and 58-61 % P *(ibid.)*. Alternatively, the calculated shares are similar to some data on annual N input (LAIHO / PRESCOTT 1999) on pine, fir and spruce forests (yearly input of N and P from CWD was up to 5 % to total N and P release from litter). However, two possible sources of overestimation of nutrients release should also be taken into account in our study: i) the time for release in our study (51 years accounted for in the calculations) can only be applied tentatively; ii) the biomass calculation was based on the absolute density of the measured CWD volume, while the basis for calculation should ideally be basic density.

4.4 FINAL DISCUSSION
SKLEPNA RAZPRAVA

The general processes regulating nutrient flow within an ecosystem are those associated with i) uptake by higher plants, ii) translocation and re-use by these plants, iii) nutrient return to the soil surface, iv) mineralization and immobilization of returned nutrients by micro-organisms and v) nutrient leaching through soil profile (COLE 1991).

During decomposition, logs undergo considerable structural and chemical changes, certain components may decay more rapidly than others (i.e. bark), the wood becomes soft and cracked and the density steadily decreases (e.g. ALLEN *et al.* 2000). A number of authors (e.g. FRANGI *et al.* 1997, STONE *et al.* 1998 etc.) represent decomposition of CWD using the decomposition constant (k). It is calculated as the logarithm of the mass ratio at two different times divided by the time of exposition (i.e. time since death). Therefore, it depends on the initial mass and its disappearance with time.

Our data (Table 9, Figures 6 and 7) shows decay phase related density, pH and C : N ratio decline, and moisture, N, S, P rise. K content showed a decline only in decay phases 4 to 6.

Due to the restrictions in age determination from our study, only tentative age-decay phase model resulting in tentative nutrient release estimates could be produced. Nutrient and age-decay phase studies were done in the Slovenian forest ecosystems for the first time. Presently, they represent a valuable basis for all future studies. Since species richness has been compared to decay phases, volume, moisture, nutrient contents and their ratios in CWD (ALLEN / BUCHANAN / CLINTON / CONE 2000), such comparisons (with data published by KUTNAR *et al.* 2002, ODOR / VAN DORT 2002, PILTAVER *et al.* 2002) will also be part of our future studies.

5 CONCLUSIONS
SKLEPI

Physical and chemical characteristics of beech coarse woody debris (CWD) were studied in two forest reserves in the Dinaric Alps in southern Slovenia.

The total volume of beech CWD in the sampled area in Rajhenavski Rog was 100 m^3/ha (or with respect to the average density 46,646 Mg/ha) and 192 m^3/ha of silver fir CWD; for the sampled area in Krokar the total beech CWD volume was 57 m^3/ha and silver fir CWD 88 m^3/ha. The biomass of beech CWD per ha was used for calculations of nutrient storage and release of nutrients in / from CWD.

Density declined with increasing decay phase classes (absolute density was measured).

Moisture content (in average 209 m^3/ha) showed that CWD is an important source of water needed for CWD dependent organisms. It increased with increasing decay phase from DP class 2 to 6.

The pH value decreased with decay phase.

N, S and P concentrations rose with the decay phase, while the C : N ratio declined. An increase of concentrations of N, S, P and a decrease in C : N ratio might be applied as indicators for decomposition phases.

The total C, N, S, P and K content in CWD was 21,78 Mg/ha C, 140 kg/ha N, 17 kg/ha S, 5 kg/ha P, and 74 kg/ha K.

From 214 trees, 93 samples from the decay phases 1 to 3 (4) were used for dendrochronological dating of age since death. Due to rotting, only 58 could be analysed and from these only 44 were used for production of age-dependent decay curves. The expected time for decay above decay phase 4 was over 32 years, the total decomposition time used for calculations of yearly release of nutrients was 51 years. However decay phases 2 and 3 have shown a number of overlapping dendro-chronologically dated ages, therefore the number of dated trees should be increased in future.

6 POVZETEK

Prostorska in časovna razporeditev velikih odmrlih lesnih ostankov (CWD) ima pomembno vlogo: (i) kot substrat in vir hranil za organizme, ki uspevajo na ali v CWD; (ii) kot dolgoročni vir hranil za organizme, ki so drugače odvisni od CWD; (iii) za procese v gozdnih ekosistemih. V naši raziskavi, ki je bila del evropskega projekta NATMAN (QLRT1-CT99-1349), smo izbrali, opisali in vzorčili CWD bukve (Fagus sylvatica L.) v dveh (pra)gozdnih rezervatih v južni Sloveniji. Glavni namen raziskave je bil ovrednotiti vlogo CWD kot vira hranil in ugotoviti povezave med dimenzijami, starostjo, razkrojno fazo ter fizikalnimi in kemičnimi značilnostmi CWD bukve.

Raziskave so potekale v dveh gozdnih rezervatih (Rajhenavski Rog in Krokar) v Dinarskih Alpah v južn Sloveniji. V vsakem rezervatu smo izbrali prek 100 dreves. Vsako drevo (panj, če je obstajal; deblo in deli krošnje) smo oštevilčili in podrobno opisali zunanje značilnosti – fazo razkroja (1 = najmanj razkrojeno, 6 = najbolj razkrojeno); premere (cm) na različni dolžini in dolžino (m); stik s tlemi (v %); pokritost s skorjo, mahovi ter zelišči (vse v %). Položaj lesnih ostankov smo vrisali v karto; izračunali smo tudi njihovo prostornino (m3). Za manj razkrojene CWD (faze razkroja 1 do 3 (4)) smo

starost določili z dendrokronološko analizo in s primerjavo s standardizirano dendrokronologijo bukve iz tega območja. Šestdeset CWD (skupno 82 debel in panjev) smo vzorčili za analize hranil (C, N, S, P, K), pH, vlažnosti ter gostote lesa.

