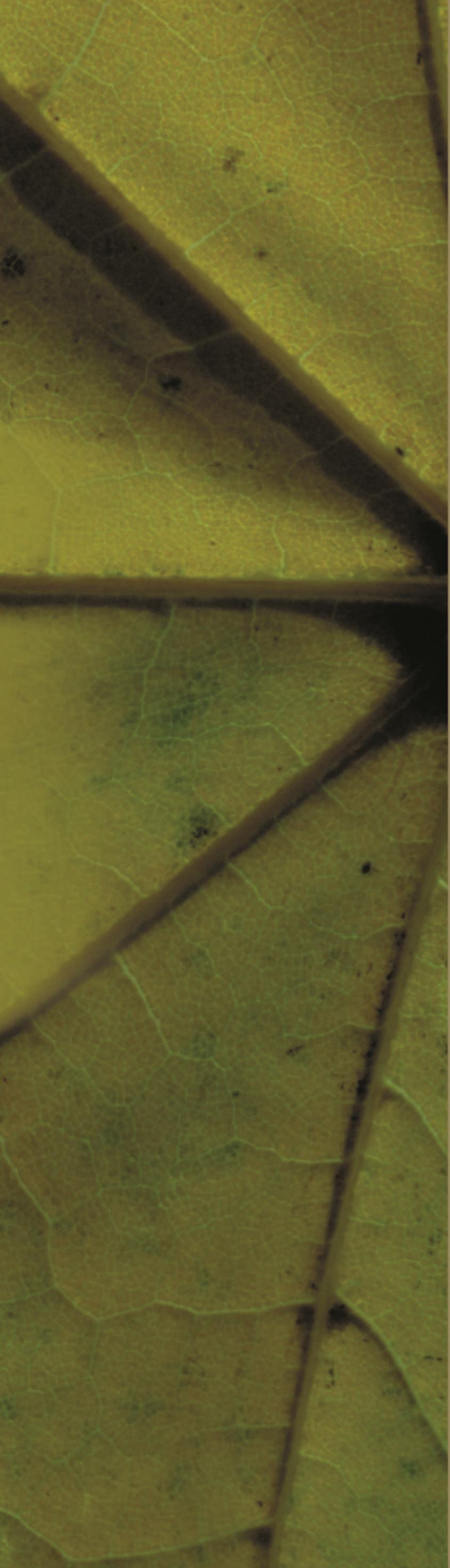

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Early Evaluation of Promising White Poplar (*Populus alba* L.) Clones in Hungary

Károly RÉDEI[a*] – Zsolt KESERŰ[a] – Gábor SZULCSÁN[b]

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Abstract – White poplar (*Populus alba* L.) and its natural hybrid, grey poplar (*Populus* x *canescens*) are native stand-forming tree species in Hungary, covering 3.4 per cent of the forested area (64 000 ha). More than 70 per cent of their stands and plantations can be found on calcareous sandy sites in the Danube–Tisza region, so they play a significant role in the poplar growing of this part of the country. One of the most important tasks ahead of Hungarian poplar growers is to improve the quality of poplar stands and plantations for wood production based on selecting relatively drought-tolerant clones and cultivars. In the paper the juvenile growth and the morphological characteristics of four micropropagated white poplar clones have been evaluated on a marginal site in central Hungary. The clones *'H-337'* (*P. alba* x *P. grandidentata)* and *'H-384*' (*P. alba* x *P. grandidentata)* appear to be especially promising for quality wood production under arid hydrological conditions.

White poplar (*Populus alba* L.) / clone selection / early growth evaluation

Kivonat – Igéretes fehér nyár klónok korai értékelése Magyarországon. A fehér nyár (*Populus alba* L.) és természetes hibridje a szürke nyár *(Populus* x *canescens)* őshonos, állományalkotó fafajok Magyarországon. Az erdővel borított terület 3,4%-át (64000 ha) foglalják el. Erdőállományaik és ültetvényeik több, mint 70%-a a Duna-Tisza közi meszes homokon található, így jelentős szerepet játszanak az ország ezen részének nyárgazdálkodásában. A magyar nyártermesztők előtt álló egyik legfontosabb feladat a nyárállományokban és ültetvényekben a fatermesztés minőségének fejlesztése relatíve szárazságtűrő klónok és fajták szelektálása révén. A dolgozat négy, mikroszaporítással előállított fehér nyár klón korai stádiumú növekedési és morfológiai értékelését mutatja be közép-magyarországi marginális termőhelyen. Száraz hidrológiai viszonyok mellett a *P. alba* x *P. grandidentata* *'H-337'* és *'H-384'* jelű klónok lehetnek a minőségi fatermesztés szempontjából leginkább ígéretesek.

Fehér nyár (*Populus alba* L.) / klónszelekció / korai növekedés-értékelés

1 INTRODUCTION

White poplar (*Populus alba* L.) and its most important natural hybrid, the grey poplar (*Populus* x *canescens*) native to Hungary. The area of poplar stands and plantations in the country was 61400 ha in 2006 (3.4 per cent of the total forested land), with a standing volume of 10.2 million m^3 (166 m^3 ha^{-1}).

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More than 70% of the white and grey poplar stands can be found on calcareous sandy sites in the Danube–Tisza region. Native poplars have been regarded for several decades as weed tree species without any value for the timber market. In spite of this fact about 35% of the new afforestation and artificial regenerations is carried out presently with white poplar in the mentioned region. White poplar has a rich gene pool in the sand dune region in the middle of the Great Hungarian Plain and in the bottomland of big rivers (Szodfridt – Palotás 1973). In the near future, due to the establishment of national parks in these regions, considerable increases can be expected in the area of native poplars. At the same time their importance will be increasing in the large areas of marginal sites which are not suitable for hybrid poplars but can accommodate native ones *(Figure 1)*.

In Hungary the range of sites optimal for poplar growing is rather limited. In the Danube–Tisza region some very important ecological factors have become unfavourable for poplar growing in the last two decades. There is insufficient precipitation during the growing season (appr.200–300 mm), and control of the rivers and canalisation have caused a drastic lowering of the ground-water table in many places. In such spots the water supply for poplars depends on the moisture content of soils, accumulating waters on the surface and on the water-storing capacity of soils. Therefore, the main aim of the selection work is to find and improve relatively drought-tolerant white poplar clones and cultivars that have good stem form providing good-quality wood material for industrial purposes (without false heartwood) and that can adapt to the changed ecological conditions (Rédei 1994).

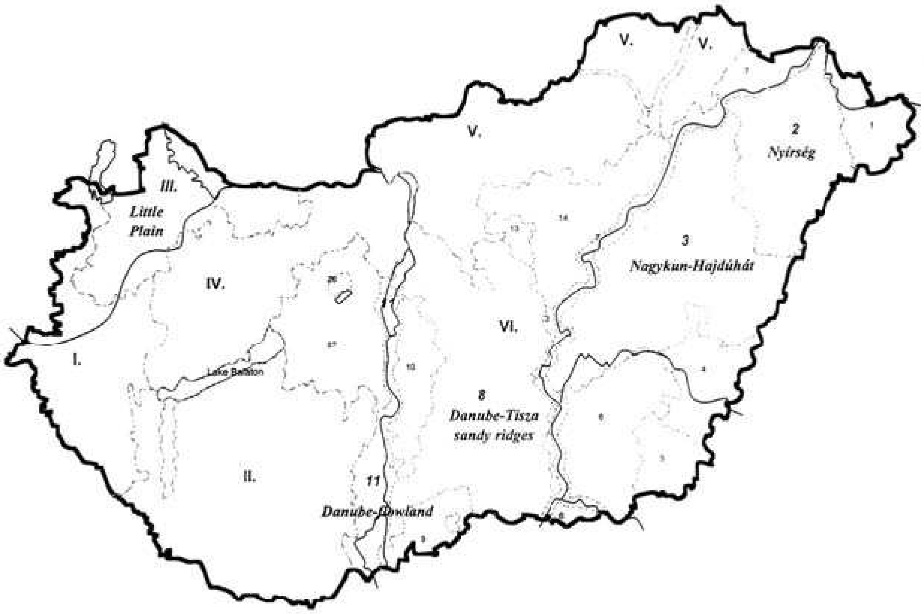

Figure 1.The main growing regions of white poplar (Populus alba L.) stands in Hungary

2 TAXONOMY AND DISTRIBUTION OF POPLARS

This section of the genus Populus (Dicmann, Kuzovkina 2008) is a complex grouping comprising the white poplars and aspens. Members of section *Populus* are distributed over temperate, boreal, and montane reaches of the Northern Hemisphere, and several are of great economic importance. As a group they are ecologically distinctive because of their clonal physiognomy and – in the case of aspens – by their common occurrence in upland habitats (Dickmann – Kuzovkina 2008).

Species crosses have yielded up to now the best results. It has to be mentioned, that the direction of crossing has importance in poplars, i.e. reciprocal crosses are genetically different. Hybrid vigour was observed in the crosses *P. alba* x *P. grandidentata* and *P. tremula* x *P. tremuloides,* which means that genetically close species, originating from different continents (usually Europe – N. America), are the most suitable partners. Such crosses may happen in nature, when the species are planted by accident close to each other *(*Mátyás 1983, Guzina 1986).

3 BRIEF SUMMARY ON BREEDING AND IMPROVEMENT OF POPLARS IN HUNGARY

The basis for the breeding and improvement programme was a series of clones obtained in the frame of co-operation, during the 1950's by the Poplar Research Institute of Italy, Belgium, the Netherlands, France, Germany and Yugoslavia, combined with the genetic heritance of Hungarian forests (*Populus nigra* and *Populus alba*). This research programme was started by the prominent scientists of the Hungarian Forest Research Institute (ERTI), Gy. Koltay and F. Kopecky. In Hungary ERTI is the most important national institution for poplar breeding and improvement. It took part in provenance testing experiments of *Populus trichocarpa, Populus deltoides* and *Populus nigra,* which were launched by FAO and IUFRO.

The number of clones selected out of progenies amounts to more than 1000. These clones, screened by early testing methods, make up a considerable part of the collection of ERTI and at the same time primary materials for clonal testing experiments. This poplar cross-breeding resulted in several excellently growing *Populus* x *canadensis* poplar clones, of which *Populus* x *canadensis Moench 'Pannonia'*, *'Kopecky'* and *'Koltay'* have been admitted to the official national poplar recommendation and are integral parts of the state approved and tested varieties.

Selection breeding was mostly directed to native poplars (Kopecky 1962, 1978). According to his research on native poplar hybrids, the *P. alba* x *P. grandidentata ‘H 422-1’*, the *‘H 422-6’*, the *P. alba* x *P. alba ‘H 425-4’* and the *‘H 325-10’* clones could have some growing-importance. The *P. alba cv. ‘Bolleana’ ‘H 427-3’*, the *P. alba* x *P. grandidentata ‘H 422-1’* and the *‘H 422-6’* clones can be planted in roadside plantations and parks for their decorative value on the whole range of suitable sites (Rédei 2000). On the calcareous sites of the Great Plain only the *P. canescens* x cv. *‘Bolleana’*, the *‘H 372-1’* and the *‘H 372-2’* can be planted.

Selection investigations on marked individuals and populations of native poplars laid the foundation for their possible *in situ* and *ex situ* conservation. Marked gene-reserves extend to roughly 100 ha and the number of registered plus-trees is about 200 (*in situ* gene preservation). In Hungary the area of native and hybrid poplar experiments amounts to 800 ha. Geographically they are dispersed in the poplar growing regions, and therefore are suitable for drawing conclusions on clone-site interactions under the typical conditions of the country (Tóth 1996).

4 METHODS OF VEGETATIVE PROPAGATION USED FOR WHITE POPLAR CLONES

Clonal selection is a variant of individual selection, a very effective one, as both additive and non additive genetic components are utilized. Asexual propagation is very important for archivation and conservation of selected genotypes. The ease of vegetative sustenance of individuals is maybe the greatest advantage of forest tree breeding as compared with perennial plant breeding.

The vegetative reproduction of white poplar clones can be implemented by auto-vegetative propagation. Cutting propagation has been practiced for centuries in horticulture and to some extent in forestry as well. Root cuttings have been proved to be the best method. Root cuttings are detached portions of root systems, generally 0.5 cm in diameter and about 5-10 cm in length. They are planted horizontally at a depth of 2 to 3 cm in a well-watered rooting medium. Good results can be archived with simple sowing of root cuttings in the nursery.

Greenwood cuttings are much more difficult to handle, as they are sensitive to drying-out. Greenwood cuttings of white poplar clones are rooted under shaded foil cover, they have to be carefully watered. The time required for root formation varies from two weeks to twelve weeks. Clones which root the best in early summer are usually over-wintered in a greenhouse because their root systems are not adequate to support the young ramets under outdoor winter conditions.

Four white poplar selected clones were micro-propagated during the last few years in the Micro-propagation Laboratory of Research Institute for Fruit growing and Ornamentals, Budapest–Érd in collaboration with the Hungarian Forest Research Institute. Plant tissue culture methods provide us with new means to speed up vegetative propagation of the selected clones and give us the opportunity to establish new clone trials and seed orchards with them (Rédei – Balla 2007). In spite of the numerous advantages of this method it has to be underlined that tissue culture plants must not be brought into cultivation before risks and costs are carefully considered.

5 EARLY EVALUATION OF WHITE POPLAR CLONES

Suitable observation techniques make it possible to observe some characteristics important for breeding already at an early stage of development of trees, while other characteristics are manifested at a later age. In our selection work the main selection criteria were:

- growth rate,
- adaptation to site conditions,
- stem form,
- branching habit,
- rootability of cuttings,
- resistance to pests and diseases and
- wood properties.

The trial demonstrated in this paper is allocated in the most important white poplar growing district in Hungary (in sandy ridges between the rivers Danube and Tisza).

5.1 Description of the study area

The trial discussed in this paper was allocated in subcompartment Kecskemét 40A in the Danube - Tisza interflow region (in central Hungary) in spring 2004. According to the Hungarian classification of forest site types, the main ecological characteristics of the studied area are the following: forest steppe climate zone; humidity of the air is less than 50% in July at 2 pm; during the period at the test area the annual precipitation is between 263.8-560.3 mm, hydrology: free draining; genetic soil type: humid sandy soil with very shallow rootable depth. The latitude and longitude coordinates of the experimental area are *N 46.883547, E 19.588868.*

5.2 White poplar clones found in the trial

In the clone trial the clone *'H 325'* (*P. alba* x *P. alba*), *'H 337'* (*P. alba* x *P. grandidentata*), *'H 384'* (*P. alba* x_*P. grandidentata*), and *'H 425-4'* (*P. alba* x *P. alba*) as well as white poplar (*P. alba* L.) as control can be found. The experiment was set up with one-year-old micropropagated plants (in case of the clones) and one-year-old seedlings (in case of the control) in the spring of 2004. A randomised block system with three replications was used. The initial spacing was 2.5 x 2.0 m. 30 plants were planted in every replication. The total experimental area was 0,43 ha. The one-year-old *Populus* x *canescens* seedlings – as the control plants – were produced by the Kiskunsági Forestry Joint Stock Company.

5.3 Assessment of stand characteristics

The following stand parameters were measured and calculated at the age of 6 years: stem number (surviving stems), dbh.(diameter at breast height), tree height and mean tree volume. Stem volume was estimated according to the volume table for white poplar (Sopp, Kolozs 2000). According to the measurement of stem numbers the survival rate was the following: Control: 92%, 'H 425-4': 90%, 'H 337': 86%, 'H 384': 82%, 'H 325': 74%.

The collected data were analyzed by STATISTICA 8.0 (data analysis software system - StatSoft, Inc. 2008) programme including correlations and regression analysis. Analysis of variance was done for height (H) and diameter at breast height (DBH) since these parameters (particularly diameter) are highly correlated with the mean tree volume.

5.4 Tree classification

Characterization of stem quality, including their health condition was defined by using the following stem quality classes:

Class 1 – The stem is straight, cylindrical, healthy and reaching the top of the crown. Crooks are tolerated in one dimension only, up to a bend of less than twice the stem diameter. The lower two-third of the bole is free of live branches.

Class 2 – The stem is straight and healthy, forks are tolerated, but only if they are in the uppermost third of the tree. Crooks are tolerated in one dimension only, up to less than four times the stem diameter.

Class 3 – The stem is crooked, leaning and more or less damaged. Crooks may reach six times the stem diameter in one dimension and minor crookedness in a second dimension is tolerated.

Class 4 – The stem is very crooked in more than one dimension and heavy damaged. Low branching, forked trees sometimes with broken crown.

The stem quality index (see in *Table 1*) was estimated by the arithmetic average of the stem quality classes.

5.5 Results

Table 1 illustrates the most important stand structure parameters. On the basis of the data, considering the growth in height, the clones *'H 337'* and *'H 384'* provided the best results. They surpassed the control by 29 and 23 per cent, respectively. As regards the growth in DBH the above-mentioned clones surpassed the control by 24 and 23 per cent; the tendency was also the same with regard to the mean tree volume values. The effect of differences in DBH on the mean tree values seems to be very considerable (an additional 50 and 40 per cent for the above-mentioned clones). As the stem quality index is concerned, the succession from best to worst is: '*H 337*', '*H 384'*, '*H 425-4'* and '*H 325*'. According to the significance test at P = 5% level, significant differences were found in height ($SD_{5\%} = 1.31$ m), in DBH ($SD_{5\%} = 1.22$ cm) and in the mean tree volume values ($SD_{5\%} = 2.90$ dm^3).

Table 1. Stand characteristics of white poplar clones at age of 6 years.

Name of clone	Mean H		Mean DBH		Mean tree volume		Stem quality index (1-4)
	m	%	cm	%	dm^3	%	
‘H 325’	5.1	106	6.0	97	9	90	1.7
‘H 337’	6.2	129	7.7	124	15	150	1.1
‘H 384’	5.9	123	7.6	123	14	140	1.4
‘H 425-4’	5.6	117	6.7	108	12	120	1.5
Control	4.8	100	6.2	100	10	100	1.9

6 CONCLUSIONS

The trees in the clone trial demonstrated in the paper thrive under site conditions that are only partly favourable for poplar growing. Considering this fact, the early evaluation showed that mostly the clones *‘H-337’*and *‘H-384‘* seem to be suitable for poplar growing, while the clone ‘*H 425-4’* could be considered an alternative one for wood production.

The experiments have also demonstrated that micropropagated plants can be successfully transplanted into soil, hardened and grown in the field. Micropropagated trees have been exhibiting normal growth and appearance since they were planted. Hungary has got relatively much experience in white poplar growing. As the results suggest, systematic testing is essential in poplar breeding. However, results with a smaller probability of error can only be achieved after a longer period of research. The systematic evaluations of comparative trials set up in the past decades in Hungary will make it possible to select more reliably the white poplar clones which can meet all the requirements drafted in the introduction to this paper.

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Genetic Variability of Service Tree (*Sorbus domestica* L.) in the Hungarian Middle Mountains – Based on cpDNA Analysis in Two Regions

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Abstract – A genetic inventory was conducted at maternally inherited chloroplast DNA (cpDNA) gene loci of 196 adult service trees (*S. domestica*). The sampled trees represent autochthonous collectives/populations originating from 2 distant regions, from contrasting habitats, a forested area (eastern part of the Dunazug Mountains) and cultured habitats (Zemplén Mountains), respectively.

Strong intrapopulation variation was observed; percentages of molecular variance were: between regions 27%, among populations/regions 6%, within populations 67%. Considering all samples, the major part of total diversity ($h_t = 0.752$) was contributed by intrapopulation diversity ($h_s = 0.583$).

Species diversity was represented differently in individual populations. E.g. the population Kácsárd contains only one haplotype: the doubtless sign of local human cultivation. The population Buda Hills has an average differentiation considering the whole sampled material but the highest when evaluating the region north from Budapest separately. That points to the dispersion after an introduction event, probably parallel to adaptive radiation under selection influence.

In the study genetically polymorphic populations containing unique haplotypes were detected, providing important information for forest management, gene conservation and nature protection activities. The described work is part of *ex situ* gene conservation projects of the species in Hungary.

cpDNA diversity / PCR-RFLP / differentiation / representativity / genetic distances

Kivonat – Középhegységi házi berkenye (*Sorbus domestica* L.) populációk genetikai variabilitása – két régió cpDNS vizsgálata alapján. 196 házi berkenye egyed vizsgálatát végeztük el cpDNS-markerekkel. Az idős fák kollektívumait két tájegységben mintáztunk: a Dunazug-hegység keleti felének erdőborította részéből, illetve a Zempléni-hegység szőlőhegyi kultúr-élőhelyeiről. Az élőhelyek ugyan különbözőek, viszont a mintázott populációk őshonosaknak tekinthetőek.

A molekuláris variancia 27%-a régiók közötti, a régiókon belüli populációk között ez 6%, míg a populációkon belüli érték 67%. A minták összességét tekintve az összdiverzitás (h_t = 0,752) meghatározó részét a populáción belüli diverzitás teszi ki (h_s = 0,583). Az elkülönített populációk eltérő reprezentativitási avagy differenciálódási értékeket mutattak a minták összességéhez viszonyítva. A kácsárdi populáció pl. csak egyetlen haplotípust őriz, mely a helyi kultiváció biztos jele. A Budai-hegyek populációja különlegesnek bizonyult: a teljes növényanyaghoz viszonyítva

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átlagos differenciálódást mutatott, viszont a Budapesttől északra levő populációk között a legjobban differenciált. Mindez a behurcolást követő szétáramlásra utal, amely együtt járhatott szelektív befolyás alatti adaptív radiációval is.

cpDNS-diverzitás / PCR-RFLP / differenciálódás / reprezentativitás / genetikai távolságok

1 INTRODUCTION

Forest species, particularly wind pollinated species, exhibit a very effective gene flow. Unlike the patterns of nuclear DNA encoded alleles, maternal inheritance of the DNA of cell organelles maintain local patterns of allelic structure for long time periods (Mátyás 2002). Intraspecific chloroplast DNA (cpDNA) diversity is very effective in characterisation of population structures and in phylogeographic studies (Demesure et al 1996; Fineschi et al 2000). Organelle DNA markers are suitable for tracking of postglacial species migration routes (Petit et al 2002/b), for introgression or hybridisation testing, for kinship relations or descent analysis (Heinze 1998 in: Mátyás 2002).

Service tree (*Sorbus domestica)* is an insect pollinated and animal dispersed, rare species, and is of high interest both from silvicultural as well as from nature and gene conservation aspects. The natural distribution area of the species is concentrated on Southern Europe. Core areas are the Balkans and Appenines, eastern Spain and southern France (Rotach 2003). The easternmost occurrences are found on the Crimean peninsula and in Asia Minor. The northern boundary of natural occurrence is uncertain, because since the Roman period this species was repeatedly cultivated and dispersed for its fruits (Kausch Blecken von Schmeling 2000, Gyulai 2001). A contiguous distribution is present in southern Germany (Kausch Blecken von Schmeling 2000), Lower Austria (Klumpp – Kirisits1998) and in southern Slovakia (Kárpáti 1959/60, Paganová 2008).

In Hungary, the species is distributed mostly along the Hungarian Middle Mountains range and in South and West Transdanubia *(Figure 1).* The habitats are in mountainous regions, usually dry oak or scrub forests, rocky, open woodlands, but also forest margins, abandoned vineyards and fruit orchards.

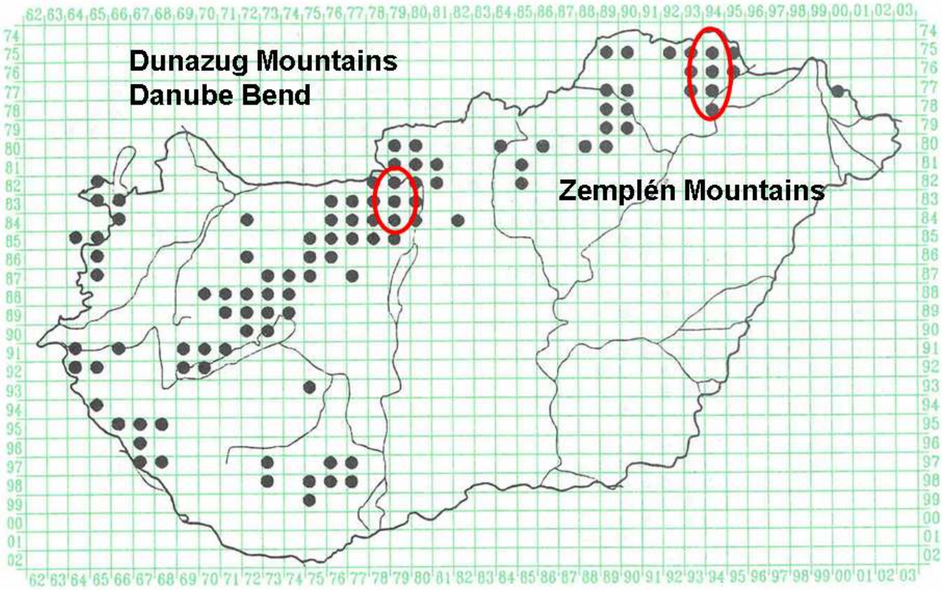

Figure 1. Natural distribution range of Sorbus domestica in Hungary (after Bartha – Mátyás 1995) and the location of the study areas

The occurrences in the last two habitat types reflect the human influence on distribution of the species. Gyulai (2001) states that archaeological findings (seeds, fruit residuals) prove that Roman Villa-farms had a highly developed fruit and winery culture in the Roman province of Pannonia (in present-day Hungary). Seed finds from the Migration Period, and finally the study of medieval wells in Buda castle confirm the historically continuous consumption of service tree fruits and the cultivation of the tree species. Rapaics (1940) considers the service tree (*S. domestica*) as indigenous in Hungary.

S. domestica has a certain economic potential if plant material of excellent genetic quality is used (Rotach 2003). However, in most regions of Central Europe, service tree is threatened, and is regarded as a valuable biological and plant genetic resource worth to be conserved.

2 MATERIAL AND METHODS

2.1 Plant material

Samples *(Table 1.)* were collected in the Zemplén Mountains (North-Eastern Hungary), and in the eastern part of the Dunazug Mountains (Danube Bend, north of Budapest). Fresh leaves were collected from trees, afterwards frozen and stored at -80°C. 196 individuals were sampled and analysed. In the Zemplén Mts. the service trees are mostly located in cultured or semi-cultured habitats: vineyards and extensively used village margins (Nyári 2002). In the Danube Bend *S. domestica* appears in some close-to-nature forest associations, while in the Buda Hills (western limits of Budapest) the species is considered as subspontaneous (Kárpáti 1959/60, Nyári 2003).

Table 1. Sampled service tree populations in the Zemplén Mountains (codes 1-5), and in the eastern part of Dunazug Mountains (codes 6-9). The coordinates of populations represent the means of individual tree coordinates

Code	Populations	Coordinates		Number of trees
		Longitude	Latitude	
1.	Hegyköz	48°31’ 6”	21°30’38”	28
2.	Kácsárd	48°23’26”	21°35’ 5”	17
3.	Hegyalja	48°15’54”	21°23’35”	43
4.	Tokaj	48° 9’51”	21°19’54”	15
5.	Meződűlő	48°27’39”	21°18’12”	9
6.	Buda Hills	47°34’12”	18°57’33”	11
7.	Szentendre	47°43’53”	19° 3’45”	30
8.	Visegrád	47°45’ 7”	18°56’19”	29
9.	Pilismarót	47°46’31”	18°51’ 5”	14

When defining the dividing borders of sampled populations in the two regions, first of all the reproduction biology of the species was considered. Therefore, the occurrences in larger groups or significant presence in contiguous landscapes (convergent valleys, coherent vine yards, basins) were defined as populations because of favourable geographical circumstances for gene flow.

2.2 DNA extraction, amplification and digestion

For extracting total DNA from frozen leaf samples the DNeasy® 96 Plant Kit (6) (QIAGEN, Hidden, Germany) was applied. The concentration and the quality of the extracted DNA was checked by 1.5% agarose gel electrophoresis with 1xTAE as running buffer (Sambrook et al. 1989).

The fragment length polymorphisms obtained by primer pairs, combined with restriction enzymes, allow the detailed study of intraspecific variability and investigation of putative relationships between sampled genotypes. The details of amplification and restriction digestion conditions are described in Dumolin – Lapégue et al. (1997) and Demesure (1999). Seven cpDNA primer pairs HK, KQ, DT, ST, VL, CS and SFM, described originally for *Sorbus torminalis* by Demesure (1999) were tested. Amplifed products of these primers were digested with the restriction enzymes Alu I, Dde I, EcoR I, Hae III, Hinf I, Mse I and ScrF I. The restriction fragments were separated by overall 4 hours of electrophoresis on 8% polyacrylamide gel (Dumolin – Lapégue et al. 1995). The analysed samples revealed at KQ digested by Mse I seven, and at KQ digested by Hinf I four polymorphic bands, enabling the description of different cpDNA haplotypes.

2.3 Data evaluation

Genetic structures were characterized by population genetic parameters derived with GSED (Gillet 1998-2010) and GenAlEx (Peakal and Smouse 2005). Distances among haplotypes were calculated with NTSYS 4.0 beta (Sinauer Assotiation 1998) represented by TreeView (Page 2001). For diversity analysis the programs HAPLONSTAT and HAPERMUT were utilised (Pons – Petit 1996).

The diversity parameter ν - which is usually applied for haplotype genetic interpretation and analysis - is defined as follows (Pons - Petit 1996):

$$\nu = \sum_{i,j} \pi_{ij} \times x_i \times y_j$$

where π_{ij} is the distance between haplotypes *i* and *j* and x_i and y_j are observed frequencies. '*h*' is calculated by ignoring the genetic distance of two haplotypes. The resulting coefficients of differentiation are defined as N_{ST} (based on ν), or G_{ST} (utilising *h* diversity).

The N_{ST} and G_{ST} values are directly comparable by using permutation analysis, and their difference can be tested against 0 (Burban et al, 1999). Accordingly, after 1000 repetitions, the N_{ST} value is recalculated. Afterwards it is assessed whether the new value after certain repetitions is larger than G_{ST} (one-tailed test).

The differentiation parameter D_j of a subpopulation *j* was obtained according to Gregorius and Roberds (1986):

$$D_j = d_0(p(j), \overline{p}(j)) = \frac{1}{2}\sum_{i=1}^{n} \left| p_i(j) - \overline{p}_i(j) \right|$$

Here $\overline{p}_i(j)$ describes the relative frequency of the *i*th allele among the pooled material of all included samples except the *j*th. Thus, D_j indicates whether sample *j* represents the complete set of samples (= relatively low value) or has a special genetic setup as compared to the other samples (= relatively high value).

The δ gives the mean of the differentiation parameters D_j, weighted with the proportions c_j of the different samples (Gregorius 1984):

$$\delta = \sum_{j=1}^{n} c_j \cdot D_j$$

The total population differentiation δ_T (Gregorius, 1987, 1988) quantifies the amount of genetic variation within a single sample:

$$\delta_T = \frac{N}{N-1}(1 - \sum_{k=1}^{n} p_k^2)$$

The genetic distance d_0 between subpopulations was calculated inter alia following Gregorius (1974) and Prevosti et al. (1975). It quantifies the proportion of genetic elements which the two subpopulations do not share.

$$d_0(i,j) = \frac{1}{2}\sum_{k=1}^{n}\left|p_{ik} - p_{jk}\right|$$

Here i and j denote the subpopulations and p_{ik} the relative frequency of the k^{th} type (allele, genotype) in subpopulation i. The genetic distances following Nei (1972) were calculated as well.

The value of smallest genetic difference $\Delta(s)$ is based on the consideration that it quantifies the change to be made in the frequency of the trait states in one population in order to match the frequency distribution of the second population, under the requirement that trait states be shifted to the most similar trait state possible. The minimum change in the sense of linear programming is relevant, taking into account the characteristics of the place of traits during optimization (smallest difference) through the application of the principle (Gillet et al. 2004). Therefore:

$$\Delta(s) = \sum_{a,b} s(a,b)d(a,b)$$

$$\Delta = \min_s \Delta(s)$$

3 RESULTS

Polymorphisms were observed by means of PCR-RFLPs. The primer pair KQ was used to amplify the non-coding region between trnK and trnQ of the chloroplast genome. The amplified fragment was digested with the restriction enzymes *Mse* I and *Hinf* I and visualised on polyacrylamid (PAA) gel. Eleven polymorphic restriction fragments were observed, classifying the 196 studied trees into 16 different haplotypes (*Figure 2, 3 and Table 2*).

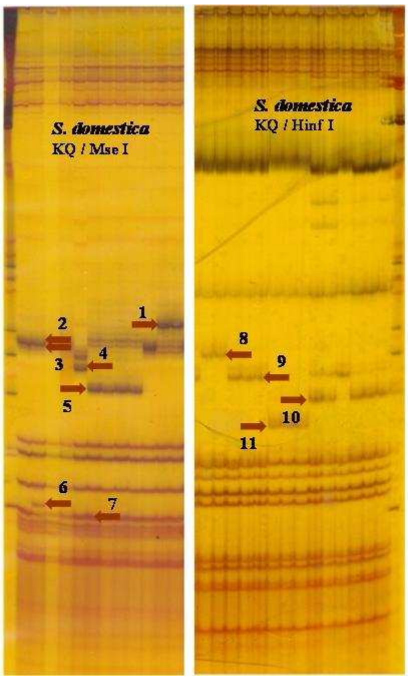

Figure 2. The RFLP restriction patterns of primer - enzyme combinations KQ - Mse I (1-7) and KQ – Hinf I (8-11) on PAA-gel. Arrows indicate the detected polymorphic bands/products.

The distances between haplotypes were calculated utilising the PAUP 4.0 beta program (Swofford 2002). From the resulting haplotype distance matrix a tree-stucture grouping without roots was constructed (Structural grouping unrooted option, program: TreeView, Page 2001). The resulting UPGMA diagram is shown in *Figure 3.*

Table 2. Presence (1) or absence (0) of the corresponding bands 1 to 11 of S. domestica cpDNA-haplotypes (I - XVI)

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
I	0	0	0	1	0	0	1	0	1	0	0
II	0	0	1	1	0	0	1	0	0	1	0
III	0	0	1	1	0	0	1	0	1	0	0
IV	0	0	1	1	0	0	1	1	1	0	0
V	0	1	0	0	1	0	1	0	0	1	0
VI	0	1	0	0	1	0	1	0	1	0	0
VII	0	1	0	0	1	0	1	1	0	0	0
VIII	0	1	1	0	0	0	0	0	1	0	0
IX	0	1	1	0	0	0	0	1	0	0	0
X	0	1	1	0	0	0	1	0	0	1	0
XI	0	1	1	0	0	0	1	1	0	0	0
XII	0	1	1	0	0	0	1	1	0	1	0
XIII	0	1	1	0	0	1	1	1	0	0	0
XIV	0	1	1	0	1	0	1	0	0	1	0
XV	0	1	1	0	1	0	1	0	0	1	1
XVI	1	1	1	0	0	0	1	0	0	0	0

3.1 Spatial distribution of cpDNA haplotypes

Haplotype “XI – Green” on the left upper arm of *Figure 3* is the generally distributed haplotype, prevalent in the Zemplén Mts. The haplotype was represented in 47% of the analysed samples. The “III – Blue” haplotype (on the upper right branch in *Figure 3*) represents 15% of the samples. The "V – Gray” haplotype on the lower right arm is present in 12% of the sampled specimens. The “III - Blue, V - Gray, XI – Green”, and “XIV – Pink” haplotypes were observed in both of the geographically distant regions.

Table 3. S. domestica cpDNA haplotypes in the studied populations (see Figure 3).

Haplotypes		*Population code*								
		1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*
I	Hatched light blue	0	0	0	0	0	0	0	2	0
II	Light blue	0	0	0	0	0	0	0	1	1
III	**Blue**	**2**	**0**	**0**	**0**	**0**	**1**	**15**	**9**	**2**
IV	Dark blue	0	0	0	0	0	0	2	0	0
V	**Gray**	**2**	**0**	**0**	**0**	**0**	**0**	**8**	**7**	**6**
VI	Yellow	0	0	0	0	0	0	0	0	1
VII	Orange	0	0	0	0	0	0	1	1	0
VIII	Black	0	0	0	0	0	0	0	1	0
IX	Hatched brown	0	0	0	0	0	0	0	1	0
X	Hatched pink	0	0	0	0	0	0	0	0	1
XI	**Green**	**21**	**17**	**27**	**8**	**6**	**4**	**3**	**7**	**0**
XII	Claret	0	0	1	0	0	0	0	0	0
XIII	Light green	2	0	3	3	1	0	0	0	0
XIV	Pink	0	0	3	0	0	4	1	0	3
XV	Red	1	0	9	4	2	0	0	0	0
XVI	Brown	0	0	0	0	0	2	0	0	0

Most populations include several (from 3 to 8) cpDNA haplotypes. The population of the vineyards of Kácsárd was fixed for a single haplotype which was common in other populations of the Zemplén mountains ("XI – Green"). The reason may be sought in the cultivation effect supporting the propagation of a single local haplotype (*Figure 4*). Comparing the regions, the characteristic "main" haplotypes are different (types "III – Blue" and "XI – Green" have an alternating dominance by region), or are typical for only one population. The Hegyalja, Tokaj and Meződűlő populations, as well as Hegyköz contain exclusive haplotypes which occur only in the eastern, Zemplén region ("XV – Red, XIII – Light Green").

A large number of otherwise rare haplotypes ("I – Hatched light blue; II – Light blue; IV – Dark blue; VI – Yellow; VII – Orange; VIII – Black; IX – Hatched brown; X – Hatched pink") were observed in three populations from the Danube Bend (Pilismarót, Visegrád, Szentendre: *Table 3*, *Figure 4*). The population Nr. 6 of Buda Hills contains haplotypes which are typical and dominant haplotypes for both regions ("III – Blue, XI – Green, XIV – Pink") and has a private haplotype ("XVI – Brown") as well.

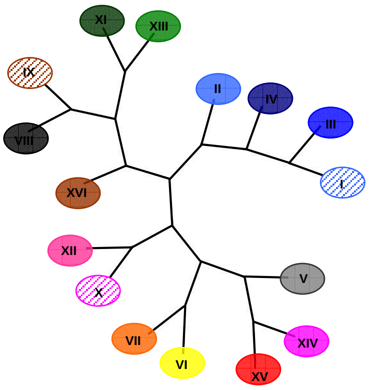

Figure 3. Unrooted UPGMA diagram of the service tree cpDNA-haplotypes (after Page 2001). The colours are corresponding to Figure 4.

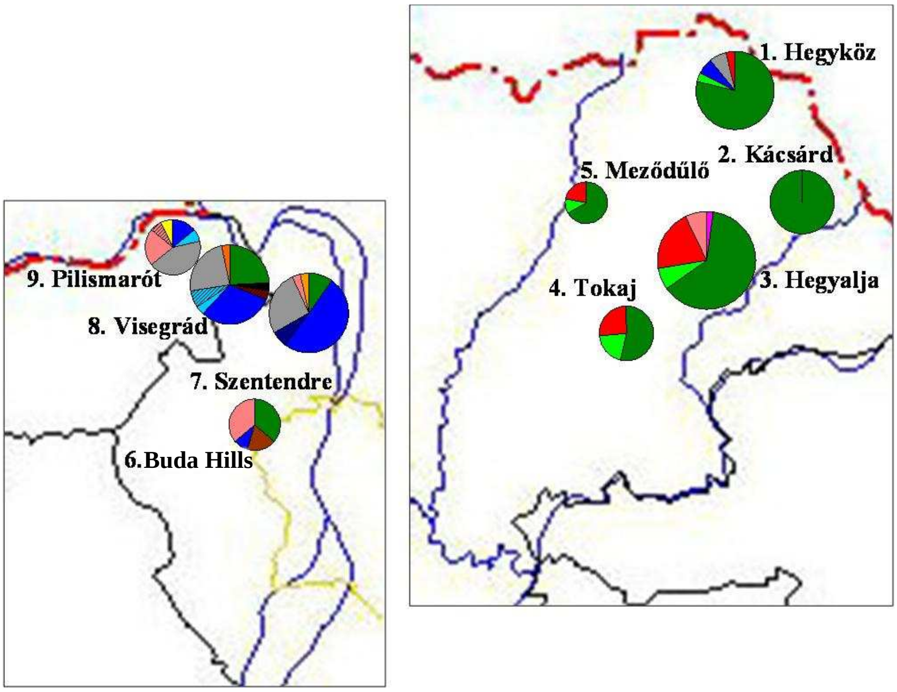

Figure 4. The spatial distribution of S. domestica cpDNA-haplotypes in the Dunazug (left) and Zemplén (right) Mountains. The circle diameters are relative to sample sizes

Considering the cpDNA-haplotype composition of the studied populations, it may be deduced that the populations dominantly indicate a mixed origin, containing numerous cpDNA haplotypes. Among these haplotypes, dominant and codominant or accompanying types are distinguishable within populations or regions. Typically, the main or dominant haplotype within a region could occupy the role of codominant haplotype in the other region.

Observed patterns of cpDNA diversity confirm the importance of endozoochorous seed dispersal and typical extinction/recolonisation dynamics. Results indicate considerable gene flow by seeds among populations within regions resulting in a high diversity within populations and sharing of haplotypes within the region, but very limited gene flow between the two regions.

An analysis of molecular variance revealed that 27% of the total variation is distributed between the two regions, 6% among populations within regions, and the remaining 67% within populations. Strong differentiation was observed between the two regions, with only 4 common haplotypes.

3.2 The cpDNA haplotype diversity and differentiation among populations

A major proportion of the total diversity (h_t = 0.752) is contributed by intrapopulation diversity (h_s = 0.583; *Table 4*). Total diversity (h_t) values are similar in the two regions (0.838 for Zemplén and 0.852 for Dunazug), however the intrapopulation differentiation is remarkably higher in the Dunazug than in the Zemplén populations (h_s = 0.761 vs. 0.678) due to other, private and rare haplotypes. The high intrapopulation differentiation indicates that a large number of mother plants participated in founding the populations.

The level of population subdivision using unordered and ordered alleles resulted G_{ST} = 0.225 and N_{ST} = 0.245, respectively, for the whole material. Analysing the two regions separately the values of population subdivision were less pronounced (*Table 4*). In the Zemplén region the G_{ST} value (0.191) was higher than N_{ST} (0.146) which is exceptional. The differences between N_{ST} and G_{ST} were not significant neither separately for the two regions, nor for all samples (U-test).

Table 4. Diversity and differentiation of S. domestica populations. Standard deviations are in parenthesis

Region	No. of populations (≥ 3 individuals)	Harmonic mean No. of individuals per populations	Number of haplotypes	h_s (standard error)	h_t (standard error)	G_{ST} (standard error)	vs (standard error)	vt (standard error)	N_{ST} (standard error)	U Nst/Gst test
Zemplén Mountains	5	21.11	9	0.678 (0.0763)	0.838 (0.0879)	0.191 (0.0135)	0.709 (0.0748)	0.830 (0.0345)	0.146 (0.1046)	-1.23 NS
Dunazug Mountains	4	17.38	13	0.761 (0.0269)	0.852 (0.0272)	0.106 (0.0303)	0.738 (0.0657)	0.858 (0.0472)	0.140 (0.0723)	0.43 NS
Overall	9	17.12	16	0.583 (0.0835)	0.752 (0.0831)	0.225 (0.0577)	0.569 (0.0932)	0.754 (0.1121)	0.245 (0.0497)	0.25 NS

NS: not significant

3.3 Genetic differentiation comparing the representativity of populations

If each service tree population is compared with the complementary material, representativity or presence of special types can be evaluated. The δ (average differentiation) value is quite high (0.51), which might be explained by the maternal inheritance, the geographical segregation, and the significant number of polymorphisms. The most representative population – including the largest number of haplotypes – is the Hegyköz population, followed by Meződűlő and by Hegyalja as well as Tokaj (*Figure 5*).

Table 5. Genetic differentiation among the S. domestica populations (Program: GSED, author: Gillet 1998-2010)

	1. Hegyköz	2. Kácsárd	3. Hegyalja	4. Tokaj	5. Meződűlő	6. Buda Hills	7. Szentendre	8. Visegrád	9. Pilismarót
C_j	0.143	0.087	0.219	0.077	0.046	0.056	0.153	0.148	0.071
D_j	0.351	0.575	0.431	0.431	0.417	0.508	0.686	0.531	0.714

C_j: differentiaton proportionally to sample sizes, D_j: differentiation versus the complementary material

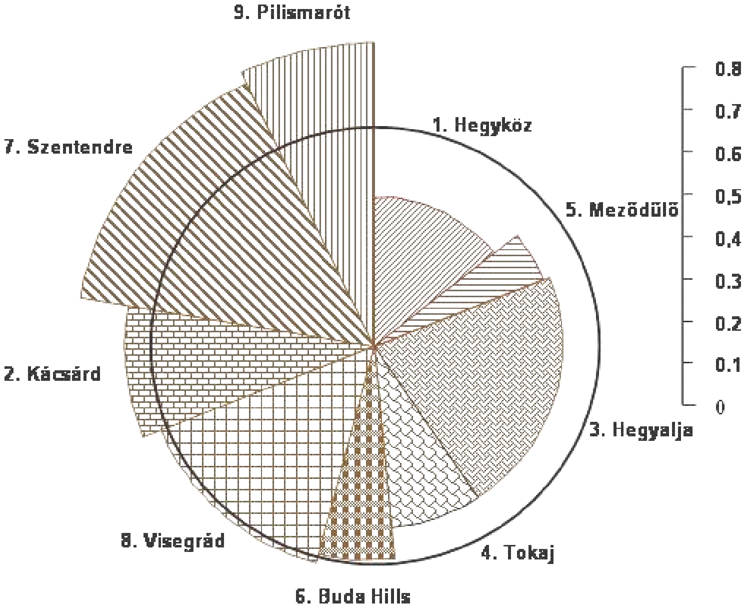

Figure 5. Genetic differentiation among populations based on cpDNA haplotypes after Gregorius and Roberds (1986). The circle displays the mean differentiation among populations (δ = 0.51)

According to the differentiation values, populations in Zemplén are more representative. Kácsárd, containing just one haplotype, is the exception. This locally cultivated cpDNA type is an autochthonous and well distributed haplotype in the Zemplén Mountains.

The differentiation of the Buda Hills population (D_j = 0.508) corresponds to the mean value among populations. It contains haplotypes commonly found in both regions and has a private haplotype: this is also reflected by the 'intermediate' position in the dendrogram (*Figure 8*).

The other populations in the Danube Bend (Visegrád, Szentendre, Pilismarót) north of Budapest, show only a lower representation (D_j > mean δ) caused by the appearance of 'new' and rare haplotypes (*Figure 5*).

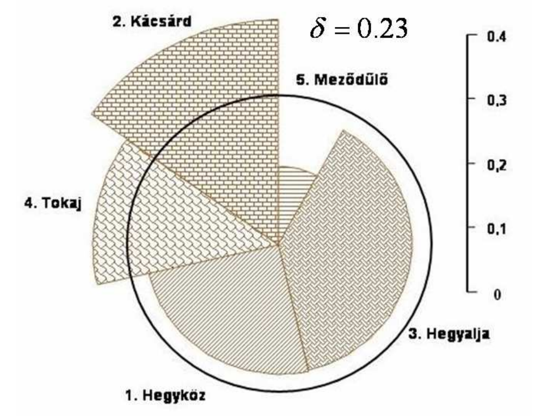

Figure 6. Genetic differentiation among the Zemplén Mts. populations (see Figure 5 for explanations)

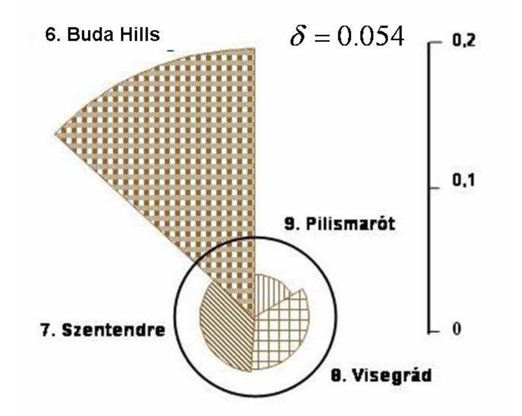

Figure 7. Genetic differentiation among the Dunazug Mts. populations.

When evaluating the Zemplén and Dunazug regions separately, the calculated mean differentiation values are lower ($\delta = 0.23$ and $\delta = 0.054$ respectively, *Figures 6 and 7*) compared to the pooled analysis. The reason is the regional separation regarding the main haplotypes (see *Figure 4*), which determines a relatively higher homogeneity within both regions. In the Zemplén Mountains the population of the vineyards of Kácsárd is the least representative due of its single haplotype. The populations of Hegyköz and Hegyalja with a large number of sampled trees and haplotypes have close to average differentiation (*Figure 6*). The Tokaj and Meződűlő display the same haplotypes but their proportion varies. This fact has a remarkable influence on the differentation calculation.

In the Dunazug region, the Buda Hills population is deviant and considerably increases the value of the average differentiation. The other populations have high representativity.

The mean differentiation values (δ) are analogous to the N_{ST} and G_{ST} population differentiation *(Table 4).*

3.4 Genetic distances among populations

Genetic distances among the 9 subpopulations were calculated according to Nei (1972), Gillet et al. (2004, smallest genetic difference), and Gregorius (1974) (software: GeneAlex /Peakall – Smouse 2006/ and GSED /Gillet 1998-2010/). When comparing the geographic and genetic distances, the Buda Hills population shows deviant values (underlined in *Table 6*).

The distances (after Gregorius 1974) are less in the eastern Zemplén region than in the Danube Bend region (*Table 6*).

The intermediate situation of the Buda Hills population was previously described: it includes main or typical haplotypes from both regions and is remarkably differentiated from the other, Danube Bend populations within the region (*Figure 7*). Based on the distances d_0 after Gregorius (1974), a cluster analysis of the analysed populations was executed (*Figure 8*). Within the SAHN (Sequential, Agglomerative, Hierarchical, Non-overlapping) classification the 'single linkage' method separates, based on the principle of minimum differences. The clustering using the single linkage method is clearly taking into consideration the geographic differentiation as well.

Table 6. Matrix of genetic distances (after Gregorius 1974) (left lower triangle) and geographic distances (right upper triangle) of the sampled populations

Geographic distance (km)

Hegyköz	Kácsárd	Hegyalja	Tokaj	Meződűlő	Buda Hills	Szentendre	Visegrád	Pilismarót	
—	15.227	29.488	41.572	16.573	*217.011*	*201.681*	*209.026*	*213.904*	Hegyköz
0.250	—	19.893	31.398	22.184	*215.666*	*201.259*	*209.035*	*214.263*	Kácsárd
0.267	0.372	—	12.119	22.761	*197.153*	*183.283*	*191.298*	*196.733*	Hegyalja
0.360	0.467	0.188	—	33.063	*188.885*	*175.710*	*183.983*	*189.638*	Tokaj
0.226	0.333	0.093	0.133	—	*200.520*	*185.121*	*192.454*	*197.334*	Meződűlő
0.565	*0.636*	*0.567*	*0.636*	*0.636*	—	19.551	20.291	24.208	Buda Hills
0.757	*0.900*	*0.867*	*0.900*	*0.900*	0.776	—	9.534	16.516	Szentendre
0.616	*0.759*	*0.759*	*0.759*	*0.759*	0.668	0.315	—	7.020	Visegrád
0.857	*1.000*	*0.930*	*1.000*	*1.000*	0.695	0.557	0.581	—	Pilismarót

Genetic distance

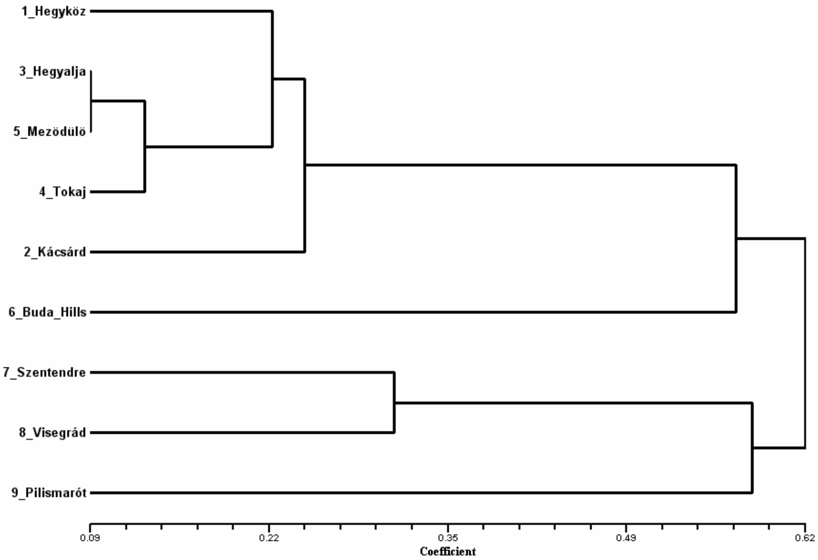

Figure 8. Single linkage dendrogram of nine S. domestica populations, based on the genetic distance d_0 after Gregorius (1974)

In our clustering, using the distances in *Table 6*, the Buda Hills was always grouped to the eastern region. It seems, that the Danube Bend populations constitute a distinctly different region regarding their haplotype composition.

4 DISCUSSION

The cpDNA analysis of this insect-pollinated, scattered species is well suited for gene flow analysis based on seed dispersal. The fruit has numerous consumers (especially thrush species) which transport the seed over greater distances and through the digestion process neutralise the effects of germination inhibitors which are in the fruit flesh (Yagihashi et al. 1998).

Oddou-Muratorio et al. (2001/c) distinguished 19 wild service tree (*S. torminalis*) haplotypes through Europe based on 7 cpDNS and 3 cpSSR primer pairs. Two main haplotypes were commonly occurring. In every population also minor or rare haplotypes were found.

In our study, regionally different major haplotypes and minor types occur as well in every analysed *S. domestica* population.

The G_{ST} values of *S. domestica* are extremely low: 0.106 (for the Dunazug region) < G_{ST} < 0.225 (for the two regions). Results for *S. torminalis* are similar: 0.13 < G_{ST} < 0.35 (Oddou-Muratorio et al. 2001/b, Oddou-Muratorio et al. 2001/c).

Wild service tree (*S. torminalis*) populations sampled over the eastern and south-eastern part of its range were studied with seven, presumably neutral nuclear microsatellite markers (Kučerová et al 2010). The differentiation level was relatively high (F_{ST} = 0.228), which comes close to our cpDNA results for a species with a fragmented occurrence at its limits.
Mohanty et al. (2002) found G_{ST} = 0.29 for the similarly insect pollinated and scattered *Prunus avium* among 23 European populations based on 16 described haplotypes.

These values appear to be lower than those for widely distributed social broadleaved species such as *Q. petraea*: G_{ST} = 0,82 (Dumolin-Lapegue et al. 1997); or G_{ST} = 0.835 (Petit et al. 2002); and *F. sylvatica*: G_{ST} = 0,83 (Demesure et al. 1996). The cpDNA markers show strong differentiation among social broadleaved populations and low levels of within population diversity. Conventional cpDNA primers shows for insect pollinated wild fruit species, that these populations are regularly fixed for numerous haplotypes. The presence of more – main and minor – haplotypes suggests numerous founders also through long distance seed dispersal.

The spatial distance between the two regions exceeds 200 km, therefore the structural differences between the Danube Bend area and Zemplén are remarkably high. The lack of additional or 'bridge' data between the two regions influences the evaluation and the interpretation as well. The reasons for the extraordinary structure of Buda Hill population could not be clarified undoubtedly, whether it is of natural origin or a product of human impact or cultivation. The influence of cultivation on the long distance dispersal is so far also not clear.

S. torminalis cpDNA results reveal, that a significant but slight geographical haplotype pattern was observable approximately up to a distance of 100 km (Oddou-Muratorio et al. 2001/a). The described cpDNA pattern was compared to isozyme-based (biparentally inherited and codominant) results, analysing the same plant material. Neither pollen nor seed dominated gene flow was clearly observable in the population structure of that species.

There are, however, countless examples for anthropogenous dispersal or cultivation effects on *Sorbus* species (Kárpáti 1959/60, Gräter 1996, 1997, Gyulai 2001). Kárpáti (1959/60) refers to Holuby's (1888) vascular flora description of Trencsén County. Trencsén[1] County is situated over the northern limit of service tree distribution. Holuby reported on centuries-old service trees. He explained: in case when accidentally detected seedlings were found in forests, which originated from seeds spread by birds, these were removed and planted at the edges of arable land. At the sites of abandoned orchards or vineyards, often established on forest clearings, these trees can still be found, putative remnants of transplanted specimens.

A very convincing example for local anthropogenous dispersal is the occurrence in the vineyards of Kácsárd, which belongs to the historic Tokaj-Hegyalja vine region. Here only the major and generally distributed ("XI – Green") haplotype was found.

Based on the communications of Boros (1944 in: Kárpáti 1959/60) the service tree in the Buda Hills is subspontaneous and distributed by birds from nearby forests. Our sampled trees in the Buda Hills are situated in private gardens, in former vineyards and in forested areas as well. Cultured habitats are in any case more frequent in the Buda Hills, than at other locations of the Danube Bend. On the other hand, occurrences in Zemplén are predominantly cultured habitats, but no exceptional or unique cpDNA haplotypes were found there.

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[1] Presently Trenčin, N-W Slovakia

5 CONCLUSIONS FOR CONSERVATION AND FORESTRY PRACTICE

Among the main species of the genus *Sorbus*, *S. domestica* requires more ex situ gene preservation, while for wild service tree (*S. torminalis*) in situ conservation methods seem sufficient for gene conservation, because this species is less endangered (Demesure 1997). In the present study genetically polymorphic populations containing unique haplotypes were detected, providing important information for forest management, gene conservation and nature protection activities of *S. domestica*.

The service tree remains rare in closed forests, and should be planted in forest edges, hedges or clearings for game food (Vancsura 1992). From the aspect of nature protection, it is important to monitor the seedling recruitment and development in regenerated stands, and where necessary, to plant artificially.

The described genetic inventory was the preparation for gene conservation breeding of *S. domestica* in both regions. Ex situ conservation measures, i.e. the planting of two grafted seed orchards for gene conservation is in preparation. The gene conservation units will represent all identified genotypes of the respective regions. Minimum 3 grafted ramets per genotype will be outplanted. The frequency of genotypes will vary according to phenotypic trait differences, following the principles of gene conservation breeding for different traits such as fruit, seed or trunk quality. The varying representation of different genotypes in the seed orchards will be based on the rating of reproductive contribution which was first applied in Hungary, in Scots pine breeding (Bánó et al. 1978).

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Parent Stand Growth Following Gap and Shelterwood Cutting in a Sessile Oak-Hornbeam Forest

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Abstract – In this paper, effects of uniform shelterwood cutting (SWC) and gap cutting (GC) on total volume and value increment of the parent stand, volume increment of individual sessile oak trees, as well as, on crown expansion of sessile oak are compared for the first five years of the regeneration period of an oak-hornbeam forest. The gaps were circular and of one tree height in diameter. During SWC, there were two harvesting occasions, on each of which 30% of the standing volume was removed. Total volume increment of the remaining sessile oak trees relative to the initial standing volume of sessile oak was approximately identical between the two methods. However, individual trees grew faster if applying SWC. Volume increment of sessile oak decreased with the distance from gap centres. Crowns expanded mostly southwards and westwards both in the cases of GC and SWC. Value increment of the parent stand did not differ considerably between the two methods.

crown expansion / gap cutting / *Quercus petraea* / shelterwood cutting / value increment / volume increment

Kivonat – Az anyaállomány növekedése ernyős felújítóvágás ill. lékvágás során gyertyános-kocsánytalan tölgyesben. Jelen tanulmányban gyertyános–tölgyesben végrehajtott lékvágásnak ill. egyenletes bontáson alapuló felújítóvágásnak az anyaállomány térfogat- és értéknövedékére, a kocsánytalan tölgy faegyedek térfogatnövedékére valamint a kocsánytalan tölgyek koronáinak növekedésére gyakorolt hatását hasonlítom össze a felújítás első öt évére vonatkozólag. A lékek kör alakúak, egy fahossznyi átmérőjűek voltak. Az ernyős felújítóvágás során az anyaállományt két alkalommal bontották meg, mindkét esetben az élőfakészlet 30%-át termelték ki. A kocsánytalan tölgy összesített térfogatnövedéke a kocsánytalan tölgy kiindulási élőfakészletéhez viszonyítva közel megegyezett a két felújítási módszer esetében. Egyenletes bontásnál azonban a kocsánytalan tölgy faegyedek gyorsabban növekedtek. A léktől távolodva a kocsánytalan tölgyfák térfogatnövedéke csökkent. Mindkét technológia alkalmazásakor a koronák leginkább déli ill. nyugati irányban nyúltak meg. Az anyaállomány értéknövedékét tekintve a kétféle eljárás nem különbözött számottevően.

ernyős felújítóvágás / értéknövedék / koronák növekedése / lékvágás / *Quercus petraea* / térfogatnövedék

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1 INTRODUCTION

One main tool of close-to-nature forestry is mimicking natural processes (Somogyi 2000, Gamborg – Larsen 2003). As temperate deciduous forests often regenerate themselves by spontaneous gap formation (Runkle 1989), it seems logical that gap cutting is one of the regeneration methods of close-to-nature forestry (Schütz 2002). However, the ecological and the economical advantages of gap cutting over the traditional uniform shelterwood system are not obvious and should be demonstrated in appropriate field trials.

Whereas shelterwood cutting of pedunculate (*Quercus robur*) and sessile oak (*Q. petraea*) stands has been practiced for a long time (e.g. Szappanos 1967a, 1969a, 1969b, Kelly 2002, Harmer et al. 2005, Harmer – Morgan 2007, Tobisch 2008), very little is known in such oak stands about spontaneous gap formation or the effects of gap cutting (Lüpke 1998, Nicolini et al. 2000, Bobiec 2007, Collet et al. 2008, Diaci et al. 2008).

Canopy closure plays a key role during natural regeneration. It influences the intensity and spatial pattern of light reaching the understory and affects soil water content (Szappanos 1967a, Bréda et al. 1995, Emborg 1998, Lüpke 1998, Ostrom 2005). For sessile oak seedlings, both light and soil moisture conditions are especially important. Although sessile oak is normally regarded as a light-demanding species (Krahl-Urban 1959 cit. Lüpke, 1998), its shade tolerance increases from northwest to southeast in Europe (Krahl-Urban 1959 cit. Kelly 2002). Therefore, under the Hungarian site conditions, survival of young seedlings is often limited by soil moisture (Magyar, 1933). It is also well-known that decreasing the canopy density during shelterwood cutting promotes weed proliferation in many sites and can lead to serious problems of sessile or pedunculate oak regeneration (Humphrey – Swaine 1997, Kelly 2002, Harmer et al. 2005, Harmer – Morgan 2007).

Although the structure of the canopy greatly influences the regeneration processes, as well as, crown size correlates with volume growth of the parent stand (Drobyshev et al. 2007), growth rate of sessile oak crowns has been rarely studied (Longuetaud et al. 2008). Sessile oak is known as a species the crown plasticity of which is very low at the age of regeneration (Szappanos 1967b) but no data is widely available on crown expansion during shelterwood or gap cutting.

Volume and value increment of sessile oak trees can be considerable even during the quite short regeneration period (lasting for maximum 10-15 years on Hungarian mesic sites) of shelterwood cutting (Szappanos 1967a, Götmark 2009) By contrast, effects of gap cutting on parent stand growth are not well-known. Based on some evidence (mainly from North America), it can be assumed that trees at the edge of gaps grow faster than those inside the closed stand (Poage – Peart 1993, Pedersen – Howard 2004). However, hardly any information is available about sessile oak in this context.

In this paper, some preliminary results of a comparative study of a sessile oak-hornbeam forest are presented. The following questions are addressed based on the first five years of the regeneration period:

1. How do shelterwood and gap cutting affect the volume and value increment of the parent stand?
2. How do size and shape of sessile oak crowns change in the shelterwood stand and at the edge of gaps?

2 MATERIALS AND METHODS

2.1 Study area

The study stand (47°42’N, 18°52’E) occurs at 470 m a.s.l. on a slight south-southwest-facing slope in Visegrádi Mountains, North-Hungary (*Figure 1*). The mean annual precipitation at the nearest meteorological station (Dobogókő, 699 m a.s.l.) is 790 mm of which 239 mm falls during the main growing period (i.e. from 1 May to 31 July). The mean annual temperature is 7.1 °C. The mean temperature of the warmest month (July) is 17.5 °C while the coldest one is January with a -4.1 °C mean.

The soil of the study stand was examined at sampling plot level (Tobisch 2009). According to these investigations, the soil is mainly of a transitional type between ranker and some brown forest soil (i.e. clay migration was noticeable but to a lower extent than in the case of brown forest soils) which is loamy and developed on andesite bedrock. The rootable depth varies between 60 cm and 75 cm. However, in one of the sampling plots, pseudogleyic brown forest soil with a rootable depth of 35 cm occurs (see the description of the sampling design). Although soil properties of this plot differed from those of the others, it was not excluded from the experiment because some useful information would have been lost if omitting this plot. Furthermore, it was possible to detect possible effects of differences in site conditions since data were evaluated at plot level.

The study stand was a sessile oak-hornbeam forest with sessile and turkey oak (*Quercus cerris*) in the upper layer and hornbeam (*Carpinus betulus*), as well as, European beech (*Fagus sylvatica*) in the lower layer. The stand was 82 years old in 2002, i.e. at the beginning of the experiment. The stand of the plots is described in details in the results section. The shrub layer was patchy and consisted mainly of *Crataegus monogyna* and *Carpinus betulus*. Characteristic type indicator species of the herb layer (sensu Majer 1963) were *Carex pilosa, Galium odoratum, Melica uniflora, Poa nemoralis*.

2.2 Experimental design, and the regeneration techniques studied

The study forest subcompartment was divided into two parts along a natural border (a little stream) and an artificial one (*Figure 1*). Five more or less circular gaps of 25-30 m in diameter (i.e. approximately one tree height) were cut in one part (hereinafter abbreviated as GC stand where GC refers to ‘gap cutting’) during the winter of 2002-2003. Distances between margins of neighbouring gaps were at least one tree height. The other part of the study area (hereinafter abbreviated as SWC stand where SWC refers to ’shelterwood cutting’) was evenly opened at the same time. Around one third of the trees (in respect of volume) of the SWC stand was removed. Here, a second cut was carried out with the same intensity as the first one during the winter of 2006-2007.

2.3 Sampling

Eight sampling plots of 55 m x 45 m in N-S and E-W direction, respectively, were distributed in the study area (*Figure 1*). Five of them were regenerated by gap cutting (hereinafter called GC plots), three of them were regenerated by shelterwood cutting (hereinafter called SWC plots). In the former case, gap centres were located approximately 5 m south to the plot centres. In this way stands at the north edge of the gaps in which sunlight penetrates most deeply and for the longest time (Mihók et al. 2005, Ritter et al. 2005) can be studied more thoroughly. All plots but No. 4 and 7 were fenced to study the effects of browsing on regeneration (data not published in this paper).

All trees of the parent stand of the eight plots were sampled on two occasions, after the vegetation period of 2002 and after that of 2007. In 2002, separate point maps of all trees of the sample plots were created by theodolite (Zeiss – DAHLTA 010A) and sonic distance measurer (SONIN Combo PRO). Furthermore, the longest horizontal crown radii of all trees were measured in direction of N, W, E and S. Moreover, two perpendicular diameters (dbh) of each tree were recorded. Height of one average tree of each 1 cm-wide diameter class was measured by standard hypsometer (Vertex III) in each plot to generate diameter-height curves for each species (if it was necessary due to the high number of trees).

In contrast to 2002, height of all trees was measured in 2007 since it was supposed that trees surrounding the gaps had not grown at the same speed. Furthermore, in GC plots, the crown radii of only trees directly at the edge of gaps were measured because crown expansion of trees inside the closed stands surrounding the gaps was assumed to be very low (Longuetaud et al. 2008).

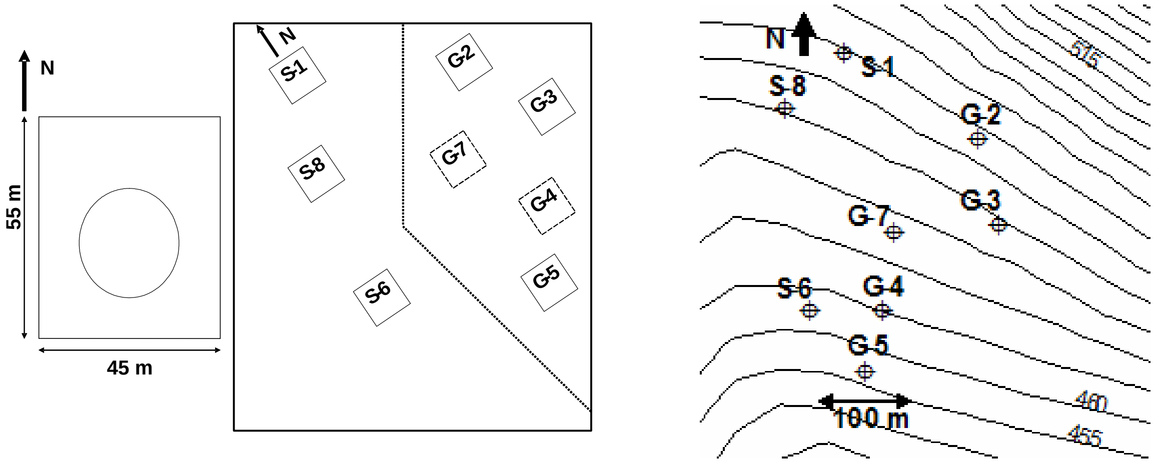

Figure 1. Experimental design. On the right side a schematic map of the study stand is shown with the six fenced (delineated by solid lines) and the two unfenced plots (delineated by broken lines) and a plot of gap cutting can be seen. The area of the gap is indicated by a circle. On the left side the real topographical position of the plots is indicated. G – plots of gap cutting; S – plots of shelterwood cutting; dotted lines – border-lines of the two regeneration methods. The numbers refer to plot numbers. Source of the topographical map: Hungarian Institute of Geodesy, Cartography and Remote Sensing.

Beside the two sampling occasions of the complete parent stands (i.e. all living trees), diameters of those trees which were cut in the winter of 2006-2007 (i.e. at the second cut of shelterwood cutting) had been measured after the vegetation period of 2006. Height of these trees was calculated from the diameter-height curves.

2.4 Data analysis

Data of each plot (except for those on crown expansions) were analyzed separately. Thus, the applied significance tests were performed pairwisely which means that every SWC plot was compared with every GC plot. In this way, possible effects of small-scale differences in site conditions or tree stand structure between the plots on parent stand growth could be revealed.

Diameter-height curves were created from diameter and height data of 2002 by natural logarithmic regression (Veperdi 2008) for each tree species per plot. These curves were then used to estimate the height of those individuals which were not measured directly.

Total above-ground volume of each tree was calculated for 2002 and 2007 using the Hungary-specific Király volume function (Király 1978). Volume of those trees which were cut in the winter of 2006-2007 was calculated by the same method for 2006. Total increment of the remaining trees of each species was examined at plot level for the first five years of the regeneration. Total increment of the remaining trees of a given species was divided by the total initial volume of all trees of that species and multiplied by 100. Thus, total increment of the remaining trees was expressed on a percent scale relative to the initial standing volume of the given species. Furthermore, total volume of the removed trees was studied by the same method.

Increment of the remaining sessile oak trees in absolute, as well as, in relative value was analyzed also for the first five years of the regeneration (individual-level analyses). The differences occurred in these types of increment were compared by single classification ANOVA-s. However, increment distributions were both non-normal and heteroscedastic therefore the classical F test of ANOVA cannot be used. Furthermore, it has been shown recently that even the non-parametric Kruskal-Wallis test assumes the equality of variances (Fagerland – Sandvik 2009). Thus, significance of the F statistic was checked by sampled randomization tests with 1000 resamplings (Sokal – Rohlf 2003, McDonald 2009). The randomization tests were performed by randomly permuting the assignment of observations to the groups (i.e. to the plots). The sizes of the groups were fixed.

Kendall's rank correlation coefficient was applied to analyze the relation between the distance from the gap centre in the four cardinal directions and the increment of sessile oak trees. If the correlation proved significant Kendall's robust line fit method was used to fit a regression line on the data.

Crown expansion of sessile oak trees was examined in two ways. On the one hand, SWC and GC plots were compared according to the expansions of crown quarters (N, E etc.). The applied method was the Kruskal-Wallis test because distributions of the expansions were non-normal but homoscedastic as indicated by Levene tests. On the other hand, trees of all plots were grouped according to the regeneration type, as well as, in the case of GC, according to the location (N, S, E, W) relative to the gaps. Thus, five groups (one group of SWC and four groups of GC) were distinguished. The expansions of crown quarters were then compared by groups using Wilcoxon's signed ranks tests. These tests were carried out as unplanned comparisons (every possible comparison was done). In this way, expansion of a crown quarter of a given tree was compared to that of the other three crown quarters of the same tree (paired comparisons, Sokal – Rohlf 2003). Due to the unplanned character of the tests, significance levels were modified according to the Bonferroni-Holm method (Sokal – Rohlf 2003). It should be noted that by the Bonferroni-Holm method, significance tests become conservative which means that the power (the probability of rejecting the null hypothesis when it is false) of the tests decrease. Thus, the null hypothesis is accepted too often. However, there were no reasons to make *a priori* decided (planned) comparisons.

Value increment of the parent stand was analyzed using the mean market values (without VAT) of the local forestry practice in 2008 (*Table 1*). Harvesting costs and selling revenues apply to net volume which was calculated as 80% of the total above-ground volume following the local forestry practice. 30% of the harvested sessile oak wood was considered as industrial wood while the remaining 70% was regarded as firewood following the local practice again. 100% of the harvested wood of other species was considered as firewood.

Table 1. Costs and revenues by forestry operation used for economical calculations. The applied exchange rate (as of November 2008) was 1 EUR to 260 HUF.

Forestry operation	Costs/revenues (EUR/m^3)
harvesting	11.54
revenue from selling industrial timber	84.62
revenue from selling firewood	50.00

Value of all living trees was calculated for the initial stage of the regeneration ($value_i$) and for the fifth year of that ($value_f$) from the revenues and costs of wood harvesting and selling (*Table 1*). Furthermore, value of the removed trees ($value_r$) was calculated by the same method. Value increment (I_v) of the parent stand referring to the first five years of the regeneration was then expressed as interest from the following equation:

$$I_v = \left[\frac{\left(value_f + value_r \right) - value_i}{value_i} \right] * 100$$

Data were evaluated by the BIOMSTAT 3.3 (2002) program.

3 RESULTS

3.1 Standing volume at the initial stage and volume of the removed trees

Tree stand structure of the plots was diverse at the initial stage of the experiment (*Figure 2*). Volume of the removed sessile oak trees varied between 20% to 56% in the SWC plots whereas almost all trees of the associated species were cut from here during the first five years of the regeneration (note that some beech trees were removed only on the second harvesting occasion, thus due to their increments, volume of the removed trees was higher than 100% in plot No. 1; *Figure 3*). 20-30% of sessile oak and the same amount of turkey oak were cut in most GC plots. In plots No. 2 and 3, 40% of hornbeam while in plots No. 4 and 7 20% of that was removed.

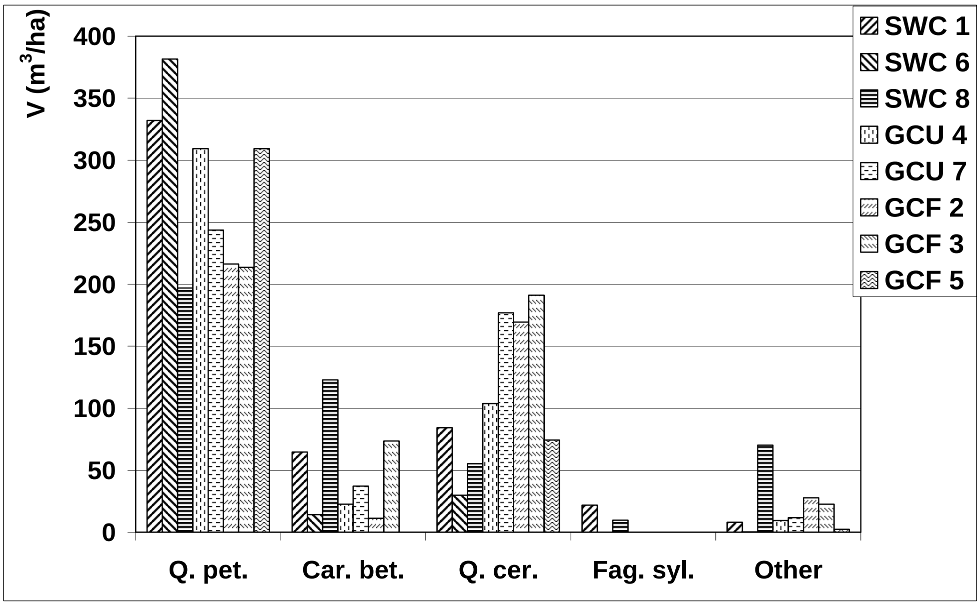

Figure 2. Initial standing volume of tree species. The numbers refer to plot numbers. SWC – plots of shelterwood cutting; GCU – unfenced plots of gap cutting; GCF – fenced plots of gap cutting; Q. pet. – Quercus petraea; Car. bet. – Carpinus betulus; Q. cer. – Quercus cerris. Fag. syl. – Fagus sylvatica.

3.2 Volume increment

Total increment of the remaining sessile oak trees relative to the initial standing volume of sessile oak was approximately identical, 7–9% in most of the plots (plot-level analyses, *Figure 4*). The only exception is plot No. 8 in which it was higher, 12%. However, considering the absolute, as well as, the relative increment values, sessile oak trees grew significantly faster ($p \leq 0.01$ and $p \leq 0.05$, respectively, in all the 15 possible cases) in SWC plots according to the pairwise randomization tests (individual-level analyses, *Figure 5*).

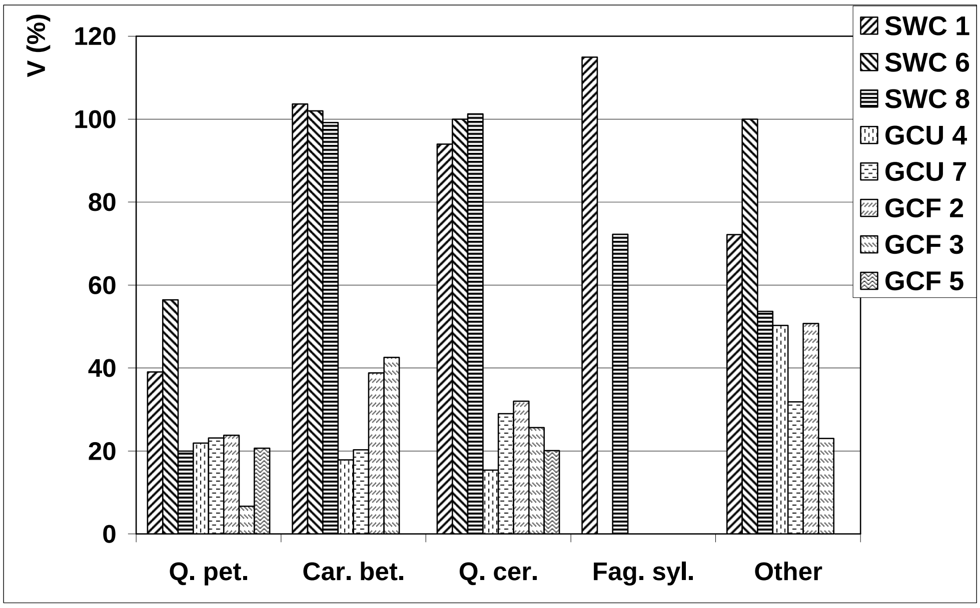

Figure 3. Volume of the removed trees by species relative to the initial standing volume of the given species during the first five years of the regeneration. For abbreviations see Figure 2.

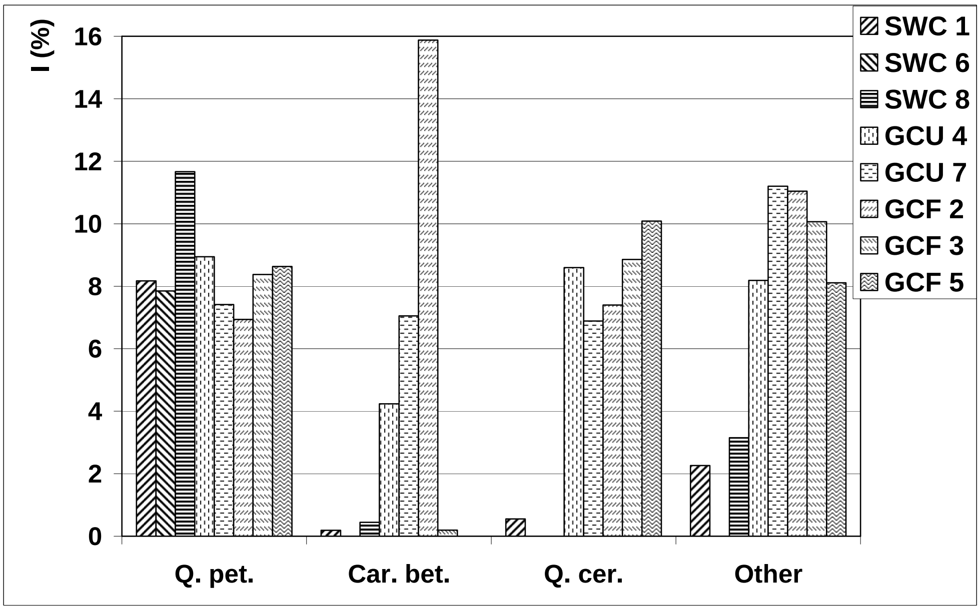

Figure 4. Total increment of the remaining trees by species relative to the initial standing volume of the given species during the first five years of the regeneration (plot-level analyses). For abbreviations see Figure 2.

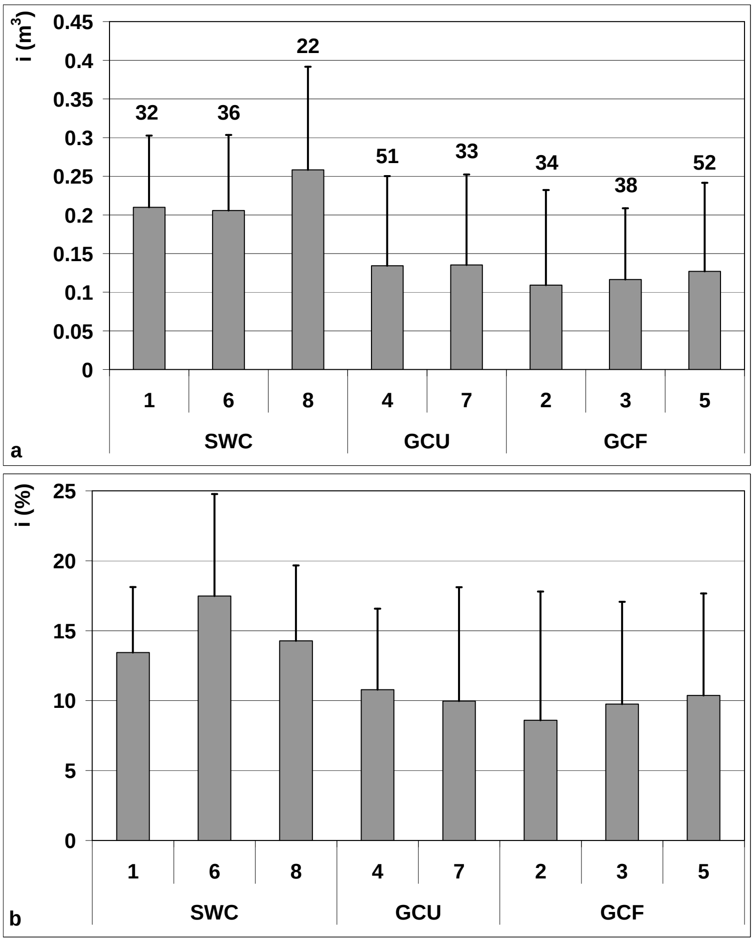

Figure 5. Increment (i) of the remaining sessile oak tress in absolute (a) and in relative value (b) during the first five years of the regeneration (individual-level analyses). Standard deviations are indicated by whiskers above which observation numbers are shown on Figure 5a. For abbreviations see Figure 2.

In GC plots, significant negative correlations were found between distance from gap-centre and growth of sessile oak trees mainly northwards (in three out of the five possible cases; *Table 2*). In addition, the correlation was significant eastwards (in two cases) and westwards (in one case). Increment of those trees, which were located farther away than 30–35 m from the centre of the gaps was usually lower than 0.1 m^3 (*Figure 6*). Increment of turkey oak was similar to (or, in plot No. 5, somewhat higher than) that of sessile oak in GC plots (*Figure 4*). Growth of hornbeam and the other associated tree species was very diverse, no regularity could be found in that issue.

Table 2. Kendall's rank correlation coefficients (τ) between increment of sessile oak trees and distance from the gap centres in the four cardinal directions.

	N		E		S		W	
	τ	n	τ	n	τ	n	τ	n
GCF 2	–0.35*	16	–	3	0.17	9	–0.33	6
GCF 3	–0.49*	15	0.02	11	0	4	–0.29	8
GCF 5	–0.02	20	–0.62*	7	–0.6	5	–0.32*	20
GCU 4	–0.16	23	0.07	10	–0.07	6	–0.06	12
GCU 7	–0.35*	15	–0.87*	6	0.71	7	-0.2	5

Kendall's robust lines corresponding to the significant correlations (*; p ≤ 0.05) are shown on *Figure 6*. Abbreviations are given at *Figure 2*.

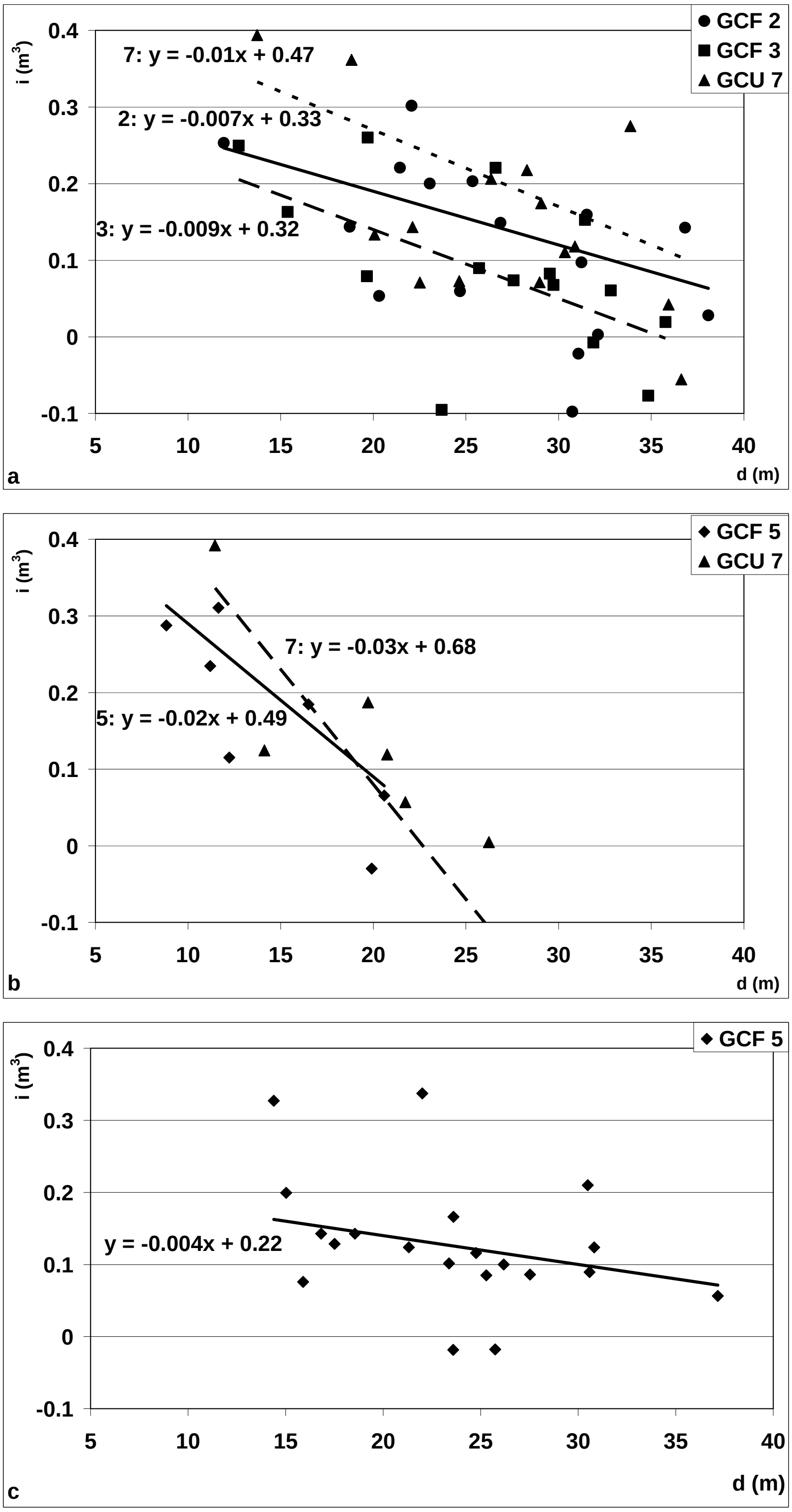

Figure 6. Kendall's robust lines for the significantly negative correlations between distance from the gap centres (d) and increment of sessile oak trees (i) northwards (Figure 6a), eastwards (Figure 6b) and westwards (Figure 6c). The negative increment values are consequences of crown breaks or measurement errors. Equations of the robust lines are shown on the diagrams with the corresponding plot numbers. For abbreviations see Figure 2.

3.3 Crown expansion of sessile oak trees

Results of the Kruskal-Wallis tests (*Table 3a*) do not prove that SWC and GC affect crown growth differently. The differences are often not significant and no clear trend can be recognized even in the significant differences.

Sessile oak crowns expanded mainly southwards and westwards in the SWC plots. The expansion was often considerable (even several meters as indicated by the standard deviations; *Table 3b*). Effects of the gaps on crown expansions are not always obvious if considering the location of the oak trees relative to the gaps (*Table 3b*). The expansion of many crowns was the highest not towards the gaps but southwards again (even by up to 5.5 m) though the differences between the expansions of crown quarters were not always significant.

Table 3a. Crown expansions (ce) of sessile oak trees in the four cardinal directions.

	ce (m)				n
	N	E	S	W	
SWC 1	0.0 (0.9)	0.4 (1.0)	2.2 (1.0)	1.7 (0.7)	32
SWC 6	0.1 (0.8)	0.7 (1.3)	2.3 (0.8)	1.1 (0.8)	36
SWC 8	0.4 (0.9)	1.0 (0.8)	1.8 (1.6)	0.9 (0.6)	23
GCU 4	0.5 (0.9)^{1}	1.0 (0.8)	1.9 (1.1)	1.2 (0.9)	16
GCU 7	0.5 (1.0)	1.3 (1.1)^{1}	2.2 (2.3)	–0.3 (0.9)^{1,6,8}	9
GCF 2	0.2 (1.0)	0.3 (0.7)^{8}	1.3 (0.9)^{1,6,8}	1.5 (0.8)^{8}	14
GCF 3	0.4 (1.0)	0.8 (0.9)	1.5 (1.5)^{6}	0.3 (1.3)^{1}	10
GCF 5	1.0 (0.5)^{1,6,8}	–0.3 (1.4)^{6,8}	1.3 (1.0)^{1,6,8}	1.5 (0.6)^{8}	12

Table 3b. Crown expansions (ce) of sessile oak trees at different positions relative to the gaps and in the SWC plots in the four cardinal directions.

Position	ce (m)				n
	N	E	S	W	
N	0.6 (1.0)^{a}	0.9 (1.2)^{a}	1.8 (1.3)^{b}	1.0 (1.3)^{a,b}	24
E	0.3 (0.9)^{a}	0.4 (1.3)^{a}	1.7 (1.0)^{b}	1.0 (1.0)^{a,b}	14
S	0.3 (0.6)	0.4 (0.8)	1.3 (1.4)	0.8 (1.0)	10
W	0.9 (0.9)	0.4 (0.8)	1.5 (1.7)	1.1 (0.9)	13
SWC	0.2 (0.9)^{a}	0.7 (1.1)^{b}	2.1 (1.1)^{c}	1.2 (0.8)^{d}	91

Standard deviations are shown in parentheses. The numbers in the upper index of cell values of *Table 3a* indicate the numbers of those SWC plots from which the given GC plot is significantly different ($p \leq 0.05$). In *Table 3b*, mean values of significantly different crown expansions are marked with different letters in the upper index (comparisons were carried out by positions). For abbreviations see *Figure 2*.

3.4 Value increment

There were no substantial differences in value increment of the parent stand between the plots of the two regeneration methods (*Figure 7*). Value increment of plots No. 4, 5 and 6 was slightly higher than that of the other plots.

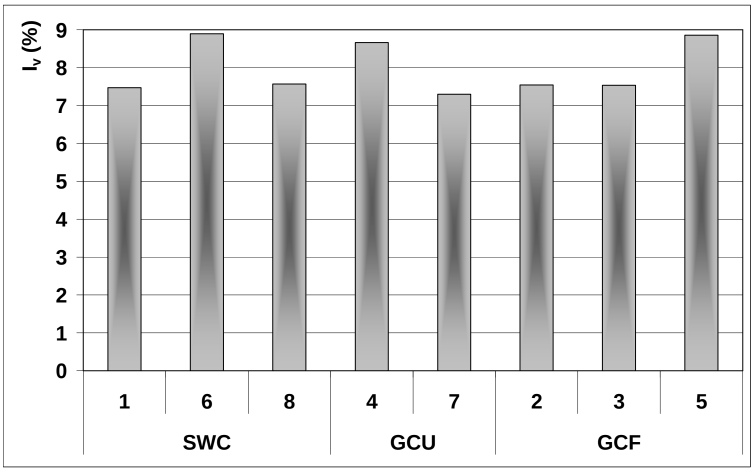

Figure 7. Relative value increment (I_v) of the tree stand. For abbreviations see Figure 2.

4 DISCUSSION

4.1 Volume increment

Although total increment of the remaining sessile oak trees relative to the initial standing volume of sessile oak was approximately identical in most plots, the same amount of increment was produced by relatively much fewer trees in two SWC plots (No. 1 and 6; *Figure 3*). Furthermore, volume of the removed sessile oak trees in plot No. 8 was similar to that in the GC plots but relative total increment of sessile oak was higher in the former (*Figure 4*). These results indicate that in the SWC plots individual trees had larger increments in absolute value than those surrounding the gaps, as it was proved by the pairwise randomization tests. The explanation of the higher plot-level increment of sessile oak in plot No. 8 compared to the other SWC plots is the fact that relatively more trees remained (volume of the removed trees was smaller) in plot No. 8 than in the other SWC plots.

The higher absolute increment of sessile oak following SWC could be explained by two distinct reasons. On the one hand, it would be possible that trees grew really relatively faster due to the reduced competition occurred in the tree stand. On the other hand, it could also be assumed that the differences between SWC and GC plots are only results of artificial selection of the larger trees in the former case. That is, all trees were removed from gap areas and all of them remained in the stand nearby the gaps irrespectively of their size when applying GC, whereas with SWC, trees were selected according to their attributes, including size as well. Therefore, even if the larger trees of the evenly opened plots had grown relatively similarly to trees surrounding the gaps, their increments would have been larger in absolute value. However, the results of pairwise tests on relative increment values disprove this assumption. Moreover, it can be stated that differences in soil properties did not influence the character of differences in effects of the regeneration methods. That is, the contrasts between SWC and GC plots were of the same nature independently from the unique site conditions of plot No. 8.

Presumably, the significant decreases of increment of sessile oak trees northwards and eastwards from the gaps are related to crown expansions (Drobyshev et al. 2007). The crown of these trees grew southwards to a significantly greater extent than eastwards and northwards. The southwards growth of crowns seems to be the most advantageous for sessile oak trees (see below).

Apart from the asymmetric expansions, differences in illumination of crowns could also influence the spatial pattern of volume increment of sessile oak trees surrounding the gaps. Crowns of trees north to the gaps were illuminated by direct sunshine for the longest time, whereas those of trees south to the gaps were shaded mostly by the closed stand nearby (see Mihók et al. 2005 and Ritter et al 2005). That can be the reason for the phenomenon that the most frequent direction in which increment of sessile oak trees significantly decreased was north, whereas the opposite was true for south. Consequently, the results indicate that growth of the assimilating surface of sessile oak can mostly be facilitated by cutting elliptical gaps with the long axis oriented E-W (on south-facing slopes). However, increase of the assimilating surface is obviously not the primary goal of regeneration. Several other factors must be taken into consideration (e.g. seedling mortality, seedling growth, wood quality of the parent trees etc.).

4.2 Crown expansion of sessile oak

Crown expansions in the SWC plots show that southwards growth of crowns was the most advantageous for sessile oak trees. Again, the results were independent from soil differences between the plots. The asymmetric crown expansion can be caused by the extra high solar energy which the south part of the crowns gained (Péczely 1998). This effect was further facilitated by the S-SW aspect of the slope on which the stand can be found since the intensity of light received by the south part of the crowns became even higher.

It is not so clear, however, why west crown parts grew significantly faster (horizontally) than east parts following SWC. One possible explanation is that the angle of incidence of west light on west crown parts is smaller (i.e. the amount of solar energy per unit surface area is higher) than that of east light on east crown parts due to the southwest aspect. Another reason can be that light of warm afternoons may be more advantageous to the photosynthesis of sessile oak than that of cooler mornings. However, this assumption is very difficult to verify since photosynthesis is influenced by many factors simultaneously (Kramer – Kozlowski 1979 cit. Collet et al. 1998).

The results show that SWC and GC do not affect crown growth differently if considering trees at the edge of gaps and if overlooking the location of those trees relative to the gaps. However, in the case of GC, crowns are expected to expand towards (over) the gaps to gain more light (Muth – Bazzaz 2002). The present study disproves this assumption.

Although expansion of crown quarters of trees west and south to the gaps was not significantly different, growth rate of these crowns was highest southwards, similarly to that of crowns of trees at the two other locations. Considering also the fact that by the Bonferroni-Holm method significance tests become rather conservative, it can be supposed that irrespectively of the position of the trees relative to the gaps, crowns grew more or less alike. Thus, effects of angle of incidence of sunlight and those of Sun moving on crown expansion of sessile oak seem to be stronger than gap effects.

Despite the stand age, sessile oak crowns were rather plastic. Therefore, the results contradict the widespread theory that, after the age of selective thinnings, crown plasticity of sessile oak decreases greatly (Szappanos 1967b).

4.3 Value increment

Value increment of the parent GC stand was considerably influenced by the associated tree species. Although sessile oak trees grew significantly faster and volume of the removed trees was much higher in the SWC plots, increment of the associated tree species was higher in the stands nearby the gaps. The reason for this phenomenon is not only the differences between the initial tree stand structures of the plots but mainly the fact that fewer trees of the associated species were cut from the GC plots than from the evenly opened stands (*Figure 3*). Therefore, growth of the associated tree species could balance the value increment between the two regeneration methods. The unique soil properties of plot No. 8 did not cause any differences in value increment between the SWC plots.

The reason for the phenomenon that the value increment of plots No. 4, 5 and 6 was higher than the average is the tree stand structure of these plots. That is, initial sessile oak volume in these plots was higher than the average and sessile oak was the only species in the study forest which produced industrial wood. Despite the high initial sessile oak volume of plot No. 1, the value increment of this plot was lower than that of the three other plots rich in sessile oak. The difference between plot No. 1 and the others is that individuals of the associated tree species were cut to a great extent from the former plot while in two of the latter plots (No. 5 and 6) hardly any individuals of the associated tree species could be found at the beginning of the experiment or in the third plot (No. 4) they were not removed to such a great extent. These results suggest that the initial structure of the tree layers modified slightly the value increment both in the cases of SWC and GC. However, these modification effects did not cause any substantial differences between the two regeneration methods.

4.4 Additional considerations

Gap cutting should also be examined in long-term because wood quality of sessile oak trees located directly at gap edges can be greatly reduced by epicormic branches since their stems are exposed to direct sunshine. This question is of high importance since these are the trees, the volume increment of which is the largest. With uniform SWC, epicormic branch development is a less serious problem because due to shading by the neighbouring trees and to the short regeneration period, it does not decrease wood quality considerably (Szappanos 1967a, Papp 1983 see also Johnson et al. 1998).

Another important issue in connection with gap cutting is the spatial distribution of gaps. The present study shows that increment of trees far away from the gaps can be much lower than that of trees at gap edges. Thus, increment at stand level strongly depends on gap distribution. The results point out that if between-gap distances are larger than one tree height (~ 30 m), volume and value increment at stand level are smaller with the applied GC than with the applied SWC until the third (final) cut of the latter one. However, regeneration period of the stand is longer in the former case, which means that trees have more time to grow. Further long-term research is needed to evaluate the effects of the gap cutting system on parent stand growth at stand level.

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Water Balance Study of a Groundwater-dependent Oak Forest

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Abstract – The objectives of this study were (1) to estimate the water balance components of an oak stand by calibrating a Hydrus 1-D model, (2) to determine the groundwater consumption by the water table fluctuation method and (3) to compare the results of the modelling with a remote-sensing based estimation.

Model simulation described the observed soil moisture and groundwater level relatively well, the root mean square errors varied between 12.0 and 14.9% for the soil moisture measurements and 5.0% for the groundwater level. Groundwater consumption was estimated also by the water table fluctuation method, which provided slightly different groundwater consumption rates than estimated by the Hydrus model simulation. The simulated evapotranspiration was compared with results of a remote-sensing based estimation using the surface temperature database of MODIS.

According to the Hydrus model, the estimated evapotranspiration resulted from transpiration (73%), interception loss (23%) and soil surface evaporation (4%) in the two-year study period. The proportion of groundwater consumption was 58% of the total transpiration. During the dry growing season of 2007 the groundwater consumption was significant with 66% of the total transpiration. Water supply from groundwater was found to be less important in the wet growing season of 2008 with 50%. The remote-sensing based estimation of evapotranspiration was about 4% lower than the model based results of nearby comparable sites.

groundwater / evapotranspiration / hydrus 1-D

Kivonat – Egy tölgyes vízforgalmi vizsgálata. A jelen tanulmány célja (1) egy kocsányos tölgyes állomány vízforgalmi komponenseinek becslése egy numerikus modell (Hydrus 1-D) alkalmazásával (2) a két felszín talajvízfogyasztásának becslése a talajvíz fluktuáció módszerének segítségével és (3) a modellezett evapotranszspiráció összehasonlítása egy távérzékelési módszeren alapuló párolgás eredményével.

A modell szimuláció jól követte a megfigyelt talajnedvesség- és talajvízszint értékeket. A talajnedvesség átlagos négyzetes gyök eltérése (RMSE) 12.0 és 14.9% között változott, míg a talajvízszint esetén 5.0% körüli érték volt jellemző. A talajvíz-fluktuáció módszerével becsült talajvíz-fogyasztás kissé eltérő értékeket szolgáltatott a Hydrus modell eredményénél. A vegetációs idejű evapotranszspiráció összegeket összehasonlítottam a MODIS felszínhőmérsékleti adatbázis felhasználásával becsült párolgás értékeivel.

A modell eredmények szerint a teljes vizsgált időszakban (2007.04.01–2009.03.31.) az evapotranszspiráció mintegy 73%-a származott növényi párologtatásból, 23%-a intercepciós párolgásból és mindössze 4%-a talajfelszín párolgásból. A talajvíz-fogyasztás a teljes transzspiráció 58%-a volt. A 2008-as vegetációs időszakban a talajvíz-fogyasztás aránya (50%) lényegesen kisebb volt a 2007-ben becsültnek (66%), mivel a csapadékos időszakokban az intercepciós veszteség és a telítetlen zóna párolgása dominált. A modell által becsült evapotranszspiráció 4%-kal volt kisebb a hasonló mintaterületeken – MODIS felszínhőmérséklet alapján – becsült értéknél.

talajvíz / párolgás / hydrus 1-D

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1 INTRODUCTION

In recent years, knowledge about the amount of recharge to the groundwater has become an important issue because groundwater has become a scarce resource in some areas. Changes of the vegetation cover, e.g. afforestation may be one of the factors, influencing the long-term changes of groundwater levels e.g. in the Hungarian Great Plain.

The vegetation cover influences significantly the interception loss, the transpiration and consequently the groundwater recharge. Interception loss is considerably higher at forested sites, compared to herbaceous vegetation due to higher leaf area index and much higher atmospheric conductance over forests (McMillan – Burgy 1960).

Evapotranspiration from forest is considerably larger than from any other crop or grassland and the amount of water left for groundwater recharge is relatively low. Gácsi (2000) found that deep recharge was significantly greater under bare soil than under a scotch pine forest on sandy soil in Hungarian Great Plain. Local studies of water balance of forests and other vegetation covers have found mainly that the forests have higher water consumption (Major 1990, Ladekarl et al. 2005, Nachabe et al. 2005, Schilling 2007), whilst some studies have demonstrated little difference in water consumption of different vegetation covers (Járó – Sitkey 1995, Roberts – Rosier 2005).

The present study intends to determine the water balance components of an oak stand on sandy soil in North-East Hungary to obtain actual evapotranspiration, calibrated with a Hydrus 1-D model by soil moisture and groundwater level measurements. Groundwater consumption was estimated also by the water table fluctuation method. The simulated evapotranspiration was compared with results of a remote-sensing based estimation using the surface temperature database of MODIS.

2 MATERIALS AND METHODS

2.1 Study area

The study area is located in the North-East part of the Hungarian Great Plain *(Figure 1)*, characterized by sand dunes, built up from river deposits during the early Pleistocene (Borsy et al. 1981).

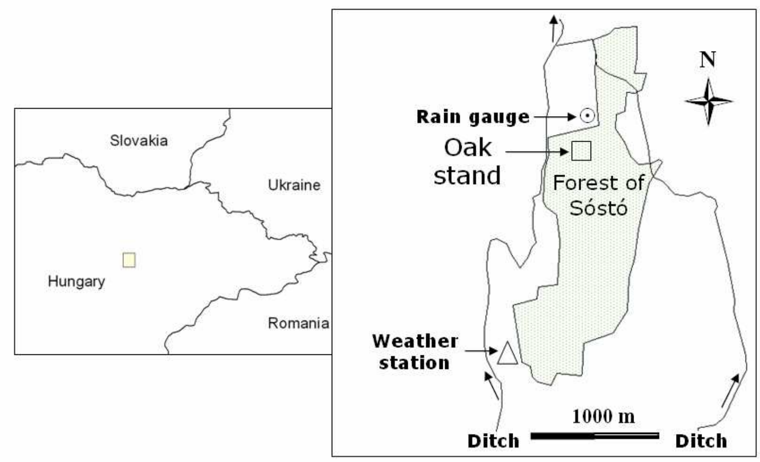


Figure 1. Location of the study site

The climate is continental, the mean annual precipitation (1951–2000) is approximately 520 mm and mean monthly temperature (1951–2000) ranges from –2.4°C in January to 20.5°C in July. The original vegetation was dominated by pedunculate oak (*Quercus robur*).

Much of these forests have been cleared and transformed into pasture and agricultural fields. The stand has a slope of less than 2‰ with no sign of surface runoff.

The stand is located at the discharge part of the local groundwater flow system, characterized by shallow groundwater depth and groundwater inflow. The groundwater level apparently did not responded to the water table changes of the nearby (distance: 300 m) ditches.

The stand is situated in the northern part of a native forested area, which was naturally regenerated in the 50s of the last century. The forest is a mixed stand of pedunculate oak (*Quercus robur*), sycamore maple (*Acer pseudoplatanus*) and black locust (*Robinia pseudoacacia*). The trees are 20–25 m high and the stand density is about 270 trees/ha.

The vertical distribution of the root density was determined by taking three replicate volumetric soil core samples from six different depths (0–0.2 m, 0.2–0.4 m, 0.4–0.6 m, 0.6–0.8 m, 0.8–1.0 m and 1.0–1.2 m). Fine roots (diameter < 2 mm), responsible for most of the water uptake, were separated by sieving the soil core samples. Fine root length decreased approximately linearly with depth and below 1 m of soil depth only little amount of fine roots were found. Root depth was estimated approximately 1.5 m, considering deeper penetrating roots below the trunks.

The particle size distribution of the soil profiles was determined by sieving and hydrometer analyses of samples, taken at 0.2 m intervals down to 3 meter depth. The soil texture is dominated by compacted fine sand (0.02–0.2 mm) near the surface and varies between 85–99%. The clay and silt fractions increased significantly with depth and reach 35 and 20% respectively, which corresponded to the sandy clay loam texture class (Dingman 2001). Three replicate samples for the determination of water retention were taken at 0.1, 0.3, 0.5, 0.7, 0.9 and 1.2 m by cylinders of 100 cm^3.

The saturated hydraulic conductivity was not measured in the upper soil horizon, but it was obtained from measured water retention curves and soil texture data by the Rosetta lite 1.1 pedotransfer software (Schaap et al. 2001). Below the deepest measured horizon the saturated hydraulic conductivities were estimated by slug tests. Saturated hydraulic conductivity was used for model calibration *(Table 1).*

Table 1. Main parameter values

Field measured parameters		
Maximum LAI	(m^2/ m^2)	3.9
Free throughfall coefficient	(%)	14
Root depth	(m)	1.5
Estimated parameters from literature and database		
Reference height	(m)	20.1
Albedo	(%)	10–16
Maximum leaf conductance	(mm/s)	6.3
Roughness length	(m)	0.9
Displacement height	(m)	15.12
Light coefficient of extinction	(–)	0.5
Stem flow ratio of precipitation	(%)	3
Calibrated parameters		
Canopy storage capacity	(mm)	
Vegetation season		1.17
Dormant season		0.5
Litter storage capacity	(mm)	0.5
Saturated hydraulic conductivity	(mm/day)	
Root-zone		$0.9 \times 10^3 – 2.9 \times 10^3$
Below the root zone		1.4×10^2
Specific yield		0.032

Maximum Leaf Area Index (LAI) was estimated from leaf litter and the seasonal change of LAI was described using remote sensing images.

During late autumn 2007 leaves were collected from five (1 m × 1 m) plots. The decomposition of leaves did not begin at the time of collection and the old leaves from previous years has already decomposed to an extent that it was easy to separate from new leaves by careful collection. The leaves were dried in an oven (105°C for 24 hours), then some of the leaves were scanned and the ratio of weight to leaf area was determined for this subset of leaves and subsequently for the whole sample. According to average of the five samples, the maximum LAI was 3.9 m^2/m^2.

The seasonal change of LAI was estimated using the 16-day Enhanced Vegetation Index (EVI) product of MODIS (Moderate Resolution Imaging Spectroradiometer). The 250 m resolution EVI was transformed to LAI by an empirical relationship (Wang et al. 2005). According to the satellite images, the maximum LAI was 4.2 m^2/m^2 in 2007, which was a about 8% higher than the results of the leaf litter collection. During the dormant season the images showed approximately 1.5 m^2/m^2 LAI, which may be accounted for the herbaceous vegetation below the forest canopy *(Figure 2).*

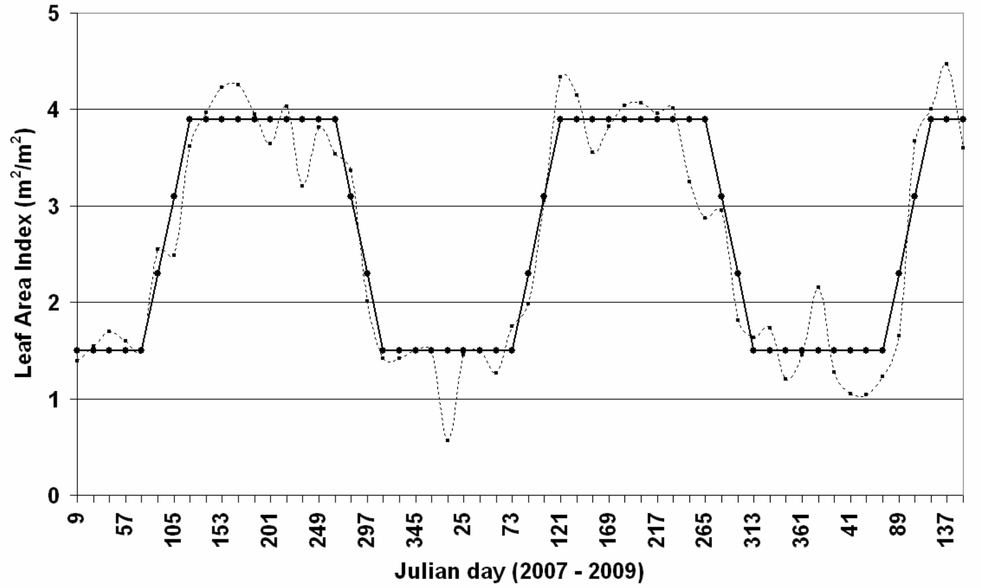


Figure 2. Seasonal change of LAI
(dashed line - MODIS data, solid line - applied in the model).

The seasonal change of albedo was estimated using the 500 m resolution images of MODIS. Daily albedo values were interpolated from the 16-day estimates and missing values were considered as snow cover. During these periods we used an albedo of 45% (Kondratiev 1969). During the vegetation period albedo had a value of 14–16%, while it decreased considerably in the dormant season.

2.2 Monitoring at the field site

2.2.1 Meteorological measurements

Meteorological variables (air temperature, relative humidity, solar radiation, wind speed) were measured hourly at 2 meter height by an automatic weather station (iMETOS, Pessl Instruments, Austria), about 3 km distance from the oak stand *(Figure 3).* Additionally, an automatic rain-gauge (Rainlog Data Logger, Rainwise, USA) was installed in 2007 at a distance of 500 m from the forest stand. Air temperature and relative humidity data, as measured were applied above the forest canopy, which probably influenced the potential transpiration estimate to some extent. Interception loss was not measured.

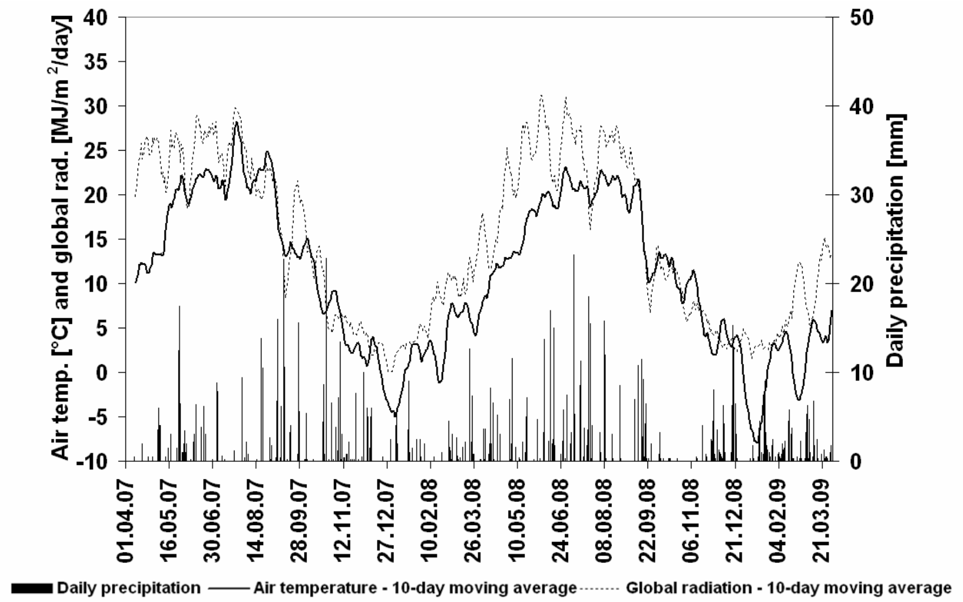


Figure 3. Meteorological conditions during the study period

The vegetation period (April to September) of the year 2007 was unusually dry with only 260.9 mm precipitation while 2008 was relatively wet with 401.4 mm rainfall. Air temperature was above average during almost the whole study period.

2.2.2 Soil water content in the root zone

The volumetric water content was measured by FDR (Frequency Domain Reflectometers) with Decagon EC-5 probes (Decagon Devices, Pullman, USA). The probes were inserted at 0.1, 0.3, 0.5, 0.7 m depth, respectively.

FDR measurements were verified by the gravimetric method using bulk density to convert gravimetric water content to volumetric. The accuracy of the FDR measurement was ±3.7%, which did not differ significantly from ±3%, given by the manufacturer (Decagon Devices, Pullman, USA).

2.2.3 Groundwater level

Shallow monitoring well was installed in spring 2007. Groundwater level was monitored by Dataqua DA-S-LRB 118 pressure transducer with an accuracy of 1 mm.

Besides the continuous monitoring, occasionally, groundwater level was measured also manually to check the reliability of the automatic groundwater monitoring.

2.3 Water balance modelling using Hydrus 1-D model

The Hydrus 1-D model (Simunek et al. 2005) was used for estimation of the water balance components *(Figure 4).* Hydrus 1-D 3.0 is a Windows-based modelling environment for analysis of water flow and solute transport in variably saturated porous media. Details can also be found at http://www.pc-progress.com/en/Default.aspx?HYDRUS-1D.

The base of the Hydrus 1-D model is the variable saturated vertical soil domain, where water flow is simulated.

The upper boundary condition (BC) was set to atmospheric BC with surface layer. The lower BC was set to variable flux, according to the groundwater supply (Q_{NET}), computed by the daily diurnal groundwater fluctuation method (Gribovszki et al. 2008b).

Input meteorological variables on the upper boundary of the 1-D model included the daily potential transpiration (T_P), the potential evaporation (E_P) and the effective precipitation (P_{EFF}).