V rezervatu Rajhenavski Rog je bila skupna prostornina bukovih CWD na vzorčeni ploskvi 100 m^3/ha (oziroma 46,646 Mg/ha ob upoštevanju povprečne gostote lesa), jelovih CWD pa 192 m^3/ha; v rezervatu Krokar je bila prostornina bukovih CWD na vzorčeni ploskvi 57 m^3/ha, jelovih pa 88 m^3/ha. Vsebnosti N, S in P so z večanjem razkroja naraščale, vsebnost K in C/N razmerje pa sta padali. Skupne količine makrohranil v CWD so bile 21,78 Mg/ha (C), 140 kg/ha (N), 17 kg/ha (S), 5 kg/ha (P) in 74 kg/ha (K).

Z večjim razkrojem sta padali vrednost pH in gostota lesa, naraščala pa je njegova vlažnost. Analize vlažnosti (skupna količina vode v CWD je bila 209 m^3/ha) so pokazale, da predstavljajo CWD pomemben vir vlažnosti; to velja zlasti za organizme, ki so odvisni od CWD (npr. glive, mahovi, višje rastline, vključno s semenkami gozdnega drevja).

Na osnovi 44 dreves, za katere smo dendrokronološko določili čas odmrtja, smo določili časovne funkcije razkroja. Pričakovani čas za razkroj do 4. faze je daljši od 32 let. Izmerili smo tudi več različnih časov odmrtja za nižje razkrojne faze, vendar bi za natančnejšo določitev hitrosti razkroja v tem območju potrebovali večje število meritev.

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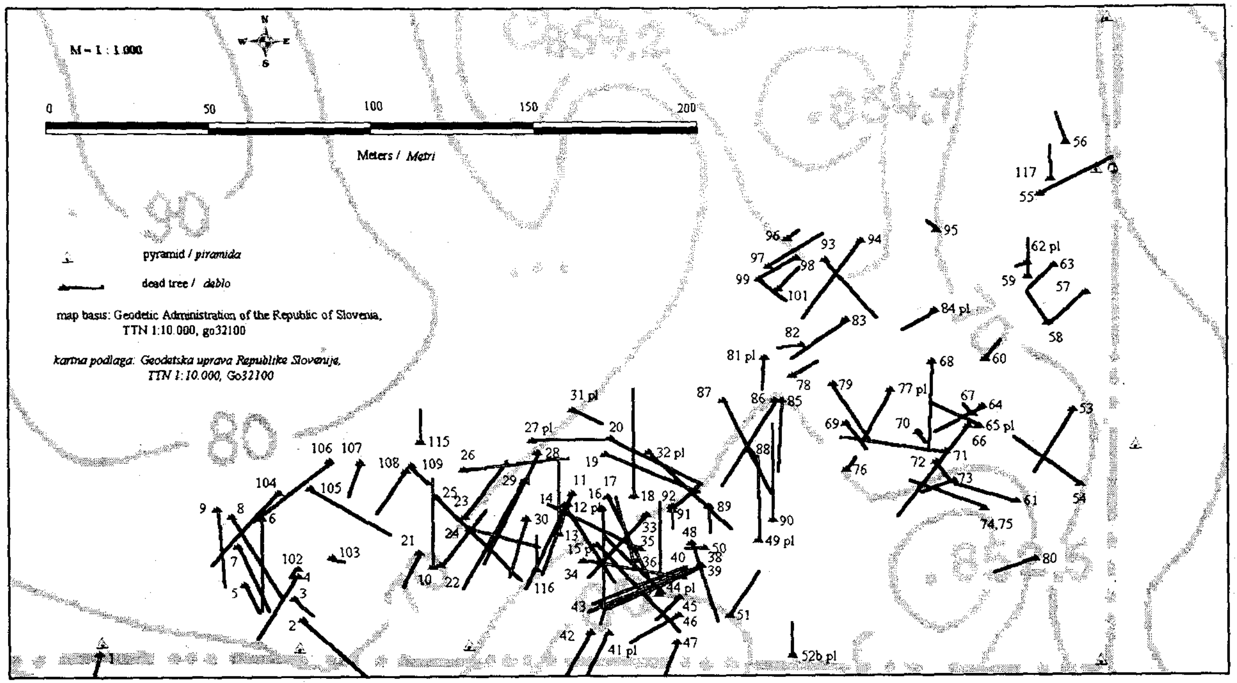
8 APPENDIX
PRILOGA



Appendix: Position and orientation of the studied dead beech trees (CWD) in Rajhenavski Rog. Pyramid (empty triangle) - permanent pyramids, made of rocks, for delineation of the outer borders of the forest reserve; dead trees - position of the enumerated beech CWD, localized by GPS (full triangle) and their orientation (lines, length according to the total length of CWD, diameters not to scale) (Map prepared by S ŽITNIK, GPS position by I. KOPŠE, CWD orientation by M. RUPEL).

Priloga: Položaj in usmeritev odmrlih dreves (CWD) v rezervatu Rajhenavski Rog. Piramida (prazen trikotnik) - trajne kamnite piramide, ki označujejo zunanji rob gozdnega rezervata; odmrlo drevje - lega oštevilčenih bukovih debel, določena z GPS (polni trikotniki) in njihova usmeritev od panja k vrhu (nekdanje) krošnje (črte; dolžina ustreza skupni dolžini CWD, premer ne ustreza razmerjem). (Karto je izrisal S. ŽITNIK, z GPS izmeril I. KOPŠE, azimute CWD je določil M RUPEL).