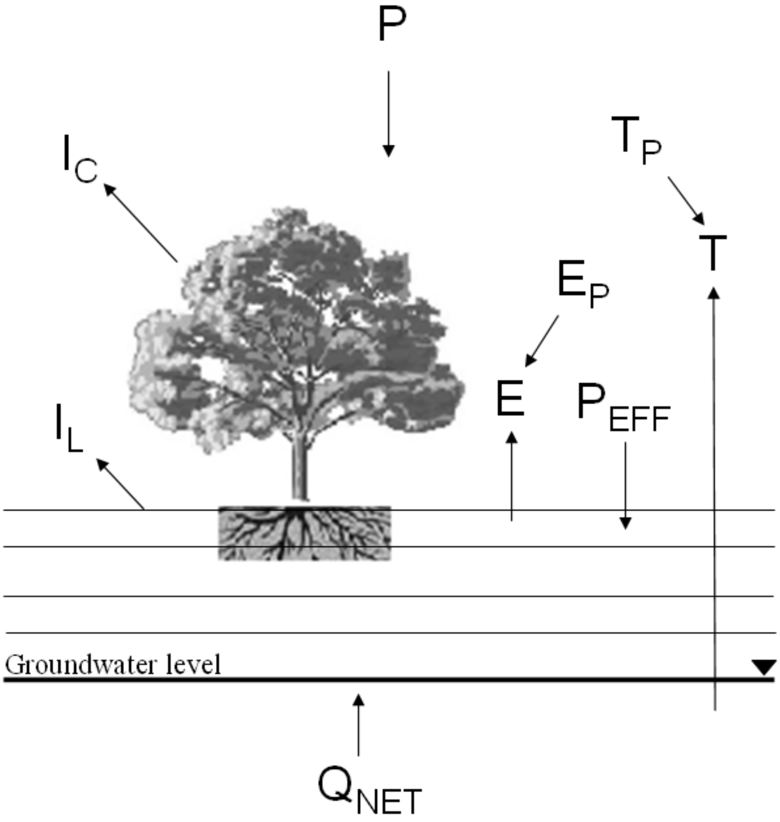


Figure 4. Water balance components of the numerical model
(P: gross precipitation, P_{EFF}: effective precipitation, I: interception loss,
I_C: canopy interception loss, I_L: litter interception loss, T_P: potential transpiration,
T: actual transpiration, E_P: potential soil surface evaporation,
E: actual soil surface evaporation, Q_{NET}: net groundwater supply.)

Potential transpiration and evaporation were calculated using the Penman-Monteith equation (Monteith 1965). The infiltrated rainfall into the mineral soil (effective precipitation) required the estimation of interception loss from canopy (I_C) and litter (I_L) from gross rainfall measurements (P).

The model simulated the presence of vegetation by root water uptake. Actual value of transpiration (T) was computed by the Hydrus 1-D model by water uptake reduction function. The S-shaped model for water uptake reduction was used, proposed by van Genuchten (1987). The actual value of soil surface evaporation (E) was estimated by the model, according to the moisture conditions at the topsoil.

Water retention variables and the saturated hydraulic conductivity functions were required to be specified for each soil horizons. The van Genuchten (1980) function was applied to describe the water retention of soil layers. The RETC software (van Genuchten et al. 1991) was used to fit the soil water retention curves.

2.3.1 Input data

The input data of the model is discussed separately as the upper and the lower boundary condition. Potential transpiration, potential evaporation and effective precipitation are discussed as the upper while variable bottom flux is analysed as the lower boundary condition.

Upper boundary condition

Potential transpiration was determined after Jarvis (1976) by estimating the leaf conductance C_{leaf} (mm/s).

$$C_{leaf} = g_{l\min} + f_T\, f_D\, f_R\, f_W\, f_C (g_{l\max} - g_{l\min}) \tag{1}$$

where g_{lmax} (mm/s) and g_{lmin} (mm/s) are the maximum and minimum leaf conductance respectively and f_T, f_D, f_R, f_W, f_C are reduction factors, varying between 0 and 1, that account for effects of temperature, vapour pressure deficit, radiation, leaf water stress and atmospheric carbon dioxide concentration respectively, on stomatal opening. Canopy conductance was computed by multiplying the leaf conductance with the leaf area index.

Potential evaporation from soil surface was also estimated by the Penman-Monteith equation, based on estimates of net radiation, aerodynamic and surface resistances applicable at the soil surface. Net radiation at the soil surface was computed using Beer’s low, leaf area index and extinction coefficient.

Effective precipitation was calculated by the estimation of the interception loss. For herbaceous vegetation evaporation from canopy during and after rainfall events plays little importance (McMillan – Burgy 1960), thus solely the storage capacity can be used for estimation of interception loss. Conversely, due to the high atmospheric conductance above the forest canopy, the evaporation of intercepted rain cannot be neglected.

Canopy interception was estimated by the Gash model (Gash 1979). This model was chosen, because it yields accurate estimation and only needs a few parameters to describe interception (Dolman 1987). Gash considered rainfall to occur as a series of discrete events, each comprising of a period wetting up, a period of saturation and a period of drying out after the rainfall. The canopy has sufficient time to dry out between rainfall events. Canopy parameters (free throughfall coefficient, storage capacity of canopy, stem flow proportion) were based on literature values and field observations.

The value of storage capacity of canopy S (mm) was estimated by a logarithmic saturation curve (Wattenbach et al. 2005):

$$S = f\left[\log(1 + LAI)\right] \tag{2}$$

where f is a species-specific parameter, which was set to 1.5, thus the value of S was 1.17 mm at the LAI of 3.9. During the dormant season the storage capacity of stems and branches were assumed to be 0.5 mm (Larcher 1994).

Rainfall and evaporation intensities were computed as monthly averages from hourly meteorological variables, where the rainfall rate exceeded 0.5 mm/h (Gash 1979). The rainfall interception was calculated on a daily basis. The evaporation rate was computed by the Penman equation.

Beyond the vegetation period we used the daily interception method to estimate the daily interception loss I (mm), proposed by Menzel (1997):

$$I = S\left(1 - e^{(-cp_i)}\right) \tag{3}$$

where p_i (mm) is the daily precipitation amount and c (–) is species-specific parameter, which was set to 0.7 (Wattenbach et al. 2005).

Litter storage capacity was estimated to be 0.5 mm during the model calibration. The total storage capacity (canopy + litter) was 1.67 (1.17 + 0.5) mm during the vegetation period and 1.0 (0.5 + 0.5) mm in the dormant season.

Lower boundary condition

The lower boundary condition was set to variable flux, according to the groundwater inflow, calculated by the water table fluctuation method (Gribovszki et al. 2008b). Beyond the vegetation period the groundwater level responded apparently to significant rainfall events, however these responses were slow and gradual due to the relatively deep (1.5–2.3 m) groundwater level.

In general, the lower boundary variable flux was set to zero for the period without observable daily groundwater fluctuation.

2.3.2 Result variables

Reduction of potential to actual transpiration was calculated by the model for all soil layers, where the normalized root density was above zero (Simunek et al. 2005). The S-shaped function (van Genuchten 1987) was applied with recommended parameters to describe the water uptake stress response function.

Actual evaporation was estimated internally by the model from the prevailing soil moisture conditions near the soil surface.

2.4 Estimation of groundwater consumption by the water-table fluctuation method

Significant diurnal fluctuation of groundwater level and streamflow rate can be seen at shallow groundwater areas during periods with no rainfall (Bond et al. 2002, Gribovszki et al. 2008a). This fluctuation is caused mainly by the diurnal variation of transpiration, originated by the vegetation cover.

Groundwater consumption T_G (mm/day) was estimated from groundwater level readings. An empirical version of the technique, developed by Gribovszki et al. (2008b), was applied. Gribovszki et al. (2008b) upgraded the White-method (White 1932) based on the fundamental assumption that groundwater supply per unit area, Q_{net} (mm/day), exhibits a significant daily variation due to hydraulic gradient changes over the day. Groundwater consumption values were calculated as the difference between the net inflow rate and the storage change (Gribovszki et al. 2008b).

$$T_G = Q_{net} - S_y \frac{dh}{dt} \tag{4}$$

where S_y (–) is the readily available specific yield was estimated from soil sediment texture data. According to the trilinear diagram of Loheide II et al. (2005), S_y varied from 0.03 to 0.10. Low specific yield values are further justified by the shape of the water retention curves of the lowest measured horizons and the low hydraulic gradient of the adjacent areas (Maidment 1993).

Days with less than 5 mm precipitation did not present any problem for the ET estimation, because these light rainfall events cannot produce any measureable groundwater recharge due to interception loss. Larger rainfall events (> 5 mm) can affect the estimation for up to 2 days, so those periods were excluded from the analyses (Gribovszki et al. 2008b). During the excluded periods the groundwater consumption can be considered negligible due to interception and evaporation loss from topsoil.

While this method aims to describe storage changes within the saturated zone only, implicitly it accounts (at least partially) for moisture withdrawal from the vadose zone as well, depending on the depth of the water table. Consequently, this method shows water extraction amounts from variable soil profile height, according to the groundwater depth and capillary fringe.

2.5 Comparison of the simulated local evapotranspiration data with ET results based on remote-sensing

Recently several remote-sensing based estimations of areal actual evapotranspiration (ET) were developed (Gowda et al. 2008). Szilagyi – Kovacs (2010) recently presented an ET estimation method based on the daytime land surface temperature of MODIS. Areal evapotranspiration rates were achieved by a linear transformation of the MODIS daytime land surface temperature employing the complementary relationship of evaporation.

The method was validated in the USA (Szilagyi – Józsa, 2009) and also in Hungary. The spatially distributed ET rates corresponded well with soil/aquifer properties and the resulting land use type. Validation of the ET rates has been performed at three sites in Hungary by Eddy-covariance measurements.

Monthly actual ET rates for 2000-2008 were mapped for Hungary at a spatial scale of about 1 km. Various meteorological data (sunshine duration, air temperature and humidity) and the daytime land surface temperature of MODIS was used for the estimation of ET.

A comparison of the model estimated ET of the oak plot with the remote-sensing based estimation has been carried out. Since the horizontal coverage of the oak plot (where the estimated ET values were valid) is smaller than 1 km, the direct, pixel-based comparison was not possible. For the comparison we have chosen suitable sites, (shallow groundwater table and similar leaf area index) in the vicinity.

2.6 Testing of the model performance

To test the performance of the model, time series of simulated soil water contents and groundwater levels were compared with observed values. Three performance criteria were used to quantitatively examine model performance: the coefficient of determination (R^2), the root mean square error (*RMSE*) and the Nash–Sutcliffe modelling efficiency (*ME*).

3 RESULTS AND DISCUSSION

3.1 Calibration of the Hydrus model

Measured soil moisture and groundwater level were used to calibrate the Hydrus model. Soil water measurements showed a cyclic variation seasonally, drying began in April, wetting started usually in September. Very dry conditions prevailed during late summer in 2007, soil water content dropped close to wilting point in the upper layers. Soil frost caused significant drop in soil water content during January of 2008 and 2009.

In *Figure 5* the soil moisture measurements and model predictions are shown.

Soil moisture measurements and model simulation generally compare well both in the dry (2007) and wet year (2008). However, there was a slight overprediction of the water contents in summer 2008. Unfortunately, the model, applied for daily time-resolution was not able to simulate accurately the transpiration on days with short and high-intensity rainfalls.

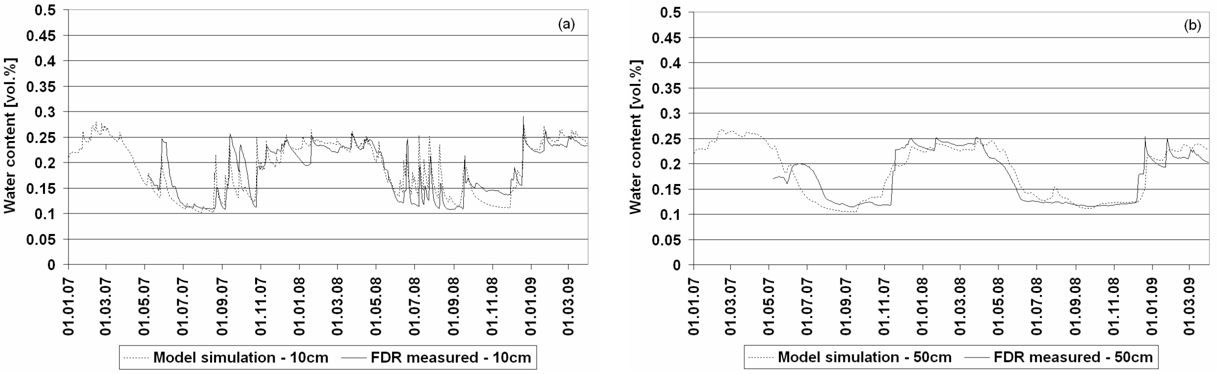


Figure 5. Comparison of measured and simulated water content for 10 cm (a) and 50 cm (b)

Groundwater levels showed also a cyclic seasonal variation during the study period and dropped deeper in the growing season of 2007 than in 2008 due to dry weather conditions in 2007. During the growing season groundwater levels showed a diurnal fluctuation, which is caused mainly by the diurnal variation of transpiration *(Figure 6)*.

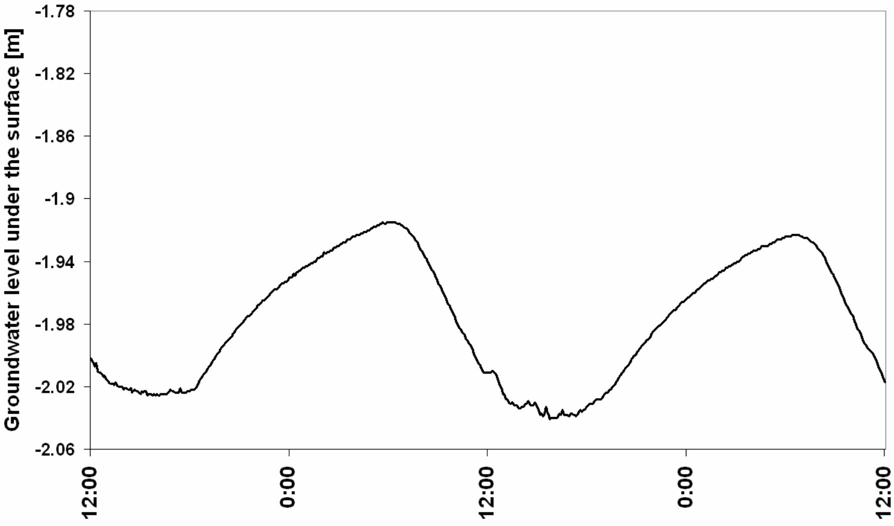


Figure 6. Diurnal fluctuations in groundwater level between 27.06.2007 and 29.06.2007.

Model simulations of groundwater levels compared fairly well with observations *(Figure 7)*. We observed a significant divergence during early autumn, namely simulated groundwater level was lower than the measured levels. Percolating rainwater could not explain the abrupt rise of groundwater, because it took months for the wetting front to reach groundwater at 2 meter depth. Macropores might also caused similar effect, but water level rose from 4th to 24th September 2007, while precipitation event already ended on 12th September. This behaviour was not typical for preferential flow. The estimated groundwater consumption was only 19 mm in September and 11 mm in October 2007, therefore it could not be the cause of the divergence.

Possible explanation of the divergence is that during late summer, groundwater is significantly lowered under the forest stand, compared to the neighbouring landcovers. At late summer evaporation forcing and transpiration usually cease abruptly and the groundwater depression disappears quite quickly due to groundwater supply from background. During this early autumn period the background groundwater supply was estimated from the mean of the smallest time-rate of change in the predawn hours. This time-rate of change was decreased linearly by the time of equilibrium groundwater level.

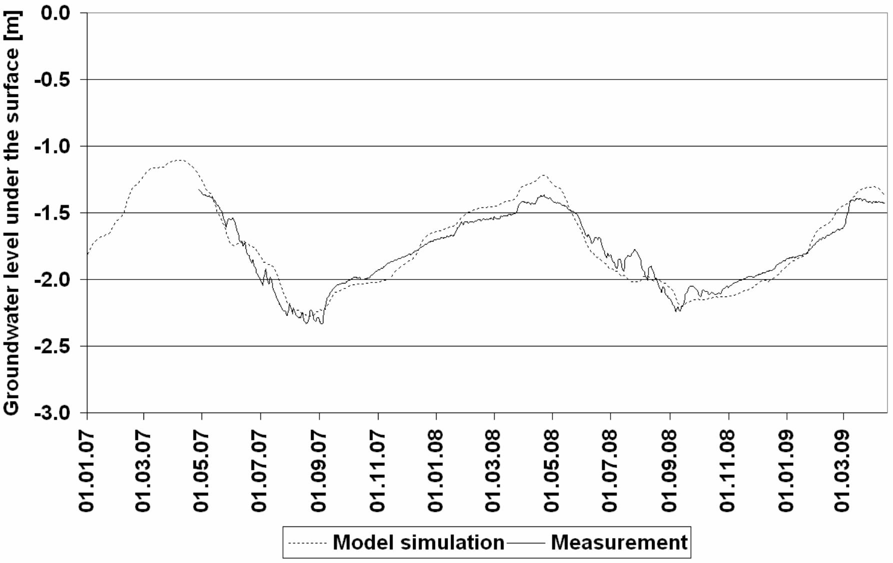


Figure 7. Comparison of measured and simulated groundwater level

Table 2 gives an overview of the obtained performance criteria.

Table 2. Various model performance criteria

Oak site	R^2	*RMSE%*	*ME*
Soil moisture (10cm)	0.73	14.91	0.69
Soil moisture (30cm)	0.83	11.95	0.80
Soil moisture (50cm)	0.79	13.52	0.77
Groundwater	0.92	5.03	0.88

Day-by-day comparison was used to analyse the deviations between the observed and simulated soil moistures and groundwater levels. We found no systematic deviation of the simulation from the observed values. The average deviation was –0.008 vol% for the soil water content and 0.009 m for the groundwater level.

Model calibration was accomplished primarily by trial-and-error adjustment of the storage capacity of vegetation and soil hydraulic parameters to minimize the root mean-squared error and optimize graphical fit between simulated and observed soil moisture content of each layer and groundwater level.

The storage capacity determined interception loss to a considerable extent. The value of *f (Equation 6)* was changed between 1.0 and 3.0 and finally was set to 1.5, opposed to the suggested 2.0 (Wattenbach et al. 2005). The storage capacity of canopy was 1.17 mm at *LAI* of 3.9, which was in good agreement with other study results. In Andre et al. (2008) the interception capacity of an oak dominated stand was 1.19 mm with *LAI* of 3.8. Rutter et al. (1975) and Dolman (1987) suggested 0.8 mm for oak stands. In the dormant season the storage capacity of stems and branches were not changed from the initial value of 0.5 mm, suggested by Larcher (1994). The value of the storage capacity of litter has been decreased during the calibration from 1.1 mm to 0.5 mm.

The α and n shape parameters of the soil water retention curves were slightly adjusted during the calibration.

Initially, the saturated hydraulic conductivity (K_S), estimated by the Rosetta Lite 1.1 software, was used for the root-zone (< 1.5 m) of the soil profile. Below the root-zone the mean of the results of the slug tests was used.

The calibrated K_S values varied between 2.9×10^3 mm/day in the upper most horizon and 0.9×10^3 mm/day at about 1 m depth. In the saturated zone the calibrated K_S value differed only slightly from the measured value.

Specific yield was used for estimating the bottom boundary flux in the Hydrus models via the water table fluctuation method. It was used for model calibration, since the magnitude of the bottom boundary flux was quite sensitive to the specific yield. The diagram of Loheide II. et al. (2005) suggested specific yield in the range of 0.03–0.10, based on the soil texture. During the calibration process the best fit with groundwater levels were achieved by lower values of specific yield. Finally, the calibrated value was 0.032.

3.2 Water balance components

3.2.1 Interception loss

According to the model, canopy interception was 27.7% and litter interception 7.6% of the rainfall amount during the study period, which was in good agreement with other study results (Führer 1994). The effect of evaporation during and after rainfall events raised the interception loss rapidly *(Figure 8).*

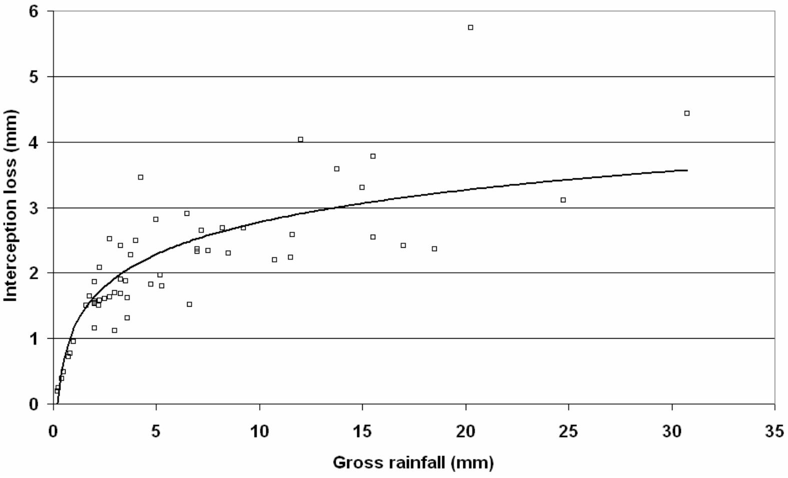


Figure 8. Relationship between gross rainfall and interception loss in the growing season of 2008

Although the amount of interception loss was larger in the growing season of 2008 (128 mm), than in 2007 (98 mm), the relative interception loss (% of precipitation) was slightly larger in 2007 (37.6%) than in 2008 (33.3%) due to occurrence of more frequent rainfall events in 2007 with low amount.

3.2.2 Actual transpiration and groundwater consumption

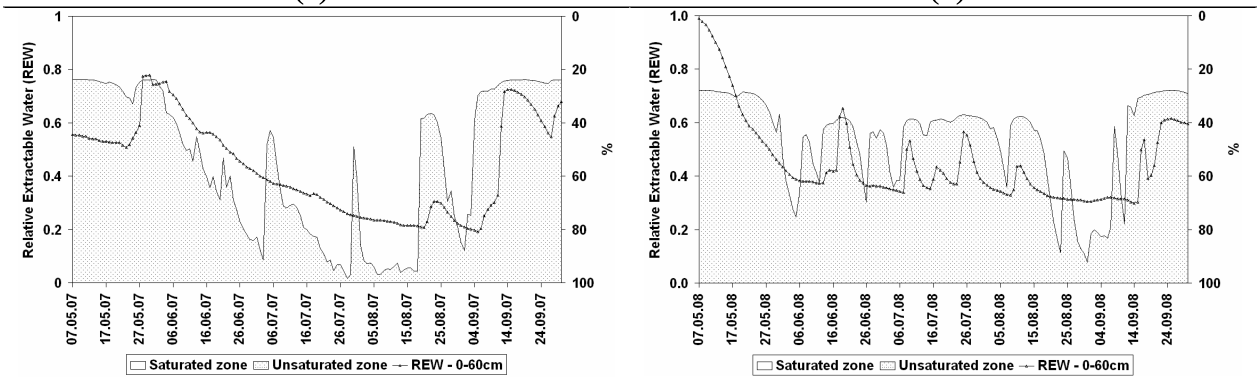
Actual transpiration was similar to the potential value in our experiment. This is not surprising, since the root system of the vegetation was in connection with the saturated zone via the capillary fringe throughout the year. Gazal et al. (2006) found the transpiration of a cottonwood forest was not limited at groundwater table depth of 1.5–1.8 m. Hence, transpiration of riparian vegetation responds less to changes in soil moisture because of their direct access to the groundwater table (Oren – Pataki 2001).

Groundwater consumption was determined by the simulated soil water content changes and capillary fringe dynamics of the Hydrus models. The depth of separation was the field capacity of the soil layer, containing the capillary fringe. According to the Hydrus model simulation, the groundwater consumption of vegetation was approximately 66% of the total simulated transpiration in the growing season of 2007 and 50% in 2008.

Relative extractable water (REW) was calculated for the upper 60 cm of the soil profile from soil hydraulic properties (Granier et al. 1999), namely water content at field capacity (W_{fc}), the actual water content (W) and permanent wilting point (W_{pwp}):

$$REW = \frac{W - W_{pwp}}{W_{fc} - W_{pwp}} \tag{5}$$

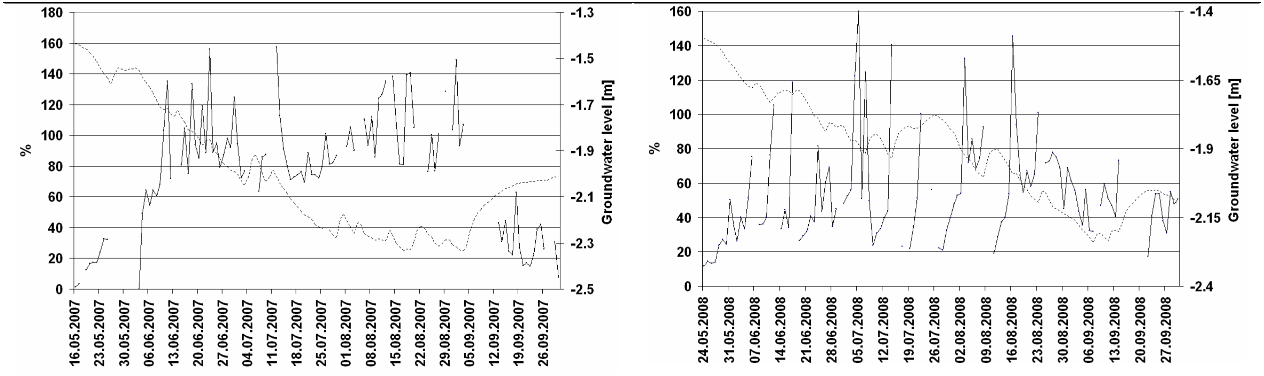
During the growing season of 2007 the REW declined almost continuously at the upper 60 cm of the soil profile, because of severe drought in summer. Accordingly, the proportion of groundwater consumption increased up to 90% for periods during late summer. In 2008 several rainfall events increased considerably the water content of the unsaturated zone, thus the groundwater consumption was less than in 2007 *(Figure 9).*



(a) (b)

Figure 9. Proportion of the modelled water uptake from the saturated and unsaturated zone and the relative extractable water (0-60 cm) during the growing season of 2007 and 2008

The groundwater fluctuation method showed that groundwater consumption was 69% of the total simulated transpiration in the growing season of 2007 and 44% in 2008. The daily groundwater consumption showed large fluctuation during the growing season and exceeded sometimes considerably even the daily potential transpiration *(Figure 10).* Despite of the deeper groundwater level, groundwater consumption was higher in 2007 than in 2008. In 2008 large rainfall events interrupted often the continuous groundwater consumption of vegetation. The gaps in the groundwater consumption denoted the days with larger rainfall events.



(a) (b)

Figure 10. Ratio of the groundwater consumption to the potential transpiration (solid line) and groundwater level (dotted line) in 2007 (a) and in 2008 (b)

The estimated groundwater consumptions of the groundwater fluctuation method were slightly different than the results of the Hydrus simulations. The differences between the approaches may be attributed to the slightly subjective determination of the minimum and maximum rate of groundwater supply in the groundwater fluctuation method. Namely, the values of Q_{net} are quite sensitive to atmospheric changes (e.g. clouds), which may have confounded the determination of the amount of groundwater supply. Besides, the water table daily net variation reflects the net variation of several fluxes (recharge, baseflow, evapotranspiration, subsurface flow), as a result, the estimated groundwater consumption probably includes some subsurface redistribution of water (Healy – Cook 2002). The determination of the daily groundwater consumptions from the soil water content profile of the Hydrus model simulations had also several uncertainties (e.g. position of the capillary fringe, root depth).

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According to the groundwater fluctuation method, the daily groundwater consumption varied between 0.8 and 5.8 mm, which is in good agreement with other study results. Bauer et al. (2004) obtained riparian ET rates of 0.06–4.3 mm/day (potential ET was between 150–200 mm) for different vegetation cover (trees, shrub, grass) and soil characteristics, where continuous groundwater level readings were used for the estimates (groundwater depths varied around 2 m from the surface). Schilling (2007) obtained transpiration rates in Iowa (USA) between 5.0 and 6.3 mm/day at a forest during mid July at groundwater depths between 0.9–1.2 m under the forest.

3.2.3 Actual soil surface evaporation

Model results showed that actual soil surface evaporation was only 3.7% of the evapotranspiration during the study period. The sum of the actual evaporation and the litter interception was 11.6% in our experiment. Forest floor evaporation, including litter interception, varied between 8 and 11% of the total evapotranspiration in deciduous forests during the growing season (Moore et al. 1996, Wilson et al. 2000).

During summer of 2007 actual evaporation was only 42% of the potential value due to the low water content of the upper soil layer, initiated by drought periods. During summer of 2008 the rainy weather allowed actual soil surface evaporation close to potential value.

3.2.4 Summary of the water balance analyses

The simulated water balance components for the vegetation periods between 2007.04.01–2007.09.30 and 2008.04.01–2008.09.30 are shown in *Table 3*. The intervals of uncertainties were determined by the root mean square errors, expressed in % of the mean observed variable.

Table 3. Estimated water balance components (mm) for vegetation periods of 2007 and 2008

Vegetation period	P	T_p	ET_a	I	T_a	E_a	Q_{net}	ΔS
2007	261	659	730±83	98±11	609±69	23±3	289±33	–180±20
2008	383	551	678±77	128±15	513±58	37±4	184±21	–111±13

P: precipitation, T_p: potential transpiration, ET_a: actual evapotranspiration,
I: interception, T_a: actual transpiration, E_a: actual soil surface evaporation,
Q_{net}: net groundwater inflow, ΔS: soil water storage change

3.2.5 Comparison of the results of the modelled and remote-sensing based evapotranspiration

Two large forest areas (E1 and E2) along the river Tisza were chosen for comparison with ET results of Hydrus simulation *(Figure 11).*

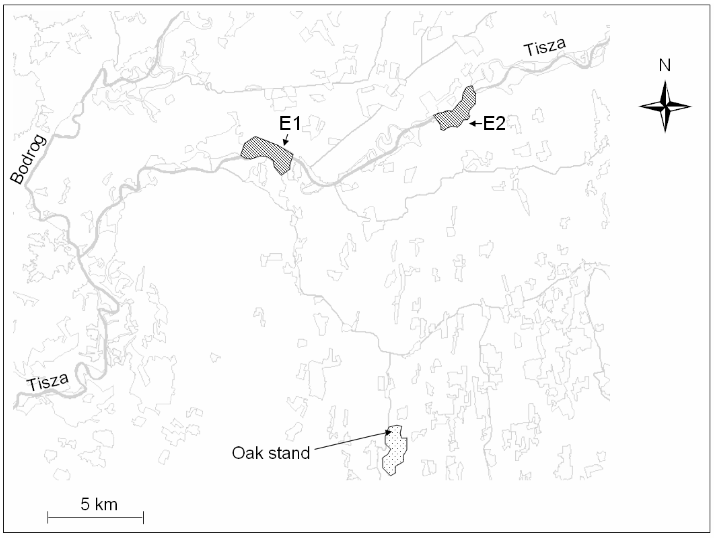

Figure 11: Location of the study plot and the chosen sites for comparison (E1, E2)

The E1 and E2 forest areas are located close to the river Tisza, characterized by shallow (1–2 meter deep) and fluctuating groundwater level. We have selected the pixels, where the leaf area index was closest to the maximal value of the oak stand. ET of the vegetation period was compared with 4 and 5 pixels, respectively *(Table 4).*

Table 4. The evapotranspiration and the average maximal leaf area index of chosen pixels of the two sample areas, compared to the model

Area	E1			E2		
	ET		LAI	ET		LAI
Growing season	2007	2008		2007	2008	
Pixel1	717	684	5.0	673	657	3.9
Pixel2	727	688	5.1	682	662	4.0
Pixel3	681	667	4.1	699	657	4.5
Pixel4	713	685	4.5	688	667	3.7
Pixel5	709	676	4.7	–	–	–
Average of pixels	709	686	4.7	680	661	4.0
Hydrus model	730	678	3.9	730	678	3.9

Evapotranspiration results of the Hydrus simulation were closer to the higher values of the remote-sensing based ET estimation. The deviation from the results of the remote-sensed based estimation was not larger than 4% from the mean of the sample area.

4 CONCLUSIONS

In this study, the water balance components of an oak stand was estimated for a two-year period (Spring 2007 – Spring 2009). The study site was located at the discharge part of the local groundwater flow system, characterized by shallow groundwater depth and groundwater inflow.

Water balance components were estimated by calibrating the Hydrus 1-D model to fit measured soil moisture and groundwater level. Groundwater supply from background – estimated by the water table fluctuation method – was applied as the lower boundary condition in the Hydrus models. Model simulation described the observed soil moisture and groundwater level relatively well, the root mean square errors RMSE varied between 11.95% and 14.91% for the soil moisture measurements and 5.03% for the groundwater level.

According to the Hydrus model, the estimated evapotranspiration resulted from transpiration (73%), interception loss (23%) and soil surface evaporation (4%) in the two-year study period. Canopy interception loss was 27.7%, while litter interception loss reached 7.6% of the precipitation. Actual transpiration was similar to the potential values, which was not surprising, since the root system of the vegetation was in connection with the saturated zone via the capillary fringe throughout the year. Soil surface evaporation was not significant.

The proportion of groundwater consumption was 58% of the total transpiration. During the dry growing season of 2007 the groundwater consumptions were significant with 66% of the total transpiration. Water supply from groundwater was found to be less important in the wet growing season of 2008 with 50%. Climate change projections predict that summer temperature may increase by up to four degrees by the end of this century in Hungary (Gálos et al. 2007). Increasing temperatures may raise the evapotranspiration demand, thus groundwater consumption of forests can be expected greater due to increased ET as long as the groundwater is available for roots for water uptake.

Groundwater consumption was computed also by the water table fluctuation method. We found that the groundwater fluctuation method provided slightly different groundwater consumption rates by 8,5%, than estimated from the Hydrus model simulations. The cause of the difference may be originated from the uncertain estimation of the groundwater supply from background, but probably also from the Hydrus model simulations (e.g. position of the capillary fringe, root depth). The remote-sensing based estimation of evapotranspiration was approximately 4% lower than the model based result of nearby similar sites.

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Effects of Building a Highway and Wildlife Crossings in a Red Deer (*Cervus elaphus*) Habitat in Hungary

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Abstract – We examined how the movement of red deer (*Cervus elaphus*) was modified in an area that had a new fenced off highway built across it. The first step was the collection of data from the track marked for construction. We continued collecting data on wildlife crossings after the construction of the highway and the completion of the fences. After the completion of the highway, it was observed that only 5.9% of the original deer track counts remained, spread across the crossings. After the construction was finished, the wider crossing structures were used more often by deer for crossing to the other side of the highway than the smaller ones. During construction of the highway, a number of animals chose to walk tens of kilometres to get around the construction site instead of using the crossings. An existing highway, or a highway under construction not only changes the frequency of deer crossings, but affects their distribution as well.

Wildlife crossing structure / red deer / *Cervus elaphus* / linear constructions / fragmentation / barrier effect

Kivonat – Az autópálya építés és a vadátjárók hatása a gímszarvas területhasználatára. Vizsgáltuk, hogyan változik a szarvasok mozgása egy olyan területen, melyen megépült egy kerítésekkel kísért autópálya. Első lépésben adatfelvételezést végeztünk az épülő autópálya egy szakaszának nyomvonalán, majd folytattuk a felvételezést a megépült autópálya vadátjáróin, még az úttestet kísérő kerítés felállítása után is. Az autópálya építkezést követően a kezdetekben tapasztalható „szarvas-forgalomnak” csupán a töredéke (annak 5,9%-a) maradt meg és oszlott el a megépített vadátjárókon. Az, hogy melyik átjárót használják szívesebben, már rögtön a megépítést követően látszik, mint ahogy az is, hogy az egyedek nem használják az átjárókat, amíg akár több tíz kilométer árán is, de meg tudják kerülni az épülő útszakaszt. Az épülő ill. megépült autópálya nem csak a szarvasok gyakoriságát változtatja meg az egyes szakaszokon, hanem azok eloszlási arányait is.

vadátjáró / gímszarvas /*Cervus elaphus* / vonalas létesítmények / fragmentáció / barrier hatás

1 INTRODUCTION

Linear constructions have significant impact on the density of various wildlife species and diversity of the communities (Bissonette 2002). The impact can be direct (loss of habitat, population decline, etc.) and indirect (isolated population, deteriorating gene pool) (Bellis et al. 2007). These constructions (e.g. roads, railroads, waterways, forest fences, etc.) form a

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border line in both the ecological and the visual sense. The result is the “barrier-effect,” which is the root cause of habitat fragmentation, and the most serious problem caused by linear constructions (Spellerberg 1998). The fragmentation effect is greatly affected by the width of the linear construction, its permeability, amount and speed of traffic and the existence of fences. Roads split up evenly distributed populations, forming smaller, sometimes completely isolated sub-populations (Forman – Alexander 1998). Fragmentation may inhibit species from spreading, reaching adequate food, mating and can lead to declining gene diversity due to smaller population size. These adverse effects can lead to further shrinking of the population, can cause serious depression of viability and fecundity and increase the risk of extinction (Standovár – Primack 2001).

The “border-effect” is another serious consequence of habitat fragmentation. Conditions along the borders of a fragmented habitat are different from those deep within the habitat. The micro-climate can change (light, temperature, humidity, wind speed) that can seriously affect community composition of the area, or the survival of the species. For example, the dense vegetation that grows along the borders of forests may lead to increased density of large herbivores. This may result in over-grazing of several sensitive plant species in a belt possibly several kilometers wide, reaching into the depths of the forest (Alverson et al. 1994).

Building fenced highways or similar structures creates a barrier that makes it difficult for wildlife to move from one side of the road to the other. Installing wildlife overpasses and underpasses allow animals to pass safely over or under the highway, mitigating these effects.

Building wildlife crossings requires a considerable amount of funds, so it is essential to know their effectiveness and to monitor how often they are used by different species. A number of methods are used to monitor the use of a wildlife crossing structure in wildlife management investigations – for example counting tracks, video recordings, and GPS-telemetry (Hardy et al. 2003; Cuperus et al. 1999; Dodd et al. 2004; Ford et al. 2009; Trombulac – Frissel 2000). These methods are useful not only for the examination of the use of wildlife crossings, but also for the study of the behaviour of wild animals when they are forced to approach artificial barriers that could otherwise be avoided or overcome.

In this study we collected data along the line of a highway before, during and after construction. According to earlier observations, the deer spotted the 2.4 m high fences protecting the highway from several kilometers away, and walked around them when possible (Alexander – Waters 2000; Mata et al. 2008). When deer could not find a by-pass, the animals were presumably “forced” to use the newly constructed overpasses and/or underpasses. Because of the increasing number of fences that fragment and limit the sizes of habitats, it is becoming more and more important to understand how these fences affect deer movements in these areas, and which type and size of crossings are more efficient.

Our main objective in this study was to examine if the animals were presumably „forced” to use the new highway crossings and in which degree, when they could not find another way. In addition, we examined whether there is a detectable drop in population size along the highway, when we compare track counts before and after the construction of the highway. Finally, we suggest methods to increase the use of the crossings

2 STUDY AREA

The study was conducted on the Hungarian M7 highway, in Somogy County (south of Lake Balaton) between the overpass north-east of the Road 68 crossing and the underpass with a water canal near to Balatonújlak. There were farm fields on both side of the highway, mostly corn and canola.

3 MATHERIAL AND METHODS

After marking the highway on the ground, but before commencing construction, the number of deer tracks that crossed the entire width of the planned highway was systematically recorded. The first recording took place in February of 2006, about one year before crossings were built with fences (January – February of 2007. The last recording was in November of 2008. We divided the planned trace into two sections. After the highway construction each section had two crossings built on it. After the completion of the crossings, we continued counting the tracks that crossed the entire length of the overpass and the underpasses.

Professional hunters employed by Somogyi Hunor Vt. (the association authorized to hunt in the area) helped us collect these data. There were four crossings constructed in the study area, one overpass (at the west end of this section) and three underpasses. The overpass (bridge S67 in highway segment 169 + 770) was 62 meters long and 27 m wide. The next underpass in the direction of Budapest was the S66 in highway segment 168 + 755. It was 25 m long and 16.3 m wide. There was a very similar underpass (called S64) in the same direction, in highway segment 166 + 996, 25 m long and 15 m wide. The last underpass is wider than the other underpasses, since there is a railway and a canal ("Nyugati-övcsatorna.") This was 25 m long and 132 m wide, located in highway segment 166 + 430. We calculated monthly averages from data collected on a weekly basis. To avoid duplicate counts, after each count, the tracks were covered by brushing over the soil with a tree branch. During, and right after construction, the ground where we counted the tracks was soft and tracks were clear, visible and easy to count.

The data did not match the normal distribution curve even after any transformation. For this reason, we decided to use the non-parametric Mann-Whitney test, the Kruskall-Wallis test, and the Spearmann rank-correlation.

4 RESULTS

According to the Mann-Whitney test which was applied to the data recorded before the construction between the two parts of the selected section, there was no difference in track density *($Z = –0.558$; $p = 0.577$).* However, when we compared the results based on the data from two crossings in each of these two sections, we found a significant difference *($Z = –4.514$; $p < 0.001$).* This definitely differs from the results before the construction *(Figure 1).*

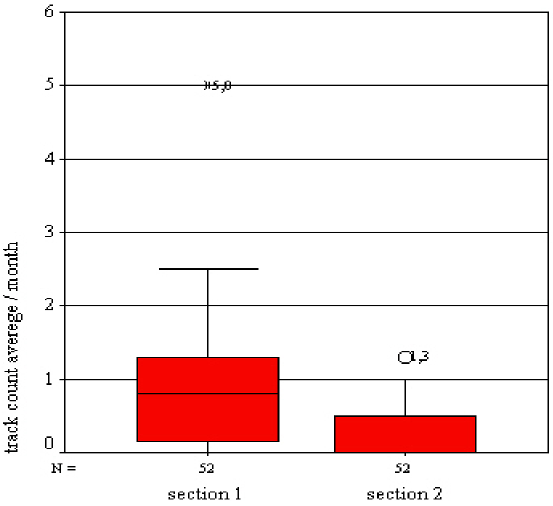


Figure 1. Comparison of two sections of the highway based on deer track counts recorded on two wildlife crossings at each section

This indicates that the number of red deer tracks was altered after the construction of the crossings. The section further away from the parts of highway still under construction had a higher frequency of use compared to the other section.

Comparing the conditions before and after the construction, the significant difference is evident not only in the altered proportion, but also in the entire recorded track density *(Figure 2).*

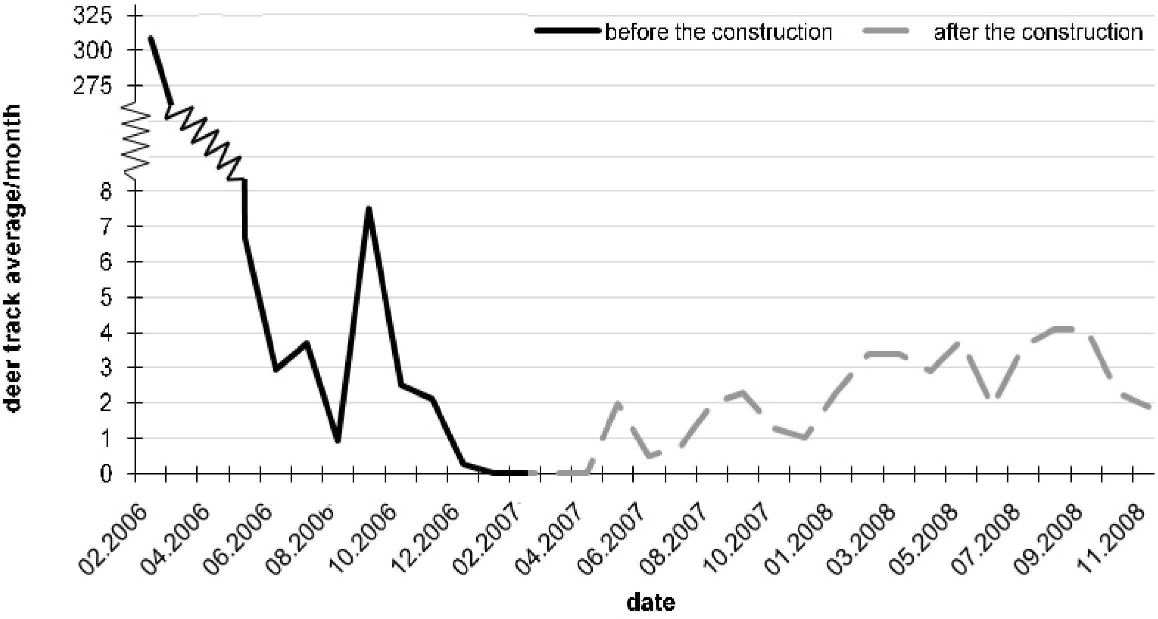
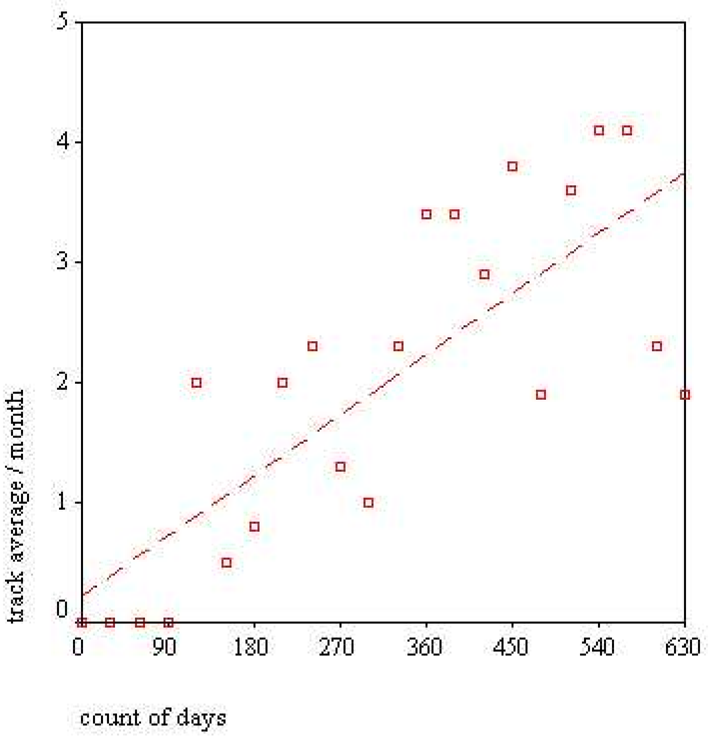


Figure 2. Comparison of deer track counts before and after the construction of wildlife crossings

Looking at monthly averages, before construction started, we observed more than 300 deer tracks for both sections each month. After the construction, this value at all crossings summarized was below 10, and often 0. The number of deer tracks was dramatically reduced after the highway construction *(*Mann-Whitney U test $Z = -1.755;\ p = 0.79$*)*

From the beginning of December, 2006, until end of January, 2007, the number of track counts of crossing deer was zero. This is the time period when the entire length of the road was closed off with a fence, with the exception of the uncompleted crossings. The second part of *Figure 2* shows that after this time, the presence of deer in the crossings was detectable again. Using Spearmann rank-correlation, we looked for a connection between the time and the track density. Based on the statistical analysis and the trend-line fitted on the scatter-type figure, there is an unambiguous correlation between the number of days that passed and the track density, so as time passes the track density in the crossings increases *(Figure 3).*



Figur 3. Deer track density progress in time,
after the deflecting fences of the given section were set up

The number of tracks of deer using each of the four crossings is different. *Figure 4* shows how the use was divided between each of the crossings in the period when they were built. The non-parametric Kruskall-Wallis test proved that in the same time period, the widest crossing (marked as Nr. 1 on *Figure 4*) experienced a significantly larger traffic than the others *(Chi-square = 23.509; p < 0.001).*

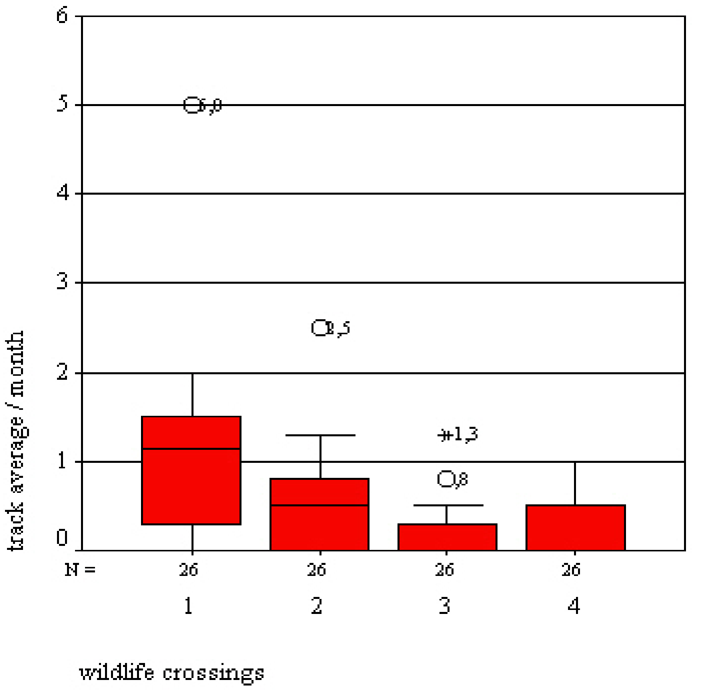


Figure 4. Comparison of monthly averages of deer track frequency
recorded in each of the crossings

We compared the only overpass with the underpass in the same section to have a comparison of two main types of crossings. As result of a Mann-Whitney U test, there is no significant difference shown between the frequency of the use of overpass (Nr. 4 on *Figure 4*) and underpass (Nr. 3 on *Figure 4*) in section two by deer. ($Z = -0.041$; $p = 0.967$)

5 DISCUSSION

A number of other investigations have examined the ecological implications of linear structures using track counts, just like our current study. Among their findings, they agree that the impact on wildlife is determined by the density of roads (Mech et al., 1988), and the size and speed of traffic (Gagnon – Dodd 2007; Clevenger et al. 2001).

Our results showed that shortly after the construction of the crossings, the animals did not use them, since they could still get around the fenced-off section in the near distance. This „getting around” behaviour was also observed when the fences were built in two parts. After the first section was built, the number of vehicle-wildlife collisions along the second unfenced section increased significantly.

Red deer used the “getting around” strategy as long as the energy invested was worth it. After that they were compelled to use the crossings. However, the construction work likely influenced their use. Servheen (2003) and Kusak et al. (2009) found positive correlation between disturbance and the use of wildlife crossings. In our study the crossings that were the furthest away from the construction site were the ones that were used first. As the construction moved away, and the disturbance affecting the animals decreased, the use of the crossing increased.

The above observations explain why the crossings on the first part of the section were used sooner. If the assumption is right, the difference should disappear with time after the completion of the entire M7 highway. If the phenomenon is caused by preference for one or two crossing types or locations, then the difference will remain detectable.

If a wildlife crossing has a low use, it does not necessarily mean that the location or its construction was wrong. Sometimes a few years are necessary for wildlife to get used to the crossing structures, and a few years with low use can be followed by sudden and significant increase (Clevenger – Waltho 2003). However, we must strive to decrease the “getting-around” behaviour due to the changed environment, since otherwise the number of car collisions with wildlife will increase. An animal won't consider a crossing that is 8-10 meters wide, since the animal won't even approach it, due to the presence of fences and the environment that was changed during the construction. Vegetation helps animals get used to it and increases the chances of it being used. Vegetation is especially important for an overpass because it makes the overpass more natural, and it will decrease the noise and light of the traffic as well, eliminating most of the disturbances.

To increase the effects of vegetation, it is advisable to equip the overpass edges with peg or noise reducing walls (Bekker – Vastenhout 1995). In addition to the vegetation, making the deflector fences cone-shaped can also help the animals to get used to the crossing. This form will not only lead the animals towards the crossing structure, but will make it more noticeable for the animals as well. This is important, as a deer might approach the fence at a given section, but won't see a 6-10 meter wide “hole” in it as a crossing point. Making these „holes” wider with deflector fences in a coned shape will give the animals a chance to carefully try and explore it before getting used to the new conditions.

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Consumer Behaviour Model on the Furniture Market

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Abstract – This study introduces the furniture purchasing behaviour model. The study describes the behaviour model and characteristics of decision making and the environmental factors affecting the individuals besides emphasising the family character of furniture purchase. We introduce a chapter from the primary research verifying the model that analyses the validity of customer behaviour trends defined as elements of the impersonal environment on the furniture market. We touch on our lifestyle based segmentation model which is elaborated in our work in detail. The method of primary research is quantitative, personal interview. While working out our research model we applied a method that enables multi-level cross-section and cohort analyses. Our work has verified the need for trend researches on the furniture market so we suggest the construction and the near-future launch of a trend research system consisting of several modules that reveals the specific factors on the furniture market besides verifying the validity of general behaviour trends.

consumer behaviour model / trend research / lifestyle

Kivonat – Vásárlói magatartásmodell a bútorpiacon. A tanulmány bemutatja a szerzők által kidolgozott bútorvásárlói magatartásmodellt, amely a bútorvásárlás családi jellegének hangsúlyozása mellett fordít figyelmet a döntésben résztvevők személyes adottságaira, az individuumra ható környezeti tényezők vizsgálatára. Bemutatjuk a modellt igazoló primer kutatás egy fejezetét, amely a személytelen környezet elemeként értelmezett vásárlói magatartástrendek érvényességét vizsgálja a bútorpiacon. Ennek mentén érintjük a munka során részletesen is kidolgozott életstílus alapú szegmentációs modellünket. A primer kutatás módszere kvantitatív, személyes megkérdezés. A kutatási módszer kidolgozásánál olyan eljárást alkalmaztunk, amely többszörös keresztmetszeti vizsgálatok, kohorsz-elemzéseket tesz lehetővé. Munkánk igazolta a bútorpiaci trendkutatások szükségességét, ezért javaslatot teszünk egy olyan több modulból álló trendkutatási rendszer felállítására, és a közeljövőben történő bevezetésére, amely az általános magatartástrendek érvényességének igazolásán túl a bútorpiaci specifikumokat is feltárja.

vásárlói magatartásmodell / trendkutatás / életstílus

1 INTRODUCTION

The aim of customer behaviour researches is on the one hand the analysis of preceding reasons of mass phenomena, on the other hand, the prognosis of the future. One criterion of this is the analysis of psychic phenomena. Customers with individual personalities show

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various behaviours when affected by different environmental stimuli. The researchers of customer and consumer behaviour attempt to typify individual decisions and, as a result of this, several customer behaviour models have been created since the 1960s. In the majority of these models the process of decision making can be interpreted by the chain of problem recognition – information search – evaluation – purchase – use – follow-up evaluation, these are then determined by factors the different authors consider important.

Our innovative customer behaviour model, created in 2009, *(Figure 1)* can be applied on the market of durable goods, is based on the role of individuals in making family decisions and is verified by the analyses of the mechanisms of furniture acquisitions.

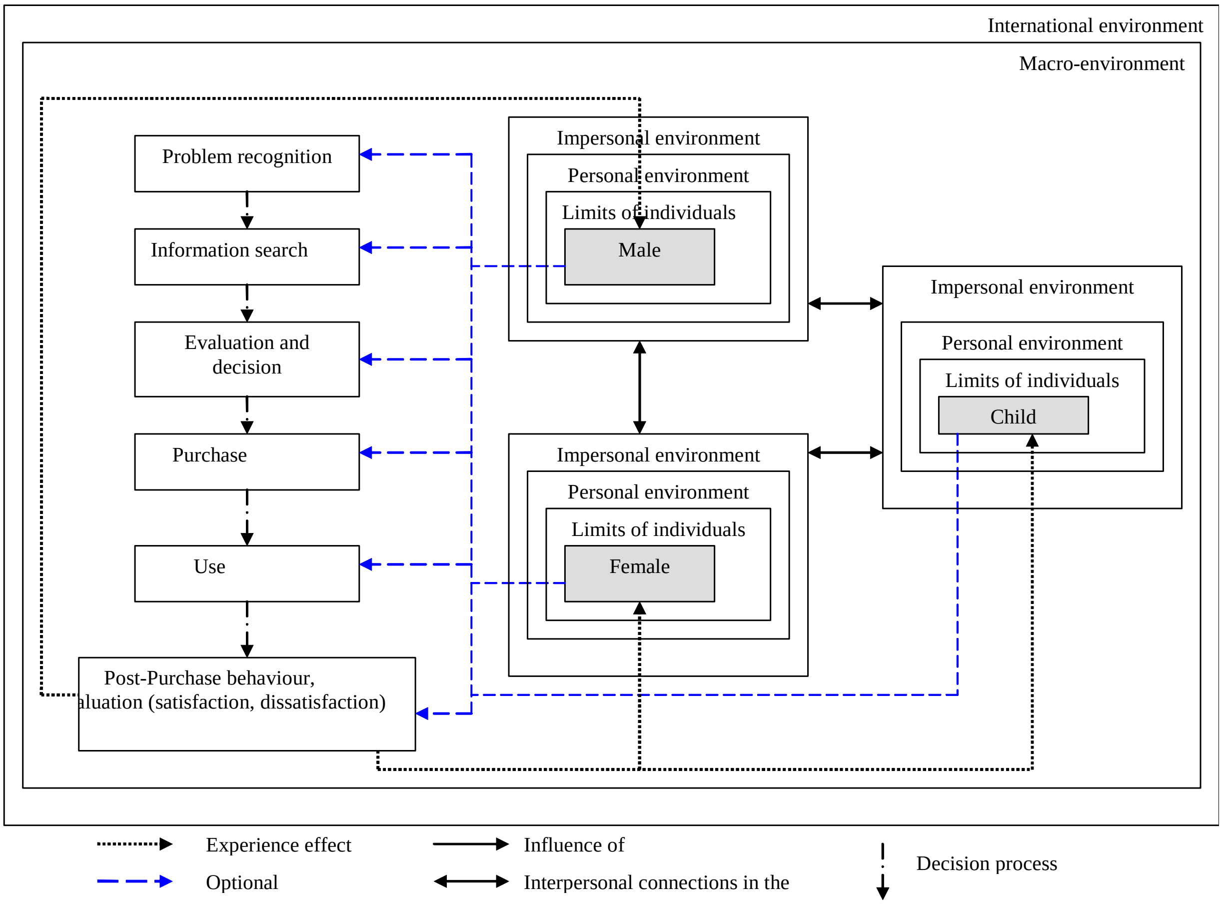

Figure 1. Customer behaviour model on the durable goods market

The behaviour models of Hoffmanné (1977), Pakainé (1997) and Törőcsik (2007) have been considered in our work.

This model designed for the durable goods market supposes that complex environmental stimuli affect members of families (men, women, and children) as *individual decision making elements*. In accordance with behaviour trends, *children* are also involved in purchase decisions in our model since they affect them. The male, female members and children in a family are directed into each period of purchase decisions by an optional type of relation, which signals that certain members take part in decision making to a different degree in line with the male-female-child roles characteristic to the given society. The relationship between the individuals determines the family character of decision making and the roles of individuals in decision making are unravelled. It is an important part of our model to analyse which periods of decision making do individual family members take part in and with what intensity. The *experience effect* impacts each family member, the results appear in the consumer habit of the next decision making. We would like to emphasize that *international environment* also affects the process of decision making.

We verified this theoretical customer behaviour model on the *Hungarian furniture market* in accordance with an aspect-system determined by the primary research. We analysed the impacts of impersonal environment on furniture purchases by researching the validity of general customer behaviour trends on the furniture market. We found it necessary to analyse the family character of furniture purchase decisions, to survey family roles in each period of the decision process (problem recognition, information search, decision, purchase) based on the model. The primary research enabled us to group furniture uses and purchases *according to theoretical categories* and to *segment the market based on lifestyle*, which is of outstanding importance for small ventures and medium-sized business enterprises of the branch (Hetesi et al. 2007, Veres et al. 2006, Hradil 1995, Lazer 1971).

2 METHODS

The method of research is a descriptive, quantitative, personal interview based on a structured questionnaire. Our aim was to obtain statistically valid, quantifiable data on a sample representing Hungarian furniture purchasers, the population of the research. In keeping with the aims of the research, we considered those persons furniture purchasers who are planning to buy furniture in the next two years, who take part in the decision making process in the family and who do not work in the branches wood industry, furniture manufacturing, furniture trade, furniture design or inner architecture.

While elaborating the research method we aimed at assembling a questionnaire that is appropriate for conducting multi-level cross-section and *cohort analyses*. Multi-level cross-section researches enables to make comparisons on conspectus levels but they do not make it possible to measure changes in the opinions of individual respondents since our samples are made up of different persons each time. That is why it is advisory to use these multi-level cross-section researches as cohort analyses, which are multi-level cross-section researches consisting of research series conducted at appropriate time periods. We propose researches in a time period of two years in the case of the furniture industry so as to dissociate the affects of environmental trends and to acquire an impression of the tempo of development and changes. Thus cohort is a group of respondents who experience the same event at the same time period. With its help we can establish what attitudes groups of the population with identical characteristics maintain to aspects of the analysed decision making in proportion to time. In addition, it was our aim to elaborate a lifestyle based segmentation model while constructing the questionnaire that enables grouping according to value orientation and family life cycle.

We used quota sampling. Sample size was 1300 persons. Assembling the quota was done based on a preliminary omnibus survey of 1054 people in which we used the basic demographical data – significant for the topic – of people planning to buy furniture in the next two years as the basis of the quota. These were: type of settlement, gender, and age group. In keeping with the regional quota (Budapest, western Hungary, and eastern Hungary) the distribution of respondents followed national rates. According to the omnibus survey of 1054 people 18.8% of the Hungarian population was planning to buy furniture at the time of the interview. The interviews were conducted in June 2009 on neutral spots (streets).

As for the demographical characteristics of the respondents, according to the preliminarily given quota, there were slightly more men (55%) in the sample. The age distribution of the respondents was: 18–25 years: 21%, 26–30 years: 17%, 31–40 years: 23%, 41–50 years: 18% 51 years or older: 21%. Two thirds of the respondents came from towns, one third of them from villages.

3 RESULTS

During primary research we examined if general behaviour trends (Törőcsik 2007) – defined as elements of impersonal customer environment in the model – are valid on the Hungarian furniture market. All these, besides verifying the theoretical model, strongly support the marketing strategy planning of business enterprises. We analysed the validity of the following trends (we signal the marketing area of practical application in brackets):

1. Furniture purchasers need *personally tailored* products as a result of ego trends derived from modern values. (product policy, communication)
2. Price is still a very important factor in decision making. However, the trend of social responsibility, environmental protection and appraising human health may also be apprehended that is why the need for *cheap eco-products* can be expected to appear on the furniture market as well. (product policy, pricing policy, communication)
3. Besides price sensitivity characteristic for furniture purchase decisions, we can observe the *trend of cheap design and cheap chic* on the furniture market.(product policy, pricing policy, communication)
4. The impact of *personal information sources* are greater on furniture purchase decisions, which comes along with the entry of a trend indicating increase in *interest in origin of product*. (product policy, communication)
5. *Counselling, personal relations* are equally important for both sexes at the point of information obtaining when making furniture purchase decisions. The general behaviour trend that men rely more on written documents than the expertise of shop assistants does not work during furniture purchase. (communication)
6. Nowadays the 'middle-class – individualistic' value trend has spread among flat users, which puts the individual into the foreground beyond the basic functionality of the 'conventional-traditional' value trend. (product policy, communication)

According to the customer behaviour trend verified first, furniture purchasers need products **tailored to individual needs** as a result of ego trends derived from modern values. The trend found by the Trend Inspiration research group in 2008 suggests that the need for personally tailored products have become commonplace. The determinant factor of this trend is exhibitionism since everything can become a tool of self expression. This refers back to ego trend (Törőcsik 2006) which means putting the individual into the foreground and the need for personally tailored product (tailored to person). In the approaching social era, knowledge-economy, individualism will become the centre element (Horx 2000). Although the trend of 'the limit in infinity' (Trend Inspiration 2009) – suggesting that because of overflowing credits prior to the economic crisis people got used to the idea that there is no limit to their ambitions – has occurred in Hungarian trend research, in 2009 in connection with the economic crisis, people face limitations in purchasing due to credit confinements. Along with our hypothesis, all these do not affect the need for personally tailored products on the furniture market.

During lifestyle based segmentation we grouped customers according to modern and traditional values. We analysed the following statements characteristic for modern values and backing up the ego trend: flexibility is typical for my lifestyle, I like buying furniture, I look for pleasure in shopping, I often entertain guests, I often rearrange my furniture, and I would like to renew my home décor more often.

Table 1. The need for personally tailored products in the group indicating ego trend[1]

How important is personally tailoredness, uniqueness for you when choosing furniture?							
	N	Very important/important valid frequency (%)	Not so important valid frequency (%)	Not important/ absolutely not important valid frequency (%)	Average	Deviation	Variance
Flexibility is typical for my lifestyle.	470	74.3	14.3	11.4	4.04	1.19	1.39
I like buying furniture, I look for pleasure in shopping.	623	73.7	15.9	10.4	4.05	1.14	1.31
I often entertain guests.	533	70	18.4	11.6	3.98	1.18	1.39
I often rearrange my furniture.	255	73.7	14.9	11.4	4.01	1.17	1.37
I would like to renew my home décor more often.	604	75	13.1	11.9	4.05	1.18	1.39

In line with the next trend, we can expect the need for ***cheap-eco*** products to enter the furniture market as well. Eco means the commitment for the protection of both people and their environment. One of the values of the ' individualistic – middle-class' value trend is that the need for individual integrity and thus dehumanization seemed to be one of the key questions at the turn of the century (Kapitány – Kapitány 2000). Furthermore, our hypothesis is built on the previous research result that price is the first and most important aspect of choice in most furniture categories (Pakainé et al. 2007). Eco products will become characteristically cheaper along with future improvements, cheap-eco products will appear, resulting in the appearance of the cheaper versions of previous products and of eco products designed with the aim of cheapness. (Trend Inspiration 2010). Our hypothesis dealt with '*conscientious purchase*' (Trend Inspiration 2010), which means that products will be expected to have an *eco- and charitable* character. *Eco chic* trend will mean not only an eco-conscious purchase but its communication towards customers. The booming 'CSR' activities of companies back up this trend as well. According to this trend affecting furniture manufacturers, customers would like to see transparent companies; this means that customers would like to be able to have an overview on the whole production process.

In accordance with the results of the whole sample analyses, environmental protection is not a characteristic aspect among the population planning to buy furniture in the next two years. However, being detrimental to health very much is. *(Table 2)*

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[1] 1-5 scale of importance where 1 means 'absolutely not important' and 5 means 'very important'

Table 2. Environment- and health consciousness[2]

	N	Min	Max	Average	Deviation	Variance
People do not pay attention if the furniture purchased is recyclable or not.	1095	1	5	4	1.09	1.18
Most people cannot identify if a given piece of furniture is environmentally friendly.	1115	1	5	3.83	1.13	1.27
People do not take into account the effects of a product on the environment while making a purchase decision.	1113	1	5	3.96	1.04	1.09
It should be harmless to health.	1115	1	5	4.55	0.8	0.64

We examined the raison d'ętre of the need for *cheap-eco* products *first of all* among those who think that people take into consideration the effects of products on the environment. The average importance of low price was 3.69, its deviation was 1.14, and its variance was 1.29 in this group. The average agreement with the statement 'Excellent quality is more important than price when buying furniture' was 3.47 in this group. The deviation was 1.061 while the variance was 1.126. (N=355)

The estimation of price-quality ratio of furniture purchase among respondents keeping environmental aspects in mind was similar to the whole sample: on the valid frequency range (N=340) 58.8% of the respondents usually buys good quality but pays attention to the price as well and 31.2% of them generally buys average quality products for moderate prices. 2.6% of the people typically buy good quality even for higher prices and 0.9% of them look for the cheapest solutions even at the cost of quality.

The average agreement with the statement 'people do not pay attention if the furniture purchased is recyclable or not' was 4.00 in the whole sample, the deviation was 1.09 while the variance was 1.18. Price was also an important aspect (64.3%) for those respondents who keep recycling factors in mind when buying furniture (N=308). The result of the question analysing the costs of furniture purchase according to price-quality ratio in the group: on the valid frequency range 58.4% of the respondents usually buys good quality but pays attention to the price as well and 30.5% of them generally buys average quality products for moderate prices. 3.2% of the people typically buy good quality even for higher prices and 1.3% of them look for the cheapest solutions even at the cost of quality.

The number of respondents considering health protection at least moderately important was 1082 persons in the sample. 63.3% of them found low prices important or highly important. The result of the question analysing the costs of furniture purchase according to price-quality ratio in the group: on the valid frequency range 62.7% of the respondents usually buys good quality but pays attention to the price as well and 27.3% of them generally buys average quality products for moderate prices. 5.1% of the people typically buy good quality even for higher prices and 0.9% of them look for the cheapest solutions even at the cost of quality.

In summary we can say that the role of price is outstandingly important when making decisions about furniture purchase even among environment- and health-conscious groups.

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[2] 1-5 scale of importance where 1 means 'absolutely not important' and 5 means 'very important'

The research has proved that, besides price, quality also occurs to modulate the situation to some extent.

According to the next analysed trend, besides price sensitivity – which is so typical for decisions about furniture purchase – the need for ***cheap design and cheap chic*** is also characteristic for furniture markets. Cheap design means the democratization of design (Trend Inspiration 2010). Along with this trend, customers would like more imaginative, more beautiful products for lower prices. Cheap chic (Trend Inspiration 2010) is about products that become cheaper through innovativeness. A need for aesthetics occurs besides convenience in the ' individualistic – middle-class' value trend that, on the one hand, serves the needs of a society that turns outwards and seeks the acknowledgement of others to prove their own successfulness but, on the other hand, it serves the needs of the individual as well. One of the values of aesthetics is conveyed by the society assigning the greatest value to joy, attractivity (Kapitány – Kapitány 2000).

To verify our hypothesis we analysed the importance of form/design, aesthetics, fashion, functionality and durability among price-sensitive respondents. 504 respondents were price-sensitive in the sample from the aspect of the hypothesis. They did not agree with or were not certain about the attitude statement that 'the excellent quality of the product is more important than its price when buying furniture' (agree and disagree as well). According to the results summarised in *Tables 3 and 4*, durability and functionality are outstandingly important even in the case of price-sensitive customers. In proportion to importance averages, they are closely followed by aesthetics and design. Fashionableness is a moderately important factor.

Table 3. Design and functionality among price-sensitive customers 1

	N	Min	Max	Average	Deviation	Variance
Durability	491	1	5	4.71	0.523	0.274
Functionality	490	1	5	4.64	0.616	0.379
Aesthetics	488	1	5	4.48	0.696	0.484
Design	481	1	5	4.20	0.899	0.808
Fashion	481	1	5	3.31	1.202	1.446

Table 4. Design and functionality among price-sensitive customers 2[3]

	N	Important valid frequency (%)	Not so important valid frequency (%)	Not important valid frequency (%)
Durability	491	96.5	3.5	0
Functionality	491	94.5	4.9	0.6
Aesthetics	488	92.0	6.8	1.2
Design	481	81.9	13.5	4.6
Fashion	481	45.6	33.7	20.7

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[3] 1-5 scale of importance where 1 means 'absolutely not important' and 5 means 'very important', in the table: important: categories 4-5, not important: categories 1-2

According to the next analysed trend, ***personal information sources*** have greater influence on decisions about furniture purchase and this comes along with the occurrence of the trend indicating the i*ncrease in the interest of product origin*. The question dealt with *authenticity* as well and it examined the role of information coming from given sources in the decision making process. The search for *authenticity* occurs as the counter-trend of pleasure search in connection with customer expectations (Törőcsik 2006) where credibility is in the foreground and finding a trustworthy manufacturer and its store requires great awareness and commitment from the customer. The need for transparent companies originates from the fact that customers are more likely to believe their mates than companies. According to our verified hypothesis, personal information sources are observably higher rated on the Hungarian furniture market.

In case of personal information sources, friends and acquaintances turned out to be the most creditable sources from the aspect of purchase decisions, followed by furniture retailers, joiners, interior designers and building contractors (evaluation on a scale of importance where 1 means 'absolutely not important', 5 means 'very important'/How important are the given information sources for you when making decisions about furniture purchase?). The situation was modulated when we analysed the role of informants in further detail by correlating the opinions of people working in furniture trade (*Table 5*). When contradictious opinions occur, manufacturers and designers become more creditable. Respondents take into account the opinion of retailers less than that of others.

Table 5. The role of advisers[4]

Adviser	Valid frequency	N
Interior designer	73.25	1174
Retailer	26.75	
Manufacturer	77.23	1186
Retailer	22.77	
Interior designer	45.63	1166
Manufacturer	54.37	
Interior designer	37.72	1169
Joiner	62.28	
Joiner	83.84	1176
Retailer	16.16	

When we took **impersonal information sources** into consideration during our analysis, we found that friends and acquaintances were still on the top of the list. According to the importance average, besides personal acquaintances, retailers and joiners preceded any impersonal information source. The role of interior designers and building contractors were moderate, many impersonal information sources preceded them (catalogue, Internet magazine, exhibition).

In case of impersonal information sources *catalogues are the most important sources followed by the Internet, magazines, exhibition and then by flyers*. Television, local daily newspapers, women's magazines, weekly or monthly newspapers, radio stations and national daily newspapers did not turn out to be creditable information sources.

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[4] Whose opinion is determinant in case of contradicting notions?

While analsing the **interest in origin of product**, we found that the place of origin is less important when we are choosing furniture. The importance average of the place of origin (a 1–5 scale where 5 means 'very important') was 2.9, deviation was 1.28 and variance was 1.62. If we take a closer look we find that: 31.1% of the respondents found this aspect important or very important, 31.6% of them found it moderately important and 37.3% of them thought it was not important (or absolutely not important). The difference between 'important' and 'not important' categories is only 6.2% in favour of the 'not important' category.

The situation was modulated when we asked a concrete question: do you prefer buying Hungarian furniture? 59% of customers prefer Hungarian furniture. This rate of preference was independent of age, region and gender (Chi square test, 0.05 significance level).

Among people preferring Hungarian furniture we asked an open question about the type of criteria they require Hungarian furniture to meet. Quality was mentioned most often (69%) followed by price (51%), guarantee (31%), repair services (21%), complementary services (5%) and reliability in 2% of spontaneous remarks.

We examined in our research the need for furniture purchase at *joiners*. 61% of the respondents would not have his/her furniture made by a joiner but 10% of them were sure to order furniture from a joiner, and this is reassuring. While analysing significant differences in opinions (Chi square test, 0.05 significance level) we found that younger people were more open to order from joiners and people living in eastern and western Hungary also prefer ordering from joiners while those living in Budapest do not. The spontaneously mentioned and most important reasons for ordering from joiners: meeting unique requirements (53%), personal acquaintanceship (14%), credibility, reliability (13%), quality (8%), low price (8-8%), precision of joiners (4%) and the statement 'Hungarian joiners are good' (4%). Spontaneously mentioned reasons of those not planning to order from joiners: higher price of joiners (25%), longer time (8%), the simplicity of shopping in a department store (8%), 'preferring to see what they buy' (7%), wider choice in department stores (6%), not reliable, not creditable (5%), longer acquisition time (5%), joiner cannot make it (3%) and 'do not know any joiners' (3%).

Reliability/credibility occurred among spontaneously mentioned reasons for buying from close, local members. It was also confirmed that the role of personal connections, informants is significant in connection with furniture purchases.

The trend that ***counselling***, personal relations are more important for women since men rely more on written documents during purchases was not confirmed on the furniture market. The need for *counselling* is a general behaviour trend characteristic for our time (Törőcsik 2006), which signals that customers entrust certain decisions they have little knowledge about to experts. The role of shop assistant is dominant in making furniture purchase decisions (Pakainé 1997), appropriately trained people can determine the decision making process since consumers need tangible help and counselling when making decisions about furniture purchase.

We examined the differences in opinions between personal and impersonal information sources – analysed in connection with the previous hypothesis – in proportion to gender to examine this hypothesis. We did not find any significant difference in the opinions in personal aspects (One Way ANOVA, 0.05 significance level).

Table 6. Opinions about personal information sources among men[5]

	N	Categories 4–5 valid frequency (%)	Moderate	Categories 1–2 valid frequency (%)
Friend, acquaintance, relative	530	68.3	21.5	10.2
Joiner	512	62.1	27.7	10.2
Retailer	526	59.5	29.3	11.2
Interior decorator	506	40.1	20.6	39.3
Building contractor	500	28.4	27.6	44.0

We verified the assumption that the ***' individualistic – middle-class ' value trend*** **has spread** among flat users which puts the individual into the foreground beyond the basic functionality of the 'conventional-traditional' value trend. The motto of this new value trend is to feel oneself comfortable; self-expression has become typical in furnishing. This, on the one hand, serves the needs of a society that turns outwards and seeks the acknowledgement of others to prove their own successfulness but, on the other hand, it serves the needs of the individual as well. The shift between the two value trends became multitudinous in the 1960s in Hungary and in a certain way that resulted in mixed forms. The two value trends mixed and gradually shifted towards the individualistic value trend (Kapitány – Kapitány 2000).

The lifestyle based segmentation carried out during the research confirmed that there are two groups among Hungarian furniture purchasers that own the modern values of the 'individualistic – middle-class' value trend characterised by Kapitány – Kapitány (2000). These two groups are the 'modern, innovative' (21%) and the 'demanding, modern' (19%) amounting to 40% of furniture purchasers. Evidences of modern values can be detected in the additional three groups (escapist 10%, style-less 29%, frustrated 21%) but they more or less stick to traditions. The practice of segmentation according to values is widespread in lifestyle based models. The Gallup model identifies groups in a space determined by traditional-modern or individualistic-social values. The Lifestyle Inspirational model segments groups according to pace of life and value orientation. The SINUS milieu model creates groups according to basic value orientation, everyday activities, general attitudes and everyday aesthetics. The analysis of the role of values was confirmed by Lazer (1971) who stated that lifestyle is the result of factors such as resources, culture, values, rules, punishments and symbols.

In our work we aimed at developing a model – in connection with the customer behaviour model dealt with in the introduction – that enables us to segment furniture purchasers based on lifestyle. That is why segmentation was done according to the following variables:

1. Socio-demographic: taking into consideration age, region, qualification, subjective living standard, character of flat/house, and especially life cycle: the age of oldest child, marital status (single, couple), age and economic activity.
2. According to questions of attitude: they served the analysis of attitudes towards traditional-modern values, furniture purchase and home décor and that of factors of furniture choice. According to value orientation we determined modern and traditional furniture purchasing and using values in accordance with *Table 6*.

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[5] 1-5 scale of importance where 1 means 'absolutely not important' and 5 means 'very important', in the table: important: categories 4-5, not important: categories 1-2

Table 7. Modern and traditional values in lifestyle based segmentation

Modernity	Tradition
Self-expression, the individual is in the centre (colour, form, design, fashion, brand products, tailored to person). Flat as the source of joy.	Functionality in furniture use (long endurance, manufacturing precision, cleanness and order as basic value).
Furnishing principle: 'feel comfortable', sacrifices time, and goes into details.	Functionality in home décor.
Provoking positive reaction from the social environment by self-expression. This means fear/risk at decision making. Mutual presence of confidence and fear.	Provoking positive reaction from the social environment by correspondence, adjustment to others.
Chosen relationships are higher valued, more frequent guests; accessible spaces are created in accordance with this.	Less guests.
Changes, rearrangements are typical.	Continuity, rearrangements are not typical.
Eclectic home décor (memorabilia from the past together with modern objects in one space).	Respect tradition in home décor, influenced by average standards, mediocre principle, follows uniform style determined by tradition.
The role of the Internet, virtual objects, pictures.	Written text, personal communication.
Flexible pace of life (workplaces mixed into each other).	Considerate, slow pace of life.
Self-expression penetrates working areas.	Strict functionality (kitchen, pantry, workshop).
Search for experiences is characteristic for lifestyle.	Aspiring safety in lifestyle.
Critical approach, need for authenticity.	
Basic value: *joy, self-centred, measures own success through acknowledgement of others.*	*Basic value:* *belonging somewhere, rules, norms, authority*

We used the k-mean cluster statistic method for determining groups. *Figure 2* shows the segments according to family life cycle and value orientation.

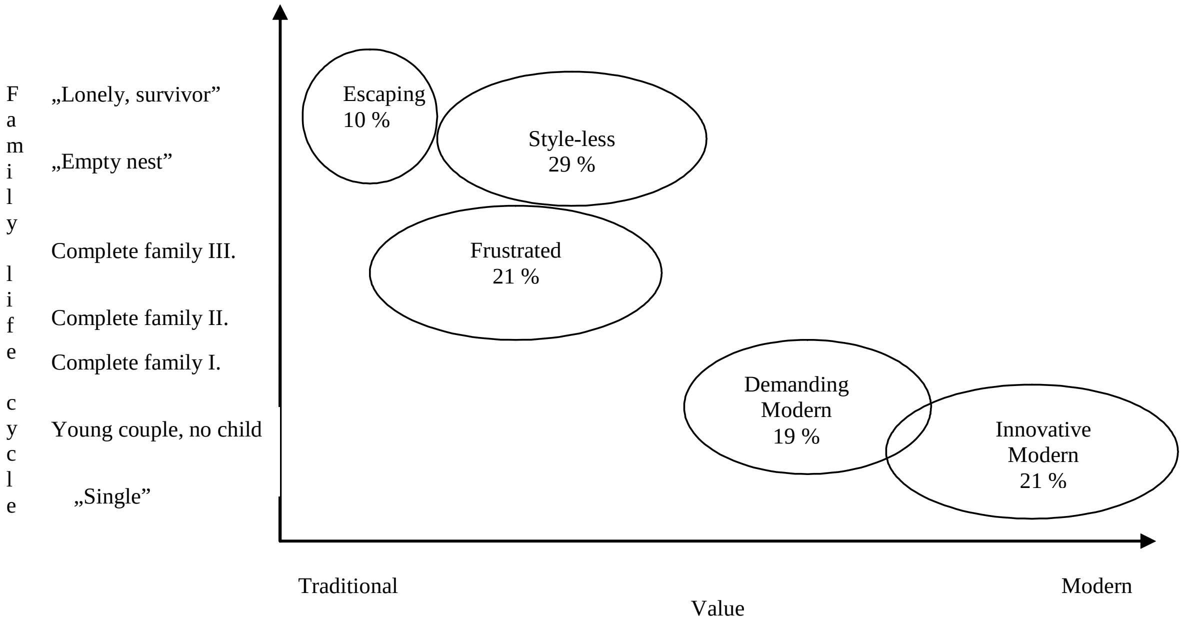
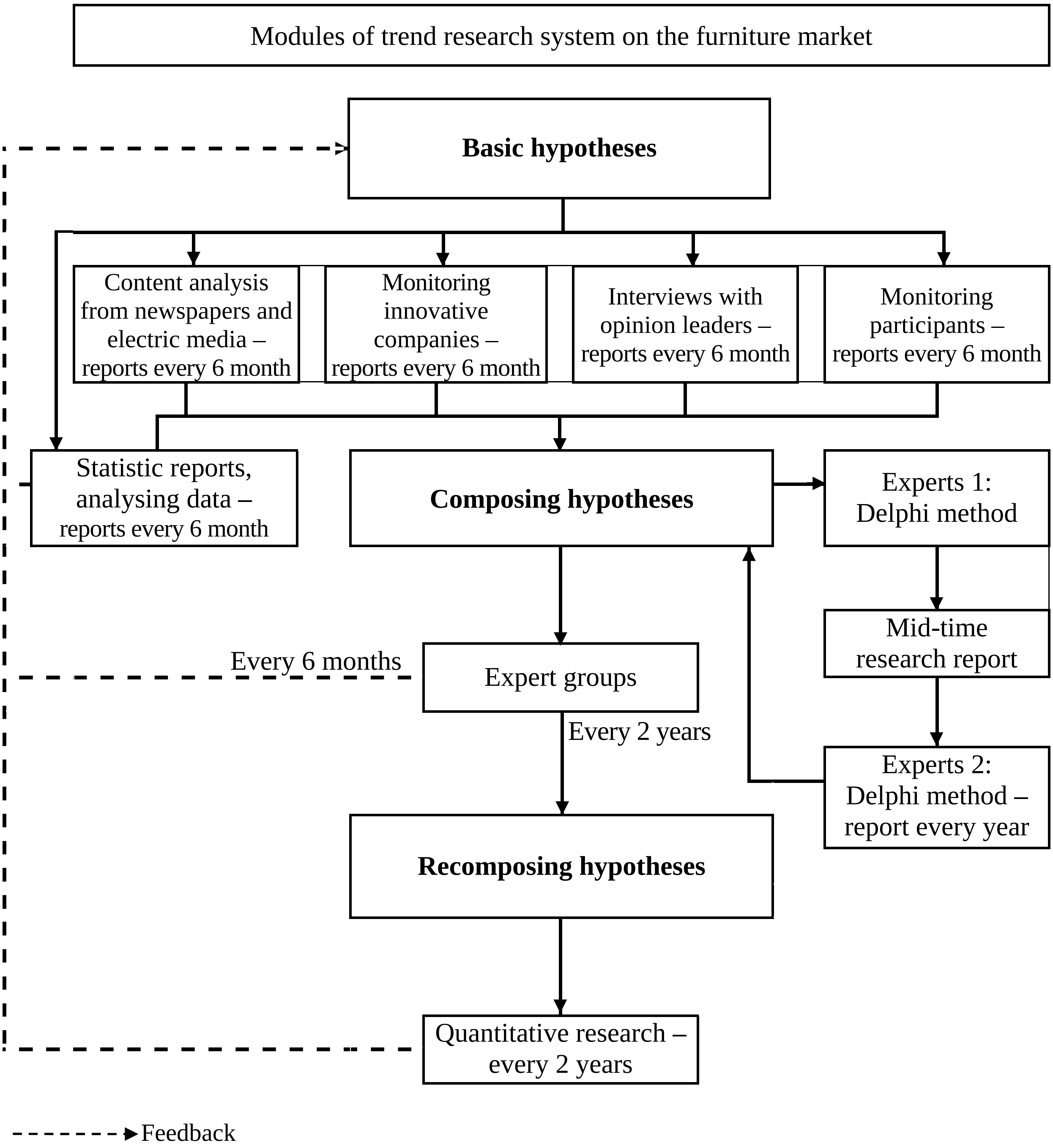


Figure 2. Home décor style groups in Hungary

4 DISCUSSION

The result of our research confirms the necessity of trend analysis on the furniture market verifying the validity of several general behaviour trends on the furniture market. We recommend a *research system of multi-level modules* focusing on the furniture market that could reveal special characteristics of this market besides monitoring and testing general trends. It is our aim to explore greater correlations about the living standards of customers, consumers, about the changes in values, the features of lifestyle so as to help companies to adapt to the market. Qualitative research methods are primarily needed to reveal new phenomena but we cannot neglect quantifiable results either. An interdisciplinary approach will be further needed in future researches taking into account mainly the research results and methods of sociology and psychology. It is essential to give exact frames and systems of criteria before starting researches. The research methodology we suggest *(Figure 3)* refers to the furniture market and undertakes exclusively the revelation of the trends in furniture use and purchase. Besides these, it constantly monitors general behaviour trends, analyses their interpretability and validity from the aspect of the furniture market. We need to examine the results of trend researches from time to time; we have to monitor changes, the spreading process, time and pace of the phenomena.

We are planning to further research certain elements of the *customer behaviour mode*l outlined in the introduction: the effects of marketing activities as elements of the impersonal environment and the role of reference groups, opinion leaders given as elements of the closer social environment in decision making. Our aim was to create a customer behaviour model that is valid on the market of durable goods because of its cogency on the furniture market but which has to be further confirmed on additional markets. *Figure 3* demonstrates the trend research system suggested for the furniture market.



Research aim revealing trends on the furniture market, constant monitoring, analysing the validity of general behaviour trends

Figure 3. Trend research system on the furniture market

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Introduction to the FAGUS 2010 Symposium papers on European beech

European beech (*Fagus sylvatica* L.) is an important species of Central and Southern Europe where it holds dominant position according to its share in growing stock and overall economic value. Although adaptable by its genetic system, due to climate change the future status of this species remains uncertain. By strengthening the perception of vital problems which affect beech at present and by emphasizing the necessity of their further analysis, it is possible to diminish potential risks and provide adequate answers. Implementation of results will support future management of this valuable broadleaf species

In the series of similar symposia, the international scientific symposium on beech FAGUS 2010 "Is There Future for Beech – Changes, Impacts and Answers" was jointly organized by the Croatian Forest Research Institute CFI and the Hungarian Forest Research Institute ERTI, with the cooperation of the Institute of Environment and Earth Sciences, Faculty of Forestry, University of West Hungary in Sopron. Under the support of IUFRO WP 1.01.07 on Ecology and Silviculture of Beech and the European Forestry Institute, altogether 190 participants from 14 countries (Bosnia and Herzegovina, Czech Republic, Croatia, France, Germany, Hungary, Iran, Japan, Poland, Serbia, Slovakia, Slovenia, Sweden, and Turkey) participated in a 2-days conference in Varaždin, Croatia. 28 papers and 16 posters were presented, covering the field of forest ecology, silviculture, genetics and reproduction, modeling, forest protection, phytopatology, physiology and management. A field trip to Zala county, Hungary followed the conference. The presented paper's abstracts have been published as trilingual FAGUS 2010 Book of Abstracts, while the complete Summary of the FAGUS 2010 Symposium is available as a separate document[1].

In cooperation with the editorial board of ASLH, conference participants were invited to submit manuscripts. The papers were selected and reviewed through the FAGUS 2010 reviewing process based on scientific excellence and actuality of the problem investigated. The reviewers were all members of the international scientific community with confirmed expertise in forest science. It is the expectation of the organizers that these papers will contribute to the better understanding of the challenges facing beech in the upcoming era of predicted climate change.

Igor Kolar[2]
guest editor

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[1] Summary of the FAGUS 2010 International Scientific Symposium, October 27th – 29th 2010,Varaždin, Croatia and Zala county, Hungary. Croatian Forest Research Institute, Jastrebarsko, Croatia

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Future of Beech in Southeast Europe from the Perspective of Evolutionary Ecology

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Abstract – The aim of this study is to provide quantitative information on the effect of climatic change on the growth and vitality of European beech: although the species is considered in its optimum highly plastic and adaptable, it becomes climate-sensitive closer to its xeric (lower) distribution limits. The future of beech in Southeast Europe requires special attention because this region harbours significant populations living at or near their xeric distribution boundary. Even though the low elevation occurrences are uniquely vulnerable to climatic shifts, observations and modelling studies pertaining to this region are particularly scarce.

Out of climatic factors determining the xeric distributional limits for beech, Ellenberg's drought index (*EQ*) appeared as the most influential. Growth response analyses in comparative tests have confirmed the existence of macroclimatic adaptation of beech and have proven that warming and more arid conditions lead to decline of growth and vitality, while no decline was observed if *EQ* changed in the opposite direction. The response to weather extremes was investigated in field plots. Recurrent summer droughts of 3 to 4 consecutive years, above mean *EQ* value 40-42 resulted in pest and disease attacks and mass mortality.

The discussed approaches indicate consistently a high level of uncertainty regarding the future of beech at the xeric limit in Southeast Europe. According to field observations and bioclimatic data in Hungary, a large part of low-elevation beech forests presently in the zone of *EQ* index ≥20 might be threatened by the warming in the second half of the century, while higher-elevation occurrences may remain stable.

The interpretation of the results bears some stipulations, such as the consequence of ecological and human interactions in influencing present distribution patterns, the unclear role of persistence, natural selection and plasticity and uncertainties of climate projections. Grim projections may probably be partly overwritten by the mentioned stipulations and by careful and prudent human support.

genetic adaptation / climate change / drought tolerance / range retraction / xeric limits

1 INTRODUCTION

Adaptation strategy of forest trees is receiving growing attention in view of expected climatic changes. Scarcity of reliable information on responses to macroclimatic changes is a central problem and obstacle of planning for the future. In order to formulate realistic predictions, both

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the nature of adaptation to past and current climate, and the level of sensitivity to sudden environmental changes have to be understood and properly interpreted.

Conflicting approaches and unclear role of different factors determining adaptability keep adaptation to macroclimate still unresolved, in spite of its importance for practical forest management, for response prediction and risk management. Species-level (genetic) adaptation pattern is the basis for setting the rules of reproductive material use, for concepts to conserve genetic resources and for strategies to adapt to expected effects of environmental changes (Mátyás et al. 2009a).

The distribution of European beech extends across ecologically and climatically variable regions. Compared to other wide-spread tree species of Europe, it is still the one which was left in a relatively natural condition as – although in a distributional range reduced by man – it was seldom regenerated artificially and its reproductive material was not subject to large-scale commercial relocations such as oaks or Scots pine. Thus, present populations of European beech are still close to a "wild state". Therefore beech is a well suited model species to study adaptation strategy of long-living, deciduous climax species to climate and to changes of climate. The species is considered climate-sensitive and vulnerable to changes. Therefore its response to predicted large-scale changes of climate is a critical issue.

In this study an attempt is presented to trace, quantify and project the impacts of macroclimatic change on the distribution and vitality of beech, with results interpretable for the practice, as such information is urgently needed to develop adaptation strategies for both forestry and conservation. Investigations were concentrated to the xeric limits in SE Europe. This region, where the retreat of the species is imminent, has been largely neglected by European studies (Jump et al. 2009, Mátyás 2010, Lindner et al. 2010). The authors consider the detailed, practice-oriented investigation of climate impacts at the xeric limits of primary importance because especially the low elevation occurrences of beech in the region are uniquely vulnerable to climatic shifts.

Although climatic selection acts on the local, microclimatic level, macroclimate is generally considered as an appropriate surrogate. We also follow this convention in this study mainly for two reasons: available climatic scenarios define changes on macro-level only, and on the other hand, in forestry, local data on micro- and meso-climate are in most cases lacking or unreliable.

1.1 Hypotheses of adaptation strategy and pattern of beech – ecotypes, random effects vs. macroclimatic clines

Hypotheses in contemporary silviculture on the adaptation strategy of K-strategist or climax tree species are originating from ecology. Considering the strong and lasting effects of local selection, a close (“ecotypic”) adaptation has been implicitly assumed for K-strategist tree species’ such as beech. This view has been further supported by numerous field experiments with perennials, starting with Clausen et al. (1940). Studies on intraspecific genetic variation patterns of beech also explain spatial differentiation mostly as ecotypic (e.g. Wühlisch et al. 1995, Kleinschmidt – Svolba 1995, Jazbec et al. 2007), i.e. as result of close adaptation to local ecological conditions. As a corollary, beech is generally considered to be a climate-sensitive species throughout its entire European distribution area.

Recent developments of phylogeography and molecular genetics provide arguments pointing towards the role of random effects in counteracting close adaptation. First, the postglacial return of beech from various refugia to Central, and especially to Northern Europe is relatively recent, and its migration speed to follow climatic shifts is low (Davis 1981). Its genetic structure seems to have been impacted by random separations and mergers of lineages (Magri et al. 2006, Gömöry – Paule 2010). This renders a very close adaptation to local conditions less probable. Long-range gene flow and genetic interaction between distant populations, although less intense than in the case of widespread conifers, is also acting against well differentiated ecotypes. For example, a recent study identified beech pollen transport – depending on wind trajectories – as distant as from NE France to Catalonia (Belmonte et al. 2008). There are a number of other biotic reasons why the genetic system of tree species may robustly counteract strict local adaptation (Mátyás 2007).

Annual growth and development cycle of beech is governed besides the photoperiod by the amount of physiologically effective heat sum (Kramer 1994, Chuine et al. 2003) and of course precipitation. As the latter two are unevenly distributed across the range of the species, it may be assumed that diverging direction and intensity of climatic selection leaves also traces in the adaptive genetic variation pattern within the species. Proofs of macroclimatic selection are however surprisingly seldom found in beech. For instance, the range-wide analysis of metabolic allozyme gene loci has established correlations of allelic frequencies with climate-dependent factors such as altitude and continentality (Comps – Mátyás et al. 1998). Traces of genetic similarity among geographically distant populations growing on climatically similar sites point in the same direction (A. Borovics pers. comm.). The patterns of phenological behaviour observed in early phase of beech provenance trials also suggest a clear effect of macroclimate on genetic differentiation within the species. For example, bud break of beech shows a clinal East-West pattern: Atlantic coast provenances[1] are late, while Alpine and SE-European continental ones are early flushing (Wühlisch et al. 1995, Führer et al. 2009, Gömöry 2009).

Considering the pace of expected changes as compared to the generation length of beech, it is obvious that adaptation to rapid changes and to extreme events can function only if a strong component of plasticity (and, possibly, not yet identified epigenetic effects) is augmenting the inefficiency of selection and gene flow to adjust genetically set responses (Mátyás et al. 2010a, Finkeldey – Hattemer 2010). Surprisingly this aspect is largely missing from the agenda of ecological and genetic research in beech, but also generally in forest tree species.

1.2 The threat to xeric limits in SE Europe

Xeric (or rear, trailing) limits at the low latitude and low altitude end of distribution ranges are determined by climatic aridity (Mátyás et al. 2009b). Xeric limits of beech are apparent along lower elevations of Mediterranean mountain ranges, however on the temperate-continental plains and hills of SE Europe they are more difficult to follow due to more complex ecology and human disturbance. These limits are handled by contemporary statistic and process-oriented models with considerable uncertainty (Kramer et al. 2010).

At the xeric limit ecosystems are dependent on a volatile minimum of rainfall and are therefore sensitive to prolonged droughts. What makes this zone especially vulnerable to climatic shifts is the magnitude of the *latitudinal lapse rate* in flat terrain. It is generally known that the altitudinal lapse rate (gradient) for temperature (i.e. the rate of change with increasing elevation) amounts to 5.0–6.5 ºC/1000 m. At the same time, the latitudinal lapse rate is less recognized: in the temperate zone its mean value is around 6.9 ºC/1000 km – a difference of three magnitudes (Jump et al. 2009). One degree of temperature increase causes a shift upwards along a mountain slope of approximately 170 m: the same change on a plain triggers a shift of close to 150 km northward. A consequence is that obviously even minor changes of temperature *affect disproportionately larger tracts on plains* as compared to mountainous regions. Presuming a spontaneous migration speed for beech of approx. 20 km/century (Davis 1981, Mátyás 2007) an increase of temperature of just 1ºC would imply for beech a horizontal migration time of 750 years to follow the change. This fact explains the much larger vulnerability of low elevation occurrences in Southeast Europe.

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[1] The term "provenance" is used in the paper synonymously for "transferred population of known origin”.

According to calculations of the IPCC (Christensen et al. 2007), predicted temperature changes of the critical summer climate at the end of the century are much milder in North Europe between latitude 50º and 70º N, as compared to South Europe between 50º and 30º N. *Table 1* shows that changes are more extreme in summer than those of annual averages. Drought projections for Southern Europe are also serious, while none are predicted for North Europe.

Table 1. Predicted annual and summer climate changes for the period 2080-2099 vs. the reference period of 1980-1999, according to the A1B scenario (data from the IPCC, Christensen et al. 2007)

	Change of				
	mean annual temperature dT (°C)	mean summer temperature dT (°C)	mean annual precipitation dP (%)	mean summer precipitation dP (%)	percentage of dry summers (%)
South Europe, Mediterranean	+3.5	**+4.1**	- 12	**- 24**	**42**
North Europe	+3.2	**+2.7**	+ 9	**+ 2**	**0**

The expected drought frequency was separately modelled by us for the Carpathian Basin due to the importance of this climate factor (Gálos et al. 2007). The results of the projection, using the regional climate model REMO developed by the Max Planck Institute for Meteorology (Hamburg) indicate a very similar outcome: in the second half of the 21st century every second year could bring major summer drought events *(Table 2).* Projected summer precipitation change is of special significance at the xeric limits which may affect profoundly the available climatic niche of dominant forest species, such as beech. This justifies the separate treatment of the Southeast European region.

Table 2. Frequency of recent and projected drought events for Hungary, according to scenario A1B, calculated with MPI's REMO regional climate model. Reference period: 1961-1990 (Gálos et al. 2007)

Period	Drought summers		
	number of years (out of 50 years)	mean of precipitation anomalies (%)	mean of temperature anomalies (°C)
1951–2000	15	–28.0	+0.9
2001–2050	17	–19.8	+1.5
2051–2100	26	–37.6	+4.2

1.3 Climatic factors of the xeric distributional limits for beech in SE Europe

The actual climatic envelope (niche) of beech has been repeatedly modelled (e.g. Kölling 2007, Fang – Lechowitz 2006, Bolte et al. 2007, Kramer et al. 2010). However, the studies focus on continental-scale effects of climate change, using low resolution climatic and species distribution data.

To identify the limiting macroclimatic factors at the xeric distributional limits of beech forests a regional modelling analysis was carried out in Hungary (Czúcz et al. 2010). Only data of occurrences were analysed which fulfilled the criteria of zonality (i.e. primarily determined by macroclimate). The stands have been grouped by the inventory grid system of the Forest Service (~1.5×1.9 km cells). The response variable was the percentage of presence of beech in the respective cell.

The probability of presence of beech was modelled by the variables seasonal and monthly temperature and precipitation means, interpolated for the grid cells. In addition Ellenberg's climate quotient (*EQ*, Ellenberg, 1988) was also applied, defined as the mean temperature of the warmest month (July, T_{07}) divided by annual precipitation (P_a):

$$EQ = 1000\ (T_{07} / P_a)$$

Ellenberg's climate quotient is a simple index expressing the joint effect of temperature and precipitation, and it has been generally used to express humidity conditions in Central Europe.

As the main modelling tool we used conditional inference-based regression trees (Hothorn et al. 2006). This technique identifies at every branching only the most influential variable. We fitted several regression tree models to subsets of the data in a bootstrap-like framework, using different calibration and evaluation data sets each time (for details see Czúcz et al. 2010). Examples of regression tree models are presented in *Figure 1.*

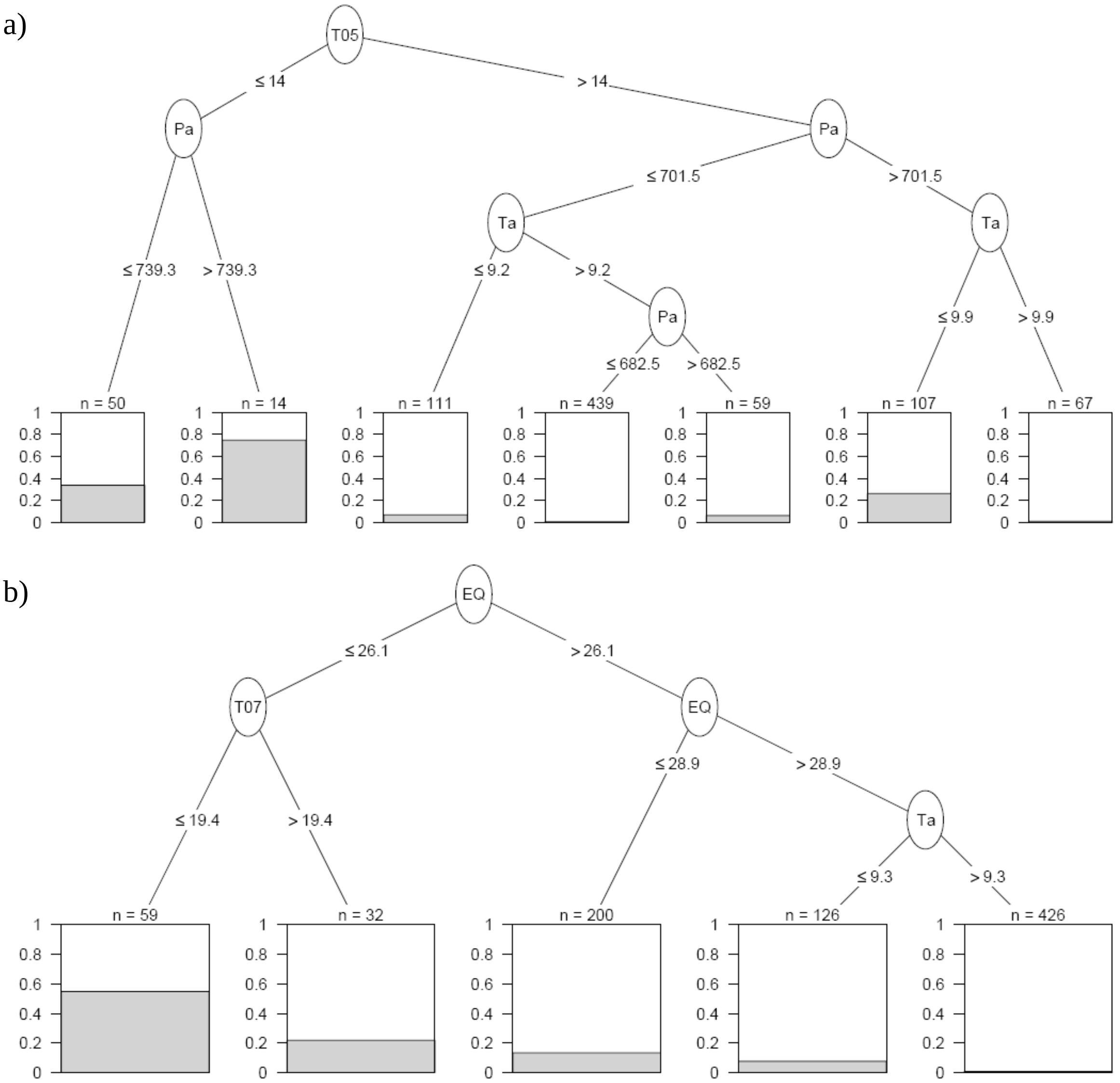

Figure 1. Examples of regression tree models for the xeric limits of zonal beech forests, determined by (a) basic climatic predictors only; and (b) with EQ included. In the terminal nodes bar diagrams visualize the probability of presence. (n: number of cells in the node). See text for variable names (Czúcz et al. 2010)

Out of the basic set of climatic variables late spring (May) temperature (T_{05}) appeared as the most influential predictor. In addition, annual precipitation (P_a) also played a significant role in determining the presence of beech near its xeric limit *(Figure 1a)*. Grid cells with high late spring temperatures (T_{05} > 13.5–14 °C) contained relatively few beech stands. Alternatively, cells with the highest probability of presence had relatively cool May temperatures (T_{05} <14 °C), and received a higher amount of rainfall (>740 mm) per year.

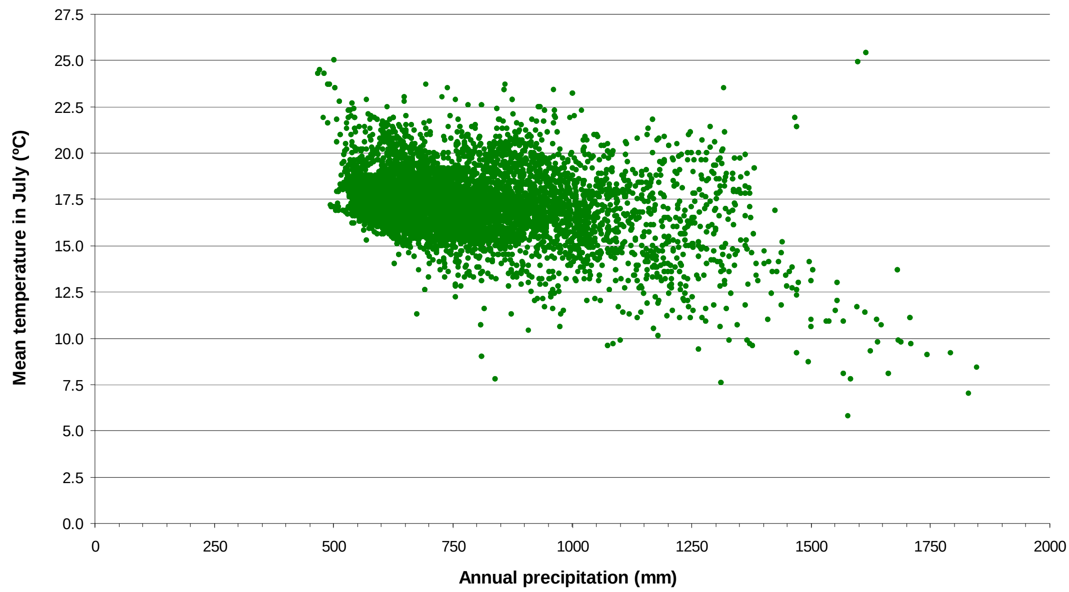

Figure 2. The climate envelope of beech in Europe using long term (1950-2000) climatic average of annual precipitation and mean July temperature. Climate data were extracted from the WoldClim high resolution interpolated climate database. (Compiled for EUFORGEN beech distribution data by E. Rasztovits)

If Ellenberg's climate quotient (*EQ*) was included among the predictor variables, it almost always appeared as the most distinguishing predictor. In the example of *Figure 1b* its maximum (limiting) value was 28.9. Apart from *EQ*, May temperature and annual temperature appeared again in other runs of bootstrapped decision tree models (Czúcz et al. 2010). The obtained results for limiting climate conditions for beech at low latitude/low altitude were compared with other, published ones *(Table 3)*.

Table 3. Comparison of results of the present analysis with literature data on xeric limits of beech occurrence (Czúcz et al. 2010)

Source	Temperature limit (°C)	Precipitation limit (mm)	*EQ* index limit (°C/mm)
Fang and Lechowicz 2006	ann. mean < 13.5, July mean < 23.0	ann. mean > 900	29.0
Kölling 2007, cool-dry limit	ann. mean < 9.5	ann. mean > 500	–
Kölling 2007, warm-humid limit	ann. mean < 13.5	ann. mean > 850	–
Goetz in: Bolte et al. 2007	–	ann. mean > 500	–
Hoffman in: Bolte et al. 2007	July mean <19.0	–	–
Czúcz et al. 2010, "xeric limit"	ann. mean < 9.3	ann. mean > 680	28.9

* warmest month: 23.0 °C

The climate envelope of beech *(Figure 2)* indicates practically no presence below 500 mm annual precipitation and the bulk of occurrences stay below 20°C July mean. Most of the marginal points around the "main cloud" may be presumed to be non-zonal occurrences utilising surplus humidity (e.g. seeping water on slopes etc.). Data of *Table 3* show that the precipitation conditions at the continental xeric limit in Hungary are much drier than at the warm-humid limit in SW Europe, where the higher annual mean temperature requires significantly more rainfall. The study of Fang and Lechowicz (2006) analysed a large number of climate factors and indices, among them Ellenberg's index. Their "xeric limit" values refer to the hottest sites beech might tolerate. Despite the limited scope of their dataset, the closeness of the estimated *EQ* limit of 29.0 to ours is surprising.

It is obvious that when modelling the probability of presence of beech, neither temperature nor precipitation can be considered as a single factor. This is illustrated also on the example of the two climate factors determining *EQ (Figure 2). EQ* index seems to characterise the climate conditions for beech in the region reliably and will be used for analysing responses to changing conditions in the followings.

2 GROWTH RESPONSE TO CHANGING CLIMATIC CONDITIONS (TRANSFER ANALYSIS)

The response of populations to changed climatic environment is analysed on the basis of the genetic tolerance limit hypothesis. According to the hypothesis, the fitness of a population adapted to a certain environment declines rapidly with worsening conditions. Natural selection intensifies simultaneously and adjusts the genetic makeup to the changed environment, depending on available genetic variability. At the genetic tolerance limit climatic selection ends up in mass mortality, where the genetic and ecological possibilities of adaptation are exhausted (Mátyás 2010a, *Figure 3*). Due to competitive or trophic interactions in the ecosystem, fitness is usually sooner lost than the genetically set critical tolerance, through pest and disease attacks or competition by other tree species. In ecology, this is expressed as the difference between "physiological" (in reality: genetic) and ecological tolerance.

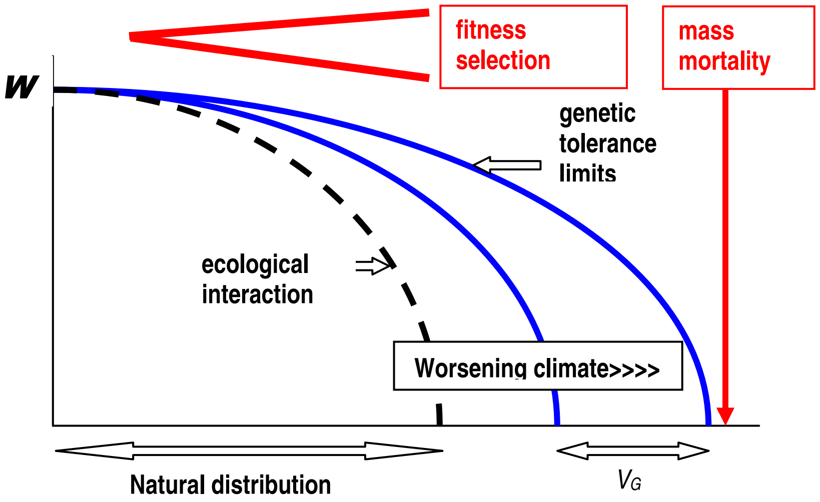

Figure 3. Ecological-genetic hypothesis of fitness loss along a climatic cline: tolerance decline and mortality triggered by worsening of climatic conditions. The genotypic variance of limits of tolerance (V_G) represents the basis of natural selection. The dashed line marks the ecological limitations of the species (Mátyás et al. 2010a)

Quantitative, adaptive genetic differentiation among provenances (in growth, phenology, and health) measured in common garden tests may be utilized to model the result of climatic selection and to forecast the effects of climatic change, as the response of populations at the test site can be interpreted as a simulation of environmental changes. Climate change as experienced by tested populations in the common garden is expressed as *ecodistance* ("space for time substitution" Mátyás et al. 2009a, 2010a).

For beech, growth response projections have not been validated thus far by field tests. The all-European beech provenance trials initiated by Muhs and collaborators (Muhs – Wühlisch 1993, Wühlisch 2007) are likewise suitable for modelling growth response to climatic changes through transfer analysis. For this purpose, experiments of the 1998 test series have been selected in SE Europe (Mátyás et al. 2009a). In this study results of two sites are introduced. For ecodistance calculation, Ellenberg's climate quotient (*EQ*) was applied. 10th year heights, measured in winter 2005/2006, have been used for the analysis.

The mid-elevation site in Straža, Slovenia provides climatically optimal conditions, while the Hungarian one (Bucsuta) is continental and relatively close to the xeric (trailing) limits of the distribution of beech, as shown by the Ellenberg indices *(Table 4).*

Table 4. Geographic, climatic data of two beech provenance trials (from Mátyás et al. 2009a)

Reg. Nr.	Country	Location	Altitude a.s.l. (m)	July mean temperature (^{o}C)	Annual mean precipitation (mm)	Ellenberg index (*EQ*)
2012	Slovenia	Straža	545	19.3	1260	15.3
2015	Hungary	Bucsuta	200	19.7	747	26.3

In *Figure 4*, data of 10 populations are shown which are represented in both tests. The ecodistance between the *EQ* at origin and *EQ* at the test site (*ΔEQ*) expresses the change of climate, where positive values indicate transfer to warmer/drier, and negative ones transfer to cooler/more humid conditions.

At the warm-continental site in Hungary (*EQ* = 26.3), all the 10 provenances have been transferred into an environment with increased continentality, higher mean temperatures and higher drought stress. On the other hand, in the Slovenian test (*EQ* = 15.3) the majority of the selected populations has been brought into an environment cooler/wetter (i.e. less stressful) than their original climate.

Response regressions were calculated between mean heights of provenances and ecodistances expressed in *EQ* values. The polynomials *(Figure 4)* express that response of provenances depends on the difference of climatic conditions at the origin and the test sites, i.e. ecological distance is a valid concept for explaining responses and substantiate the existence of macroclimatic adaptation. At the warm site in Bucsuta, Hungary, the calculated polynomial shows a clear decline of height growth beginning from *ΔEQ* value 4. Such a clear effect of changed climate is not visible at the cool, humid site in Slovenia. In this case most provenances were brought into a cooler, wetter environment than they were adapted to (*ΔEQ* reached nearly the same values as in Hungary, however in opposite direction); therefore no growth depression was detectable with growing ecodistance. This illustrates that negative response to changing environment is triggered only if the shift happens toward warmer/drier climate. The presented results for beech are supported by data of other species such as pine, larch and spruce species (for review, see Mátyás et al. 2010a) where very similar trends have been found.

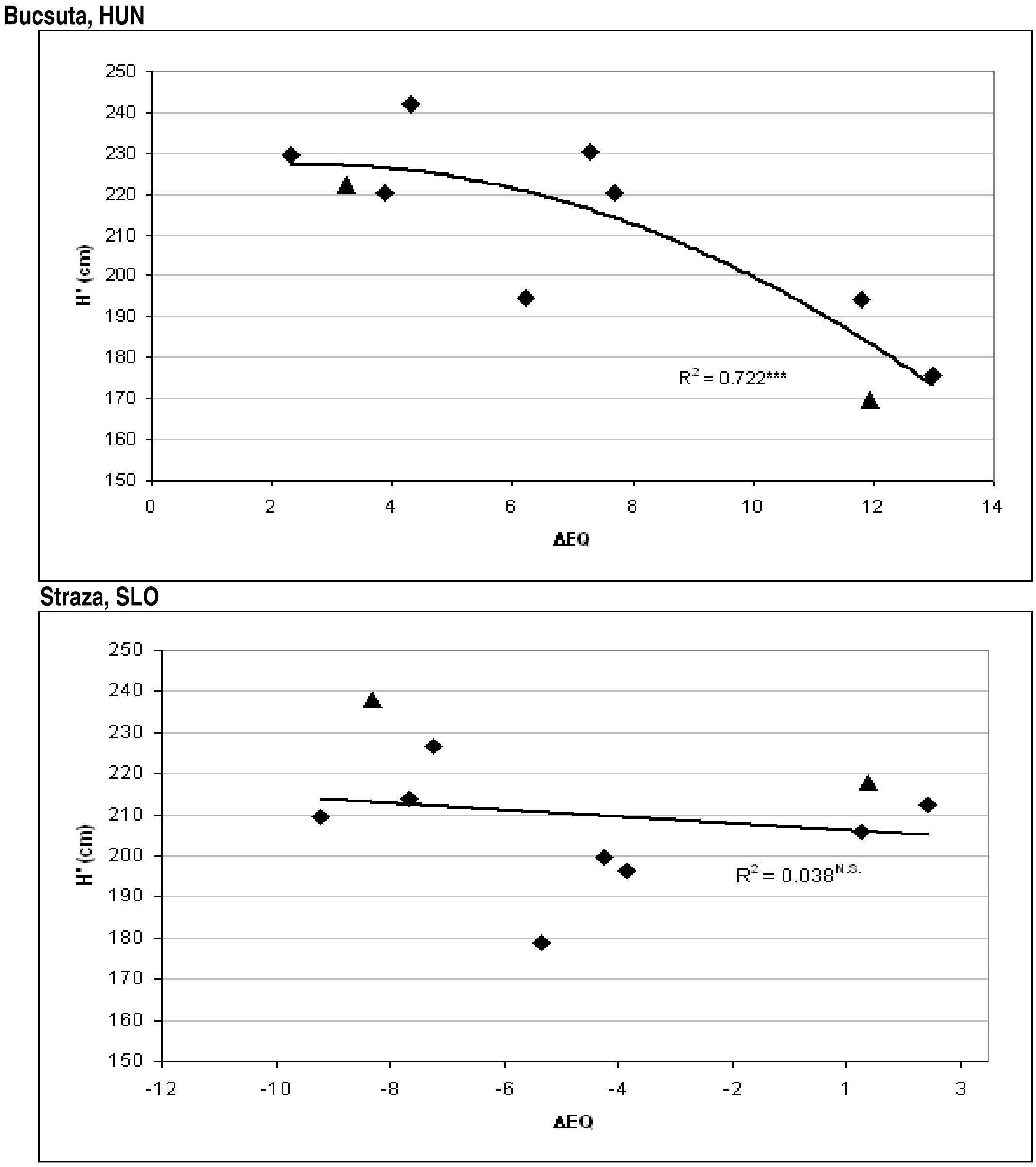

Figure 4. Regression of 1o-year height (H') of 10 identical provenances with ecodistance, at two sites with strongly differing EQ values. The sequence of provenances is the same. Compare the two provenances marked with ▲ for interaction: Tarnawa (POL, left) and Plateaux (FRA, right). Both mountain populations perform much better at higher elevation in Slovenia than in Hungary (Mátyás et al. 2009a)

The individual response of a population to changing environmental conditions along an ecological gradient is described by the term *phenotypic plasticity*. In general, plasticity has been found much more significant than expected from a "closely adapted" species. This is illustrated by the data of the Slovenian test site *(Figure 4*). Even relatively distant transfers (with high *EQ* values) do not show growth depression. Similar effects could be observed in other trials across Europe. However, close to the xeric limit, in Hungary, the buffering of plasticity does not function, as described before. Distinct interactions could be identified only in individual cases *(Figure 4).*

The growth response (or transfer) analysis of the SE European beech trials yielded the following main conclusions:

- a climate-dependent component of adaptive genetic response could be identified across populations of different origin, i.e. adaptation to (and consequently, selection effect of) macroclimate exists in beech in spite of counteracting evolutionary and ecological effects;
- the change of climatic conditions toward warming and more arid conditions lead to decreasing height growth and vitality, while vitality is not affected if changes happen in the opposite direction.
- phenotypic plasticity of all populations is considerable, but near the xeric limit its effect ceases.

2.1 Response to weather extremes

Effects of climatic change are described as shifts of vegetation zones, realised through “migration” of species. In case of forest trees, “migration” means loss of competitive potential and subsequent decline of vitality followed by pest and disease attack. However, the response of forests to drought – contrary to grass or crop vegetation – is not immediate. Forest stands, even drought-sensitive beech, survive single extreme summers and recover merely with yield loss. This is the result of deep rooting of trees, utilizing deeper soil water resources. The situation is different if drought years happen consecutively.

In the literature “mortality syndrome” (Worrall et al. 2008) cases have mostly been treated as isolated, transient problems related to extreme events, rather than as a consequence of a long-term climate shift. This is because the gradual, relatively slow change of climatic means does not express the current effect of extremes at the xeric limits. Spontaneous climatic selection is driven by recurrent drought events and the symptoms of change appear usually quite abruptly. Climatic means in models should be regarded therefore rather as surrogates for extreme events. The long-term, gradual shift of climatic factors has merely a *predisposing* role. Besides climate, the site conditions, age and structure of stand play also a predisposing role. *Inciting* factors are mainly connected to climatic anomalies especially at the xeric limits. Pests or diseases attacking populations of weakened vitality are then the *direct or proximate causes* of mortality.

Health and vitality loss due to climatic extremes: case study of beech in SW Hungary

The gradually growing moisture deficit in Hungary has led to health problems in Hungarian beech forests since the 1990s, first of all in the Southwest of the country where climatic changes were the strongest, and where the stands are at low elevation and close to the xeric limits. The weakened trees became more sensitive to secondary pests and pathogens and showed symptoms of health deterioration (early leaf abscission, sparser crowns, etc.).

The extent of climate damages of the drought years 2000–2004 has been investigated in two West Hungarian state forest companies. In 460 damaged forest compartments (total area: 3900 ha) 87.7 thousand cu.m. of damaged timber was harvested. The damaged stands were mostly above 60 years (T. Szép, unpubl. data).

The area most damaged was the Zalaegerszeg forest district (Zala county), where mass mortality was triggered in mature beech stands after regeneration cuts, when the canopy closure was opened up. This led to the outbreak of the otherwise harmless beech buprestid (*Agrilus viridis*). Damage of *Biscogniauxia nummularia* disease and of the beech bark beetle (*Taphrorychus bicolor)* occurred together with the buprestid damage. As a consequence close to 70,000 cu.m. of sanitary felling had to be executed in 2005 in that forestry district alone (*Figure 5,* Lakatos – Molnár 2009). The type of damage supports the observation of forest protection experts that disturbance of the closed canopy increases the risk of climate damage.

Figure 5. Symptoms of beech decline in 2004 in Zala county, following the damage of Taphrorychus bicolor on the trunk (Molnár – Lakatos 2009)

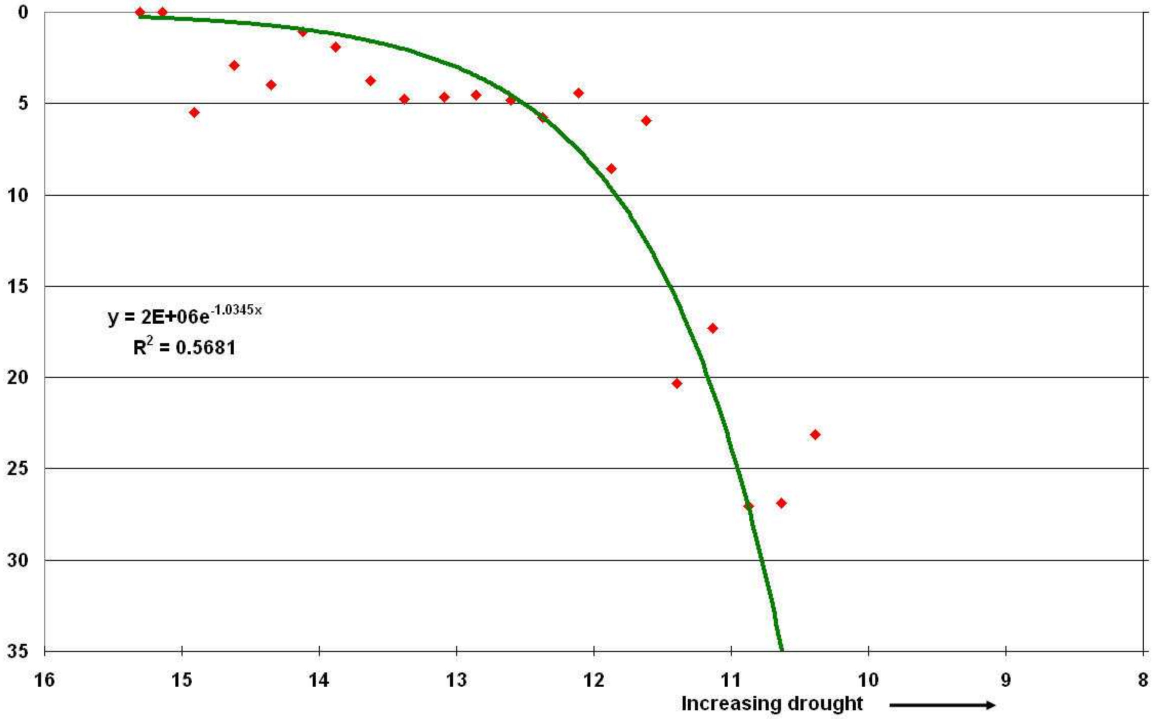

Figure 6. Percentage of compartments in West Hungarian forest companies damaged by drought events 2000-2004 (vertical axis) in relation to their climatic position (climate worsens toward lower tolerance index values, horizontal axis). Compare with hypothetic graph in Figure 3. Explanation in the text (T. Szép, unpublished data)

A close correlation was found between the climate classes and the percentage of stands damaged to various degrees *(Figure 6)*. Berki's tolerance index was used for climate classification which considers in addition to summer temperature and precipitation also spring rainfall (Berki et al. 2009).

Extrapolating the correlation onto the national forest area, 23% of the 104 thousand ha of beech forests may be assumed as threatened with 9 million cu.m. of total standing volume. For 2065, a tripling of these figures was extrapolated (76%, 29 million cu.m.). To avoid further increase of damages, a faster rotation (lowering of rotation age) is proposed by silviculturists (T. Szép, unpubl. data).

Analysis of drought events

For the closer definition of extreme weather effects leading to the “mortality syndrome” in beech, threatened stands have been selected in different parts of the country. Criteria of selection were: at least medium-age, zonal site (primarily climate dependent site, at least medium deep soil with no defects, no hydrological influence) and position as close to the xeric limit as possible. Weather conditions and mortality events in the stand in the recent past were reconstructed.

For the analysis on annual basis, *EQ* had to be modified to be suitable to characterise individual years’ weather. Mean temperature of the 3 summer months was used for the annual *EQ* index instead of just July’s, to avoid random effects of individual months (in case of 30-year climate averages, this is not a problem). Investigation of mortality frequency has shown that single drought events did not threaten the stability of populations. The recurrent drought period lasting up to five years in some areas, has however resulted in very serious mortality in the investigated beech stands, in one case the population went extinct *(Figure 7)*. As an example, effects of consecutive drought events are shown for a South Hungarian beech forest at the xeric limits of distribution. The stand has been selected at the edge of the xeric limit which is indicated by the frequency of droughty years. Years with EQ indices significantly above 30 have been considered as drought events. Mass mortality started in 2003, in the fourth year of consecutive drought, after an extremely dry summer *(Figure 8).*

Observations at other locations have confirmed that in case of beech, recurrent drought events of 3 to 4 consecutive years (depending on severity) lead in general to irreversible mass mortality and local extinction (Berki et al. 2009). It was also found that not only the number of consecutive years, but the severity of drought period has an influence on the decline. Data of selected observation plots near the xeric limit *(Figure 7)* confirm a direct, causal link between health and drought. Mean summer drought severity above *EQ* value 40–42 seem to trigger a mass mortality syndrome.

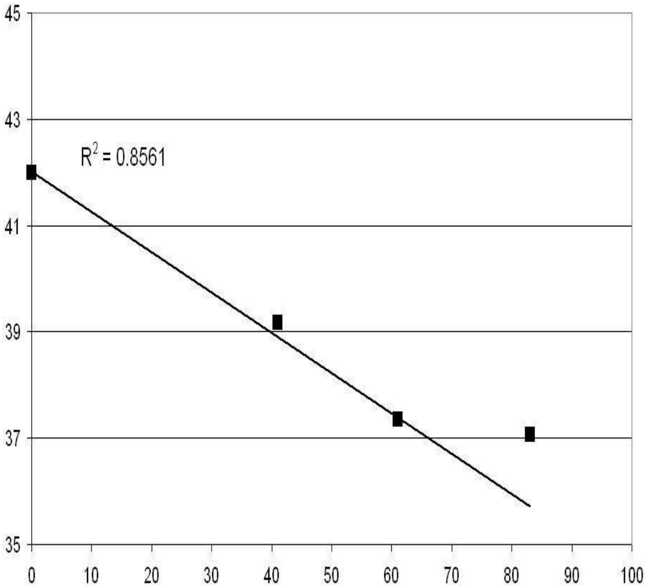

Figure 7. Average EQ value of the drought years 2000-2004 (vertical axis) and the health condition of selected mature beech plots at the xeric limit, at the end of the period (percentage of healthy individuals, horizontal axis) (unpublished data of Berki and Móricz)

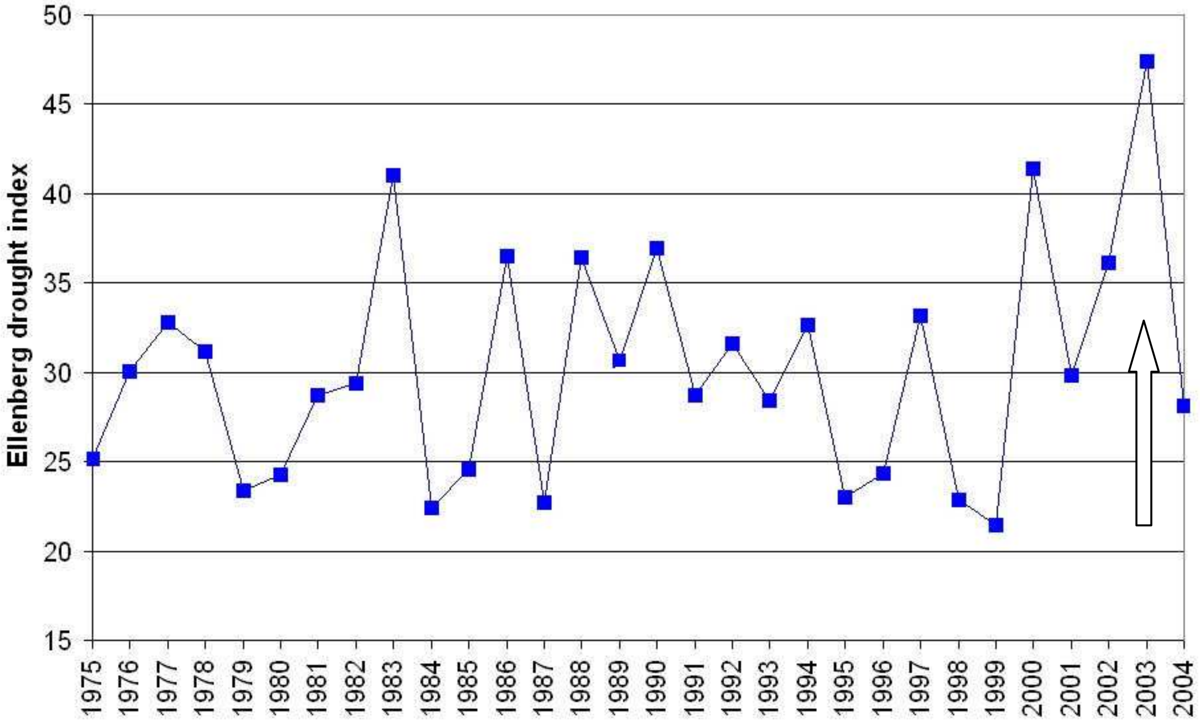

Figure 8. Drought frequency and the initiation of mass mortality of beech at the location Fiad (South Transdanubia). Years with EQ indices (vertical axis) significantly above 30 have been drought events. Mass mortality started in Fiad in 2003, in the fourth year of consecutive drought (arrow) (after Berki et al. 2009)

3 PROJECTIONS INTO THE FUTURE

How exactly xeric limits of beech will shift in the future is poorly explained by currently available models. Predictions about the role of selection and adaptation are ambiguous, as judgements of genetic adaptive potential rely first of all on model results with neutral traits, and neither statistical nor process oriented models handle conditions at the xeric limits properly (Kramer et al. 2010). Although the possibility of selection sweep as a consequence of adaptation is acknowledged but no studies exist at the trailing limits of distribution, where extreme selection for fitness comes into effect. The reliability of existing models is first of all hampered by not considering the main limiting factor at the xeric limit, i.e. the occurrence of droughts. In addition, human effects (forestry, land use) have to be considered not only for the past, but also for the future. It is also important to reiterate that present projections and models practically ignore the region, and this is supported by a detailed European study by Lindner et al. (2010). In the followings, projections for SE Europe are discussed according to the three approaches presented before.

3.1 Bioclimatic models

For predicting future distribution of beech on the basis of bioclimatic models, climatic projections of the Intergovernmental Panel on Climate Change (IPCC, Christensen et al. 2007) were applied *(Table 5)*.

Table 5. Expected changes of climatic conditions by 2050 and estimated climatic space of zonal beech (Δbeech) forest stands in Hungary. Projected changes in summer half year temperature (ΔTs °C) and precipitation (ΔPs, percents) are shown for six IPCC AR4 climatic scenarios (extracted from Czúcz et al. 2010)

	HADCM3 A2	HADCM3 A1B	HADCM3 B1	CNCM3 A2	CSMK3 A2	GFCM21 A2
ΔTs	+2.9	+3.3	+2.6	+2.4	+1.8	+2.1
ΔPs (%)	–13.4	–10.9	–12.4	–9.6	+ 0.4	–11.4
Δbeech (%)	97–99	94–99	97–99	97–99	56–96	92–99

Table 5 reveals surprisingly high levels of range reduction, relatively independently from applied scenario projections. The projected potential distributions indicate a drastic reduction in macroclimatically suitable sites for beech, as 56–99% of present-day zonal beech forests might be outside their optimal bioclimatic niche by 2050. However, the projections of analysis only pertain to zonal beech forests in plachor position and other uncertainties of the projections are also high (Czúcz et al. 2010).

3.2 Responses predicted from transfer analysis

Predictions in the literature based on the hypothesis of close local adaptation envisage a general decline across the whole range of the species ("decoupling": Jump, Penuelas 2005). As it was shown in *Figure 4*, plasticity of populations is significant, and it may be anticipated that except for regions in the vicinity of xeric limits, productivity of beech will not decline (in sufficiently humid areas, even increase) until *EQ* values do not reach the critical maximum.

With worsening climatic conditions, vitality decline reaches 20% of height loss according to *Figure 4a*, around +13 *ΔEQ* in the Bucsuta test site. Based on field experience this amount of decline may be judged as a limit for competitive survival and a vitality decline where attack of pests and diseases may lead to mass mortality.

For the sake of a simple exploratory calculation let us assume that climatic changes will result in relatively homogeneous shifts in EQ values throughout the SE European distributional range of beech. Using the projected statistics of IPCC for Southern Europe (partly presented in *Table 1*), the climatic shift until 2080 was calculated as +11 *ΔEQ*. This suggests that – using the distribution limit value of 29 *EQ* – at locations with present *EQ* values below 29 – 11 ≈ 18~20 *EQ,* beech may survive, even if under stress. The larger part of the distributional range, especially Atlantic NW Europe as well as the higher elevation occurrences of the continental mountains (e.g. the Carpathians or the Balkan Range), fall into this group.

On the contrary, at the low-elevation xeric limits *EQ* would rise in 2080 from 29 to 40 *EQ*. Theoretically, part of these populations could survive as well, assuming that mass mortality starts only if the difference from the originally adapted climate surpasses +13 *ΔEQ* as stated above – if no extreme events and subsequent pests, epidemics occur in this time period. This assumption seems rather unrealistic. It has to be emphasized that all modelled responses were measured within the present distribution range of beech; there is no test site *outside* the xeric limits (which is a deplorable, but understandable drawback of the provenance test series). It is therefore impossible to formulate a more realistic estimate based on transfer analysis for the locations close to the limits.

3.3 Responses validated by field observations

The future frequency of drought events has been analysed for the territory of Hungary. The projected frequency of drought summers (precipitation decline exceeding 15% of the seasonal mean) were calculated with MPI's REMO regional climate model *(Figure 9)*. It is highly remarkable that from 2050 onward, the model projects at least one occasion per decade when 3 or more consecutive years with drought summers will happen, while only three such periods are projected for the first half of the century. Although droughts hit usually regionally, the predicted drought frequency may have an impact on the most part of the investigated beech area at least once during the century. The close link between extreme events and pest outbreaks exacerbate the expected damages *(Figures 6-8)*. Drought will have its effect also on natural regeneration of stands as well (Czajkowski et al. 2005). These results support the grim outcome of the bioclimatic forecast for the second half of the century.

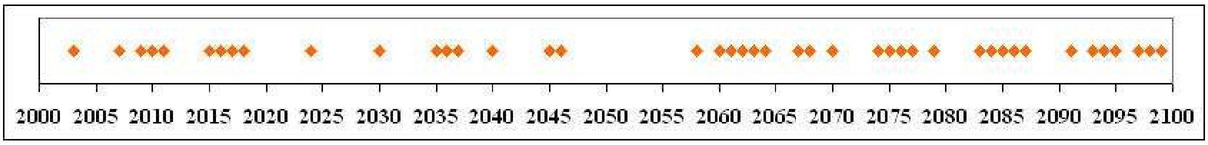

Figure 9. Frequency of consecutive drought events for Hungary, according to scenario A1B, based on results of the REMO model. Symbols depict years of droughty summers (Gálos et al. 2007)

Concluding, the outcome of the projections indicates a high level of uncertainty regarding the future of beech in Southeast Europe. According to the bioclimate approach 56–99% of present-day zonal beech forests might be outside their optimal climatic niche by 2050. The extrapolations of field observations on "drought plots" at the xeric limit also point toward a nearly complete loss of all beech stands in course of the century. Both analyses were carried out predominantly in mature, grown-up stands. For the transfer analysis performed on common garden populations only juvenile, 10 year old saplings were available. This approach confirmed the stability of mountain populations of SE Europe but provided no clues for the low-elevation zone close to the xeric limit. Although plasticity may support adaptation potential to a certain limit, *the part of the SE European continental range of beech where EQ values are currently above 20, has to be considered as a potential mass mortality zone* and respective precautionary measures should be taken.

4 CAVEATS OF INTERPRETATION OF THE RESULTS

Numerous studies (Gessler et al. 2007, Hlásny – Turčáni 2009, Kremer et al. 2010, Lindner et al. 2010) and also IPCC's 2007 report forecast a decline in growth and production of forest stands for East Europe. This projection is not measurable yet as a general trend (e.g. Somogyi 2008) although significant warming of the climate was already taking place. It should be noted that one reason for the missing evidence for gradually worsening vitality of beech in Southeast Europe has to be sought probably in the improper contents of datasets. Analyses are usually based on large-scale forest inventory data or wide-mesh monitoring points which are not precise enough to trace complex effects of opposing trends of environmental effects acting simultaneously across climatic gradients. For example, an international monitoring program (ICP Forests[2]) has gathered in Europe an immense body of information about the decline of tree health, including beech. The data have been of limited use for modelling trends because of low representation of threatened regions; there are too few sample points and insufficient ecological and genetic background data (Mátyás 2010).

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[2] International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests

A general bias of both statistical and process-based modelling is caused by assuming actual limits of beech being in equilibrium with the ecological niche. This may imply an instant breakdown if climate conditions change ("decoupling") which is obviously not the case. For example, the xeric limit described by *EQ* 29 follows fairly exactly the distribution of beech at the beginning of the last century in Hungary. If limits would have been in ecological equilibrium, the present area of beech should have shrunk to its half during the 20th century, following the observed climate shift, a mean temperature increase of approx. 0.6°C *(Figure 10).* This extent of area contraction did not happen, although the mass mortality events in the SW part of the range were located in this zone.

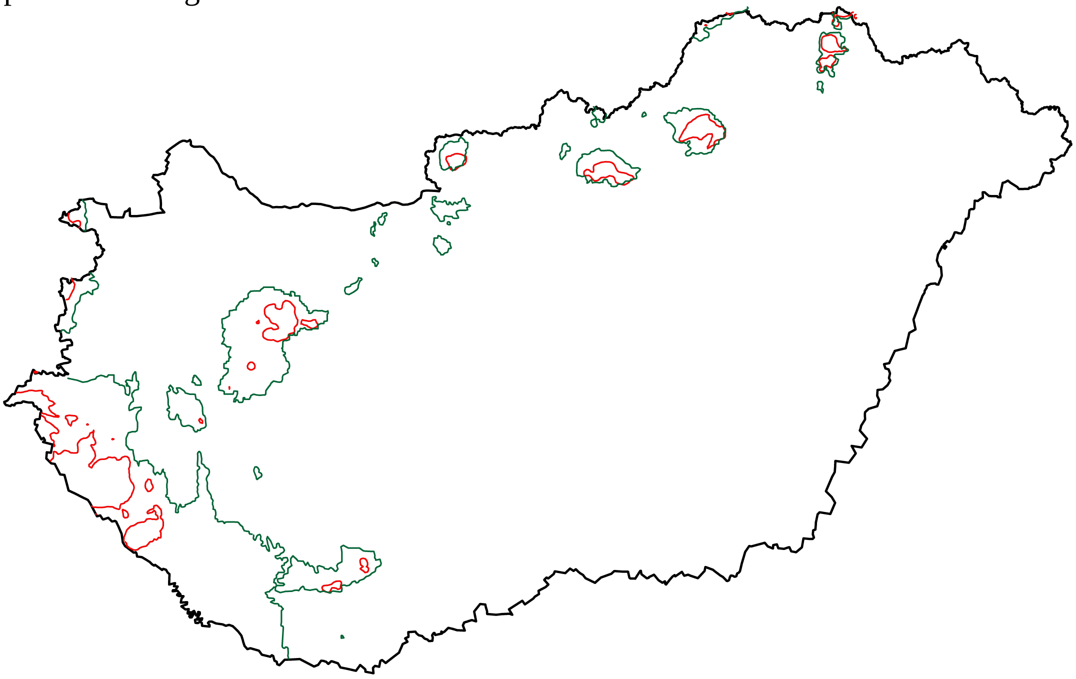

Figure 10. Shrinking of the climatic xeric limit of beech (EQ = 29) in Hungary between the beginning of the 20th century (1900-1930, green) and for the period 1975-2004 (red). (design: E. Rasztovits)

Projection of limits of genetically and ecologically set climatic tolerance has numerous additional constraints. For better interpretation of the results of this study the following four are highlighted: the consequence of ecological and human interactions in determining distribution patterns, the role of persistence, plasticity and natural selection, and uncertainties of climate projections, especially of precipitation conditions.

Genetically set (potential) tolerance limits are *per definitionem* wider than realized actual ones. It is a well known ecological rule that actual distributions of species are regulated by complex, often hidden interactions between host, competitors and consumers which may modify tolerance limits. The change of climatic environment affects also consuming and pathogenic organisms; the selection pressure by consumers may be rearranged. Forecasts are unreliable in this respect, because previously unknown pests and diseases may appear or harmless ones may change their virulence any time.

Modelling of adaptive response fails to regard not only biotic interactions and migration limitations (Jeschke – Strayer 2008, Jump et al. 2009) but especially human interference such as planned forest management. Planned forestry means that the structure, species composition and demography conditions of forests are determined by current management concepts, strategies and laws. Spontaneous processes are suppressed or tolerated only as far as they fit into the accepted strategies (Mátyás et al. 2010a). Therefore the predictive power of bioclimatic models has its limitations; nevertheless it is still the common projection method.

Accordingly, models based on bioclimate data do not consider the intrinsic persistence of tree species, which is mostly linked to longevity. The actual absence of seeding and reproduction may also mislead locally, as reproduction may happen anytime during the century-long lifetime of a tree, if suitable weather conditions favour it. In addition the extent of plasticity forest trees can rely on is still insufficiently known (see in detail in: Mátyás et al 2010a).

At the same time the results of the common garden tests support the opinion that predicted climatic changes may lead to production increase in the central-northern part of the range and at higher elevations due to the plasticity of the species (Mátyás et al. 2010a). It is strongly cautioned however from overestimating the plasticity potential in regions close to the lower (xeric) limit of the range.

Present ecological models of phenotypic behaviour usually treat temperate tree species, including beech as monolithic, genetically uniform entities (e.g. Kramer 1994, Chuine et al. 2003, Czúcz et al. 2010) and necessarily disregard within-species adaptive genetic differentiation. It is a general problem of bioclimatic models that consequences of genetic selection and adaptation is still not properly handled (Jeschke – Strayer 2008, Mátyás 2010, Lindner et al. 2010). The expectation that populations under extreme climatic stress may acclimate and genetically adapt infinitely is deceptive, as resources for adaptation and plasticity cannot be extended beyond the limitations set by the genetic system of species *(see Figure 3 and 6)*, and this is valid for beech as well.

Bioclimatic models usually do not count with the effects of extreme weather events, which have shaped also the past distribution ranges. Also, the limited precision of predicted precipitation changes are not stressed enough. This is of special significance in particular at low elevation plains and hills which are extremely sensitive to relatively minor humidity variations. For example, Hungary lies very close to the climatic division line separating areas of increasing (N. Europe) and decreasing (S. Europe) precipitation both in summer and winter (Christensen et al. 2007). Close to the xeric limits, relatively slight deviations in the climate pattern may seriously affect summer precipitation dependent beech. This is illustrated by the projections calculated from the different climatic scenarios *(Table 5).* The CSMK3 scenario predicts no decrease in summer rainfall, which affects the projection significantly. The effect of relatively minor changes visualises the uncertainty of projections generated by potential reversion of precipitation trends (Czúcz et al. 2010). Further details on uncertainties of projections may be found in Mátyás (2009), Czúcz et al. (2010), and Mátyás et al. (2010a).

5 FINAL CONCLUSIONS

Summing it up, projections into the far future may be biased by a number of uncertainties, first of all by the uncertainty of climate projections themselves. This part lies however beyond the expertise of a forester. Taking the ensemble of deductions of current, fairly deviating projections for granted, the comparison of very different approaches confirm the probability of serious climate impacts on distribution, health and productivity of beech. These effects will appear nonetheless differentiated, according to the ecological and genetic status of local beech occurrences. It is also important to note that contrary to mortality events and health decline along the xeric limits of the species, "compensatory" colonisation at the thermic (or front) limits, as projected by ecological models, will not happen spontaneously because of human obstacles to colonisation and due to the fairly low migration speed of beech compared to other deciduous species (Davis 1981, Mátyás 2009, Jump et al. 2009).

The verification of the existence of macroclimatic adaptation patterns justifies genetically based regulations for use of reproductive material. Regarding the sensitivity of beech to macroclimatic changes, the results show that adaptive pattern and plasticity of the species is fairly comparable to better explored conifer species such as pines, spruces. Observations of mortality events close to the lower (xeric) limit of the species indicate that stability and vitality of populations depend not only on shifts in climatic means. Extreme weather events (droughts) may weaken physiological condition of populations relatively fast and may lead to insect and disease outbreaks also in regions generally suitable for the species. Differences in growth performance and plasticity of provenances left unexplained by macroclimatic factors sustain earlier assumptions that local genetic adaptation also exists ("ecotypes") and maybe also epigenetic effects (Mátyás et al. 2010a). It seems that in beech, local differentiation co-exists with macroclimatic adaptation and with well developed plasticity.

The shrinking of future distribution of beech as suggested by various bioclimatic models (e.g. Thuiller et al. 2005, Czúcz et al. 2010) represent probably pessimistic scenarios which may be alleviated not only by the mentioned features but also by prudent human support (e.g. artificial regeneration and other silvicultural measures, see Mátyás 2010a). In the major part of the range the predicted changes will not trigger any decline due to the plasticity of the species: the predicted "decoupling" is improbable (Jump, Penuelas 2005). It would be however misleading to expect the same level of persistence and plasticity at the threatened xeric limits as across the rest of the range.

Therefore the forecasts have to be taken serious close to the xeric limits, and especially at low elevations. Field observations near the retracting distributional limits confirm that the decline process is ongoing in many locations (Penuelas et al. 2007, Berki et al. 2009). Considering the rapid shrinking of suitable bioclimatic space and the increasing selection pressure of abiotic and biotic stressors at the xeric limits, the results underline the importance of adaptive strategies both for management and conservation of forest resources. This calls also for relevant, well designed field studies and further development of prediction methods and modelling (Mátyás 2010).

The results of this study may contribute to the adjustment of adaptation and mitigation policy in forestry and nature conservation, to the revision of rules for deployment of reproductive material and also to validating evolutionary and ecological hypotheses related to climate change effects.

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Is there a Future for the Isolated Oriental Beech (*Fagus orientalis* Lipsky) Forests in Southern Turkey?

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Abstract – Oriental beech (*Fagus orientalis* Lipsky) is mainly found in the northern region of Turkey. There is also an approximate 40,000 ha of isolated relict oriental beech forest in southern Turkey. This relict population differs somewhat from the northern distribution in terms of average altitudinal distribution, health conditions, and reactions to climate change. Beech forest distribution in southern Turkey starts at about 1000 m, contrary to the northern distribution, which begins at about 150-200 m. In southern Turkey, the average temperature is higher, and summer drought occurs due to irregular rainfall. Beech trees in the south decay at earlier ages due to their sprout origins and higher temperatures than in the north. In recent decades, some part of the beech forests have shed leaves during the summer in response to severe drought. Therefore, these relict populations are on the verge of extinction under unfavorable conditions.

***Fagus orientalis* / Eastern Mediterranean / relict distribution / in situ conservation**

1 INTRODUCTION

Oriental beech (*Fagus orientalis* Lipsky) is one of the major tree species in Turkey. Most of the beech forests are distributed in the northern region of Turkey. In contrast, relict oriental beech forests are distributed in the Eastern Mediterranean region of Turkey, including the Adana, Osmaniye, Hatay, and Kahramanmaraş provinces. Beech trees in this region are coppiced and, therefore, are susceptible to decay at the stump.

It is well known that global climate change strongly impacts plant distribution and survival. It has been determined that the ability of seeds to regenerate is weakened because of the high percentage of empty seeds in the southernmost region of *F. crenata* distribution in Japan, and diameter increment has decreased over the last 50 years due to global warming (Mizunaga et al. 2005). Therefore, it has been postulated that these populations may be replaced by other species. Similarly, some unprecedented features have been observed in the beech forests in southern Anatolia in response to the summer droughts. The vulnerability of these beech forests is significantly different from the remaining distribution.

In the present study, some information is provided about the relict beech forests in the Eastern Mediterennan region, the present conditions and future problems faced by these forests. In addition, the precautions that might be taken against these anticipated negative effects of climate change are discussed in the scope of this study.

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2 BEECH FORESTS IN SOUTHERN TURKEY

There is an approximate 40,000 ha of beech forest in southern Turkey *(Table 1; Figure 1)*, which is about 2.28% of the total beech forest area of the country. The most southerly distribution is found in Hatay region.

Table 1. Beech forests in Southern Turkey (OGM 2006)

Province	Kahramanmaraş	Osmaniye	Hatay	Adana	Total
Area (ha)	5323.6	10256.5	24255.1	165.0	40.000.2

Different from the northern distribution, the beech forests in southern Turkey are located at higher altitudes, which are between 1000-2000 m. In northern Turkey, the levels of the beech forest distribution are at an altitude between 150-200 m.

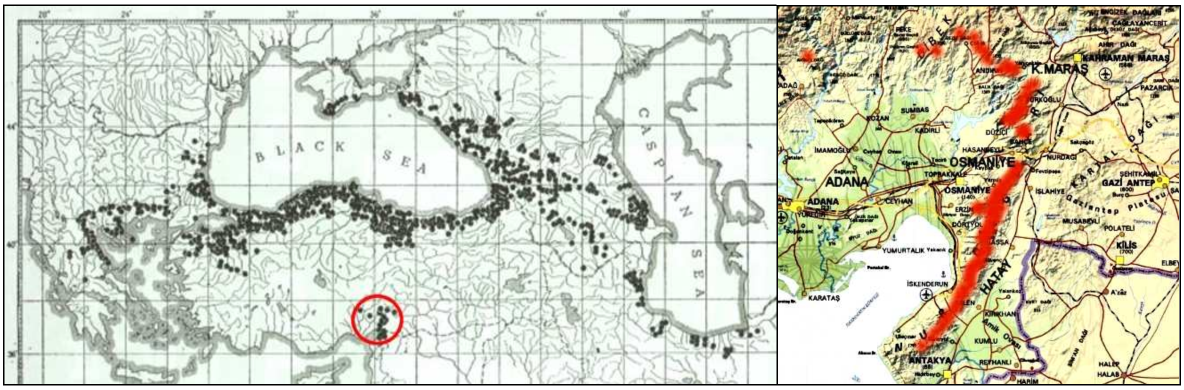

Figure 1. Distribution of the oriental beech and Southern Anatolia populations (Browicz 1982)

3 CHARACTERISTICS OF BEECH FORESTS IN SOUTHERN TURKEY

Relict: The beech forests in southern Turkey are located at a significant distance from the main distribution and are characterized as relict forests and isolated populations. They are very important relict gene sources.

Southern edge distribution: The southernmost distribution of oriental beech in Turkey is found in this region. It represents the southern edge population of the species. Similar to the edge distribution of every plant, these trees are affected by various stress factors.

High altitude: The beech forests in southern Turkey are located at higher altitudes. The distribution of the species in this region is found between 1000 and 2000 m. Lower altitudes in the region are too warm for the beech.

Sprout origin: The beech forests in this region primarily originate from sprouts. They were managed as coppice forests until the 1970s and were used as fuel or industrial wood. These coppice forests were composed of trees of 10–30 cm diameter, with some larger individuals with 50 cm diameter. For many plants, vegetative regeneration provides persistence under extreme conditions (Held 1983; Hara 1987). Similar to the relict beech forests in the Eastern Mediterranean region, coppice regeneration in these edge distributions has contributed to the sustenance of the oriental beech.

4 THE THREATS AND PROBLEMS FACING SOUTHERN OCCURRENCES

Climate change: In this region, a distinctive increase in temperature and evaporation during the last 30 years has been recorded (Karabulut and Coşun 2009; Coşun and Karabulut 2009). These significant increases threaten the edge distribution of oriental beech. Summer droughts in the years 2000 and 2008 in the Düziçi region caused beech trees to shed leaves during the drought. In September, the new leaves flushed in response to rainfall. In Hungary, mortality of beech trees was found in the edge distributions due to droughts as well (Lakatos – Molnar 2009). Similar threats to the beech forests in whole southern Turkey are expected.

Genetic stability: Since the beech forests in this area regenerate by sprouts, they have been genetically identical for centuries. The genetic resources of the populations remain unchanged in terms of time and location. The length of time period of coppice culture in the beech forests of the Eastern Mediterranean region is not known. Vegetatively regenerated forests cannot renew their abilities to adapt to changing conditions (Smith et al. 1997). Regeneration of the forests from seeds is therefore important for the genetic improvement of these valuable beech forests in Southern Turkey.

Core decay: The beech forests originating from sprouts begin to decay from the stump at early ages. Stump decay spreads to the bottom parts of other stump sprouts. The individuals arising from root suckers are unaffected by the decay of the mother tree (Nyland 1996).

Irregular stems: The beech individuals arising from sprouts usually have crooked trunks and are susceptible to wind damage (Cao and Peters 1998) and have low wood quality. On the other hand, the root suckers have straighter stems similar to individuals of seed origin.

Thinning operations: In this region, dense stands composed of young coppiced individuals are often found due to a lack of thinning cuttings in the area. It is sometimes observed that 15-20 sprout-origin trees are found together on the same stump and the individuals with small diameters compete with each other. Because of strong competition for light, long unbalanced trees have small diameters. These conditions weaken the stability of the stand. The thinning operations should not be neglected, and the excess competition in the stands must be prevented to provide suitable conditions for each individual's growth.

Conversion to high forest: Coppicing has not been applied to the beech forests in Turkey in recent decades. The beech forests in both Italy (Nocentini 2009) and France have been converted to high forests since the middle of the 20th century (Bock 2006) and they are expected to regenerate naturally. However, these forests are in need of thinning and seed tree selection before the conversion. Both genetic variability and clonal reproduction should be considered while converting the coppice forests to high forests (Valbuena-Carabana et al. 2008). The seed-originated individuals should be maintained as seed trees. To provide information about seed regeneration, the natural regeneration studies should be started in beech forests between 50-60 years of age (Odabaşı et al. 2004).

5 RESULTS AND SUGGESTIONS

The relict oriental beech forests found in Southern Turkey are important gene resources that represent the marginal distribution of the species. The performance of these local beech forests under the effects of climate change provides important insights into the general behavior of the beech forests. Therefore, changes in the beech forests of this study area should be precisely examined.

The marginal distributions of this species are sensitive to environmental conditions. Today, the impacts of global warming is well known. It is expected that the forests are better adapted to environmental conditions with improved genetic constitution when they are regenerated from seeds. It is urgent that the marginal distribution of *F. orientalis* must be naturally regenerated using local seed sources to improve its adaption to new environmetal conditions. To begin, natural regeneration should be applied in selected areas in the region. Planting of seedlings produced from local seeds would be worth trying. Local seeds should also be collected and stored for natural regeneration and nursery studies.

Seed production of beech forests is usually low in their marginal distributions (Peters 1997). The number of empty seeds is high in the beech forests of the studied region. After the empty seeds are removed, about 90% of the remaining seeds germinate (Yılmaz 2005). The seeds of this relict population should be collected in the mast year and should be stored under the appropriate conditions (Yılmaz 2008) to be used in nurseries and natural regeneration studies.

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Genetic and Ecotypic Characterization of European Beech (*Fagus sylvatica* L.) in Poland

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Abstract – European beech (*Fagus sylvatica* L.) is one of the most important forest tree species in Poland and it covers 5.2% of forest area. Present genetic structure of beech populations has been formed within the last few thousand years and influenced by many different factors, not only of environmental (postglacial) and genetic origin, but also by anthropogenic ones. In Poland, beech attains its north-eastern limit of natural range, and is limited by continental climate, winter temperatures, air humidity and soil conditions. The growth of beech stands outside the natural beech limit indicates that the species possesses a potentially wider range.

Based on their phytosociological characteristics, nine beech experimental plots of one hectare area were established in selected seed stands, representing the typical plant associations and the most important beech provenance (seed) regions. The genetic analyses were performed using isoenzyme electrophoresis for seven loci (GOT, LAP, MDH, MNR, PGM, PGI, SKDH) and DNA markers using RAPD primers. The following genetic parameters were calculated: average number of alleles per locus, percentage of polymorphic loci and heterozygosity (on the basis of isoenzyme analysis). Dendrograms based on genetic distances were constructed.

There is a slight decrease of genetic variation of beech populations towards the north of Poland, which can be explained by migration paths and selection after the glacial period. The genetic differentiation of beech in Poland does not allow distinguishing provenance regions. The data show a mosaic character of species differentiation and an ecotypic variation.

isoenzyme analysis / DNA-RAPD markers / genetic variation / genetic differentiation / progeny differentiation

1 INTRODUCTION

Beech stands cover 5.2% of the forest area in Poland (Lasy Państwowe, 2009). They dominate the typical forest associations at the lower forest belt in the Carpathians and Sudety Mountains in South of Poland and in the moraine landscape of the Pomeranian Lake District of North Poland (Wojterski, 1990).

In Poland beech attains its north-eastern limit of the natural range (Boratyńska – Boratyński 1990). The geographic range of beech is limited by the continental climate, winter temperatures, air humidity and soil conditions (Jedliński 1953, Boratyńska – Boratyński 1990). The growth of beech stands outside the natural beech limit indicates that the species possesses potentially a wider range (Brzeziecki 1995, Tarasiuk 1999).

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Present genetic structure of beech populations in Poland was formed by many different factors, among them not only environmental and genetic but also anthropogenic ones. Basic factors affecting the gene pool were the glacial epoch, the location of beech refugia, and postglacial migration paths of the species (Szafer W. 1935, Huntley – Birks 1983, Ralska – Jasiewiczowa 1983, Hazler *et al.* 1997).

Variability of environmental conditions resulted in great number of ecotypes and populations (Dzwonko 1990), resulting in a differentiation of ecological requirements, which was confirmed by provenance experiments (Giertych 1990). Some genotypes are favourable in specific environmental conditions such as certain peroxidase enzyme alleles in relation to climate continentality (Cugen et al. 1985), while non-tolerant organisms are eliminated during natural selection process (Müller – Starck 1985, Starke et al. 1996). The occurrence of beech soil ecotypes was confirmed for German and Romanian provenances where survival was found correlated with LAP A2 allele frequency in seedlings planted in open-air and in green-house conditions (Kim 1985).

Recent investigations in Poland (Sułkowska 2002, Gömöry *et al.* 2003) have confirmed high genetic diversity of beech, similar to other neighbouring European populations, with a slight decrease of average number of alleles per locus and level of differentiation towards the North of the natural range limit, which generally confirms the migration paths after glaciations but does not provide a basis to distinguish geographic regions. The differentiation of selected stands and their progenies for genetic parameters and on the basis of soil characteristics of their habitats were also studied (Sułkowska *et al*. 2008).

2 METHODS

Based on their phytosociological characteristics, nine beech experimental plots of one hectare area were established in selected seed stands, representing the following plant associations *(Table 1)*: *Galio-odorati-Fagetum* (Gryfino and Kartuzy), *Dentario glandulosae-Fagetum* (Lutowiska and Łosie), *Luzulo-luzuloides-Fagetum* (Miechów, Suchedniów, Tomaszów, Zwierzyniec) and *Dentario enneaphyllidis-Fagetum* (Zdroje). The stands are located in compact forest areas mainly in the most important beech provenance (seed) regions *(Figure 1).* A data base was established covering climate, geology and plant association data of the stands. The selected stands were practically homogenous related to site conditions, which were classified ecologically according to Zarzycki et al. (2002) as shown in *Table 1.* The largest differences were in moisture and acidity of soils. Most stands were characterised by good stem quality and crown shape.

The genetic analyses of the plant material were performed using isoenzyme electrophoresis for the following loci: glutamate-oxaloacetate transaminase (GOT – EC 2.6.1.1 – *Got-2*), leucine amino peptidase (LAP – EC 3.4.11.1 – *Lap-1*), malate dehydrogenase (MDH – EC 1.1.1.37 – *Mdh-1*, *Mdh-2*, *Mdh-3*), menadione reductase (MNR – EC 1.6.99.2), phosphoglucomutase (PGM – EC 2.7.5.1), phosphoglucose isomerase (PGI – EC 5.3.1.9 – *Pgi-2*), shikimate dehydrogenase (SKDH – EC 1.1.1.25) and DNA markers using RAPD primers H02, H12, P06, W09, W11.

Table 1. Localization and characteristics of investigated European beech populations in Poland

Forest Division	Forest Association	Soil	Average Ecological Index* L	T	W	Tr	R	D	H
Gryfino	*Galio-odorati-Fagetum*	Brown acid	2.60	3.05	3.07	3.31	3.56	3.82	3.01
Kartuzy	*Galio-odorati-Fagetum*	Typical brown	2.85	2.88	2.97	2.83	3.02	3.58	2.80
Lutowiska	*Dentario glandulosae-Fagetum*	Brown acid	2.54	3.10	3.04	3.28	3.65	3.84	2.94
Losie	*Dentario glandulosae-Fagetum*	Brown acid	2.52	3.29	3.23	3.72	4.08	4.06	2.91
Miechow	*Luzulo-luzuloides-Fagetum*	Rendzina	2.77	3.32	3.33	3.82	4.07	3.82	3.02
Suchedniow	*Luzulo-luzuloides-Fagetum*	Brown acid	2.68	3.03	3.50	3.23	3.48	4.23	3.23
Tomaszow	*Luzulo-luzuloides-Fagetum*	Typical brown	2.83	3.18	3.29	3.53	3.98	3.79	2.96
Zdroje	*Dentario enneaphyllidis-Fagetum*	Typical brown	2.53	3.26	3.28	3.65	3.96	3.79	3.04
Zwierzyniec	*Luzulo-luzuloides-Fagetum*	Grey brown	2.54	3.22	3.14	3.52	3.79	3.83	2.93

*Ecological Index (Zarzycki *et al.* 2002): Climate indices: L – light, T – thermal;
Edaphic indices: W – wet, Tr – trophic, R – acid,
D – mechanical soil components, H – humus

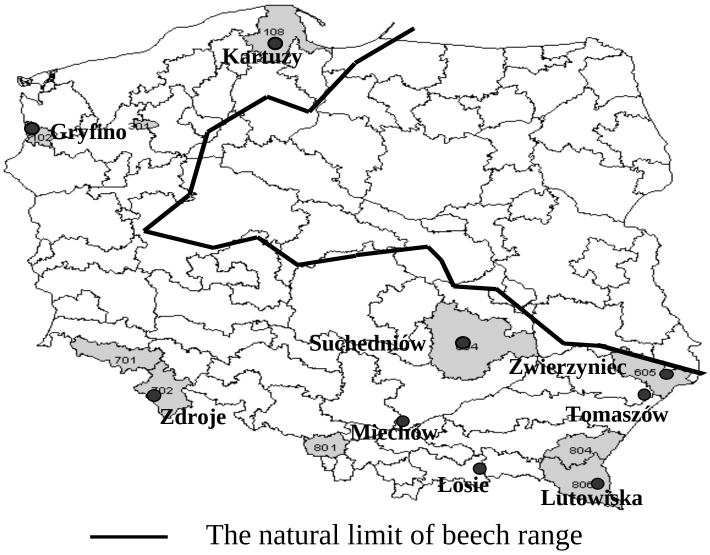

Figure 1. Location of studied populations in Poland on the map of beech seed regions

Proteins from buds were extracted with 0.1 M Tris-HCl buffer pH 7.0. Based on the results of starch gel electrophoresis, genetic diversity and differentiation were estimated following Thiebaut *et al.* (1982), Merzeau *et al.* (1989) and Muller – Starck & Starke (1993). Gene diversity (expected heterozygosity) was calculated according to Nei (1978) using BIOSYS 1 program (Swoford – Selander 1981). Dendrograms were constructed based on Nei’s (1972) genetic distances.

Total genomic DNA from buds was extracted using the isolation DNeasy Plant Kits (QIAGEN). After DNA electrophoresis the qualitative and quantitative analysis of DNA was performed. On the basis of RAPD primers differentiation was estimated for chosen genetic parameters similar to isoenzyme loci (percentage of polymorphic loci, average number of alleles per locus and observed heterozygosity) and dendrograms of genetic distances were constructed using average frequencies of alleles.

3 RESULTS

Localization and description of the selected stands, representing the typical plant associations and the most important beech provenance (seed) regions, are presented in Table 1.

The genetic diversity estimated on the basis of izoenzyme and DNA analysis revealed a high variation of investigated populations (*Tables 2, 3*).

Table 2. Genetic diversity of populations on the basis of isoenzyme analysis

Provenence	Average number of alleles per locus		Percentage of polymorphic loci		Heterozygosity			
					Observed		Expected	
	M	P	M	P	M	P	M	P
Gryfino	2.0	2.7	77.8	88.9	0.245	0.237	0.209	0.221
Kartuzy	1.9	2.4	66.7	88.9	0.201	0.229	0.194	0.197
Lutowiska	2.2	2.6	77.8	88.9	0.226	0.223	0.212	0.204
Łosie	2.0	2.3	66.7	66.7	0.195	0.240	0.216	0.221
Miechów	2.3	2.6	77.8	88.9	0.208	0.241	0.221	0.207
Suchedniów	2.0	2.6	66.7	88.9	0.236	0.225	0.213	0.202
Tomaszów Lub.	2.1	2.4	77.8	88.9	0.233	0.223	0.205	0.213
Zdroje	2.1	2.4	77.8	88.9	0.216	0.238	0.202	0.208
Zwierzyniec	1.9	2.3	66.7	66.7	0.238	0.219	0.178	0.200

M – mother stands, P – progeny

Table 3. Genetic diversity of populations on the basis of DNA analysis

Provenance	Average number of alleles per locus	Effective number of alleles per locus	Percentage of polymorphic loci	Heterozygosity observed
Gryfino	2.000	1.549	100.00	0.334
Kartuzy	1.818	1.469	81.82	0.268
Lutowiska	1.954	1.528	95.45	0.314
Łosie	2.000	1.503	100.00	0.305
Miechów	1.818	1.455	81.82	0.269
Suchedniów	1.909	1.541	90.91	0.317
Tomaszów Lub.	1.954	1.484	95.45	0.300
Zdroje	2.000	1.559	100.00	0.329
Zwierzyniec	1.954	1.514	95.45	0.309

The dendrograms *(Figure 2*) constructed on the basis of Nei's (1972) genetic distances do not offer possibilities to distinguish beech regions similar to the European beech differentiation pattern. The provenances originating from fertile sites were characterised by higher differentiation value of genetic parameters, as e.g. Miechów provenance. For the mother stand of provenance Miechów (South Poland) average number of alleles per locus (isoenzyme markers) was estimated at 2.3, while percentage of polymorphic loci was 77.8% and for its progeny 2.6 and 88.9% respectively. The lowest average number of alleles per locus (1.9) was found for the Zwierzyniec mother stand (South-East Poland, at the natural range border), with 66.7% polymorphic loci and for its progeny the values were 2.3 and 66.7% respectively. The mother stand of provenance Kartuzy (North Poland) was also characterised by low values of analysed genetic parameters: average number of alleles per locus 1.9, with a percentage of polymorphism 66.7%, but for the progeny the values were higher: 2.4 and 88.9% respectively.

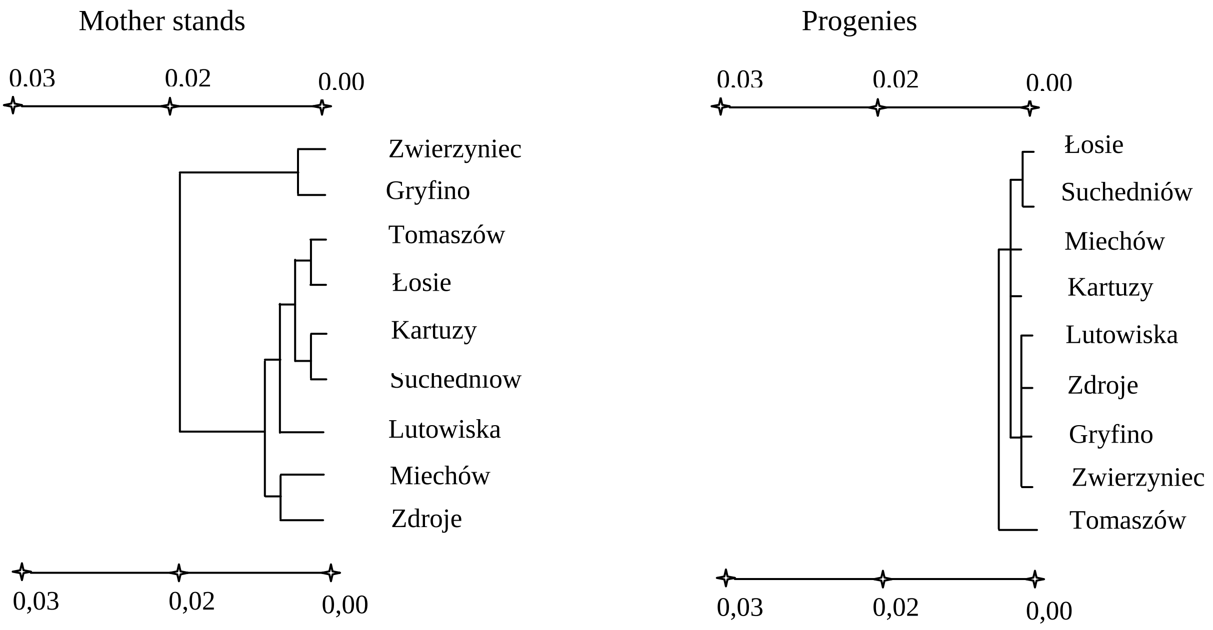

Figure 2. Genetic differentiation of mother stands and their progeny on the basis of average frequency of alleles

4 DISCUSSION

Geographical locations are not in accordance with genetic diversity patterns of investigated beech populations. This result corresponds with recent investigations of beech diversity in Poland (Sułkowska 2002, Gömöry *et al.* 2003, Sułkowska *et al.* 2008). Low range of values of genetic differentiation of investigated beech populations point toward homogenous characteristics of ecological conditions as expressed by indices (Zarzycki *et al.* 2002).

The slight decrease in the average number of alleles per locus and in the level of differentiation towards the natural range limits confirms the effect of migration after the last glaciation. The Kartuzy and Zwierzyniec provenances, located close to the border of natural beech range were characterized by the lowest values of genetic variation for isoenzyme markers.

On the basis of isoenzyme markers, estimated values of the expected and observed heterozygosity do not show differences. This is typical for genetically stable populations with a random mating system (Hartl 1988) – except the populations Gryfino and Zwierzyniec. The high value of observed heterozygosity of Gryfino, a fertile Pomeranian beech site, can be explained by the origin of the stand (stand of probably artificial origin). The difference between observed and expected heterozygosity in population Gryfino and Zwierzyniec (the latter located close to the natural border of the range) can be caused by selection processes occurring in the stands.

On the basis of DNA-RAPD markers, slight decrease of average number of alleles per locus and level of differentiation towards the North of Poland was observed, but the trend was not clear. The results indicate the ecotypic character of genetic variation of European beech in Poland which may be related to site differentiation. So, using of local European beech ecotypes and taking into account its plasticity seems to be the best advice for success in forest management.

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Response of Internal Conductance to Soil Drought in Sun and Shade Leaves of Adult *Fagus crenata*

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Abstract – The internal conductance to CO_2 (g_i) is an important constraint of photosynthesis, and its acclimation to environmental factors varies widely within plant functional groups, genera and even species. We measured photosynthesis and chlorophyll fluorescence response curves to intercellular CO_2 concentrations simultaneously in attached sun and shade leaves of 90-year-old *Fagus creneta* Blume trees to determine (1) how g_i varies within the crown and (2) whether soil drought affects g_i. Internal conductance to CO_2 was found to be 0.058 and 0.185 mol m^{-2} s^{-1} in lower and upper crowns, respectively, resulting in a decrease of about 70 µmol mol^{-1} in CO_2 concentration from the intercellular space (C_i) to the site of carboxylation inside the chloroplast stroma (C_c). The results suggest that g_i is as important as stomatal conductance for photosynthetic efficiency in *F. crenata*. If this large decrease from C_i to C_c was not accounted for, the maximum rate of carboxylation (V_{cmax}) in sun and shade leaves was underestimated ca 36% and 24%, respectively. When soil water supply was sufficient, leaf water potential dropped to a daily minimum in early morning, facilitating CO_2 transfer and thus photosynthesis. When soil water potential at 25 cm depth fell to –0.015 MPa, g_i and stomatal conductance decreased by 20–40% in comparison with their respective values under sufficient soil water supply. In contrast, V_{cmax} decreased by 7% in sun leaves, but there was no change in this parameter in shade leaves. Ignoring the effect of g_i on C_c under stressed conditions would lead to up to 22% underestimates of V_{cmax}, and consequently overestimates of biochemical limitations. These results suggest that CO_2 diffusional limitations have more significant effects than biochemical limitations on the rate of photosynthesis in *F. crenata* during soil drought.

light acclimation / Japanese beech / maximum rate of carboxylation / mesophyll conductance / photosynthesis / stomatal conductance

1 INTRODUCTION

Ongoing increases in the atmospheric CO_2 concentration and associated climate changes have promoted a growing interest in the function of forest ecosystems as potential carbon sinks (Baldocchi – Harley 1995). In order to evaluate these effects a number of models have been developed to aid the study of physiological processes affecting forest carbon fixation. Many investigations of carbon fixation have employed the biochemical model of Farquhar et al. (1980) at the leaf level. This model uses two key parameters: the maximum rate of

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carboxylation (V_{cmax}) and the maximum rate of electron transport (J_{max}). Variations in V_{cmax} and J_{max} within canopies are strongly correlated with their growth irradiance via the allocation of leaf nitrogen (Wilson et al. 2000a; Meir et al. 2002; Han et al. 2003). These associations between irradiance, nitrogen and V_{cmax} within canopies are widely used in scaling estimates of leaf photosynthesis to canopy level (Baldocchi – Harley 1995). The models that use these parameters have typically assumed an infinite internal conductance to CO_2 (g_i), which describes the draw-down in CO_2 concentration between intercellular spaces (C_i) and the site of carboxylation inside the chloroplast stroma (C_c) (Harley et al. 1992b). However, it is becoming apparent from recent studies that finite g_i alone are sufficient to limit the rate of photosynthesis (Harley et al. 1992a; Flexas et al. 2008). Recent studies have demonstrated that g_i also acclimates and responds both in the long term (weeks and days) and short term (hours and minutes) to environmental factors, including light, temperature, water and CO_2 concentrations (Flexas et al. 2008). For example, g_i has been found to be two-fold lower in shade leaves than in sun leaves of *Fagus sylvatica* L. crowns (Warren – Adams 2006; Montpied et al. 2009). One consequence of finite g_i is that V_{cmax} values calculated from C_i are not influenced solely by biochemical factors, but also by g_i. Therefore, these changes may be important in regulating photosynthesis in response to changes in environmental factors. Further, recent studies have indicated that variations in g_i are associated with variations in leaf forms and plant functional groups, hence there are large variations in g_i within groups, genera and even species (Hanba et al. 2002; Terashima et al. 2006; Flexas et al. 2008). This suggests that g_i is a rapidly adapting trait that may contribute to the differences in photosynthetic efficiency found among different species. Therefore, further studies are needed to fully characterize the responses of g_i to environmental factors, especially since g_i and related processes are likely to be heavily influenced by anticipated global climate changes (Flexas et al. 2008).

The most extensive deciduous broad-leaved forests in Japan are the beech (*Fagus crenata* Blume) forests, distributed from Kuromatsunai, Hokkaido (42^{o}N, 140^{o}E) to Takakuma, Kyushu (31^{o}N, 130^{o}E). These beech forests are important for wildlife and protection of water catchments, hence their ecological features and physiological traits have been extensively studied (Hashizume - Fukutomi 1978; Nakashizuka 1983; Kakubari 1991; Hiura 1998; Han et al. 1999). The cited studies have found (*inter alia*) that the photosynthetic capacity of *F. crenata* responds highly plastically to irradiance (Uemura et al. 2000; Iio et al. 2005), it is highly sensitive to drought stress (Maruyama - Toyama 1987; Uemura et al. 2004), and varies amongst ecotypes (Koike – Maruyama 1998; Bayramzadeh et al. 2008; Tateishi et al. 2010). However, g_i and the constraints it imposes on photosynthesis in this species have not been examined previously. Therefore, in this study, photosynthesis and chlorophyll fluorescence were measured simultaneously in attached sun and shade leaves of 90-year-old Japanese beech trees to determine (1) how g_i varies between sun and shade leaves and (2) the effect of soil drought on g_i.

2 MATERIALS AND METHODS

2.1 Study site

The study area was located in the Naeba Mountains in southern Niigata Prefecture, Japan (36°51' N, 138°46' E), where *F. crenata* forests are found over an altitudinal range from 550 to 1500 m. Eight permanent plots along the altitudinal gradient were established in 1970 for long-term ecological monitoring within the framework of the International Biological Program (Kakubari 1977). The bedrock is predominantly andesite and basalt, on which moderately water-retentive brown forest soil has formed. During the period 1976–2009, the mean annual precipitation and temperature were recorded as 2,214 mm and 11.5 °C, respectively, at a nearby meteorological station (36°57' N, 138°49' E, 340m asl., Japanese Bureau of Meteorology). Snow accumulates to depths up to about 3-4 m during the winter. One of eight permanent plots at the ridgeline of a south facing slope with elevation of 950 m was chosen for this study. The chosen plot was dominated by *F. crenata* (87%), with sporadic occurrence of *Quercus crispula* Blume, *Magnolia obovata* Thunb., *Prunus grayana* Maxim., *Acer rufinerve* Sieb. et Zucc., *A. japonicum* Thunb., *A. tschonoskii* Maxim., *A. palmatum* Thunb., *Kolopanax pictus* Thunb. and *Acanthopanax sciadophylloides* Franch. et Savat. The average age of the *F. crenata* trees in the chosen plot was about 90 years and the stand stem basal area was about 45.6 m^2 ha^{-1}.

2.2 Soil water measurement

Soil volumetric water content (SWC) was measured near the selected trees at 10 and 25 cm depths with time-domain reflectometry (TDR) sensors (ML2, Delta-T Devices, Cambridge, UK). Soil water potential at 25 cm depth was measured simultaneously with a tensiometer (KDC-55, Kona, Sapporo, Japan) inserted near the TDR sensors to convert SWC measurements to soil water potential during the period 2006 to 2008. These measurements were made at 10 s intervals, and data were stored as 30 min means using a data logger (DL2e, Delta-T, Cambridge, UK).

2.3 Measurements of gas exchange and chlorophyll fluorescence

Three trees with heights between 19.5 and 22 m were accessed with the aid of a research tower. Gas exchange and chlorophyll fluorescence were measured simultaneously *in situ* for leaves in both the upper and lower crowns (hereafter referred to as sun and shade leaves, respectively), between 18 August and 20 August 2009. The photosynthesis and fluorescence response curves to intercellular CO_2 concentration (A/C_i) were measured with two inter-calibrated portable gas exchange systems (LI-6400, LI-COR, Lincoln, USA) with an integrated fluorescence chamber (LI-6400-40). Dark respiration and the minimum and maximum fluorescence of dark-adapted leaves were measured at 22:00 on the day prior to the measurements of A/C_i curves. For each A/C_i curve, leaves were exposed to 360 μmol mol^{-1} CO_2 until rates of photosynthesis and transpiration were steady. Then, the CO_2 concentration in the chamber was adjusted stepwise to 300, 250, 200, 150, 100, 50, 360, 450, 600, 800, 1000, 1300, 1500 and 1800 μmol mol^{-1}, allowing at least four minutes for adjustment and stabilization at each step. Photosynthetic photon flux density was set at photosynthesis-saturated points which were 1000 and 700 μmol m^{-2} s^{-1} for sun leaves and shade leaves, respectively (Iio et al. 2005). Leaf temperatures were generally controlled at 25.0 °C, but on warm afternoons they increased to a maximum of 28.1 °C owing to the limited cooling capacity of the LI-6400. For individual leaves the variation in leaf temperature was less than 1.0 °C during the measurement periods. The vapor pressure deficit in the chamber was lower than 1.45 kPa for all measurements. Each leaf was revisited 2–3 times a day between 6:30 to 14:00 to investigate the effects of water stress on photosynthetic parameters.

2.4 Measurement of leaf water potential

After the completion of measurements for each A/C_i curve, a leaf on a neighboring shoot exposed to a similar light intensity was removed, placed in a sealable plastic bag with a small piece of humid paper towel and dropped down to the forest floor. Leaf water potential was measured immediately using a pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, USA).

2.5 Measurement of leaf nitrogen concentration

Leaves were harvested after the gas exchange measurements and their projected leaf areas were measured using a scanner (LiDE200, Canon, Tokyo, Japan) and image analysis software (LIA32, K. Yamamoto of Nagoya University, Nagoya, Japan). They were then dried at 70 °C for 48 hours, combusted with circulating O_2 using an NC analyzer (Sumigraph NC-900, SCAS, Osaka, Japan), and their nitrogen concentration per unit area (N_a) was determined using a gas chromatograph (GC-8A, Shimadzu, Kyoto, Japan).

2.6 Calculation of photosynthetic parameters

Photosynthetic electron transport (J) was calculated according to the default program installed in the Li-6400 assuming a leaf absorptance of 0.85. Internal conductance (g_i) was estimated using the "variable J method" of Harley et al (1992a):

$$g_i = \frac{A}{C_i - \frac{\Gamma^*[J + 8(A + R_d)]}{J - 4(A + R_d)}} \tag{1}$$

where the CO_2 compensation point in the absence of mitochondrial respiration (Γ^*) was taken from Bernacchi (2002), and the rate of non-photorespiratory respiration continuing in the light (R_d) was taken as half of the rate of respiration measured in the dark (Niinemets et al. 2005). Then g_i values were calculated for every step of the A/C_i curves, and C_c was calculated as:

$$C_c = C_i - A / g_i \tag{2}$$

Since the CO_2 concentration may affect g_i (Flexas et al. 2007), data in the range of $10 < dC_c/dA < 50$ were averaged to estimate a constant g_i value (Harley et al. 1992a):

$$dC_c / dA = 12 \times \Gamma^* \times J / [J - 4 \times (A + R_d)]^2 \tag{3}$$

From this constant g_i, we estimated V_{cmax} and J_{max} from A/C_c curves based on the model of Farquhar et al. (1980) using a non-linear curve-fitting routine available in Microsoft Excel (Sharkey et al. 2007). Limiting factors (the properties of ribulose 1·5-biosphosphate carboxylase/oxygenase, the rate of ribulose 1·5-biosphosphate regeneration and the rate of use of triose phosphates) were determined from J obtained by fluorescence measurements. All V_{cmax} and J_{max} values were standardized to a common temperature of 25°C. We also compared the difference in V_{cmax} and J_{max} when draw-down between C_i and C_c was, and was not, taken into account.

2.7 Data analyses

The significance of the differences in leaf traits between sun and shade leaves was tested by Tukey-Kramer's test, using StatView (SAS Institute Inc., Cary, NC).

3 RESULTS

3.1 Soil water conditions

Soil water is usually not limiting in the Naeba Mountains because of the high mean annual precipitation. However, the annual precipitation in 2009, the year in which this study was conducted, was 1902 mm (*Figure* 1b), 312 mm lower than the 2214 mm average for the period 1976-2009, and the second lowest among all years in this period. The lower than average rainfall led to prolonged soil water deficits during the summer of 2009 (*Figure* 1c). Daily average soil water potentials during the measurements of gas exchange were –0.020, –0.026, and –0.032 MPa at 10 cm depth, and –0.012, –0.013, and –0.015 MPa at 25cm depth on the 18th, 19th and 20th of August 2009, respectively. The atmospheric vapor pressure deficit during the measurements varied between 0.32–1.75, 0.35–1.26, and 0.43–1.09 kPa on the 18th, 19th and 20th August 2009, respectively (data not shown).

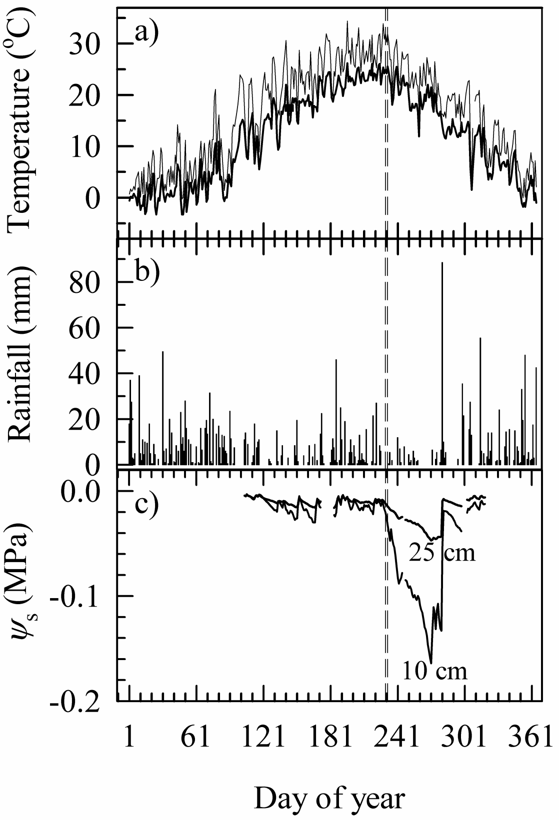

Figure 1. Seasonal course of local environmental factors during 2009.
(a) Daily mean (bold line) and maximum (thin line) air temperatures, (b) daily rainfall, and (c) daily mean soil water potential (Ψ_s) at depths of 10 cm and 25 cm. Vertical dashed lines indicate dates of gas exchange measurement campaigns

3.2 Photosynthetic plasticity within the crowns

The light-saturated photosynthetic rate at ambient CO_2 concentrations (A_{max}), g_i, g_s, V_{cmax} and J_{max} were all approximately two-fold higher in sun leaves compared to shade leaves (*Table* 1). Internal conductance to CO_2 was 0.166 mol m^{-2} s^{-1}, a similar level to g_s (0.185 mol m^{-2} s^{-1}) in sun leaves (P = 0.541). In contrast, in shade leaves, g_i was 0.058 mol m^{-2} s^{-1}, significantly lower than their g_s (0.100 mol m^{-2} s^{-1}) (P = 0.019). The decrease in CO_2 concentration from ambient to C_i varied between 76–132 µmol mol^{-1} within the crowns, and was about 56 µmol mol^{-1} higher in sun leaves than in shade leaves (*Table* 1). In contrast, the draw-down in CO_2 concentration from C_i to C_c was, on average, about 70 µmol mol^{-1} in both sun and shade leaves. The maximum rate of carboxylation estimated from A/C_i curves ($V_{cmax,\ Ci}$) was underestimated ca 36% and 24% than the value estimated from A/C_c curves ($V_{cmax,\ Cc}$) in sun and shade leaves, respectively. In contrast, estimates of J_{max} derived from the A/C_i curves and A/C_c curves did not differ significantly, for either sun or shade leaves.

Table 1. Comparison of photosynthetic parameters between sun and shade leaves of 90-year-old Fagus crenata trees without water stress

	A_{max}	g_s	g_i	C_i	C_c	$V_{cmax, Ci}$	$V_{cmax, Cc}$	$J_{max, Ci}$	$J_{max, Cc}$
Sun	12.6 ± 0.9	0.185 ± 0.024	0.166 ± 0.029	228 ± 8	158 ± 10	62 ± 5^a	95 ± 2^b	121 ± 6^a	129 ± 6^a
Shade	3.7 ± 0.3	0.100 ± 0.006	0.058 ± 0.009	284 ± 4	215 ± 5	20 ± 2^a	26 ± 2^b	44 ± 4^a	46 ± 4^a
P value	0.0006	0.027	0.024	0.004	0.007	0.00004	0.001	0.0004	0.0005

Measurements were made under light-saturated photosynthesis. Parameters determined are the rate of net photosynthesis (A_{max}, µmol m^{-2} s^{-1}) at an ambient CO_2 concentration of 360 µmol mol^{-1}, stomatal conductance (g_s, mol m^{-2} s^{-1}), internal conductance (g_i, mol m^{-2} s^{-1}), intercellular CO_2 concentration (C_i, µmol mol^{-1}), chloroplast CO_2 concentration (C_c, µmol mol^{-1}), maximum rate of carboxylation (V_{cmax}, µmol m^{-2} s^{-1}) and electron transport (J_{max}, µmol m^{-2} s^{-1}) estimated from A/C_i or A/C_c ($V_{cmax, Ci}$ and $V_{cmax, Cc}$, $J_{max, Ci}$ and $J_{max, Cc}$, respectively). Data are means ± SE obtained from measurements on two leaves from each of three *F. crenara* trees. Significance was tested by Tukey-Kramer’s test. Different superscript letters within rows indicate significant differences between the corresponding parameters estimated from A/C_i and A/C_c ($P < 0.05$).

There was no significant difference in leaf nitrogen concentration per unit dry mass between sun and shade leaves (*Table* 2). However, leaf dry mass per unit area (LMA) was 3-fold greater in sun leaves than shade leaves and thus N_a was 3-fold higher in sun leaves than in shade leaves.

Table 2 Comparison of structural parameters between sun and shade leaves

	LMA ($g\ m^{-2}$)	N_a ($g\ m^{-2}$)	N_m ($mg\ g^{-1}$)
Sun	94.94 ± 5.44	2.29 ± 0.12	24.30 ± 1.75
Shade	31.33 ± 2.42	0.74 ± 0.04	23.56 ± 0.66
P value	0.0006	0.010	0.700

Parameters determined are leaf dry mass per unit area (LMA), leaf nitrogen concentration per unit area (N_a) and per unit dry mass (N_m). The data presented are the means ± SE of two leaves from each of three *F. crenara* trees. Significance was tested by Tukey-Kramer’s test.

3.3 Responses to changes in leaf water potentials and soil drought stress

Leaf water potential at predawn was about –0.40 MPa and –0.50 MPa in shade and sun leaves, respectively (data not shown). It decreased quickly to about –1.50 MPa in the early morning and reached its daily minimum value of –2.60 MPa in mid-morning in sun leaves (refer to *Figure* 2). Leaf water potential followed a similar diurnal course in shade leaves**,** but with a minimum value of about –1.40 MPa, which was higher than in sun leaves. A_{max} did not decrease in either sun or shade leaves when soil water potential at 25 cm depth was higher than –0.013 MPa (*Figure* 2a). Neither g_s nor g_i was affected by leaf water potentials at this threshold of soil water potential (*Figures* 2b and 2c). When drought was prolonged and soil water potential fell below –0.015 MPa at 25 cm depth, g_i and g_s decreased by 20–40% in both sun and shade leaves in comparison with their respective values under unstressed soil water conditions (*Figure* 3). In contrast, $V_{cmax, Cc}$ was less affected by soil drought in shade leaves, and decreased by about 7% in sun leaves. The decrease in $V_{cmax, Ci}$ would be up to 22% in sun leaves, ignoring the effect of g_i on C_c. However, no significant difference was found between estimates of J_{max} obtained from A/C_i curves and A/C_c curves in either sun or shade leaves.

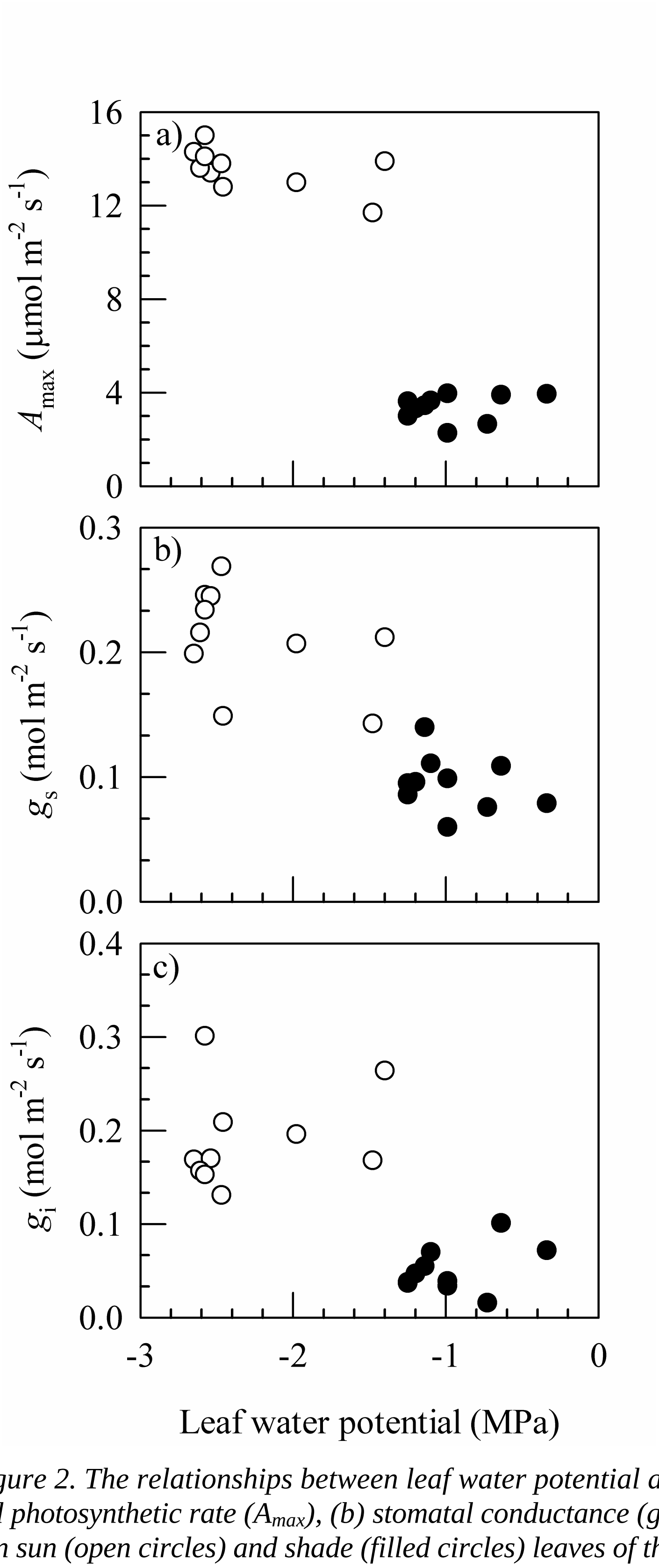

Figure 2. The relationships between leaf water potential and (a) light-saturated photosynthetic rate (A_{max}), (b) stomatal conductance (g_s) and (c) internal conductance (g_i) in sun (open circles) and shade (filled circles) leaves of three mature Fagus crenata trees when soil water potential at 25 cm depth was higher than – 0.013 MPa

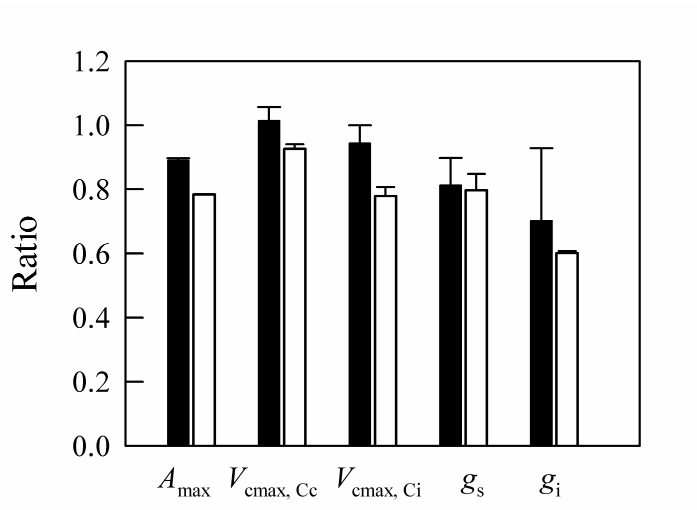

Figure 3. Effects of soil water stress on photosynthetic parameters of both sun (open bars) and shade (filled bars) leaves of three mature Fagus crenata trees when soil water potential at 25 cm depth was – 0.015 MPa (ratios between measurements on stressed leaves and unstressed leaves, measured in the preceding two days). The determined parameters are light-saturated photosynthetic rate (A_{max}), maximum rate of carboxylation estimated from A/C_c curves ($V_{cmax, Cc}$) and A/C_i curves ($V_{cmax, Ci}$), stomatal conductance (g_s) and internal conductance (g_i)

4 DISCUSSION AND CONCLUSIONS

4.1 Internal conductance of Fagus crenata

Structural (LMA, N_a) and photosynthetic (A_{max}, V_{cmax}, J_{max}) plasticity to local irradiance was observed within the *F. creneta* crown, indicating that there is great plasticity in responses to light intensity in this species. These responses have been previously documented in both *F. crenata* (Han et al. 1999; Iio et al. 2005) and *F. sylvatica* (Warren et al. 2007; Montpied et al. 2009). The internal conductance to CO_2 varied between 0.058 and 0.166 mol m^{-2} s^{-1} in lower and upper crowns of 90-year old *F. crenata* trees and resulted in a large decrease in CO_2 concentration from C_i to C_c of approximately 70 µmol mol^{-1}. To the best of our knowledge, this is the first report of measurements of g_i in *F. crenata*, although g_i has been investigated previously in *F. sylvatica* (Warren et al. 2007; Montpied et al. 2009). Internal conductance has been found to vary between 0.14 and 0.21 mol m^{-2} s^{-1} within the crown of 60-year old *F. sylvatica* trees in south-western Germany (Warren et al. 2007), and between 0.02 and 0.40 mol m^{-2} s^{-1} within the crowns of 35-year old *F. sylvatica* trees in north-eastern France (Montpied et al. 2009). These findings suggest that the magnitude of g_i is related to species ecotype, tree age and study site, as has been described for other photosynthetic parameters (Koike and Maruyama 1998; Peuke et al. 2002). In addition, assuming infinite g_i affects estimates of V_{cmax} and the interpretation of V_{cmax} in response to environmental stress. Most published estimates of V_{cmax} underestimate the true V_{cmax} by excluding the effect of draw-down from C_i to C_c (Wullschleger 1993). In *F. crenata*, use of C_i instead of C_c in modeling leads to V_{cmax} being underestimated by 24–36 %, similar to reported underestimates of this parameter in *F. sylvatica* (Warren et al. 2007).

4.2 Variation in gi between sun and shade leaves

For *F. crenata*, g_i was approximately three-fold higher in sun leaves than in shade leaves, similar to the two-fold difference found in previous comparisons between sun and shade leaves of *F. sylvatica* (Warren et al. 2007) and *Acer palmatum* (Hanba et al. 2002). Internal conductance is determined by cell wall thickness of mesophyll, the surface area of chloroplasts facing the intercellular airspace per unit leaf area (S_c), and the abundance and/or conductivity of aquaporins (Terashima et al. 2006; Flexas et al. 2008). In comparison with shade leaves of *F. crenata*, sun leaves haves larger S_c values (Oguchi et al. 2005), thicker palisade tissue (Uemura et al. 2000), and greater LMA. These structural differences may explain the difference in g_i between sun and shade leaves in *F. crenata*.

4.3 Water stress affects gi and photosynthesis

Leaf water potentials dropped to a diurnal minimum level of –2.60 MPa in sun leaves in the early morning, in accordance with previous observations at another site (550 m asl.) in the Naeba Mountains (Iio et al. 2004). In contrast, in another study of water potential in a beech forest the minimum leaf water potential was found to be about –1.50 MPa (Uemura et al. 2004). Although the reasons for such significant differences in leaf water potential are not fully understood, they may correlate with ecotypes (Bayramzadeh et al. 2008); *F. crenata* and *F. sylvatica* are known to have different characteristics that could be attributed to the climatic conditions in their original habitats, particularly to the amount of rainfall (Koike – Maruyama 1998; Peuke et al. 2002). The beech forests examined in this study are located at the side of the Sea of Japan with an average annual rainfall of 2214 mm for the period 1976–2009, whereas the study by Uemura et al. (2004) was carried out at the Pacific Ocean side with an average annual rainfall of 1408 mm for the same period.

In this study we found that g_i, g_s and A_{max} did not respond to decreasing leaf water potentials when there was sufficient soil water. Together with their rapid decline in the early morning, these results suggest that leaf water potentials fell in an adaptive response that promotes CO_2 diffusion into the carboxylation site when the soil water supply is sufficient and thus helps to maintain high photosynthetic rates. On the other hand, when soil water potential fell below a certain threshold, g_i and g_s decreased significantly in both sun and shade leaves, whereas the minimum daily leaf water potentials did not decline further. Reductions in g_i in response to soil drought rather than to atmospheric vapor pressure deficits have also been previously observed (Warren 2008). Considering this threshold of –0.015 MPa at 25cm depth for reductions in g_i, we concluded that *F. crenata* is sensitive to drought stress, as previously observed in assessments of factors affecting photosynthetic parameters of several *Fagus* species, e.g. *F. sylvatica* (Raftoyannis - Radoglou 2002), *F. crenata* (Maruyama – Toyama 1987; Uemura et al. 2004), and *F. grandifolia* (Tschaplinski et al. 1998).

Ignoring the effect of g_i on C_c resulted in an underestimation of V_{cmax}. The underestimation of V_{cmax} with water stress, found also previously (Wilson et al. 2000b), would suggest a predominant role of biochemical limitation to photosynthesis during drought. Thus, our results confirm that neglecting g_i may lead to an important overestimation of biochemical limitations. Nevertheless, V_{cmax} decreased 7% in sun leaves, even taking g_i into account, implying that the decrease in g_i due to soil drought was not fully responsible for the decrease in V_{cmax}. This finding is consistent with previous observations in *Quercus robur* L. and *Fraxinus oxyphylla* Bieb. (Grassi - Magnani 2005). In conclusion, the results of this study indicate that diffusional limitations due to both g_s and g_i affect photosynthetic rates in *F. crenata* under sufficient soil water supply, whereas biochemical limitations (i.e. V_{cmax}) are quantitatively important only during prolonged soil droughts.

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Variability of Physiological Parameters of European Beech Provenances in International Provenance Trials in Serbia

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Abstract – In this study, the variability of physiological parameters of five provenances of European beech (*Fagus sylvatica*), which were planted at two locations with different ecological conditions at Fruška Gora and Debeli Lug, was estimated. Provenance trials were established in the framework of COST Action E52: "Evaluation of Beech Genetic Resources for Sustainable Forestry". 2-3 years old seedlings originating from Croatia, Germany, Bosnia, Austria and Serbia were planted in blocks of fifty plants with a spacing of 2 x 1 m. Physiological parameters such as net photosynthesis, rate of transpiration and stomatal conductance were measured with a portable gas analysis system. Generally, provenances from Fruška Gora Mountain showed higher intensity of all physiological parameters than provenances located at site Debeli Lug. High correlations among rates of net photosynthesis and transpiration, on one side, and stomatal conductance, on the other side, were found. ANOVA test indicates that variability of net photosynthesis, transpiration and stomatal conductance of investigated provenances, at the two locations, was influenced both by environmental conditions of sites and genetic constitution of provenances.

beech provenances / net photosynthesis / transpiration / stomatal conductance.

1 INTRODUCTION

According to IPCC data, presented in 2001, the global Earth temperature has increased by 0.6 ±0.2 °C in the 20th century. Future projections indicate even more radical changes. According to those estimations, global air temperature will increase by 1.4–5.8 °C by 2100 (IPCC 2001). Due to possible scenarios about global climate changes, there is great interest and concern regarding beech ecosystems. The decline of rainfall during the vegetation period, accompanied by the intensification of summer drought and increasing concentrations of CO_2, will negatively affect beech, which is known as a species sensitive to drought (Geßler et al. 2007; Rose et al. 2009).

European Beech is the most common tree species in Serbia. According to the National Forest Inventory, pure and mixed stands of beech cover 660,400 hectares or 29.3% of the

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forest area. In total volume, beech is represented with 40.5%, while in the total volume increment beech is represented with 30.6% (Banković et al. 2009).

Networks of European beech provenance trials, which were established in six rounds so far, were aimed at research of genetic variability of populations originating from different regions, of the possibility of adaptation of different provenances at local site conditions and the study of the main environmental factors that determine the degree of adaptability of a population to specific habitat conditions (von Wuehlisch 2004). The study of adaptability of beech is particularly important as due to global climate change beech will become endangered or even lost in the course of the succession of species, in many parts of the beech range.

Previous studies have shown that the net photosynthesis is an important indicator of the vitality and competitive ability of a species at a given site (Aranda et al. 1996). Together with other gas exchange parameters in plants, net photosynthesis can be used as a criterion in the early selection of trees, in the process of breeding (Kundu – Tigerstedt 1998).

The research aimed at the study of variability of physiological parameters (net photosynthesis, transpiration and stomatal conductance) of beech plants in two international provenance trials in Serbia.

2 MATERIALS AND METHODS

2.1 Experimental fields

Beech provenance trials at Fruška Gora Mt (N 45°10'09.86", E 19°47'53.45") and Debeli Lug (N 44°19'34.01", E 21°52'20.39") were established in spring of 2007, in the framework of COST Action E52: "Evaluation of the Genetic Resources of Beech for Sustainable Forestry". Site characteristics of locations are given in *Table 1*.

Table 1. Site characteristics of "Fruška Gora" and "Debeli Lug" trials

Locality	Altitude	Exposition	Slope	Yearly average temperature	Average temperature during vegetation period	Yearly average precipitation	Average precipitation during vegetation period
	(m)		(°)	(°C)	(°C)	(mm)	(mm)
Fruška Gora	370	N	30	11.0	17.9	782	351
Debeli Lug	742	N-NE	5-7	8.8	15.1	829	455

2.2 Plant material

The tests were established by planting 2 and 3 years old seedlings in a spacing of 2 m between rows and 1 m between plants. Geographic and climatic characteristics of provenances are shown in *Table 2*.

Table 2. Site characteristics of provenances

Provenance	Country	Longitude		Latitude		Altitude	Exposition	Yearly average temperature	Average temperature during vegetation period	Yearly average precipitation	Average precipitation during vegetation period
		Deg	Min	Deg	Min						
						(m)		(t °C)	(t °C)	(mm)	(mm)
Vranica-Bistrica	BA	17	49	43	33	750	N	8.8	14.8	826	383
Fruška Gora	SRB	19	55	45	10	370	N-NE	11.2	17.9	782	351
Scharnstein, Mitterndorf	AUT	13	58	47	54	480	W	7.4	14.6	1263	706
Höllerbach	DE	13	14	49	1	755	–	5	11.7	1200	580
Sjeverni Dilj Čaglinski	CRO	18	1	45	17	350	NE	10.8	17.2	779	360

2.3 Physiological parameters

Net photosynthesis (A), transpiration (E) and stomatal conductance (gs) were measured in the second half of July 2009., using ADC Bioscientific Ltd. LCPro+ portable gas analysis system specialised for measurements of plant gas exchange parameters. Measurements were made on five plants from each provenance, in five replications per plant. The leaves were fully formed and located in the upper third part of the crown, oriented towards the south-southwest. Measurements were done in sunny and clear weather, in the period between 09:00 and 11:00 hours. Photosynthetic active radiation (PAR) has been set to volume of 1000 µmol·m^{-2}·s^{-1}, while the temperature, humidity and the concentration of CO$_2$ were measured on the spot.

2.4 Statistical analyses

The following statistical parameters and statistical analysis were applied: mean ($\overline{x}$), coefficient of variation (*CV*), standard deviation (*StD*), coefficient of correlation and ANOVA test. The data were processed by the software package "Statistica 9.1".

3 RESULTS

First the results of variability of net photosynthesis, transpiration and stomatal conductance measured in the provenance trial at Fruška Gora Mt (*Table 1*) are discussed. The highest rates of net photosynthesis (12.40 µmol·m^{-2}·s^{-1}) and stomatal conductance (0.33 mol·m^{-2}·s^{-1}) were measured on the local provenance („Fruška Gora“). The highest intensity of transpiration was measured for provenance „Höllerbach“ from Germany (4.49 mmol·m^{-2}·s^{-1}). On the other hand, the Croatian provenance „Sjeverni Dilj Čaglinski“ had the lowest value of net photosynthesis (10.41 µmol·m^{-2}·s^{-1}) and rate of transpiration (3.74 mmol·m^{-2}·s^{-1}), while the lowest stomatal conductance (0.22 mol·m^{-2}·s^{-1}) was recorded for the provenance "Scharnstein, Mitterndorf" from Austria.

The provenance „Höllerbach“ has shown the highest interprovenance variability, regarding net photosynthesis (16.93%) and stomatal conductance (19.31%). The Croatian provenance „Sjeverni Dilj Čaglinski“ had the highest coefficient of variation regarding transpiration (11.91%). The lowest interprovenance variability regarding net photosynthesis (10.71%) and transpiration (2.17%) was observed on provenance „Fruška Gora“, while the provenance "Vranica-Bistrica" showed the lowest variability of stomatal conductance (5.70%).

Table 3. Net photosynthesis, transpiration and stomatal conductance in the provenance trial at Fruška Gora Mt

Provenance	Net photosynthesis (µmol m^{-2} s^{-1})			Transpiration (mmol m^{-2} s^{-1})			Stomatal conductance (mol m^{-2} s^{-1})		
	$\bar{x}$	CV	StD	$\bar{x}$	CV	StD	$\bar{x}$	CV	StD
Sjeverni Dilj Čaglinski	10.41	16.82	1.75	3.74	11.91	0.45	0.24	18.23	0.04
Fruška gora	12.40	10.71	1.33	4.14	2.17	0.09	0.33	6.96	0.02
Höllerbach	11.35	16.93	1.92	4.49	11.68	0.53	0.24	19.31	0.05
Scharnstein, Mitterndorf	11.05	12.42	1.37	4.17	3.83	0.16	0.22	9.61	0.02
Vranica-Bistrica	11.14	11.32	1.26	3.94	3.27	0.13	0.30	5.70	0.02

Table 4. presents the results of variability of net photosynthesis, transpiration and stomatal conductance in the provenance trial Debeli Lug. Unlike Fruška Gora Mt., where the minimum value of net photosynthesis was registered for the provenance "Sjeverni Dilj Čaglinski, in the Debeli Lug, this provenance had the highest value of this parameter (12.61 µmol·m^{-2}·s^{-1}). The lowest rate of net photosynthesis was measured for the provenance “Höllerbach” (9.88 µmol·m^{-2}·s^{-1}). The highest rate of transpiration (4.81 mmol·m^{-2}·s^{-1}) and stomatal conductance (0.21 mol·m^{-2}·s^{-1}) was shown by provenance “Vranica-Bistrica” from Bosnia and Herzegovina. The lowest values of both parameters had provenance “Fruška Gora” ($E = 2.33$ mmol·m^{-2}·s^{-1}; $gs = 0.16$ mol·m^{-2}·s^{-1}).

Coefficient of variation regarding net photosynthesis (11.73%) and stomatal conductance (21.24%) was highest for provenance “Höllerbach”, while the provenance “Fruška Gora” showed the highest variation coefficient of transpiration (19.48%). The lowest coefficient of variation for net photosynthesis was found for provenance “Vranica-Bistrica” (7.77%). Provenance "Scharnstein, Mitterndorf" had the lowest coefficient of variation for transpiration (4.76%) and stomatal conductance (7.3%).

Table 4. Net photosynthesis, transpiration and stomatal conductance in provenance trial at Debeli Lug.

Provenance	Net photosynthesis (µmol m^{-2} s^{-1})			Transpiration (mmol m^{-2} s^{-1})			Stomatal conductance (mol m^{-2} s^{-1})		
	$\bar{x}$	CV	StD	$\bar{x}$	CV	StD	$\bar{x}$	CV	StD
Sjeverni Dilj Čaglinski	12.61	11.48	1.45	3.50	9.92	0.35	0.20	19.15	0.04
Fruška gora	11.23	10.66	1.20	2.33	19.48	0.45	0.16	16.12	0.03
Höllerbach	9.88	11.73	1.16	3.36	10.69	0.36	0.18	21.24	0.04
Scharnstein, Mitterndorf	10.61	10.94	1.16	3.01	4.76	0.14	0.19	7.30	0.01
Vranica-Bistrica	10.64	7.77	0.83	4.81	8.83	0.43	0.21	9.74	0.02

Results of ANOVA test for net photosynthesis, transpiration and stomatal conductance are given in *Tables 5, 6 and 7*. Significant differences were recorded among provenances (P) regarding all investigated parameters. In the case of location (L), significant differences were recorded for rate of transpiration and stomatal conductance. The interaction between provenance and locality (PxL) was statistically significant, as well.

Table 5. Analysis of variance for net photosynthesis in the studied beech provenance trials

Source	d.f.	Sum of squares	Mean square	F value
Location	1	2.859	2.859	0.7723
Error	28	103.669	3.702	
Provenance	4	30.923	7.731	5.3830***
P x L	4	63.047	15.762	10.9753***
Error	112	160.845	1.436	
Total	149	361.343		

Table 6. Analysis of variance for rate of transpiration in the studied beech provenance trials

Source	d.f.	Sum of squares	Mean square	F value
Location	1	17.944	17.944	115.541***
Error	28	4.348	0.155	
Provenance	4	21.914	5.478	50.306***
P x L	4	32.127	8.032	73.751***
Error	112	12.197	0.109	
Total	149	88.529		

Table 7. Analysis of variance for stomatal conductance in the studied beech provenance trials

Source	d.f.	Sum of squares	Mean square	F value
Location	1	0.228	0.228	180.308***
Error	28	0.035	0.001	
Provenance	4	0.055	0.014	15.856***
P x L	4	0.091	0.023	26.203***
Error	112	0.098	0.001	
Total	149	0.508		

The correlation analysis was performed between investigated physiological parameters (*Table 8*). Results indicate a high positive correlation between net photosynthesis and stomatal conductance. Positive correlation exists also between intensity of transpiration and stomatal conductance.

Table 8. Coefficient of correlation among net photosynthesis, transpiration and stomatal conductance

	Transpiration	Stomatal conductance
Net photosynthesis	0.419	0.927
Transpiration	–	0.515

4 DISCUSSION

The synthesis and accumulation of organic matter are achieved by the process of photosynthesis, and thus the influence of factors determining plant productivity could be better assessed if photosynthetic potential of individual leaves is determined (Bugbee and Salisbury, 1988). Research of numerous authors (Sheriff et al. 1986, Vaitkus et al. 1993, Kundu – Tigerstedt 1998, Orlović et al. 2001, Orlović et al. 2006) on different tree species have shown that research of net photosynthesis can provide useful information about growth potential of genotype and plant productivity. If a good correlation between growth and unit rates of photosynthesis and respiration can be established, than the effect of environment or heredity on present and even future growth may be determined easier (Bourdeau 1957).

The results of the research of net photosynthesis, intensity of transpiration and stomatal conductance of the five provenances indicate that there were highly significant differences between provenances regarding all parameters. In the case of transpiration and stomatal conductance, there was significant difference between locations as well. Adaptability of study provenances was also assessed. All parameters showed a statistically highly significant genotype x environment (PxL) interaction which indicates the existence of significant potential for adaptation.

The results of this research are corresponding with research of Ivankovic et al. (2008), who investigated variability of height growth in beech provenance trials established in Croatia and Slovenia. The authors concluded that there was a significant influence of site characteristics on height of seedlings and that different provenances had different abilities to adapt to given environmental conditions.

5 CONCLUSION

At the provenance trial established at Fruška Gora Mt., the highest rate of net photosynthesis was recorded for provenance "Fruška Gora". The local provenance had the highest stomatal conductance as well. Transpiration rate was the highest for the provenance "Höllerbach".

The lowest values of net photosynthesis and transpiration were measured for Croatian provenance "Sjeverni Dilj Čaglinski", while the lowest stomatal conductance was recorded for provenance "Scharnstein, Mitterndorf".

The highest interprovenance variability, regarding all studied parameters, was shown by the provenances "Sjeverni Dilj Čaglinski" and "Höllerbach".

At the site Debeli Lug, provenance "Vranica-Bistrica" showed the highest rate of transpiration and stomatal conductance, while the provenance "Fruška Gora" showed the lowest. Net photosynthesis was highest for provenance "Sjeverni Dilj Čaglinski", and the lowest for provenance "Höllerbach".

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Pregermination Treatment and Germination Characteristics of Oriental Beech (*Fagus orientalis* Lipsky) in the Caspian Region

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Abstract – Oriental beech is one of the most important tree species in the Caspian region that regenerates naturally.

Seed pretreatment plays an important role in beech reforestation .For this reason the seeds of three different provenances; Gilan (Asalem), Nowshahr (Makarood), Gorgan (Cheshmeh gholgholy), across the Caspian region, were collected and after viability test (TTC) placed under cold stratification (for 8-19 weeks) to overcome dormancy. The results have shown that pregermination treatments had desirable effects on seed germination. There were significant variations between three origins and different treatment duration and germination characterstics. The Nowshahr and Gilan origins showed more similarity.

***Fagus orientalis* / pregermination treatment / Caspian region**

1 INTRODUCTION

Beech is the most valuable wood producing species in the Caspian forests covering 17.6 percent of the area and represent 30 percent of the standing volume (Resaneh *et al.* 2001). Its area extends about 700 km East-West in this region. The extreme eastern border of oriental beech forests is Ziârat valley near Gorgân town, on the southern coast of the Caspian Sea in Iran. These forests extend westwards as separated spots towards the Caucasus, Asia Minor and north of Greece, Bulgaria and Romania. Oriental beech is replaced by European beech (*F. sylvatica*) in the Central and West Balkans (Sabeti 1993; Bektas *et al.* 2000). In the Hyrcanian phytogeographical region, in Northern Iran, oriental beech forests cover the northern slopes of the Alborz Mountains, between 680 to2000 m above sea level and annual precipitation between 800 to 1800 mm, decreasing from West to East.

Beech seeds require cold stratification (prechilling) for prompt germination, and current practices with European beech (*Fagus sylvatica* L.) have combined stratification and storage into a coordinated procedure. The first step is to determine how much stratification is needed to overcome dormancy (Suszka – Zieta 1977). Termination of embryo dormancy is achieved by cold moist stratification or prechilling, *i.e.* subjecting hydrated nuts to

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temperatures between +2 and +5°C with or without medium (El-Antably 1976; Suszka – Muller – Bonnet-Masimbert 1996). The time period necessary to complete dormancy release is usually quite long, ranging from 5 to 8 weeks and in some cases even up to 12 weeks (Muller – Bonnet-Masimbert 1982). The level of primary dormancy in seeds is determined by several factors of genetic and non-genetic origin (Andersson – Milberg 1998). All of these factors may cause physiological variability which is matched with differences in seed morphology (size, weight, color *etc.*) or simply heterogeneity in degree of dormancy (Bewley – Black 1994). Therefore dormancy levels vary within the seed lot of many species among them *Fagus* spp.; a few nuts germinate without cold moist stratification or prechilling, but others in the same lot will not germinate until they are prechilled. In addition, during prechilling and dormancy release, the heterogeneity usually increases (Derkx – Joustra, 1997). On the other hand variation in dormancy level among populations is a well-known phenomenon (Frost – Cavers 1975; Miller *et al.* 1976; Paterson *et al.* 1976; Naylor – Abdalla 1982; Drennan – Bain 1987; Evans – Cabin 1995; Milberg *et al.* 1996; Schütz – Milberg 1997; Andersson *et al.* 1997).

Germination is one trait that has been found to greatly vary among populations (reviewed by Baskin - Baskin, 1998). Differences among provenances, particularly in germination, can be inflated by heterogeneous environmental conditions among sites at which seeds were collected (environmental maternal effects: Gutterman 1992; Lopez – Potts – Vaillancourt – Apiolaza 2003; Pico – Ouborg – van Groenendael 2003; Roach – Wulff 1987). Significant variation in germination ability of a species among seed samples of different sources have been reported also for several species of Central Himalaya. Causes of such variability might be generally attributed either to (a) genetic character of source population/plant (Witcombe – Whittington 1972; Bewley – Black 1994), or (b) impact of mother plant environment (Fenner 1991; Andersson – Milberg 1998; Bhatt et al. 2000). A survey on effects of different treatments of beech nuts showed that germination capacity increased with increasing duration of cold - moist stratification for nuts with and without endocarp (Soltani et. al. 2005). The provenance effect, as determined by broad sense heritability, was 80% for germination capacity and 42% for germination energy. Germination energy was significantly correlated with longitude and mean annual rainfall (Loha et al, 2006).

2 MATERIALS AND METHODS

2.1 Seed sources

Lots of oriental beechnuts, used in these experiments, were collected from 10 different mother trees (in each provenance) of three different provenances in the Caspian region: in Darya-Bon Nav Asalem(Gilan), Makarood (Nowshahr) and Cheshmeh Gholgholi (Golestan) at 900, 950 and 1000 m asl. during a two weeks period in November 2008. After collection, seeds were extracted from their capsules and its physical (%MC, 1000 seed weight) and physiological (viability, germination capacity) characteristics determined at the Caspian Forest Tree Seed Centre seed laboratory according to ISTA rules (ISTA, 2008). For breaking dormancy, 4 replicates of hundred seeds from each provenance were soaked in cold water for 48 hours, then mixed at 3–5 °C with medium (sterilized sand) for a maximum period of 24 weeks (Suszka 1975) and then germinated.

2.2 Data analysis

Germination characteristics such as GC (germination capacity), GR (germination rate), GS (germination speed), MDG (Mean Daily germination), PV (peak of velocity), GV (germination value) and GE (germination energy) (Willan 1985, Panwar and Bharadwaj 2005) were calculated as follows:

$GC = (G + VS)/TS \times 100$, $GR = n/N * 100$ $GS = \sum (n/DSS)$

$MDG = FCG/T$ $PV = MCG/DSS$ $GV = PV * fMDG$

$GE = (\text{max germinated seed a day})$

where:

G = germinated seeds
VS = viable, nongeminated seeds at the end of period
TS = total seed per replicate
n = number of germinated seeds in each count
DSS = days from the start of the test
FCG = Final Cumulative germinated seed
T = total period of germination
MCG = Maximum of cumulative Germination
fMDG = final Mean Daily germination
N = number of tested seeds

Generalized linear model (GLM) or univariate variance analysis was performed to determine differences in GC and GS and one - way ANOVA for determining differences in PV, GV, and MDG between three provenances.

3 RESULTS

The results of lab analysis are shown in *Table 1.*

Table 1. The results of lab analysis

	Provenance	Physical characteristics		Physiological characteristics	
		% MC	1000 S.W.	% V.S.	% GC
1	Darya-Bon Nav Asalem (Gilan)	26/6	253/75	82	77
2	Makarood (Nowshahr)	27/7	293/62	89	89
3	Cheshmeh Gholgholi (Golestan)	18	244/16	98	84

The results of survey on the effects of cold stratification on beech nuts germination in contrast with control showed that this treatment can significantly promote germination process in all provenances. Germination characteristics of three different provenances show that

- GE in all provenances is significantly different.
- PV, GV, GS of Asalem and Makarood provenances are similar but different from Cheshmeh Gholgholi (Histograms No. 1, 2 and 4)
- MDG in Makarood and Cheshmeh Gholgholi are similar but significantly different from Asalem (Histogram No. 3)
- Treatment Duration (T.D) in Asalem and Makarood are similar but significantly different from Cheshmeh Gholgholi

Table 2. The results of treatment and germination characteristics

Provenance	% GE	PV	MDG	GV	GS	% Gr	(Week) T.D
Asalem	57	1.63	0.95	1.55	0.27	73	8–18
Makarood	71	1.69	1.14	1.90	0.25	88	8–19
Cheshmeh Gholgholi	66	3.09	1.2	3.17	0.41	81	10–19

4 DISCUSSION AND CONCLUSIONS

Germination energy may be significantly correlated with longitude and mean annual rainfall. (Loha et al. 2006). Variation in dormancy level among populations is a well-known phenomenon (Frost – Cavers, 1975; Miller et al. 1976; Paterson et al. 1976; Naylor and Abdalla 1982; Drennan – Bain 1987; Evans – Cabin 1995; Milberg et al. 1996b; Schütz – Milberg, 1997; Andersson et al. 1997). Necessary treatment duration was different in all provenances but more similar in western and central ones (Asalem – Makarood). Causes of such variability might be generally attributed either to (a) genetic characters of source population/plant (Witcombe – Whittington 1972; Bewley – Black 1994), or (b) impact of mother plant environment (Fenner 1991; Andersson – Milberg 1998; Bhatt et al. 2000).

As already described, cold stratification had significant effect on seed dormancy breaking in all three provenances of oriental beech (control had not any germination) as reported in European beech which require cold stratification (prechilling) for prompt germination, and current practices with European beech have combined stratification and storage into a coordinated procedure.(Suszka – Zieta 1977).

Germination characteristics of provenances Asalem and Makarood were similar but Cheshme gholgholi was different The difference may be caused both by provenance effect and longitudinal difference.

5 RECOMMENDATIONS

According to achievements of this study it seems that direct seeding of stored, pretreated seeds that are collected immediately after dispersal, can help to regenerate this species, because this way the seeds escape predation and the effect of rare mast years is minimised.

Regarding the importance and extended distribution of this species and missing experiences on this issue it seems that more research in this field should be done.

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Factors Affecting the Success of Natural Regeneration in Oriental Beech *(Fagus orientalis* Lipsky) Forests in Turkey

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Abstract – The success of natural regeneration using the Uniform Shelterwood Method (USM) was determined in an oriental beech (*Fagus orientalis* Lipsky.) stand, in the Bartın-Sökü Forest Range District. Number, height growth and root collar diameter of seedlings were investigated in the 10 experimental plots in the 5.0 ha regeneration area for 7 years (2004–2010). According to the result of factor analyses, it was found that amount of filled seeds, soil cover, growth status of seed trees, stand canopy closure, average crown projection area of seed trees, amount of organic substance in the upper soil layer, soil reaction in the upper soil layer and hillside status were the most effective factors determining the success of natural regeneration.

Oriental beech *(Fagus orientalis* Lipsky*.)* / natural regeneration / factor analysis / silviculture

1 INTRODUCTION

Because of variable climate and physiographic conditions, Turkey has natural forest resources with high biological and economic value both with respect to tree species and area. According to 2006 data, forest area of the country is 21.2 million hectares, reaching 27.2% of the total area. 50% of it is degraded and coppice forest. The improvement of this situation and the increase of forestry sector's portion in national income depend largely on successful regeneration practices. Oriental beech (*Fagus orientalis* Lipsky.) has the fourth largest distribution area with 1.7 million ha. Total volume of beech forests is 263.772.103 m^3, with a total annual increment of 6.130.147 m^3 (OGM 2006).

2 MATERIAL AND METHOD

2.1 Material

Forests of the Sökü district are situated in the *Northwest Euxinic* forest subzone of the *Euxinic* forest zone (Mayer – Aksoy 1998). According to inventory data for 2000, total forest area in the region is 3386.0 ha, 6.2% (208.5 ha) of it is degraded forest. Sökü region is under the effect of West Black Sea sub-climate (IIc). All seasons are rainy, the month with highest

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average precipitation is December (162.3mm), the one with the lowest is May (88.0mm). Annual average temperature is 10.6 °C, the coldest month is January (0.0 °C), and the hottest are July (19.8 °C) and August (19.7 °C). Vegetation period in the research area is 6 months (May–October). General soil type is stony, alkaline, sandy clay and sandy clayish mud of mediocre depth (OGM 2001, OGM 2002).

In compartment 27a, a pure beech stand of 5.0 hectares, a regeneration cut using the Uniform Shelterwood Method (USM) has been performed in 2003, in a seed year. During the cut the stand canopy closure has been reduced to 0.6–0.7. Tending of seedlings was continued for 3 years. To follow the increased light demand of seedlings, the canopy closure has been reduced to 0,5 in 2007. A total of 10 experimental plots with the size of 25 x 40 m have been established to follow up the regeneration process.

2.2 Method

At first, predominant habitat conditions (climatic, edaphic and physiographic factors such as exposure, slope, altitude and hillside situation) in the experimental plot have been determined. Regarding soil conditions, soil depth, structure type and rooting depth, as well as soil reaction (pH), amount of organic substances, nitrogen, phosphor and potassium have been determined. In addition, in each plot thickness of organic cover (litter and humus layers) and crown cover have been measured. For the seed trees in the 10 experimental plots, age, number, diameter, height, basal area, volume, average annual volume increment, crown width and crown projection area have been determined.

The most important criterion in determining the success of natural regeneration practices is the number of plants per square meter (Saatçioğlu 1979, Atay 1987, Nyland 2002). Not only changes in the number of seedlings but also changes in their height and the root collar diameter per year have been examined. For this purpose, 5 x 5 m sample plots were made up in the 25 x 40 m parcels. In 20 sample plots tally of seedlings, height (cm) and the root collar diameter (mm) measurements were established annually during the seven year research (2004–2010).

2.3 Statistical Analysis

SPSS (Statistical Package for Social Science) 9.0 pack program was used for the statistical analysis of data. Kolmogorov-Smirnov test has been applied to determine whether the data displayed normal distribution.

First, correlation analysis has been applied for the purpose of determining the degree of mutual relation between variables and direction. As a result of analysis, dual linear coefficient of correlation between factors have been examined whether they are meaningful or not in the level of significance 0.05 and 0.01. Factor analysis has been applied according to the coefficient of correlation between factors. The Principal Component Analysis has been applied to detect the factors explaining the variance best. “Kaiser” and “Scree Test” criterions are used mostly in determining the number of factors which will represent the relations between variables in the highest degree. In this research, the Kaiser criterion – considering the factors with eigenvalue (joining amount to variance) statistics greater than 1 – was used.

In terms of simplifying the interpretation, unturned factor matrix obtained with Principal Component Analysis should be subjected to rotation. For this purpose, the *Varimax* technique has been applied and a converted factor matrix was obtained by the selection of orthogonal rotation which takes interfactor zero correlation as basis. Interpretation and naming of factors has been made on basis of the variables with high factoral load. In some cases common reasons underlying the variables relating to factors have been taken into consideration. In the research for 7 years, the main aim was to clarify the effects of variables (climatic, edaphic and physiographic and variables relating to seed trees and seedlings) on the number of seedlings.

In this regard, the last three years (2008, 2009 and 2010) data of climate, state of weed and litter cover was used for impact of these variables determined on success of natural regeneration in recent years. For this purpose, multiple regression analysis was carried out in order to determine the effects of all investigated variables on seedling number. The number of beech seedlings per square meter in 2010 has been taken as dependent variable. In multiple regression analysis, the most important factors appeared as independent variables.

3 RESULTS AND DISCUSSION

3.1 Number of Seedlings

The success of natural regeneration practices is determined by the regrowth per square meter. Numbers of the last tally carried out in regeneration plots in 2010 is shown in *Figure 1.*

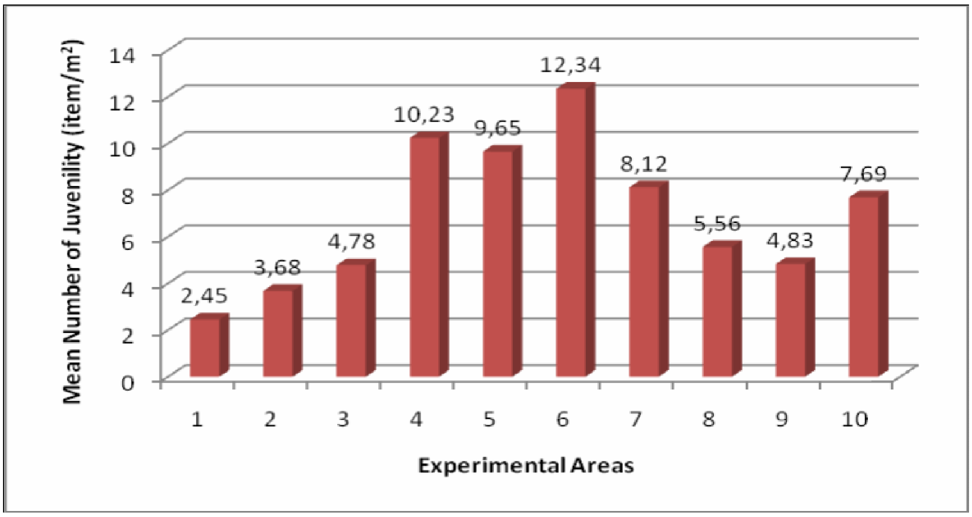

Figure 1. Mean numbers of oriental beech juvenilities according to experimental areas

The number of oriental beech seedlings ranged from 2.45 to 12.34 per m^2. In a study of beech natural regeneration practices in the Belgrade Forest, the average seedling number ranged between 4 and 80 plants/m^2 in the 3rd year and between 4 and 56 plants/m^2 in the 5th year (Saatçioğlu 1970). In Turkish practice, seedling numbers of 2–64 plants/m^2 at the end of 1st year, 1–57 plants/m^2 at the end of 2nd year and 2–71 plants/m^2 at the end of 3rd year are reported (Suner 1978). In the Bartın-Yenihan Forest Range District's 70b compartment, in a study of beech natural regeneration, recruitments between 8 plants/m^2 and 29 plants/m^2 at the end of 1st year, 7 to 28 plants/m^2 at the end of 2nd year and 6 to 26 plants/m^2 at the end of 3rd year were counted (Özel et al. 2009).

When seedling numbers in the present study are compared to other beech natural regeneration practices done with USM, the natural regeneration appears to be unsuccessful. Based on the count in 2010, it looks that 2003 was not a good seed year just a mediocre one in the Bartın-Sökü district. However, one of the reasons why the seedling number is low is that the weed control and soil cultivation in 2003 were not carried out intense enough and with appropriate technique. It was found that the density of weed cover, particularly that of pontic rhododenron (*Rhododendron ponticum* L.) presents an important problem for natural and artificial practices of regeneration in beech. In order to eliminate this problem, clearing of the regeneration area is necessary to remove particularly pontic rhododenron (Saatçioğlu 1970, Kharitonenko 1972, Suner 1978, Eşen 2000).

3.2 Height Growth

Average annual height growth of beech seedlings are shown in *Figure 2*. The mean height of 7 years old seedlings, ranged from 14.8 cm to 17.3 cm. In the Belgrade forest, oriental beech seedlings' average height ranged between 13.5 cm and 20.9 cm in the 3rd year, 13.8 cm to 23.0 cm in the 4th and 17.3 cm to 46.6 cm in the 5th (Saatçioğlu 1970). Generally, the height growth of beech seedlings in the Sökü regeneration area is found to be satisfactory.

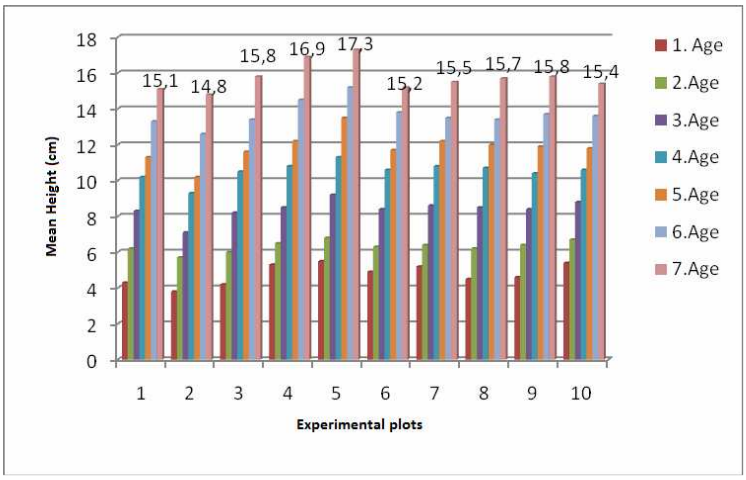

Figure 2. Mean heights of oriental beech seedlings in experimental plots

3.3 Root Collar Diameter Development

The root collar diameter growth of seedlings is shown in *Figure 3*. The mean root collar diameter of 7 years old seedlings, ranged from 18.5 mm to 21.3 mm.

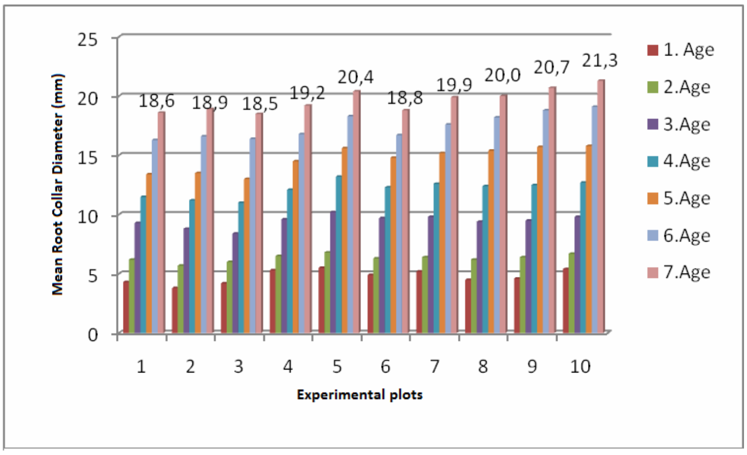

Figure 3. Mean root collar diameter of oriental beech seedlings in experimental plots

In another research in the Düzce, Cide and Akkuş regions, average root collar diameter after removal cut ranged between 15.8 mm and 23.5 mm (Suner 1978). According to this data, the beech seedlings' root collar diameter growth in the research area is found to be satisfactory too.

3.4 Factors Affecting the Regeneration Success

Factor analysis has been applied in order to determine factors that can be effective in the success of regeneration. For this purpose 52 variables were put in the analysis (*Table 1*).

Table 1. Names, dimensions and labels of investigated variables

Order	Variables	Dimension	Label
1	Altitude of Experimental Plot	m	AEA
2	Exposure of Experimental Plot	---	EEA
3	Slope of Experimental Plot	%	SEA
4	Hillside Status of Experimental Plot	---	HSEA
5	Average Diameter of Beech Seed Trees in Experimental Plot	cm	AD
6	Average Height of Beech Seed Trees in Experimental Plot	m	AH
7	Age of Beech Seed Trees in Experimental Plot	Year	ABST
8	Average Crown Form of Beech Seed Trees in Experimental Plot	---	ATF
9	Average Trunk Form of Beech Seed Trees in Experimental Plot	---	ABF
10	Number of of Beech Seed Trees	trees/ha	NBST
11	Average Volume of Beech Seed Trees	m^3/ha	AV
12	Average Annual Volume Increment of Beech Seed Trees	m^3/ha/year	AAVI
13	Average Basal Area of Beech Seed Trees	m^2/ha	ABA
14	Stand Canopy closure	---	SC
15	Mixture Ratio of Beech Seed Trees	%	MR
16	Light Density	%	LI
17	Average Crown Projection Area of Beech Seed Trees in Experimental Plot	m^2	ATPA
18	Average Crown Width of Beech Seed Trees in Experimental Plot	m	ATW
19	Absolute Soil Depth	cm	ASD
20	Physiological Soil Depth	cm	PSD
21	Rootlet Status	---	RS
22	Structure Type	---	SUT
23	Soil Type	---	ST
24	Soil Reaction in the Upper Soil Layer (pH)	---	SR
25	Amount of Organic Substance in the Upper Soil Layer (Ah)	%	AOS
26	Amount of Nitrogen in the Upper Soil Layer (Ah)	%	AZOTE
27	Amount of Phosphor in the Upper Soil Layer (Ah)	ppm	PHOSPHOR
28	Amount of Potassium in the Upper Soil Layer (Ah)	ppm	POTASSIUM
29	Saltiness of the Upper Soil Layer (Ah)	dS/m	SALTINESS
30	Amount of Filled Seeds	item/ha	AFS
31	Germination Percentage	%	GP
32	Germination Temperature	°C	GT
33	Maturation Time of Seed	day	MTS
34	Damage by Wild Animals	item/m^2	DWA
35	2008 Amount of Precipitation	mm	AP08
36	2008 Average Temperature	˚C	AT08
37	2008 Thickness of Litter Layer	cm	TLL08
38	2008 Thickness of Rotten Layer	cm	TRL08
39	2008 Thickness of Humus Layer	cm	THL08
40	2008 Density of Weed	%	DW08
41	2009 Amount of Precipitation	mm	AP09
42	2009 Average Temperature	˚C	AT09
43	2009 Thickness of Litter Layer	cm	TLL09
44	2009 Thickness of Moder (decayed) Layer	cm	TRL09
45	2009 Thickness of Humus Layer	cm	THL09
46	2009 Density of Weed Growth	%	DW09
47	2010 Amount of Precipitation	mm	AP10
48	2010 Average Temperature	˚C	AT10
49	2010 Thickness of Litter Layer	cm	TLL10
50	2010 Thickness of Moder (decayed) Layer	cm	TRL10
51	2010 Thickness of Humus Layer	cm	THL10
52	2010 Density of Weed Growth	%	DW10

The number of beech seedlings per square meter in 2010 has been taken as dependent variable and factors affecting this have been examined. In factor analysis, 8 common, basic factors have been identified by using *Principal Component Analysis* and *Kaiser* Criterion (*Table 2*).

Table 2. Total variance explained for the first 12 components

Components	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative Variance (%)	Total	% of Variance	Cumulative Variance (%)
1	28.145	34.312	34.312	15.935	31.853	**31.85**
2	7.546	16.242	50.554	7.683	20.431	**52.28**
3	6.845	11.773	62.327	6.815	12.752	65.03
4	3.615	7.665	69.992	5.554	10.026	75.06
5	2.715	5.337	75.329	4.825	8.448	83.51
6	2.413	3.226	78.555	3.673	5.761	89.27
7	2.105	2.475	81.030	2.849	3.275	92.55
8	1.187	1.245	82.275	2.776	1.842	**94.39**
9	1.170	1.110	83.305			
10	1.163	1.006	84.311			
11	1.152	1.002	85.313			
12	0.996	0.785	86.098			

Extraction Method: Principal Component Analysis

As shown in *Table 2*, first 8 factors with an eigenvalue above 1 are identified. The first factor explains 31.85% of total variance. First and second factors together explain 52.28%. The 8 common, basic factors explain 94.39% of total variance.

In order to facilitate the identification and interpretation the factor, rotated factor matrix has been calculated *(Table 3)*. Factor loads smaller than 0.5 are not included in this chart for the sake of clarity.

Table 3. Rotated component matrix (if more than five components, only the first five shown)

Variables	Factors							
	1	2	3	4	5	6	7	8
AFS	0.999							
GP	0.998							
GT	0.996							
MTS	0.995							
DWA	-0.993							
TLL10		0.994						
TRL10		0.992						
THL10		0.988						
DW10		-0.985						
TLL09		0.982						
AD			0.991					
AH			0.990					
ABST			0.988					
NBST			0.983					
AV			0.980					
SC				0.989				
MR				0.985				
LI				0.980				
ATPA					0.986			
ATW					0.984			
ATF					0.979			
ABF					0.975			
AOS						0.981		
AZOTE						0.980		
PHOSPHOR						0.977		
POTASSIUM						0.973		
ASD						0.970		
SR							0.972	
SALTINESS							-0.967	
HSEA								0.970
AEA								-0.965
EEA								0.953
SEA								-0.932

Extraction Method: Principal Component Analysis
Rotation Method: Varimax with Kaiser Normalization

As seen in the rotated factor matrix, correlations among 52 variables are represented by 8 common factors. In every factor, the highest correlated variable appears in the first place. Thus, the first variable of the first factor is the amount of filled seeds, the first variable of the second factor is thickness of litter cover in the year 2010; and so on – see *Table 3* and *4*. This way the most influential factors for the success of natural regeneration of oriental beech in the Sökü experiment have been identified. The factors are listed in *Table 4* with their variance contributions.

Table 4. List of factors most influential in the regeneration success

The Name of Factor	Variance contribution (%)
1. Amount of Filled Seeds	31.85
2. Soil Cover	20.43
3. Growth Status of Seed Trees	12.75
4. Stand Canopy closure	10.03
5. Average Crown Projection Area of Beech Seed Trees	8.45
6. Amount of Organic Substance in the Upper Soil Layer	5.76
7. Soil Reaction in the Upper Soil Layer	3.28
8. Hillside Status	1.84
Total	94.39

Multivariate regression analysis was performed to examine the effects of the most important nine factors (independent variables) that were identified by the factor analysis on the beech seedlings' number. In the multiple regression analysis, the beech seedlings' number per square meter in the year 2010 (SN.10) was used as dependent variable. Results obtained by Enter Method are given in *Table 5*.

Table 5. The results of multivariate regression analysis

Model	Standardized Coefficient	Standard Error	F	R^2
(Constant)	0.782	0.651	7.895***	0.92
AFS	0.936**	0.000		
TLL10	0.00453	0.004		
AD	–0.00158	0.003		
SC	0.133**	0.000		
ATPA	0.245**	0.000		
AOS	0.237**	0.000		
SR	0.00546	0.007		
HSEA	–0.00047	0.005		

Dependent variable: SN.10 (beech seedling number per square meter in the year 2010)
(******): P=0.01 significance level
(*******): P=0.001 significance level

According to regression analysis result, 92% of the regeneration success in the research area stems from these aforementioned 8 factors. But the most important among them are AFS, SC, ATPA and AOS. These four factors affect seedling number at 99% significance level in the positive direction. According to these results, the multivariate regression model can be written as

$$\boldsymbol{Y}_{(SN10)} = 0.782 + 0.936\boldsymbol{X}_{(AFS)} + 0.00453\boldsymbol{X}_{(TLL10)} - 0.00158\boldsymbol{X}_{(AD)} + 0.133\boldsymbol{X}_{(SC)} + \\ + 0.245\boldsymbol{X}_{(ATPA)} + 0.237\boldsymbol{X}_{(AOS)} + 0.00546\boldsymbol{X}_{(SR)} - 0.00047\boldsymbol{X}_{(HSEA)}$$

4 DISCUSSION

Out of the 8 factors that have been obtained as a result of factor analysis, amount of filled seeds takes the first place. There is also an apparent relation between amount of filled seeds and germination percentage of beech seeds. Saatçioğlu (1969), Szwagrzyk et al. (2001) and Çepel (1995) have also found that out of many factors affecting the success of regeneration, the amount of filled seed and germination percentage have evident importances.

The second factor determined by factor analysis is soil cover *(Table 3* and *Table 4)*. The soil cover includes weed and litter cover. As the density of weed cover and thickness of litter cover in the regeneration area increases, the number and growth of oriental beech seedlings decreases. It is proven that intense weed cover, particularly pontic rhododenron (*Rhododendron ponticum* L.) cover is an important problem as stated in chapter 3.1 already. Intense weed control and soil cultivation have especially positive effects on seedling development (Saatçioğlu 1970, Suner 1978).

The growth status of seed trees is the third factor having an effect on the success of regeneration *(Table 4)*. Trees in the stand should be in the age of maturity in order that regeneration practices can be carried out in a stand (Saatçioğlu 1979, Atay 1987). Trees that haven't reached the full status of maturity yet, cannot yield enough seed, especially as they haven't completed crown growth.

The next factor is the stand canopy closure *(Table 3 and Table 4)*. There is an important relation between stand canopy closure and light density. Light density is effective on germination, site condition and soil cover (weed and litter cover) (Çepel 1995). It is stated by many researchers that oriental beech, growing up slowly in the seedling period, needs protective upper cover until it gains its biological independence (Saatçioğlu 1969, Suner 1978, Atay 1987).

The fifth factor affecting the success of natural regeneration practice in oriental beech is average crown projection area of beech seed trees *(Table 4)*. Trees that haven't reached the age of maturity yet, cannot hold enough seed as they haven't completed especially crown development. On the other hand, as age advances, beech spreads its crown and crown decay starts in the upper parts. Because of the decay in the crown of oriental beech trees, capacity of seed holding decreases and this affects the number of seedlings negatively.

The amount of organic substance in the upper soil layer *(Table 3, 4)* is the sixth factor. Seedlings of beech benefit from the water and nutrients in the soil mostly in terms of root growth. In European beech silviculture it is known that the species develops best in soils which are rich in organic substance (Kerr 1995).

The seventh factor is soil reaction in the upper soil layer *(Table 4)*. There is a positive relation between amount of soil reaction in the upper soil layer and number of oriental beech seedlings *(Table 3)*. In a research carried out by Akgül and Aksoy (1976) in the Research Forest of Bolu-Şerif Yüksel, they confirmed that there is an important relation between root growth, soil reaction and the amount of organic substance.

Hillside status is the eighth factor affecting the success of natural regeneration practice in oriental beech in the research area *(Table 3, 4)*. Hillside status is an important physiographic variable influencing local habitat conditions. Depending on the changes in hillside status, microclimatic and edaphic conditions also change dramatically (Çepel 1995). Beech reaches its optimum development at middle and sub hillside (Peters 1992). Outside these conditions the density of beech stand decreases, diameter and height growth decline, crown growth weakens and crown form deteriorates. These changes of the beech trees cause the deterioration of stand structure and fertility.

5 CONCLUSIONS

In order to increase the success of beech natural regeneration in the practice the following suggestions are formulated:

- Good seed years should be identified correctly in the stands planned for regeneration.
- The presence of seed trees in sufficient quantity and homogeneity is an important precondition. Regeneration practices should be applied only in stands which are in the age of maturity.
- Before acorn fall in the regeneration area, litter and weed cover, especially pontic rhododenron should be cleared, to provide better conditions for rooting. It should be taken care of mixing litter cover with mineral soil by intensive soil cultivation. After beech seedlings appeared, the necessary tending and weeding should be applied in sufficient frequency and in time.

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Estimation of Biomass in a Submontane Beech High Forest in Serbia

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Abstract – The analysed submontane beech forest (*Fagenion moesiacae submontanum* B. Jov. 1976) is situated in Eastern Serbia (Majdan-Kučajna, compartment 33a). Stand area is 22.7 ha. Its altitude is 410-520 m and the slope is 7–28°. Parent rock consists of dense limestone, and the soil is calcocambisol. The stand is uneven-aged, managed under group selection, with a volume percentage of beech is 97%. Other statistics of the stand are: site class II, canopy closure 0.9, mean diameter 39.4 cm, and Lorey's mean height 31.0 m. For biomass evaluation, circular sample plots of 500 m^2 size were used with the area intensity of 5%. While the aboveground biomass amounts to 337.69 tons/ha or 85.9%, belowground biomass makes 55.49 tons/ha or 14.1% of the total biomass. The proportion of timber in the aboveground biomass is 89.7%, brushwood 9.3% and leaves 1.0%. Estimation of biomass of the uneven-aged beech high forest was based on the results of investigations on European beech in Central/Western Europe.

European beech / *Fagus moesiaca* / uneven-aged stand / biomass / allometry

1 INTRODUCTION

Numerous studies have examined regression equations for the estimation of biomass of different species for different regions (Marklund 1987, Jenkins et al. 2003, Zianis-Mencuccini 2003, 2005, Muukkonen 2007). Many of these papers have dealt with European beech (*Fagus sylvatica* L.), and their results have been used to develop general allometric equations for estimating beech biomass in Central Europe (Wutzler et al. 2008). Similar investigations have been conducted in Croatia for European Beech (*Fagus sylvatica* L.), pedunculate oak (*Quercus robur* L.), common ash (*Fraxinus excelsior* L.) and European hornbeam (*Carpinus betulus* L.) (Lukić – Kružić 1996). Beech has also been the subject of investigations in Greece (Zianis-Mencuccini 2003), in the Czech Republic (Cienciala 2006), in the Netherlands (Bartelink 1996) and some other countries.

Unfortunately, investigations of beech and other tree species' biomass in Serbia are missing. Therefore, the development of suitable regression equations for estimating biomass of beech trees and stands has become a growing problem.

The aim of this investigation is to estimate the total aboveground dry biomass of an uneven-aged beech high forest, as well as the estimation of the biomass of its main components (stems, branches, foliage etc.). The belowground (root) dry biomass of the stand was also estimated.

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2 STUDY AREA AND METHOD

The study area is a high forest stand of beech, situated in Eastern Serbia (stand 33a, management unit “Majdan-Kučajna“). The stand area is 22.7 ha; its altitude is 410–520 m, while its slope is 7–28°. The prevailing aspect is north-west. Parent rock consists of dense limestone and the soil is acid brown, 40-80 cm deep calcocambisol. The stand is classified as a submontane beech forest (*Fagenion moesiacae submontanum* B. Jov. 1976). It is an uneven-aged high forest, managed under group-selection, with virgin forest characteristics. Site class is II, canopy closure is 0.9, percentage of beech in the volume is 97%, stand quadratic mean diameter is 39.4 cm, and Lorey’s mean height 31.0 m. There are 274 trees per hectare, basal area is 33.4 m^2, volume is 522.5 m^3, and current annual volume increment is 8.6 m^3/ha (Koprivica et al. 2008).

For the estimation of biomass and other components, simple systematic sampling was used. Twenty-three circular sample plots of 500 m^2 were established on the area in a grid of 100 x 100 m. Diameter and height of the trees taller than 10 m were measured in all sample plots. Volume and volume increment were determined using adequate regression equations (Koprivica – Matović 2005).

For the estimation of the total biomass of a tree and its parts (as dependent variables) diameter at breast height and tree height (as independent variables) were used. General regression equations for beech in Central Europe were used (Wutzler et al. 2008) for the calculation of the total aboveground tree biomass and for the evaluation of the biomass of tree components: stem, branches, timber (d > 7.0 cm), brushwood (d < 7.0 cm), leaves and roots. The equations were developed on the basis of extensive material collected in the beech forests of Germany, Italy, France, the Netherlands, Belgium, Switzerland, and the Czech Republic. They comprise data from thirteen studies on tree biomass. Unfortunately, not all studies investigated the biomass of all tree components, which means that the number of the trees in the sample used for obtaining regression equations was different. It ranged from 48 trees for root biomass to 350 trees for total aboveground tree biomass. Diameter at breast height of model trees ranged from 1 cm to 79 cm, total height from 2 m to 37 m, age from 8 to 173 years, site index from 18 to 46 and altitude from 23 m to 1560 m. Diameter at breast height, total height, age and site index (site class) of the trees in our investigated stand have values around the upper limit of the stated ranges.

Apart from the selected regression equations, we have tested similar regression equations for estimation of beech tree biomass, obtained in Croatia (Lukić-Kružić 1996), the Netherlands (Bartelink 1996), Greece (Zianis-Mencuccini 2003) and the Czech Republic (Cienciala et al. 2005).

However, it has been concluded that these authors` equations can only be used for comparison with the results of the equations given by Wutzler et al. (2008), as the latter investigations were based on small samples of model trees (16–20) as well as on younger even-aged stands (56–114 years). Maximal diameters (35.1–62.1 cm) and heights (33.2–33.9 m) of model trees were consequently smaller.

By using the selected regression equations, we have estimated the total aboveground biomass of beech trees *(variant 1),* then biomass of stems, branches and leaves *(variant 2),* or timber (d > 7.0 cm), brushwood (d < 7.0 cm) and leaves (*variant 3*). Root biomass was also estimated. However, it turned out that different variants provided different estimation values of the total tree biomass. This problem will be discussed later. Based on the sample size of the regression equations, the first variant was the most accurate, while the other two were used only to estimate the relative proportion of the biomass of individual tree components in the total aboveground biomass. Root biomass estimation gave always the same results. Biomass of all trees in the sample plots was calculated as the sum of the biomass values for individual trees. Finally, the total stand biomass, as well as the biomass per hectare, was calculated by using a simple sample.

3 RESULTS AND DISCUSSION

3.1 Tree biomass estimation

Biomass of the most important tree components was estimated by applying general regression equations for common beech tree biomass estimation (Wutzler et al. 2008). The equations are non-linear in their parameters. In all earlier investigations, parameters of non-linear equations were estimated by applying logarithmic transformation of original values of dependent and independent variables, i.e. by linearization of non-linear model, which enables the application of the *least squares method* (Baskerville 1972, Beauchamp-Olson 1973, Sprugel 1983, Wiant-Harner 1979). However, several authors stress the shortcomings of this parameter estimation method and the quality indicators of data fitting (Van Laar – Akca 2007, Cienciala et al. 2005, Zianis – Mencuccini 2003, Wutzler et al. 2008).

Therefore, modern investigations (Bates-Watts 1988, Cienciala et al. 2005, Wutzler et al. 2008) use the method of non–linear regression with the application of the *iterative method* for estimating the parameter values and quality indicators of data fitting.

The most commonly used models are general non-linear models:

$$m = a\, d^{\,b} \qquad m = a\, (d^2 h)^b \qquad m = a\, d^b\, h^c$$

in which, biomass of a tree component (m) is a dependent variable, while diameter at breast height (d) and total tree height (h) are independent variables. Wutzler et al. (2008) used these models and developed regression equations for the estimation of tree component biomass of common beech *(Table 1)*.

Table 1. Regression equations for estimation of tree biomass of common beech

Biomass	Regression equation	Designation
above ground	$m_{ag} = 0.0523\, d^{2.12}\, h^{0.655}$	(1)
stem	$m_s = 0.0293\, (d^2 h)^{0.974}$	(2)
branches	$m_b = 0.123\, d^{3.09}\, h^{-1.17}$	(3)
timber (d > 7.0 cm)	$m_t = 0.00775\, d^{2.11}\, h^{1.21}$	(4)
brushwood (d < 7.0 cm)	$m_{bw} = 0.466\, d^{1.85}\, h^{-0.349}$	(5)
leaves	$m_l = 0.0377\, d^{2.43}\, h^{-0.913}$	(6)
roots	$m_r = 0.0282\, d^{\,2.39}$	(7)

Equations of *Table 1* were used to calculate biomass of all sample trees above a *dbh* threshold of 10.0 cm. The sample comprised 315 trees in 23 sample plots. Data processing was carried out in EXCEL programme. Total aboveground biomass was estimated in the three variants previously outlined in the study. Biomass of all trees in a sample plot was calculated as a sum of biomass of all individual trees, which was then used to estimate the biomass of the whole beech stand.

The example below illustrates the process of biomass estimation. Applying the equations of *Table 1* to a tree with the diameter at breast height *dbh* = 39.9 cm and the total height *h* = 29.4 m, we obtain the following results:

– total aboveground biomass	1186.67	kg
– stem biomass (stump biomass)	1036.89	kg
– biomass of branches	208.42	kg
– biomass of timber (d > 7,0 cm)	1106.76	kg
– biomass of brushwood (d < 7,0 cm)	131.14	kg
– biomass of leaves	13.37	kg
– biomass of roots	189.05	kg

The accuracy of the obtained results is different and dependent on the sample size (the number of model trees) and variability of the biomass components. *Variant 1* provided the most accurate estimation of the total aboveground tree biomass. It was obtained by direct fitting of biomass values for all tree aboveground parts.

It would be logical to obtain the same total aboveground tree biomass by adding up biomass values for tree components. There are two possible combinations:

- total biomass = stem biomass + biomass of branches + biomass of leaves (*variant 2*)
- total biomass = biomass of timber + biomass of brushwood + biomass of leaves (*variant 3*)

However, regression equations for estimating biomass of tree components are not mutually additive. This fact has been stressed by Parresol (2001), Lambert et al. (2005) and other authors.

In the given example:

- *variant 1* $m_{ag} = 1186.67$ kg
- *variant 2* $m_{ag} = m_s + m_b + m_l$
  $m_{ag} = 1036.89 + 208.42 + 13.37 = 1258.68$ kg
- *variant 3* $m_{ag} = m_t + m_{bw} + m_l$
  $m_{ag} = 1106.76 + 131.14 + 13.37 = 1251.27$ kg

Root biomass is 189.05 kg.

Thus, the total tree biomass is,

$$mt = m_{ag} + m_r$$

$$mt = 1186.67 + 189.05 = 1375.72 \text{ kg.}$$

The proportion of the aboveground tree biomass is 86.26%, while the belowground biomass (root biomass) amounts to 13.74%.

In order to obtain more precise estimation of the biomass of the tree components, we concluded that the biomass of *variant 3* was more accurate than the biomass of *variant 2*. There is a similar problem in the case of determining the stem volume. Therefore, the results of *variant 3* were used for the estimation of the relative proportion of the biomass of components in the total aboveground tree biomass. The proportion of timber biomass is 88.45%, brushwood 10.48% and leaves 1.07%. If we apply these percentage values to the directly estimated total aboveground tree biomass, we get:

– total aboveground tree biomass	1186.67 kg
biomass of timber (d >7.0 cm)	*1049.61 kg*
biomass of brushwood (d < 7.0 cm)	*124.36 kg*
biomass of leaves	*12.70 kg*
– biomass of roots	189.05 kg

In *variant 2*, the proportion of stem biomass amounts to 82.38%, while the proportion of branches is 16.56% and leaves 1.06%.

The results of the selected regression equations for the estimation of common beech tree biomass (Wutzler et al. 2008) were compared with the results obtained by application of regression equations developed by other authors (Cienciala et al. 2006, Bartelink 1997, Lukić – Kružić 1996, Zianis – Mencuccini 2003).

With the exception of the equation given by Zianis-Mencuccini (2003), whose equation has only one independent variable – diameter at breast height, all the regression equations developed by the mentioned authors have diameter at breast height and tree height as independent variables. All the equations have the same mathematical form and the results of their comparison are shown in *Table 2*.

Table 2. Total aboveground beech tree biomass (d = 15–90 cm, h = 19.0–34.1 m)

Diameter (cm) Height (m)	15 19.0	30 27.2	45 30.6	60 32.3	75 33.3	90 34.1
Tree biomass in kg						
Wutzler et al. 2008	112.1	616.1	1572.0	2997.2	4907.2	7335.8
Cienciala et al. 2006	114.3	638.2	1637.2	3129.5	5131.5	7680.3
Bartelink 1997	100.1	629.4	1747.4	3543.8	6091.6	9476.6
Lukić-Kružić 1996	121.4	853.0	2514.9	5313.8	9423.2	15036.6
Zianis-Mencuccini 2003	102.6	560.6	1513.8	3063.1	5291.6	8271.5
Tree biomass in %						
Wutzler et al. 2008	100.0	100.0	100.0	100.0	100.0	100.0
Cienciala et al. 2006	102.0	103.6	104.1	104.4	104.6	104.7
Bartelink 1997	89.3	102.1	111.1	118.2	124.1	129.2
Lukić-Kružić 1996	108.3	138.5	159.4	177.3	192.0	205.0
Zianis-Mencuccini 2003	91.6	91.0	96.3	102.2	107.8	112.7

Table 2 shows that the regression equation by Cienciala et al. (2006) comes closest to the equation given by Wutzler et al. (2008). Tree biomass estimation is 2–5% higher. The equations were developed on the basis of model trees with maximal diameter at breast height of 79 cm and height of 37 m in the second (Wutzler et al. 2008), and 62 cm diameter and 34 m height in the first equation (Cienciala et al. 2006).

The regression equations developed by the other authors show high percentage deviations, which in our opinion do not make them applicable to tree biomass estimation in high beech forests in Serbia. Applicability of the equations depends on the size range of the model trees, sample size, management practices and structure of the stands from which the tress are taken. In this particular case, maximal diameter at breast height of model trees was 35 cm and the height was up to 33 m. The data originate from well-managed 60 year-old even-aged stands.

To determine the wood density, we need to know the volume of all individual tree parts above ground. Assmann (1961) states that the average density of common beech timber is 560 kg/m^3, while Cienciala et al. (2006) state that the density of beech stemwood is 575.5 kg/m^3 while the density of brushwood amounts to 560.1 kg/m^3. Furthermore, the Intergovernmental Panel on Climate Change (IPCC 2003) mentions 580 kg/m^3 as the recommended wood density of beech trees. By using the local volume table for the whole aboveground tree (without leaves and stumps) (Matić et al. 1963) we estimated wood density is approximately 565 kg/m^3.

Accurate determination of the wood density of beech trees under our site and stand conditions, requires xylometry to calculate the volume of all aboveground tree parts, while the amount of biomass can be obtained by accurate measurement of the weight of all tree parts in the dry state, i.e. by seasoning at 105 $^\circ$C.

Table 3 shows the basic statistical indices of beech trees in the sample selected for the biomass estimation.

In comparison to volume, there is a larger variation in the aboveground tree biomass. The greatest variation of all biomass components is in the biomass of branches (143.4%) and the smallest is in the biomass of brushwood (89.9%). In all the other cases, coefficient of variation ranges from 110% to 120%. Since the distribution of trees by tree volume and biomass indices expresses a significant variation from the normal distribution, variability should be also determined by tree diameter classes (Koprivica – Matović 2007).

Table 3. Basic statistical indices of tree samples selected for the estimation of biomass in kg (n = 315)

Index	$X_{aver.}$	X_{min}.	$X_{max.}$	S	CV (%)	$2 \cdot \overline{CV}$ (%)	α_3	α_4
diameter	34.9	10.4	92.0	18.3	52.5	5.92	0.74	2.79
height	27.0	7.7	44.1	5.9	21.7	2.45	-0.23	3.10
volume	1.91	0.04	12.01	2.28	119.5	13.47	1.82	7.56
biomass total	1232.8	28.5	7372.3	1406.4	114.1	12.85	1.77	7.26
biomass of stem	1053.4	20.5	5783.2	1160.8	110.2	12.42	1.64	5.56
biomass of branches	257.0	5.9	2494.5	368.6	143.4	16.16	2.82	9.90
biomass of timber	1191.6	12.8	7389.1	1430.3	120.0	13.52	1.80	6.29
biomass of brushwood	123.1	13,6	597.2	110.7	89.9	10.13	1.49	5.30
biomass of leaves	13.9	0.8	94.2	15.6	112.4	12.67	2.08	8.46
biomass of roots	202.6	7.6	1392.2	242.1	119.5	13.47	2.01	7.77

3.2 Stand biomass estimation

The method described above was used to determine the total aboveground tree biomass as well as the biomass of its components for each sample plot. Tree and sample plot data were recalculated on a per hectare basis. The applied method is actually analogous to stand volume estimation.

The number of sample plots in the stand is n = 23, and the basic statistical indices are shown in *Table 4*.

Table 4. Basic statistical indices of the sampling in the sample plots for the estimation of stand biomass in tons per hectare (n = 23)

Index	$X_{aver.}$	X_{min}.	$X_{max.}$	S	CV (%)	$2 \cdot \overline{CV}$ (%)	α_3	α_4
number of trees	273.9	80	460	107.8	39.3	16.38	0.28	2.26
volume	522.2	298.7	875.0	163.6	31.3	13.05	0.54	2.54
biomass total	337.69	186.47	541.30	100.7	29.8	12.43	0.26	2.15
biomass of stem	288.54	153.16	454.77	66.0	29.8	12.43	0.25	2.10
biomass of branches	70.40	29.90	120.76	24.1	34.2	14.26	0.32	2.29
biomass of timber	326.41	179.90	557.87	105.3	32.2	13.43	0.47	2.46
biomass of brushwood	33.73	15.39	47.50	9.2	27.2	11.34	-0.17	2.10
biomass of leaves	3.80	1.95	5.47	1.13	29.8	12.43	0.05	1.75
biomass of roots	55.49	30.15	89.33	16.6	29.9	12.47	0.23	2.13

In this case, total aboveground tree biomass at the stand level also shows a slightly lower variation than the tree volume. Coefficient of variation is about 30%. The greatest variation is in the biomass of branches (34.2%) and the smallest is in the biomass of brushwood (27.2%). Coefficient of variation of other components ranges from 30% to 32%.

However, we are interested in the average biomass per hectare as well as on the whole stand area. The average aboveground stand biomasses according to the three variants are as follows:

- *variant 1* $M_{ag} = 337.69$ tons/ha
- *variant 2* $M_{ag} = M_s + M_b + M_l$

  $M_{ag} = 288.54 + 70.40 + 3.80 = 362.74$ tons/ha
- *variant 3* $M_{ag} = M_t + M_{bw} + M_l$

  $M_{ag} = 326.41 + 33.73 + 3.80 = 363.94$ tona/ha

The biomass of the tree roots in the stand is 55.49 tons/ha.

As a result, average beech stand biomass above and below ground (roots) is most likely to be,

$$Mt = M_{ag} + M_r$$

$$Mt = 337.69 + 55.49 = 393.18 \text{ tons/ha.}$$

The proportion of the total aboveground tree biomass amounts to 85.89%, while the belowground biomass makes 14.11%.

Percentage distribution of the total aboveground stand biomass by diameter classes is similar to the same distribution of its volume. To illustrate this we provide the percentage distribution of the average stand volume and biomass per hectare in *Table 5.*

Table 5. Percentage distribution of volume and biomass of aboveground beech stand

Diameter	15	25	35	45	55	65	75	85	95	Total
Volume	3.15	6.66	12.21	12.52	25.64	21.05	10.03	6.84	1.90	100
Biomass	2.36	6.08	11.74	12.61	26.21	24.78	10.31	7.70	2.00	100

The percentage distribution of biomass, with regard to the percentage distribution of volume by diameter classes in the stand is skewed to the greater diameter classes. However, the difference is small.

By using a simple sample, we estimated the average per hectare biomass of the investigated beech stand as well as the total biomass on the whole area of the stand.

We used the familiar formula:

$$\bar{m} - t \cdot s_{\bar{m}} < \bar{M} < \bar{m} + t \cdot s_{\bar{m}} \tag{1}$$

In which,

$\bar{m}$ – is average biomass per hectare in the sample,

t – is the t value from the Student distribution table - distribution for the specific probability with a degree of freedom n-1,

$s_{\bar{m}}$ – is the standard error of the average biomass per hectare in the sample,

$\bar{M}$ – average biomass per hectare in the population (stand).

Certain components in equation (1) are calculated in the following way:

$$\bar{m} = \frac{\sum m_i}{n}, \quad t\,(95\%\ \text{i}\ n-1), \quad s_{\bar{m}} = \frac{s_m}{\sqrt{n}}, \quad s_m = \sqrt{\frac{\sum (m_i - \bar{m})^2}{n-1}}$$

where:

$m_{i\,0}$ – stands for biomass per hectare for i^{th} sample plot

s_m – stands for standard deviation of biomass in the sample of n size

Which gives

$$337.69 - 2.074 \cdot 20.30 < \overline{M} < 337.69 + 2.074 \cdot 20.30$$

$$295.59 < \overline{M} < 379.79$$

Confidence interval of the average aboveground tree biomass in the stand with 95% probability is between 295.59 and 379.79 tons/ha. Sample error is ±42.1 tons/ha or ±12.46%.

Confidence interval for the total stand biomass on the whole area (A) was calculated in the same way. The following formula was used:

$$A(\overline{m} - t \cdot s_{\overline{m}}) < A\overline{M} < (\overline{m} + t \cdot s_{\overline{m}})A \tag{2}$$

It follows that

$$22.7 \cdot 295.59 < A\overline{M} < 379.79 \cdot 22.7$$

$$6709.89 < A\overline{M} < 8621.23$$

Finally, the total aboveground tree biomass in stand 33a, with 95% of probability is between 6709.89 and 8621.23 tons. Sample error is ±955.67 tons or ±12.46%. We naturally assume that the area of the stand is accurately estimated. If there is an error in the estimation of the stand area, it must be taken into consideration (Matić 1977, Van Laar – Akca 2007).

In an analogous way, it is possible to estimate biomass of any tree component in the stand. We provide the estimation of the tree root biomass at stand level. Average tree root biomass at stand level, with 95% probability ranges from 48.31 to 62.67 tons/ha. Sample error is ±7.18 tons/ha or ±12.94%. It follows that the total belowground biomass at stand level ranges from 1096.64 to 1422.60 tons. Sample error is ± 163.01 tons or ±12.94%.

4 CONCLUSION

Average dry biomass of the investigated beech high forest is estimated at 393.18 tons/ha. While the aboveground biomass amounts to 337.69 tons/ha or 85.9%, belowground (root) biomass makes 55.49 tons/ha or 14.1% of the total biomass. Aboveground tree biomass at stand level naturally has greater practical importance. Thus, average aboveground tree biomass of the studied stand is between 295.59 and 379.79 tons/ha, with 95% of probability. Sample error is ±42.1 tons/ha or ±12.46%. The proportion of timber in the aboveground biomass is 89.7%, brushwood 9.3% and leaves 1.0%. Furthermore, the total biomass of all trees on the whole area of the stand is estimated at 7665.56 tons, with confidence interval between 6709.89 and 8621.23 tons.

Estimation of biomass of the uneven-aged beech high forest was based on the results of investigations on common beech in Central Europe. Therefore, our results should be accepted only with some limitations, not only because we applied the method of sample plots, but because we used general regression equations, which were developed on the basis of model trees taken mainly from even-aged beech stands, in which silvicultural measures were regularly carried out. It is a well-known fact that development of general regression equations and tables for tree biomass estimation requires large samples, which should represent the whole range of tree sizes, age, sites and management practices. However, high forests of beech in Serbia are usually uneven-aged, under group selection and are not managed well enough. Still, we believe that we have successfully estimated the dry biomass of the investigated beech stand and that this paper has raised an important scientific and professional issue in Serbian forestry.

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Impact of Tending Measures on Assortment Structure of Fellings in Central Croatian Beech Stands

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Abstract – The effects of management of even-aged beech stands on the quality of beech timber assortments by type of cut were investigated in the region of Bjelovar. The research was carried out using Croatian timber standards. Assortment tables were developed separately for thinning and intermediate felling, and separately for regeneration and final felling in accordance with the interventions of management. The average shares of assortments maintained the same ratios by quality classes regardless of the applied standards (HRN or HRN EN). The research identified the problems in production of assortments, and justified the need for developing separate tables for thinning, intermediate felling, and for regeneration and final felling. Through forest management the quantity and quality of timber assortments may be oriented to a certain extent towards the production target. With the application of tending measures the value of the stand and timber assortments increases over time. In economic respect, the development of false heartwood shows an opposite trend. Therefore a compromise must be achieved by proper management and determination of appropriate harvesting age of beech stands.

forest management / thinning / intermediate and final felling / timber standards / false heartwood

1 INTRODUCTION

When considering assortment structure of the main forest products and the compilation of assortment tables, patterns of growth and development of stands come into conflict with the provisions of the standards for the classification of forest timber products and common practices in timber trade, subject to change over time. Presently Croatian forestry faces additional uncertainties brought by the application of new standards in beech stands.

Tables showing the share of forest timber assortments (assortment tables) are important tools necessary for the forestry staff, and common beech is the most represented species in the Croatian forests. When planning fellings and annual allowable cuts, it is necessary to know the quantity and quality of timber assortments, determined in accordance with the applicable standards. Reliable tables of timber assortments are necessary for the assessment of the efficiency of the forest harvesting process, and also for the comparison of work performed by different parts of an enterprise. Due to the diversity of their phenotype (morphology), broadleaved species are more demanding than conifers with respect to the investigation of assortment structure. Common beech almost always develops false heartwood, which

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additionally complicates the investigation. It can be concluded that in this respect common beech is the most demanding autochthonous species.

The occurrence of defects also affects the quantity and quality of timber assortments. The occurrence of defects, their size and number is of random character and cannot be correlated with measurable tree parameters. The determination of the felling time for individual trees represents a significant influence on stand structure, and also on the structure of timber assortments.

According to Benić (1987) forest assortments are standardized products determined by standards, common practices and trading practices, and can also be determined by agreement between the producer and purchaser. Assortment structure of a stand is determined by assortment proportions of individual trees. The selection of trees for felling during the rotation is a procedure based on rules and principles arising out of forest management. In even-aged beech stands, it is more convenient to investigate the assortment structure of individual cut types (felling sites) than the assortment structure of the stand. Only in clearcuts and in stands before the final felling, have the two terms the same meaning.

The basic principles of operations of forest tending and regeneration in nature close management are based on processes in virgin forests. Forests managed in this way have a strong ecological and economic foundation in all life conditions. If the forest has been managed from its establishment based on natural principles (operations of tending and regeneration) then it may be considered as natural forest management (Matić 2009).

The assortment structure of stands is directly affected by the type of forest management. The impact of management on the structure of beech stands and their timber production can clearly be seen after almost two centuries of organized forestry in the research area. This means that we no longer have virgin forest stands that developed with minimum or no human interaction. On the other hand, it is a fact that foresters have always known how to implement natural management in Croatian forests. This is best proven by the preservation of their natural structure and diversity. Natural approach to forest management in Croatia has been developed by the Faculty of Forestry of the University of Zagreb (Matić – Anić 2009).

Compilation, precision and application of tables in practice showing shares of forest assortments in the annual allowable cut (assortment tables) are connected with serious and numerous difficulties caused by the influence of biotic and abiotic factors on stand development. Among biotic factors, one of the most important is the impact of management, i.e. through implementation of criteria for selecting trees for felling. Of primary interest is the assortment structure, which can be achieved by implementing certain types of felling at a certain age of the stand, and not the assortment structure of all trees in the stand of a specific age. The effort to achieve the best possible quality of all trees in the stand of a specific age is the basis of all management procedures in even-aged beech stands.

2 RESEARCH SITE AND METHODS

2.1 Location of research

The state forests of Forest Administration Branch Office (FABO) Bjelovar involve the area of Northwest (Central) Croatia, they cover a total area of 131,820 hectares (*Figure 1*) and they are located in seven counties: Bjelovar and Bilogora, Brod and Posavina, Koprivnica and Križevci, Požega and Slavonia, Sisak and Moslavina, Virovitica and Podravina and Zagreb county. These forests owned by the Republic of Croatia are managed by „Hrvatske šume“

d.o.o. Zagreb through Forest Administration Branch Office Bjelovar. The whole area is divided into 15 forest offices and 34 management units.

In the total growing stock of these forests of almost 33,000,000 m^3, common beech is the most represented species with the volume of almost 12,000,000 m^3 or 36% (*Figure 2*). The total current annual increment is around 910,000 m^3 with the share of beech of approximately 328,000 m^3 or 37%. Beech in this area is vital and healthy. This is highly supported by the information on the average 3.3% of emergency beech felling compared to the annual allowable cut of beech in the area of FABO Bjelovar in the period 2001 to 2009. Within the research area (Forest Office Bjelovar) for the same period the average annual share of emergency felling in the annual allowable cut of beech was only 2.3%.

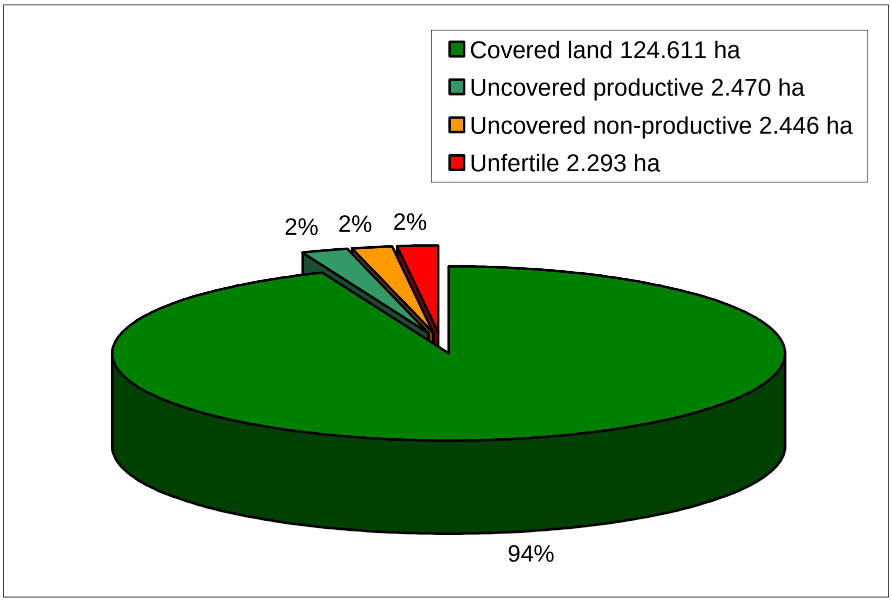

Figure 1. The area of FABO Bjelovar

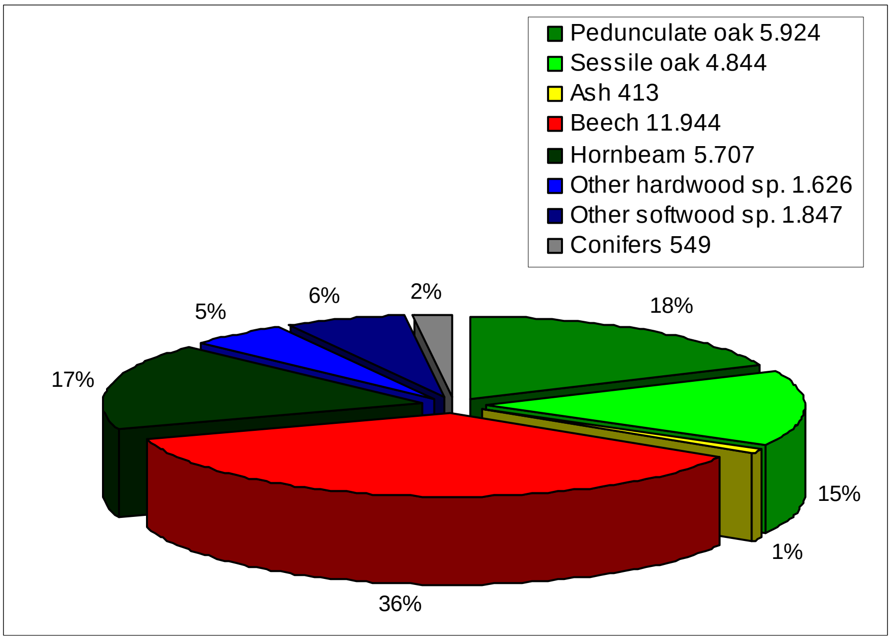

Figure 2. Growing stock of FABO Bjelovar (thousand m^3)

The research was carried out in the management unit „Bjelovarska Bilogora” of the Forest Office Bjelovar, FABO Bjelovar. All research compartments belong to the ecological-management type II-D-11 and management class BEECH with a 100-year rotation, whose share in the area of the management unit is 76.1%, and in the growing stock 80.6%. The management unit „Bjelovarska Bilogora” is located on Southwest and South slopes of Bilogora, at the altitude ranging between 115 m and 307 m above sea level. Its total area is 7632.62 ha, of which 7444.17 ha is stocked. The management unit is divided into 180 compartments and 533 sub-compartments. In 2003 the total growing stock was 2,317,147 m^3. In the growing stock, beech, as the most represented species, accounts for 1,036,386 m^3 or 44.73%. The total 10-year allowable cut for I/1 management semi-period is 586,231 m^3, of which 443,752 m^3 is main felling, and 142,479 m^3 is thinning. The share of beech in the 10-year allowable cut is 297,753 m^3 (67.2%) in the main felling and 45,939 m^3 (32.2%) in thinning, or a total of 343,692 m^3 (58.6%).

The total allowable cut of the main felling of the Forest Administration Branch Office Bjelovar is approximately 400,000 m^3 with the share of beech considerably higher than 50%. The total felling in the period 2001 to 2009 in the area of Forest Administration Branch Office Bjelovar can be seen in *Table 1.* Along with a continuous growth of the allowable cut in this period (from approximately 600,000 m^3 to approximately 700,000 m^3), an increasing share of beech can also be seen in the average wood volume (from approximately 34% to approximately 45%). Similarly, it can be said that the share of the main felling has increased considerably (from approximately 60% to almost 75%) in an average wood volume of beech in the area of FABO Bjelovar. The survey of fellings performed in the research area (Forest Office Bjelovar, *Table 2*) show the same increasing trend of allowable cuts (from approximately 50,000 m^3 to approximately 85,000 m^3), increase of beech share in the total wood volume (from approximately 40% to 50%) and considerable increase of the main felling (to more than 90%) in the average allowable cut of beech in the area of Forest Office Bjelovar (*Figure 3*). These trends are the effect of the growing stock structure of the research area, disproportion of age classes, as well as some inconsistencies in determining the rotation of beech stands. They should be taken into account when planning the development of both forestry and wood-processing activities in the area of Bjelovar.

Table 1. Felling from 2001 to 2009 - Forest Administration Branch Office Bjelovar

Year	Beech						Allowable cut				
	Main felling		Thinning		Total		Main felling		Thinning		Total
	m^3	%	m^3	%	m^3	%	m^3	%	m^3	%	m^3
2001	122 384	60,4	80 340	39,6	202 724	***33,7***	325 923	54,1	276 139	45,9	602 062
2002	129 999	59,0	90 525	41,0	220 524	***35,7***	289 554	46,9	327 778	53,1	617 332
2003	171 831	69,6	74 934	30,4	246 765	***40,0***	338 814	54,9	278 530	45,1	617 344
2004	184 957	72,1	71 729	27,9	256 686	***39,6***	366 680	56,5	282 180	43,5	648 860
2005	192 115	70,6	79 925	29,4	272 040	***41,2***	339 610	51,4	320 912	48,6	660 522
2006	205 372	71,2	82 895	28,8	288 267	***43,6***	383 765	58,0	277 367	42,0	661 132
2007	199 731	70,9	81 923	29,1	281 654	***41,7***	388 054	57,4	288 013	42,6	676 067
2008	226 122	72,4	86 313	27,6	312 435	***45,8***	375 802	55,1	306 020	44,9	681 822
2009	227 579	74,6	77 307	25,4	304 886	***43,9***	413 830	59,6	280 435	40,4	694 265
Total	1 660 090	69,6	725 891	30,4	2 385 981	***40,7***	3 222 032	55,0	2 637 374	45,0	5 859 406

Table 2. Felling from 2001 to 2009 - Forest Office Bjelovar

Year	Beech						Allowable cut				
	Main felling		Thinning		Total		Main felling		Thinning		Total
	m^3	%	m^3	%	m^3	%	m^3	%	m^3	%	m^3
2001	13 570	55,1	11 048	44,9	24 618	***39,7***	30 991	50,0	31 011	50,0	62 002
2002	6 447	61,8	3 992	38,2	10 439	***21,7***	23 789	49,5	24 243	50,5	48 032
2003	27 702	84,7	5 018	15,3	32 720	***47,9***	43 746	64,0	24 603	36,0	68 349
2004	30 567	87,7	4 281	12,3	34 848	***48,4***	49 513	68,8	22 426	31,2	71 939
2005	36 268	92,1	3 110	7,9	39 378	***51,3***	49 766	64,8	27 049	35,2	76 815
2006	33 606	90,6	3 489	9,4	37 095	***49,2***	51 794	68,7	23 635	31,3	75 429
2007	27 084	81,9	5 979	18,1	33 063	***38,1***	58 030	66,9	28 760	33,1	86 790
2008	34 263	81,2	7 938	18,8	42 201	***49,9***	55 132	65,2	29 450	34,8	84 582
2009	28 379	82,1	6 194	17,9	34 573	***41,9***	53 970	65,4	28 517	34,6	82 487
Total	237 886	82,3	51 049	17,7	288 935	***44,0***	416 731	63,5	239 694	36,5	656 425

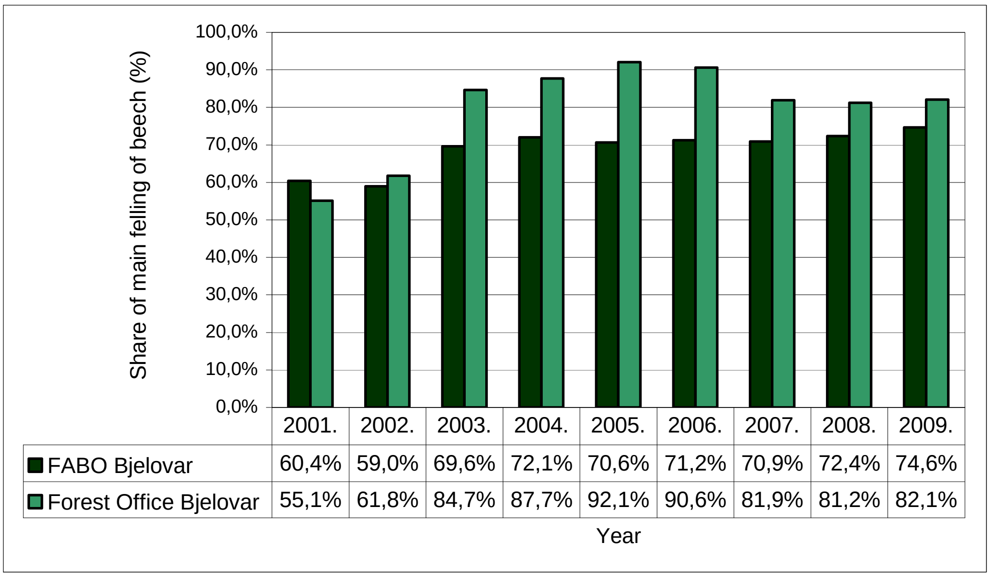

Figure 3. Share of main felling in felled volume of beech from 2001 to 2009

2.2 Method of work

The age of felling sites ranged between 59 and 91 with thinning operations, between 94 and 110 with intermediate felling, between 100 and 112 with regeneration felling and between 98 and 114 with final felling. The sample of model trees was taken by random selection of approximately 10% of marked trees. Moving around the stand at predetermined azimuths all marked beech trees found in the travel direction were included in the sample.

In the period of 1997 to 2007, the field research involved a total of 3776 model trees. *Table 3 and 4* show the number of model trees by research compartment according to the type of cut and applied standard.

Table 3. Distribution of model trees according to the standard HRN (1995)

Type of felling															
Thinning				Intermediate fellings				Regeneration fellings				Final fellings			
Forest Block	Number of marked trees	Number of trees in the sample	%	Forest block	Number of marked trees	Number of trees in the sample	%	Forest block	Number of marked trees	Number of trees in the sample	%	Forest block	Number of marked trees	Number of trees in the sample	%
7c	292	60	20,5	9a	1198	102	8,5	11a	1667	177	10,6	20d	394	46	11,7
13a	665	65	9,8	11a	683	78	11,4	21a	2112	108	5,1	21a	1201	74	6,2
13b	285	51	17,9	17a	865	91	10,5	38a	1308	109	8,3	42a	1239	118	9,5
20e	569	66	11,6	19b	490	58	11,8	59c	409	41	10,0	42c	876	104	11,9
29a	368	46	12,5	21a	1166	132	11,3	83a	166	31	18,7	59c	438	44	10,0
29b	229	34	14,8	38a	1164	102	8,8	94b	650	76	11,7	75a	547	55	10,1
37a	631	83	13,2	42a	456	63	13,8	95b	439	64	14,6	83a	445	42	9,4
37c	335	48	14,3	42c	394	42	10,7	-	-	-	-	89b	145	23	15,9
39b	368	56	15,2	60a	862	97	11,3	-	-	-	-	155f	953	57	6,0
65b	164	24	14,6	66a	577	64	11,1	-	-	-	-	166c	135	20	14,8
66b	163	31	19,0	73a	888	100	11,3	-	-	-	-	-	-	-	-
69b	515	67	13,0	94b	343	54	15,7	-	-	-	-	-	-	-	-
80b	46	17	37,0	95b	306	42	13,7	-	-	-	-	-	-	-	-
82a	159	49	30,8	-	-	-	-	-	-	-	-	-	-	-	-
162a	371	45	12,1	-	-	-	-	-	-	-	-	-	-	-	-
162c	282	45	16,0	-	-	-	-	-	-	-	-	-	-	-	-
Total	5442	787	14,5	Total	9392	1025	10,9	Total	6751	606	9,0	Total	6373	583	9,1

Table 4. Distribution of model trees according to the standard HRN EN

Type of felling															
Thinning				Intermediate fellings				Regeneration fellings				Final fellings			
Forest Block	Number of marked trees	Number of trees in the sample	%	Forest block	Number of marked trees	Number of trees in the sample	%	Forest block	Number of marked trees	Number of trees in the sample	%	Forest block	Number of marked trees	Number of trees in the sample	%
7c	292	59	20,2	9a	1198	102	8,5	11a	1667	174	10,4	11a	721	76	10,5
13a	665	65	9,8	11a	683	78	11,4	38a	1308	109	8,3	38a	879	102	11,6
13b	285	51	17,9	17a	865	91	10,5	59c	409	41	10,0	42a	1239	118	9,5
20e	569	66	11,6	19b	490	58	11,8	66a	953	138	14,5	42c	876	104	11,9
29a	368	46	12,5	38a	1164	102	8,8	73a	1077	155	14,4	59c	438	44	10,0
29b	229	34	14,8	60a	862	97	11,3	94b	650	76	11,7	94b	711	133	18,7
37a	631	83	13,2	66a	577	64	11,1	95b	439	64	14,6	95b	378	68	18,0
37c	335	48	14,3	73a	888	100	11,3	124a	1134	105	9,3	-	-	-	-
39b	368	56	15,2	94b	343	54	15,7	-	-	-	-	-	-	-	-
65b	164	24	14,6	95b	306	42	13,7	-	-	-	-	-	-	-	-
66b	163	31	19,0	-	-	-	-	-	-	-	-	-	-	-	-
69b	515	67	13,0	-	-	-	-	-	-	-	-	-	-	-	-
80b	46	17	37,0	-	-	-	-	-	-	-	-	-	-	-	-
82a	159	50	31,4	-	-	-	-	-	-	-	-	-	-	-	-
162a	371	45	12,1	-	-	-	-	-	-	-	-	-	-	-	-
162c	282	45	16,0	-	-	-	-	-	-	-	-	-	-	-	-
Total	5442	787	14,5	Total	7376	788	10,7	Total	7637	862	11,3	Total	5242	645	12,3

Model trees were processed in accordance with the requirements of the *Croatian standards for forest harvesting products* (former JUS – standards of ex Yugoslavia) of 1995 (HRN D.B4.020, HRN D.B4.022, HRN D.B4.027, HRN D.B4.028, HRN D.B5.023), and «bucking simulation» was made on the same trees in accordance with the Croatian standard *Hardwood Round Timber – Qualitative classification, Part 1: Oak and beech HRN EN 1316-1:1999*. The defects of wood and processed round timber were measured in accordance with the terms of the standards HRN D.A0.101, HRN D.B0.022, and HRN EN 1309-2, HRN EN 1310, HRN EN 1311 and HRN EN 1315. Many other characteristics were also measured or assessed on model trees: diameter at breast height, tree height, trunk height, length of logs, trunk diameter, length of cut logs (1 m and longer), diameters of cut logs (1 m and longer), lengths and diameters of fuel wood up to 4 m, length of waste wood, diameters of waste wood, bark thickness, false heartwood and described tree markings.

Out of the total number of model trees, 693 were processed and measured only in accordance with the requirements of the *Croatian standards for forest harvesting products* of 1995, on 2308 trees the measurements and classification of roundwood were carried out in accordance with the requirements of both standards, while 775 model trees were measured and then roundwood was classified in accordance with the requirements of the Croatian standard Hardwood Round Timber – *Qualitative classification, Part 1: Oak and beech HRN EN 1316-1:1999.*

In this way the sample for the preparation of assortment tables in accordance with the requirements of Croatian standards for forest harvesting products of 1995 covered 3001 model trees (*Table 3*). On the other hand, in accordance with the requirements of the Croatian standard HRN EN 1316-1:1999, assortment tables were prepared on the basis of the sample of 3082 model trees (*Table 4*).

3 RESULTS AND DISCUSSION

Obstacles related to processing, precision and practical application of assortment tables, and to the increase of reliability of business decision-making in planning the assortment structure of managed beech stands usually arise out of the following facts:

- quality of trees and of the whole stand is the result of continuing impact of different abiotic and biotic factors,
- total volume of the stand cannot be used as the basis for planning the felling, processing and extracting, and first of all not as the basis for calculating the financial income,
- usable volume of trees and stands varies in a wide range between values from approximately 30% to 80% (or more) compared to the total volume,
- distribution of timber assortments in individual trees is determined by the diversity of their phenotype (morphology) and occurrence of defects on and in the tree,
- occurrence of defects, their size and number on and in the tree is of random character and it cannot be correlated with measurable tree parameters,
- timber assortments of the same quality are not always produced from trees with the same dimensions and equal quality characteristics,
- there are differences between the classification of timber assortments in different countries, and the classification standards are subject to changes in time,
- in determining the quality of timber assortments, there is also a component of subjectivity,
- analysis of the structure of timber assortments achieved in the process of wood production provides no possibility to make final conclusions primarily because there is no correlation between breast-height diameters of individual trees and the produced assortment structure, and due to the effects of the market and other effects on the production process.
- assortment structure of managed stands is partly the result of human impact, and these have not been sufficiently researched or recognized.

Due to the above reasons, the method for determining the assortment structure that would be relatively quick, simple and accurate is still to be found. In all methods used so far, model trees were used for determining the total volume and volume assortments by sectioning of standing and felled trees.

Tables showing shares of timber assortments determined in accordance with the *Croatian standards on forest harvesting products of* 1995 and in accordance with the Croatian standard

HRN EN 1316-1:1999 Hardwood Round Timber – Qualitative classification, Part 1: Oak and beech were developed separately for thinning and intermediate felling, and separately for regeneneration and final felling. This was done due to numerous reasons stated and explained above, and due to results of research published before. The reasons for separating thinning and intermediate felling trees into special assortment tables are as follows:

- thinning sites and intermediate felling sites have an exceptionally high share of undamaged trees of abnormal growth and generally a higher percentage share of trees with negative impact on assortment structure of the felling site in the total number of marked trees compared to regeneration and final felling (Prka 2005, 2006),
- marked trees of thinning and intermediate felling have on average a lower trunk height and consequently a lower share of industrial roundwood is made of tree trunks compared to regeneration and final felling (Prka 2005, 2006),
- validation analysis of trees by type of cut shows that thinning and intermediate felling trees have lower index values compared to trees from final and regeneration felling (Prka 2003, 2005),
- total percentage share of industrial roundwood in the net volume of trees is lower with thinning sites compared to other types of cut and it increases from thinning towards final felling (Prka 2005),
- analysis of total deviations of percentage shares of timber assortments of the highest quality from the plan (analysis carried out in a three-year period in the research area) shows that tables of timber assortments, currently in use, overestimate the percentage share of veneer logs and peeling logs in thinning and intermediate felling sites (Prka 2003),
- in thinning and intermediate fellings, the occurrence of trees with the highest quality assortments of industrial roundwood is less probable (F – veneer and L – peeling logs – A and B quality class) and consequently the percentage share of timber assortments of the highest quality in the volume of large dimension timber is also smaller compared to trees of regeneration and final felling (Prka 2005, 2008, Prka – Krpan 2007),
- occurrence of false heartwood is not significant in felling sites up to the age of approximately 90 years. In older thinnings false heartwood may be expected in around 15% of the trees. On the other hand in felling sites aged from 100 to 110 false heartwood is quite significant as it can be expected in more than 50% of marked trees (Prka 2003, 2005, Prka et al. 2009, Krpan et al. 2006),
- number of trees with false heartwood increases from thinning towards final felling, as well as the length of industrial roundwood with false heartwood and shares of industrial roundwood affected by false heartwood (Prka 2005, Prka et al. 2009, Krpan et al. 2006),
- regeneration and final felling compared to thinning and intermediate felling show higher shares of the highest quality timber assortments depending on the diameter class by: approximately 8 to 14% (veneer logs and peeling logs) with the application of the Croatian Standards for Forest Harvesting Products (1995), and approximately 11 to 13% (A and B – quality class) with the application of Croatian standard HRN EN 1316-1:1999 Hardwood Round Timber – Qualitative classification, Part 1: Oak and beech (Prka 2005, 2008, Prka – Krpan 2007),
- percentage shares of timber assortments by quality classes retain the same ratios (of course not the same percentage shares) regardless of the applied standards (Prka 2005, 2008, Prka – Poršinsky 2009).

A common feature of the marked trees in thinning and intermediate felling is that they are chosen by selection criteria, which become irrelevant when the intermediate felling is completed because the key role in selecting trees for felling in the regeneration phase is then played by seeding, presence and growth of regeneration and spatial distribution of remaining trees.

In short, when determining the mathematical model for the development of volume of timber assortments, it should be taken into account that it depends on natural laws of development, which are not well known and which are affected during the rotation cycle by changing the stand structure and by applying the system of standards and trade conventions, both subject to change in time.

Factors affecting the assortment structure of even-aged beech felling sites when implementing sustainable management of beech forests are therefore as follows:

- selection criteria of trees for felling by which the prescribed type of cut is performed in managing natural beech stands,
- technological level of wood production which involves both technical equipment and development of forest infrastructure, as well as professional competence of all participants in wood production and the whole forest management,
- defects of beech wood formed as the consequence of natural development of beech stands and human impact, among which false heartwood is the most conspicuous**,**
- procedures with beech roundwood during and after operations of wood production and the prescribed ways of measuring and calculating the volume,
- market relationships, which besides demand and supply are also greatly influenced by the development of capacities for processing beech into wood products and other products (energy and similar),
- level of knowledge of management of natural beech stands, and operational application of such knowledge.

4 CONCLUSION

There are many factors affecting the assortment structure of managed beech stands, and their impact is very complex. These factors are partly the result of natural laws of growth and development of beech stands and trees, and partly the result of human and environmental impact. Some of these factors are objective and their impact cannot be avoided, while others are of a subjective nature.

The effects on quantity and quality of assortments of a certain type of cut in even-aged stands are related to:

- abiotic factors such as climate, edaphic and orographic conditions, and their continuous and interdependent impact,
- biotic factors mostly affected by human interference although there are also others (bacteria, fungi, insects, game etc.),
- historic development of beech stand management, i.e. advance in forest sciences, operational practice and education of forestry staff,
- actual comprehensive management of beech stands and organization of forest economic activities, as well as position of these activities in a wider business (social) environment,
- technological level of wood production that provides the basis in the production of beech forest assortments, including technical equipment and professional competence of all participants in the process of wood production,

- occurrence and quantity of wood defects, although they are of random nature, can be partly affected by silviculture,
- rotation age, which is particularly important in this species due to the occurrence and pattern of development of false heartwood,
- bucking of beech industrial roundwood, precision of measurement and consistent use of applicable regulations (standards) for the classification of forest timber assortments into quality classes,
- research and application of research results with the aim of developing more precise assortment tables, more objective planning and control of production of beech assortments,
- development of standards for the classification of forest assortments as well as development of market relationships.

Production potential of managed stands are limited, they are more or less stable. Forestry is not in a position to achieve, in a short term, a considerable increase (if any) of the productivity of natural stands. The decisions may only affect where the increment of wood volume will be accumulated and when it should be sold. Short-term silvicultural interferences make optimal use of the stands and preserve the production potential, and leave stable stands of a potentially higher quality to future generations.

By managing beech stands, meeting scientific and professional requirements, the outlined impacts on the quantity and quality of forest timber assortments may be directed to a certain extent, towards the production target. With the application of tending procedures the value of the stand and that of timber assortments produced by individual type of cut increases in time. The positive selection of trees that determine the development of the stand and natural regeneration provide the transfer of the best properties to future generations. In economic context, the development of false heartwood in beech trees displays an opposite trend. A compromise must be accepted therefore by proper management and determination of harvest age.

Unfortunately, during the last turbulent 20 years, wood production in the region of Bjelovar has been losing the potential based on traditional and natural resources. This has a negative effect both on forestry and the development of this region as a whole. The reasons are manifold, and one of the most important is the lack of objective planning of the achievable assortment structure of the allowable cut. Although such analyses are part of decision making at the strategic level, in the Republic of Croatia they have not been implemented satisfactorily.

Regardless of the degree of (de)centralization of management, the profit of forestry activities should not be the primary interest of the state. The permanent interest of the owner (society as a whole, the state) should be to employ as many people as possible based on sustainable and economic principles of forestry, and utilize natural potentials.

Compared to timber assortments of some other species, the market demand of beech assortments is less stable. Therefore, beech roundwood (e.g. compared to roundwood of pedunculate oak) is often treated as necessary evil in commercial and processing context. On the other hand, the quality of beech timber and its share in the allowable cut of this area show that such attitude should be changed. This requires considerable changes in the approach to this problem of all involved in this segment of Croatian economy, especially on regional and local level.

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Quality and Assortment Structure of Beech High Forests in Serbia

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Abstract – The paper presents research results on quality and assortment structure of uneven-aged beech high forests in Central Serbia. Eleven representative stands of submontane beech forest (*Fagenion moesiacae submontanum* B. Jov. 1976) and montane beech forest (*Fagenion moesiacae montanum* B. Jov. 1976) were selected. Their altitude ranges from 450 m to 1350 m. Site class ranges from I/II to III/IV, canopy closure from 0.7 to 0.9 and volume from 290 m^3/ha to 522 m^3/ha. Total area of the stands is 241.9 ha. Sample plots of 500 m^2 were established in a systematic grid of 100 x 100 m. From silvicultural aspect, 16% of the standing volume (384 m^3/ha) is class one, 39% is class two and 45% is class three. From the aspect of forest utilization 37% of the volume is class one, 34% is class two, 19% is class three, and 10% is class four. In the assortment structure of the average stand volume, industrial wood accounts for 42%, cordwood 48% and waste 10%. It has been concluded that beech high forests in Serbia have unfavourable quality and assortment structure. This situation should be improved in future by taking adequate management measures.

European beech / stand volume / stand structure / wood quality / assortments

1 INTRODUCTION

Beech is a dominant tree species in the forests of Serbia since it accounts for 60% of the total tree volume of all high forests (Stojanović et al. 2005). In the past different management systems of beech forests were used the main ones were: selection felling system, regeneration felling system, and group selection system.

Until the planned conversion of beech virgin forests into productive forests at the beginning of the twentieth century, selection management system was solely applied (single tree selection). The system was used up to the sixties. The selection system then was assessed as unsuitable for beech forests and it was replaced with the management system of group selection felling. This system was developed by Milin (1988) both in theory and in practice, and was introduced in the period from 1960 to 1990. The system was later also considered as unsuitable for beech forests and a new change of management system was implemented. The system of forest management by regeneration felling with short regeneration periods was proposed. This system is still the most commonly applied in management plans, but it is seldom put into practice.

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Generally, there is a great difference between management planning of beech high forests in Serbia and putting these plans into operation. Depending on the stand structure (even-aged, uneven-aged and selection stands with various transitional forms), either regeneration, group selection or selection felling is planned. However, single tree selection felling and selection felling of trees in small groups are most commonly used in practice. This is due to a number of reasons, particularly to the wrong approach to claim that most uneven-aged forests are almost even-aged and to determine the intensity of felling on stand level, rather than on management class level. Beech stands in Serbia are predominantly group-selection all-aged, while there is an insufficient confidence of the measured stand parameters, required for the planning of the forest management on the stand level (Koprivica 2006).

Implementation of different management systems of beech high forests in Serbia and their frequent change have resulted in exceptionally heterogeneous structural development of beech high forests, which has had a particularly unfavourable influence on the quality and natural regeneration of the stands.

Inventory of these forests is still focused on the size and diameter structure of the basic taxation elements: number of trees, basal area, volume and volume increment. Evaluation of the quality and assortment structure of stands and overall classification of forest management units has not been given enough consideration. In forest management plans data on stand quality structure are usually given descriptively, while their assortment structure is determined based on the experience gained during the assortment production in a particular locality or region. However, this approach is often subjective in its nature and there is a permanent need for development, improvement and application of a more objective and precise method of assessing quality and assortment structure of stands.

Dendrometry textbooks (Mirković-Banković 1993, Pranjić-Lukić 1997) describe several methods of assessing quality and assortment composition. However, different methods have different reliability as well as different potentials for their practical implementation. Therefore, the Institute of Forestry in Belgrade has initiated a research project under the title "Method of assessment of quality and assortment structure of beech high forests in Serbia". The project was successfully carried out in the period of 2005 to 2007. A part of the obtained results has been published so far (Koprivica et al. 2006, 2007, 2008, 2009).

The task and the aim of this paper is analyze and synthesize the results of older and recent investigations of the quality and assortment structure of beech stands in order to determine more precisely the quality of beech high forests in Serbia and to plan suitable management measures.

2 STUDY AREA AND METHOD

The research was performed in eleven high, pure, uneven-aged beech stands, selected from six forest complexes located in Central Serbia. These are: Severno Kučajsko, Jablaničko, Podrinjsko-Kolubarsko, Donje-Ibarsko, Golijsko and Rasinsko with a total area of 241.9 ha. Average stand area is 22.0 ha, while individual stand areas range from 9.8 ha to 32.3 ha. Average altitude of the stands is 850 m, while individual stand altitudes ranging from 445 m to 1330 m. Average slope is 21°, individually from 11° to 27° . The most frequent exposure is northwest. Parent rock consists of different types of rocks (sandstone, slates, limestone, granite, gneiss, granodiorite, andesite, etc.). The most frequent soil type is acid brown soil (dystric cambisol), with the depth of approximately 40 to 80 cm. The stands belong to the submontane (*Fagenion moesiacae submontanum* B. Jov. 1976) and montane beech forests (*Fagenion moesiacae montanum* B. Jov. 1976). By silvicultural treatment and structure, they are group-selection uneven-aged stands of beech high forest, in operational (economic) use.

Average site class is II/III, ranging from I/II to III/IV. Average canopy closure degree is 84%, ranging from 69% to 94%. Average percentage of beech in the stand volume is 97%, stand mean diameter is 34 cm and Lorey's mean height 28 m. The average number of trees (with diameter above 10 cm) per hectare is 298, basal area 27 m^2/ha, volume 384 m^3/ha, volume increment 8.3 m^3/ha (Koprivica et al. 2006, 2007, 2008).

A special method was designed (Koprivica et al. 2005) for collecting and processing data needed for the research of quality and assortment structure of beech high forests in Serbia. We shall present only the basic characteristics of the applied method. The size and the structure of taxation elements, particularly the volume and its quality and assortment structure, were determined by partial measurement (samples). Simple circular sample plots, sized 500 m^2 were used. They were distributed in the stands in a 100 m quadratic grid. The intensity of sampling was 5% of the stand area. Altogether there were 242 sample plots. The quality of the 3611 trees in all sample plots was evaluated by using three different methods: the method of the Faculty of Forestry in Belgrade (Stamenković-Vučković 1988), the method of the Faculty of Forestry in Sarajevo (Matić 1977) and Priesol`s method (Mirković-Banković 1993).

In this paper we used Matic`s (Matić 1977) method. This method includes two classifications of trees: silvicultural-technical and technical. The first classification is used to determine the quality of the growing stock and the yield, while the second is used to determine the proportions of assortments in the stand volume, as well as in the marked volume. The classifications are based on the diameter and the quality of the trees, or more precisely trunks. The silvicultural-technical classification is defined primarily from the aspect of silviculture, while the technical classification is defined from the aspect of forest utilization. The second classification is derived from the first one. The criteria for these classifications are described in detail in the paper by Matić, V. (1977).

This paper gives only the general characteristics of these classifications. According to their diameter, trees are classified in the following categories: 5-10, 10-20, 20-30, 30-50, 50-80, and above 80 cm, while their quality is assessed according to different criteria. A number of different stem characteristics are assessed: origin, health condition, leaf colour, forks, butt end, tree trunk, sweep, twist, dents, damage, frost cracks, overtopping, supression, crown damage, snapped or dry tops and infection. According to silvicultural-technical classification, there are three classes of trees:1, 2 and 3. The first class is the best, while the third is the worst.

The first silvicultural-technical class comprises healthy and normally formed trees, with trunks beginning at the stump, suitable for the production of logs of the best and good quality (or potentially so when a tree reaches mature stage). Leaves should be healthy and green. The third silvicultural-technical class comprises severely damaged, diseased and decaying trees, as well as healthy trees which can be used only for the production of fuel and pulp wood, and possibly the lowest quality logs (e.g. „wolfs"). The second silvicultural-technical class (2) comprises all other trees.

According to technical classification, trees are classified into four classes: 1, 2, 3 and 4. The first class is the best, while the fourth is the worst. Trees are classified according to their previously established silvicultural-technical and diameter class, while taking other criteria into consideration as well, primarily those relating to the technical quality of trees. For example, a tree with a dry or a snapped top classified as a tree of the third silvicultural-technical class can be classified as a tree of the first technical class because the quality of its trunk is the same as the quality of a tree in the first silvicultural-technical class etc.

The provisional marking of the trees for felling was performed exclusively for silvicultural purposes (positive selection).

The assortment structure was assessed by the stand assortment tables for beech in Bosnia (Vukmirović 1971), with some corrections (Koprivica et al. 2005). These assortment tables show the proportion of forest assortments in the total volume of the trees (with diameter above 3 cm at the thinner end) expressed in percentage. The inputs in these tables are technical class and diameter class, as well as the kind of assortment, the proportion of which is assessed. For a given technical class, the percentage of a particular kind of assortment, by its diameter class can be read directly from the tables. The total tree volume, previously classified into technical and diameter classes, is used to determine assortment structure expressed in m^3. The volume of each class is simply multiplied by the appropriate percentages read from the tables and then they are added up.

Field data were processed with the SORTIMENT computer software which was specially designed for this purpose (Marković et al. 2007).

3 RESULTS

Out of the numerous study results, we shall only present the results concerning the size and structure of the basic beech stand taxation elements. The focus will be naturally on the stand volume.

3.1 Size and structure of beech stand taxation elements

The average values for the number of trees (N), basal area (G), volume (V) and volume increment (I_v) of the beech stands (per hectare at the time of measurement) are presented in *Table 1*, while *Table 2* shows the values for the marked part of the stands and *Table 3* for the unmarked part.

The average per hectare value of the taxation elements of all stands at the time of measurement was as follows: number of trees 298, basal area 27.0 m^2, volume 383.9 m^3 and volume increment 8.3 m^3.

Table 1. Beech stand taxation elements (total)

Elements	Stand										
	33a	42a	42b	122a	27a	31a	46a	8a	8b	44a	116a
N	274	321	308	214	259	301	298	352	482	294	314
G, m^2	33.4	31.7	31.5	29.0	23.1	21.5	23.2	30.8	29.5	31.0	22.2
V, m^3	522.4	379.6	333.2	503.6	353.7	290.8	316.0	385.2	361.0	502.0	289.9
I_v, m^3	8.6	6.6	5.0	10.5	8.0	6.4	10.1	8.9	6.7	9.2	8.0

Table 2. Beech stand taxation elements (marked part)

Elements	Stand										
	33a	42a	42b	122a	27a	31a	46a	8a	8b	44a	116a
N	135	179	142	110	127	155	136	146	230	110	167
G, m^2	19.0	17.1	17.2	14.0	10.6	9.9	11.5	12.2	11.8	13.7	11.8
V, m^3	304.5	203.3	189.1	242.1	159.8	130.7	157.8	152.9	142.1	229.1	152.9
I_v, m^3	4.3	3.3	2.3	4.9	3.6	2.7	4.7	3.3	2.2	3.5	3.9

The average per hectare value of the taxation elements of the part which is included in the provisional marking of all stands is: number of trees 145, basal area 13.2 m^2, volume 188.6 m^3 and volume increment 3.7 m^3.

Table 3. Beech stand taxation elements (unmarked part)

Elements	Stand										
	33a	42a	42b	122a	27a	31a	46a	8a	8b	44a	116a
N	139	142	166	104	132	146	162	206	252	184	147
G, m^2	14.4	14.6	14.3	15.0	12.5	11.6	11.7	18.6	17.7	17.3	10.4
V, m^3	217.9	176.3	144.1	261.5	193.9	160.1	158.2	232.3	218.9	272.9	137.0
Iv, m^3	4.3	3.3	2.7	5.6	4.4	3.7	5.4	5.6	4.5	5.7	4.1

The average per hectare value of the taxation elements of the part which is not included in the provisional marking of all stands is: number of trees 154, basal area 13.8 m^2, volume 195.3 m^3 and volume increment 4.6 m^3.

The given data on the existing state of beech stands and the part which has not been included in the provisional marking of trees clearly show that the current state of beech high forests in Serbia is very bad. Provisional marking included on the average: 48.5% of trees, 48.9% of basal area, 49.1% of volume and 44.6% of volume increment.

Distribution of stand volume per diameter classes is one of the most important parameters of the quality and assortment structure – in the sense that, with approximately the same quality of healthy trees, the stand with a higher percentage of larger diameter trees is more valuable. In order to better understand the differences in the stand volume structures per diameter classes; their percentage distribution is presented in *Table 4.*

Table 4 shows that in all stands altogether the percentage of the trees with diameter above 60 cm (threshold diameter of felling size) is 26.7% of the average volume. The volume of the trees with diameter above 60 cm in individual stands range from 0 to 41.0%. It can be assumed that the stands with a higher percentage of thicker trees have better quality and assortment structure, but this cannot be proven yet. Above all, it depends on the quality of the trees.

The volume of the trees included in the provisional marking in the stands is presented in *Table 5.* The table shows that the percentage of the trees with diameters above 60 cm in the provisionally marked volume of all stands amounts to 36.0% in the average. Individual stand percentages of the trees with diameters above 60 cm are in the range from 0 to 52.0%. This is in accordance with the percentage distribution of the stand volume presented in *Table 4.* It further shows that provisionally marked trees are distributed in all diameter classes, which supports the previous conclusion that the trees were exclusively marked from the aspect of silviculture (stand tending).

Table 4. Structure of the beech stand volume per diameter classes,in %

Stand	Diameter class (cm)									Total, %
	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100	
33a	2.4	6.1	11.7	12.6	26.2	21.5	10.3	7.2	2.0	100.0
42a	1.7	9.5	24.1	27.6	24.6	10.7	1.8	-	-	100.0
42b	1.9	7.9	9.9	28.7	27.5	17.4	6.7	-	-	100.0
122a	1.6	4.0	9.5	18.9	21.5	29.7	12.1	2.7	-	100.0
27a	3.4	8.8	18.9	20.5	26.1	18.0	4.3	-	-	100.0
31a	4.7	10.6	21.3	38.2	11.0	11.2	3.0	-	-	100.0
46a	4.9	9.3	14.7	21.0	29.0	13.2	7.9	-	-	100.0
8a	1.7	15.5	35.8	30.9	16.1	-	-	-	-	100.0
8b	6.6	20.8	27.6	26.8	18.2	-	-	-	-	100.0
44a	3.3	6.5	9.5	16.0	19.2	21.0	21.2	3.3	-	100.0
116a	5.4	10.2	24.4	26.8	16.0	10.4	4.5	2.2	-	100.0
Average, %	3.3	8.7	17.2	22.9	21.2	16.3	8.1	2.0	0.3	100.0

Table 5. Structure of the provisionally marked volume in the beech stands per diameter classes, in %

Stand	Diameter class (cm)									Total, %
	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100	
33a	1.8	3.8	9.4	8.3	24.7	22.9	13.4	12.3	3.4	100.0
42a	1.9	10.9	23.9	24.1	20.3	15.6	3.3	-	-	100.0
42b	1.6	5.1	6.5	20.1	24.3	30.6	11.8	-	-	100.0
122a	1.7	5.3	11.1	15.3	20.2	27.7	13.0	5.7	-	100.0
27a	3.8	11.5	18.6	14.2	26.3	20.8	4.8	-	-	100.0
31a	6.8	10.8	14.1	30.4	11.6	19.7	6.6	-	-	100.0
46a	4.7	7.6	13.3	14.4	24.9	19.3	15.8	-	-	100.0
8a	2.4	16.7	27.6	31.8	21.5	-	-	-	-	100.0
8b	12.0	18.0	9.7	28.2	32.1	-	-	-	-	100.0
44a	2.8	5.1	4.0	8.7	16.6	21.3	34.3	7.2	-	100.0
116a	5.8	11.2	17.9	29.7	11.0	14.9	5.2	4.3	-	100.0
Average, %	3.6	8.3	13.5	18.5	20.1	19.5	11.9	4.1	0.5	100.0

However, intensity of marking (per volume) is rather high and amounts to around 49.1%. Intensity of marking in individual stands ranges from 39.4% to 58.2%. Apart from the high percentage of the trees with diameter above 60 cm in the stand volume, this is primarily the consequence of the poor quality of the trees. The percentage of the trees with diameter above 60 cm in the unmarked average volume of all stands is 17.6%, while there are no trees with diameter above 80 cm.

3.2 Quality structure of beech stand volume

The study results include the quality structure of the existing stand volume, provisionally marked volume, and the stand volume which would remain after the provisional marking (tree felling) has been carried out.

The percentage distribution of the existing stand volume per silvicultural and technical classes is shown in *Table 6*.

Table 6. Quality structure of the existing beech stand volume, in %

Stand	Silvicultural class			Total, %	Technical class				Total, %
	1.	2.	3.		1.	2.	3.	4.	
33a	10.8	36.4	52.0	100.0	27.9	36.1	24.6	11.4	100.0
42a	11.3	39.6	49.1	100.0	38.9	36.6	18.5	6.0	100.0
42b	5.9	22.0	72.1	100.0	18.5	22.7	39.9	18.9	100.0
122a	30.2	43.3	26.5	100.0	56.0	33.0	9.3	1.7	100.0
27a	24.6	45.9	29.5	100.0	57.9	26.3	10.2	5.6	100.0
31a	17.3	35.1	47.6	100.0	37.7	31.4	17.4	13.5	100.0
46a	5.0	35.6	59.4	100.0	25.2	39.3	22.0	13.5	100.0
8a	6.9	42.9	50.2	100.0	23.7	38.3	26.9	11.1	100.0
8b	10.0	43.7	46.3	100.0	26.1	33.7	20.7	19.5	100.0
44a	19.7	47.5	32.8	100.0	44.2	37.0	13.5	5.3	100.0
116a	9.5	32.6	57.9	100.0	26.6	32.8	25.0	15.6	100.0
Average, %	15.5	39.5	45.0	100.0	37.4	34.0	18.9	9.7	100.0

Table 6 shows that the quality structure of the existing beech stand volume is rather unfavourable. The percentage of the trees of the third (the lowest) silvicultural class in the existing volume is 45.0%, ranging from 26.5% do 72.1%. The percentage of the trees of the third and fourth technical class (the lowest classes) in the existing volume is approximately 28.6%, ranging from 11.0% to 58.8 %. This results in an exceptionally high intensity of the provisionally marked volume, 49.1%, ranging from 39.4% to 58.2%, which means that practically half of the existing stand volume should be removed in the next three or four decades. This is the consequence of the high share of trees with large diameters and poor quality, and the failure to apply adequate tending measures in the past. Approximately 23.5% of the trees in the stands are strongly damaged or affected by canker or decay. The volume of such trees accounts for 25.5% of the existing beech stand volume.

We came to similar conclusions in our earlier investigations for the Jablaničko and Severno-Kučajsko forest areas, where the quality structure of the volume of the beech stands was also rather unfavourable (Koprivica et al. 2006, 2008). However, the quality structure of the volume of the beech stands in Kolubarsko-Podrinjsko forest area was far better (Koprivica et al. 2007). The best quality beech stands are in the Boranja (122a i 27a) and Željin (44a) region.

Earlier studies concluded that the quality of beech high forests in Serbia was far from being satisfactory (Mirković 1971). The recent evaluations of the quality of beech forests in Serbia have proven the same fact (Stojanović et al. 2005).

The quality structure of the volume of the trees included in the provisional marking in the stands is presented in *Table 7*. It shows that the provisional marking includes mostly trees of the third silvicultural class, on average 71.8%, ranging from 49.8% to 96.8%, then trees of the second and finally a negligible percentage of the first class trees. The share of the third and fourth technical classes (together) in the provisionally marked volume accounts for about 46.4%, ranging from 17.4% to 87.0%. Therefore, the quality structure of the provisionally marked volume is much less favourable than the quality structure of the existing stand volume, which could have been expected. In short, the planned volume yield of the beech high forests has a rather unfavourable quality structure, which will be more clearly shown in the analysis of the assortment structure of the stand volume.

Quality structure of the unmarked tree volume in the beech stands is shown in *Table 8*. The data show the quality structure of the stand volume which should be achieved in the next three to four management periods (30–40 years) by applying the stand tending principle of positive selection.

Table 7. Quality structure of the marked beech stand volume in %

Stand	Silvicultural class			Total, %	Technical class				Total, %
	1.	2.	3.		1.	2.	3.	4.	
33a	-	26.4	73.6	100.0	10.2	36.3	35.2	18.3	100.0
42a	1.3	24.1	74.6	100.0	15.1	44.0	29.8	11.1	100.0
42b	-	3.2	96.8	100.0	2.1	10.9	54.8	32.2	100.0
122a	11.9	38.3	49.8	100.0	35.5	47.1	14.0	3.4	100.0
27a	7.1	41.2	51.7	100.0	39.6	30.7	17.6	12.1	100.0
31a	0.5	20.0	79.5	100.0	15.2	29.7	27.1	28.0	100.0
46a	-	13.7	86.3	100.0	0.8	46.1	27.2	25.9	100.0
8a	-	20.3	79.7	100.0	6.2	30.0	39.1	24.7	100.0
8b	-	11.4	88.6	100.0	5.2	19.6	30.4	44.8	100.0
44a	8.1	35.0	56.9	100.0	22.9	46.3	20.4	10.4	100.0
116a	-	11.4	88.6	100.0	7.0	30.2	34.4	28.4	100.0
Average,%	3.4	24.8	71.8	100.0	16.5	37.1	27.8	18.6	100.0

Table 8. Quality structure of the unmarked volume of the beech stands, in %

Stand	Silvicultural class			Total, %	Technical class				Total, %
	1.	2.	3.		1.	2.	3.	4.	
33a	25.9	50.4	23.7	100.0	52.6	35.8	9.9	1.7	100.0
42a	22.8	57.5	19.7	100.0	66.3	28.1	5.4	0.2	100.0
42b	13.5	46.8	39.7	100.0	40.0	38.3	20.2	1.5	100.0
122a	47.1	48.0	4.9	100.0	75.2	19.8	4.9	0.1	100.0
27a	39.0	49.8	11.2	100.0	73.0	22.7	4.1	0.2	100.0
31a	31.0	47.4	21.6	100.0	56.1	32.7	9.5	1.7	100.0
46a	10.0	57.4	32.6	100.0	49.6	32.5	16.8	1.1	100.0
8a	11.4	57.8	30.8	100.0	35.2	43.8	18.9	2.1	100.0
8b	16.4	64.7	18.9	100.0	39.7	42.7	14.4	3.2	100.0
44a	29.4	58.0	12.6	100.0	62.1	29.2	7.6	1.1	100.0
116a	20.2	56.3	23.5	100.0	48.5	35.8	14.6	1.1	100.0
Average, %	27.2	53.5	19.3	100.0	57.4	31.2	10.3	1.1	100.0

The average share of the third silvicultural class in the provisionally unmarked volume accounts for 19.3%, while the third and the fourth technical class amounts to 11.4%. This goal is difficult to attain in the management practice, but we should do our best to reach it. Naturally, we should also consider a very important issue of natural regeneration of the beech stands and the intensity of tree growth above the taxation limit (10 cm).

3.3 Assortment structure of the beech stand volume

Table 9 presents the assortment structure of the existing volume of the beech stands. The assortment structure of the existing volume in the studied beech stands is unfavourable. The share of the best quality assortments (FT/TL and PT1) is 60.3 m^3/ha or 15.7%. The percentage of industrial wood in the volume is 41,7%, cordwood 48.4% and waste 9.9%.

Table 9. Assortment structure of the existing volume of the beech stands, in m3/ha

Stand	Volume of the products and waste, m^3/ha									Total, m^3/ha
	FT/TL*	PT1	PT2	PT3	C	O1/O2	O3	S	OTP	
33a	31.5	40.7	64.4	77.1	85.0	70.1	68.6	28.2	56.8	522.4
42a	26.5	34.2	47.7	52.7	65.6	47.6	44.4	25.2	35.7	379.6
42b	12.1	18.4	32.8	49.3	61.1	52.5	47.5	19.0	40.5	333.2
122a	55.3	60.0	72.0	69.5	69.4	49.5	54.8	28.1	45.0	503.6
27a	38.0	38.4	43.7	46.3	54.4	40.9	37.9	23.0	31.1	353.7
31a	17.9	24.2	32.7	38.8	51.6	41.0	35.7	19.9	29.0	290.8
46a	15.8	23.6	38.3	42.9	56.0	45.0	42.0	19.5	32.9	316.0
8a	14.6	22.6	41.9	53.9	78.1	59.2	47.8	28.2	38.9	385.2
8b	11.8	20.7	35.9	44.2	75.6	60.6	47.8	27.1	37.3	361.0
44a	44.0	51.4	68.9	68.9	75.3	57.7	60.0	27.9	47.9	502.0
116a	13.3	20.0	31.9	38.7	53.7	44.3	38.5	19.1	30.4	289.9
Average, m^3/ha	26.9	33.4	47.2	52.6	64.5	50.3	47.2	23.8	38.0	383.9
%	7.0	8.7	12.3	13.7	16.8	13.1	12.3	6.2	9.9	100.0

* FTTL –veneer log and rotary log, *PT1, PT2 i PT3* – saw logs of the first, second and third class, C- pulpwood,*O1, O2 i O3* – fuelwood of the first, second and third class, S- small round billets and OTP - waste

Table 10 shows the assortment structure of the provisionally marked volume of the beech stands. The assortment structure of the provisionally marked volume of all the stands is on average rather unfavourable, which is due to unfavourable quality structure. The share of the best quality assortments (FT/TL and PT1) is 20.2 m^3/ha or 10.7%. The percentage of the main groups of products is as follows: industrial wood 36.2%, cordwood 52.4% and waste 11.4%.

Table 10. Assortment structure of the marked volume of the beech stands, in m^3/ha

Stand	Volume of products and waste, m^3/ha									Total m^3/ha
	FT/TL	PT1	PT2	PT3	C	O1/O2	O3	S	OTP	
33a	11.1	17.9	34.9	47.5	49.1	46.4	45.6	14.4	37.6	304.5
42a	7.9	12.8	24.4	29.0	37.3	30.7	26.9	13.1	21.2	203.3
42b	2.3	4.8	14.0	29.5	35.8	34.8	31.5	9.1	27.4	189.2
122a	19.0	24.2	35.5	34.7	36.0	27.5	28.7	13.4	23.0	242.0
27a	13.8	14.0	18.7	20.6	25.7	22.5	18.9	10.3	15.3	159.8
31a	4.5	6.5	12.4	17.5	24.2	22.7	19.2	8.2	15.5	130.7
46a	3.2	7.7	18.1	22.3	27.8	26.2	24.8	8.7	19.0	157.8
8a	2.9	4.8	13.3	20.8	31.8	28.4	22.4	10.6	17.9	152.9
8b	2.3	4.0	9.3	15.4	28.8	30.4	24.0	9.8	18.1	142.1
44a	14.0	19.7	32.6	32.7	33.5	29.2	32.1	10.8	24.5	229.1
116a	3.7	6.5	14.0	20.7	28.5	28.0	23.5	9.4	18.6	152.9
Average m^3/ha	8.3	11.9	21.5	26.6	32.3	29.0	26.7	10.8	21.5	188.6
%	4.4	6.3	11.4	14.1	17.1	15.4	14.2	5.7	11.4	100.0

It is interesting to see the assortment structure of the unmarked volume of the beech stands *(Table 11).* Although this structure can be calculated from the data in *Tables 9 and 10*, we will present it here in full to make the study of the stand volume structure complete. As a matter of fact, this is a model which should be strived for in the beech forest management and which can be brought about by changes in the quality structure of the trees in the stands.

The data in *Table 11* show that the difference in assortment structure of unmarked stand volume is smaller than the difference in the marked volume. The share of the best quality assortments (FT/TL and PT1) is 40.1 m^3/ha or 20.5%. The percentage of the main groups of products is as follows: industrial wood 47.0%, cordwood 44.4% and waste 8.6%.

Table 11. Assortment structure of the unmarked volume of the beech stands in m3/ha

Stand	Volume of products and waste, m^3/ha									Total, m^3/ha
	FT/TL	PT1	PT2	PT3	C	O1/O2	O3	S	OTP	
33a	20.4	22.7	29.5	29.6	36.0	23.7	23.0	13.8	19.2	217.9
42a	18.6	21.4	23.2	23.7	28.3	16.9	17.6	12.1	14.5	176.3
42b	9.8	13.6	18.8	19.8	25.3	17.7	16.0	9.9	13.1	144.0
122a	36.3	35.8	36.4	34.8	33.3	22.0	26.1	14.8	22.1	261.6
27a	24.2	24.4	25.0	25.6	28.7	18.4	19.0	12.7	15.9	193.9
31a	13.4	17.8	20.3	21.2	27.4	18.3	16.5	11.7	13.5	160.1
46a	12.6	15.8	20.3	20.6	28.2	18.8	17.3	10.7	13.9	158.2
8a	11.7	17.7	28.6	33.1	46.3	30.9	25.4	17.6	21.0	232.3
8b	9.5	16.7	26.5	28.9	46.8	30.2	23.8	17.3	19.2	218.9
44a	30.0	31,7	36.7	36.1	41.7	28.5	27.8	17.1	23.3	272.9
116a	9.7	13.6	17.9	18.0	25.1	16.3	15.0	9.6	11.8	137.0
Average m^3/ha	18.6	21.5	25.5	26.2	32.2	21.1	20.3	13.1	16.8	195.3
%	9.5	11.0	13.1	13.4	16.5	10.8	10.4	6.7	8.6	100.0

4 DISCUSSION AND CONCLUSION

The results of the quality and assortment volume structure of the studied beech stands show that according to the quality of their volume, the stands can be classified into three groups: the stands of good, medium and poor quality. Stands 122a, 27a, 44a belong to the group of good quality, stands 42a, 33a, 31a, 46a medium quality and 116a, 8a, 42b, 8b are poor quality stands.

In order to give a full insight into the quality of the studied beech stands, we applied the stratified sample. The quality and assortment structure of the present volume, provisionally marked volume and unmarked volume are compared (*Table 12* and *13*).

Table 12. Quality structure of the volume of all beech stands, together

Stand volume	Silvicultural class(%)				Technical class (%)				
	1.	2.	3.	Total	1.	2.	3.	4.	Total
Present	15.5	39.5	45.0	100.0	37.4	34.0	18.9	9.7	100.0
Marked	3.4	24.8	71.8	100.0	16.5	37.1	27.8	18.6	100.0
Unmarked	27.2	53.5	19.3	100.0	57.4	31.2	10.3	1.1	100.0

The data in Table 12 show that the quality of the trees i.e. their volume in the studied beech stands in Serbia is rather bad. The percentage of the third silvicultural class in the marked volume is 71.8%, while the third and the fourth technical class account for 46.4%. The percentage of the third silvicultural class in the provisionally unmarked volume amounts to 19.3%, while the third and the fourth technical class make 11.4% altogether.

Table 13. Assortment structure of the volume of all beech stands, together

Stand volume	Products and waste (%)								
	FT/TL	PT1	PT2	PT3	C	O1/O2	O3	S	OTP	Total
Present	7.0	8.7	12.3	13.7	16.8	13.1	12.3	6.2	9.9	100.0
Marked	4.4	6.3	11.4	14.1	17.1	15.4	14.2	5.7	11.4	100.0
Unmarked	9.5	11.0	13.1	13.4	16.5	10.8	10.4	6.7	8.6	100.0

Unfavourable quality structure of the stand volume has a negative impact on their assortment structure, i.e. the structure of the present volume, provisionally marked volume and unmarked volume. The share of the best quality assortments (FT/TL and PT1 in the present stand volume is 15.7% (10.9% in the marked volume and 20.5% in the unmarked volume). The percentage of the main groups of products in the above three states of the stand volume is the following:

Stand volume	Industrial wood (%)	Cordwood (%)	Waste (%)	Total (%)
Present	41.7	48.4	9.9	100.0
Marked	36.2	52.4	11.4	100.0
Unmarked	47.0	44.4	8.6	100.0

To improve the present unfavourable quality and assortment structure of beech stands in Serbia, an appropriate management system should be implemented consistently, which implies that tending and regeneration measures should be applied in a permanent, planned and professional way. Since these are all pure uneven-aged beech stands, we think that the forest management should continue to support the group-selection structure of stands. This statement is further supported by the following facts: the present structural and spatial development of beech stands, the present state and emergence of regrowth, unfavourable tree quality on a large area, and steep terrain on which the stands are located. Apart from their production function, there are numerous other forest functions which should be taken into consideration in forest management planning and practice. To put it briefly, it is our opinion that only a „permanent forest” can fulfil all the requirements of multifunctionality.

Management should gradually strive towards achieving a quality and assortment structure for unmarked volume calculated in this research. We think that in the next four decades, disciplined and professional work can improve the existing unfavourable quality and assortment structure of beech high forests in Serbia.

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Investigation of Welded Joints with Linear Turned Beech Elements

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Abstract – Welding of wood is a process where chemical and physical reactions take place, heat is formed during the friction, which melts and softens the structure of wood, and a firm joint is formed by cooling of the melt.

The paper discusses the present knowledge about wood welding and the results of wood welding research obtained in the Faculty of Forestry, University of Zagreb. The results were obtained on samples (solid beech wood) with tapered entrance holes 9 mm in diameter, the bottom of the hole 7 mm in diameter and dowel lengths of 20 mm and 30 mm, as well as samples with 8 mm hole diameters and dowel lengths of 20 mm and 30 mm. The tensile strength of welded joints was analysed. The analysis results show that there is a big difference in tensile strength between the samples with 20 and 30 mm long dowels and profile holes. 30 mm long dowels give better results than the 20 mm dowels.

wood welding / tensile strength / beech / longitudinal bonding of turned elements

1 INTRODUCTION

The wood welding technique is a newer way of connecting wooden parts without using glue, using high temperature which is generated by the friction of elements that are being connected. During the welding process, due to the influence of pressure and temperature, the lignin and hemicellulose in the layers that are in mutual contact, is melted.

Welding of metals, metal alloys and plastics with friction has been developed nearly 50 years ago, while the use of similar processes in wood was shown and patented only when Suthoff and others (1996) patented their research conducted in Germany. This patent (Suthoff – Kutzer 1997) demonstrated and showed that wood can be welded with friction heat resulting from rotation or linear movement. They suggested the possibility of joining wood with dowels. In the welding zone, the density of wood is significantly increased, because the cells are completely destroyed. Cell walls are destroyed due to thermal effects, pressure and chemical reactions during the cooling of wood.

The results of recent studies have shown that the welding of wooden dowels into the substrate with mechanical friction at a certain rotation frequency (without adhesive), gives connections with satisfactory strength. This technology is environmentally friendly, using natural materials only. Recycling or burning welded products does not lead to the release of

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toxic components, and the combustion of products which are connected this way is safe for human health (Stamm and others, 2005).

The results of previous studies have shown that by using the rotation and insertion of the dowel or plug in the hole, friction develops the temperature that causes welding. Pizzi and others (2008) showed in their studies that the welding of wooden dowels with a certain rotation frequency gives a connection of fairly high strength. The quality of the connection is affected by factors such as: species of wood, the difference in diameter between the dowel and the hole, welding duration, the frequency of the wooden dowels' rotation (very important for the bonding strength), the use of hot dowels, cross-incised dowel tops, the use of ethylene glycol, etc.

Pizzi and others (2004, 2006), Kanazawa and others (2005) and Ganne-Chedeville and others (2005.) have shown in their studies that the welding of wooden dowels with a high rotation frequency without glue provides high-strength connections. Best results were obtained in the frequency range of 1200 - 1600 rpm, especially between 1500 and 1600 rpm. The frequency was dependent on mechanical limitations of the drill that was used for welding.

Leban and others (2008) explored the dependence of dowel welding on rotation frequency and welding depth. The results showed that if the dowel is welded deep enough, in their case 46 mm, the bond strength is greater than the tensile strength of the dowels. When the depth of the welding was 22 mm, the tensile strength of the dowels was greater than the bond strength.

Besides the depth of welding and the diameter difference between the dowel and the hole, the shape of the hole into which the dowel is welded is also important. When welding dowels deeper (over 30 mm), it is necessary to drill stepwise to increase the strength of welded joint (Župčić and others, 2008), because it comes to detrition at the top of the dowel, as difference in diameter between the dowel and the hole is reduced too much and welding is not achieved.

The shape of the hole (cylindrical or tapered) at longitudinal bonding of turned elements using plugs or dowels (smooth and grooved) affects the magnitude of applied force (Župčić 2010). The average tensile force for samples joined by welding 20 mm long dowels in cylindrical holes is 5726 N, and for 30 mm dowels, also welded into cylindrical holes, is 6603 N. If welding is applied with grooved dowels cylindrical holes result in less tensile force compared to tapered holes, while using smooth dowels, the difference is statistically significant.

The aim of this study was to determine the effect of welding depth and of the shape of the hole on the strength of the linearly connected turned beech elements. Such connected components could be used for manufacturing furniture and furniture parts.

2 MATERIALS AND METHODS

2.1 Welding of samples

Research on welding dowels in holes was carried out at the Faculty of Forestry, University of Zagreb. The samples were made of beech wood with tapered holes, 9 mm and 7 mm in diameter at the entrance and at the bottom, respectively, with dowel lengths of 20 mm and 30 mm. Another set of samples with cylindrical holes of 8 mm diameter, and dowel lenghts of 20 mm and 30 mm were also prepared. The average diameter of the dowel was 10.2 mm, so the diameter difference between the dowel and the hole was 2.2 mm. The samples were connected longitudinaly by rotation welding. Welding of the dowel into the hole was carried out with a constant rotation frequency of 1520 rpm. Sketches of test samples are shown in *Figures 1 to 4.*

Table 1. List of notations

Sample code	Description
2_8	Dowel length 20 mm, hole diameter 8 mm
3_8	Dowel length 30 mm, hole diameter 8 mm
2_9/7	Dowel length 20 mm, tapered hole 9/7 mm
3_9/7	Dowel length 30 mm, tapered hole 9/7 mm

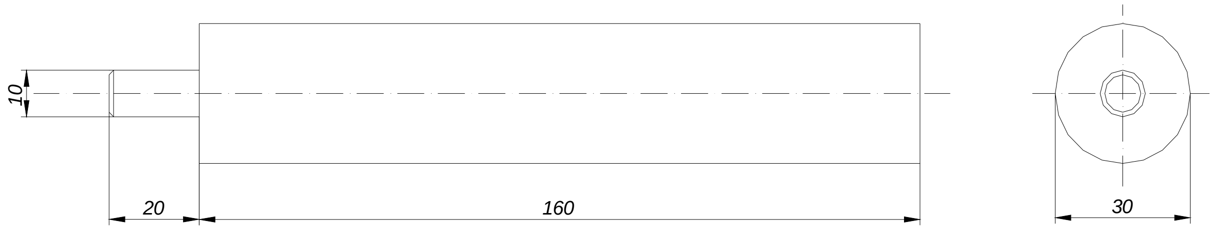

Figure 1. Turned test sample with 20 mm dowel length

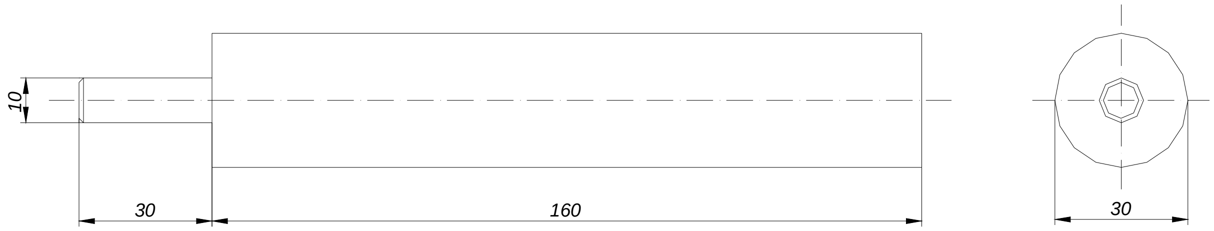

Figure 2. Turned test sample with 30 mm dowel length

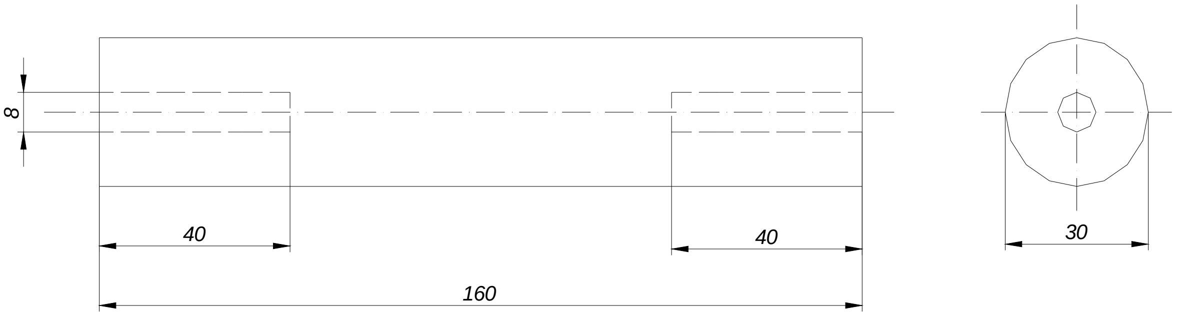

Figure 3. Turned test sample with 8 mm hole diameter

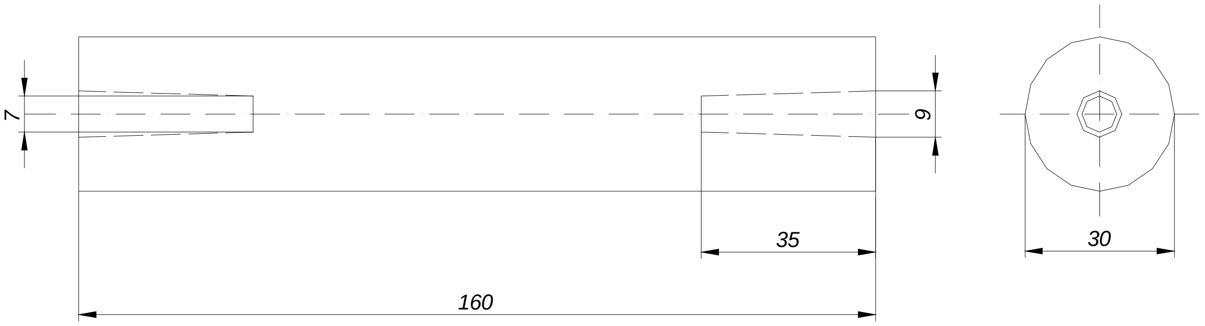

Figure 4. Turned test sample with 9/7 mm tapered hole diameter

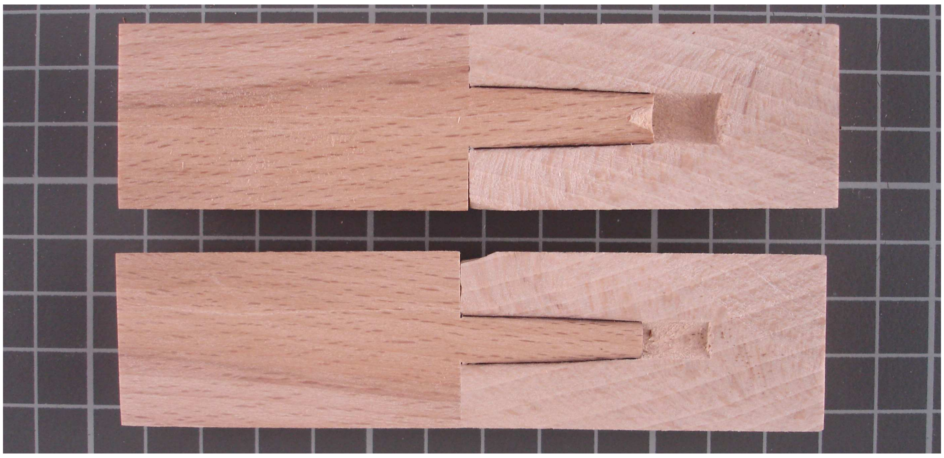

Figure 5. The longitudinal cross section of turned beech elements with 30 mm dowel length (Župčić, 2010.)

2.2 The determination of moisture content and density

Before welding, the samples had been kept in climatised conditions (temperature 23 °C, relative humidity 50%) for approximately three months, but the moisture content of the wood was not measured. After testing the tensile force for each sample, the moisture content was determined. All samples were dried to 0% water content (at 103 ± 2 °C) to constant mass. Moisture content was determined according to HRN ISO 3130:1999. (Croatian standard for determining the moisture content for physical and mechanical tests of wood). The average moisture content was 8.3% (min. 8.1% and max. 9.0%).

After determining of the moisture content, wood density was determined on the same samples according to HRN ISO 3131:1999. (Croatian standard for determining the density of wood for testing physical and mechanical tests of wood). The average density (ρ_0) was 0,69 g/cm³ (min. 0,59 g/cm³ and max. 0,78 g/cm³).

2.3 Test method

After welding, the samples were again conditioned (temperature 23 °C, relative humidity 50%) for eight days, and then tensile force was examined on a universal testing machine. The loading rate of the test was 5 mm/min. From the total of 60 welded samples, 57 were used in the test, as 3 samples cracked during welding.

3 RESULTS AND DISCUSSION

The research results are presented in *Table 2* and *Figure 6*. Linear turned elements can be successfully bonded with the dowel welded into a cylindrical or tapered hole. Research results show that by increasing the depth of welding, tensile force, respectively bond strength generally increases both for cylindrical and tapered holes. It would be logical to assume that with increasing depth of welding bond strength increases, but it is not always the case. With increasing depth of welding, bond strength is gradually increasing until the depth of 30 mm (Župčić 2010.). At this depth, however, it is visible even to a naked eye that the top of the dowel is not properly welded (the weld line is much thinner than in the middle of the hole, or is missing), which certainly affects the bond strength.

In this test series, drilling tapered holes did not lead to a statistically significant increase in tensile force, but the tapered hole reduces the sample’s cracking during welding and is therefore certainly justified. When welding in cylindrical holes, in the first few millimeters rapid wearing of the top of the dowel and expansion of the hole occurs. As a result, there is extra load on the wall of the hole which leads to the cracking of the samples. In addition, to prevent the cracking of the sample during welding samples with tapered holes, the force required for pressing the dowels during welding is lower (Župčić 2010).

Table 2. Descriptive statistics of results of tensile force depending on the depth of welding and the shape of the hole

N=57

Sample code	Tensile force (N) Mean	Number of samples (n)	Tensile force (N) Std. Dev.	Tensile force (N) Minimum	Tensile force (N) Maximum
2_8	4527,692	13	982,905	2780,000	6220,000
3_8	5384, 000	15	1019,915	3450,000	6850,000
2_9/7	4760,714	14	628,704	3880,000	5800,000
3_9/7	5366,000	15	803,108	4220,000	6900,000
All groups	5030,877	57	927,680	2780,000	6900,000

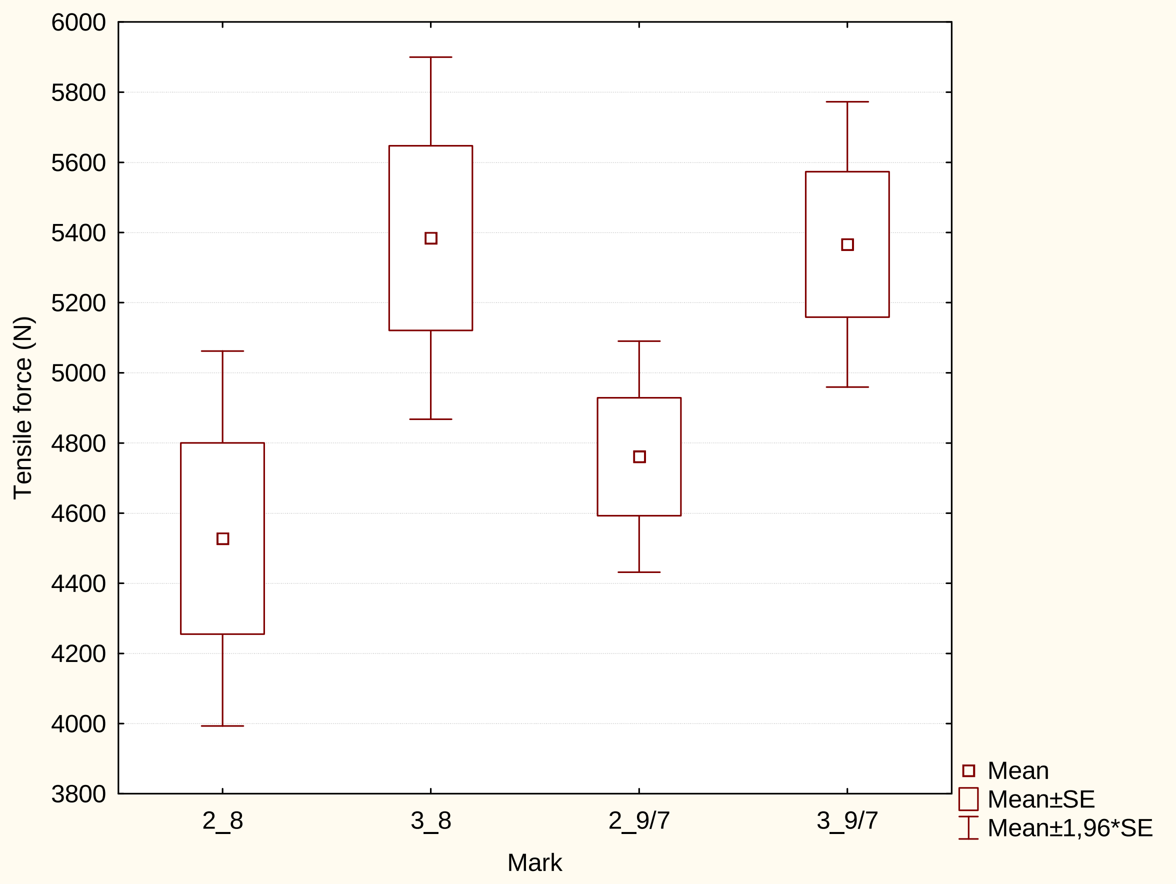

Figure 6. Dependence of tensile force on the depth of welding and the shape of the hole

4 CONCLUSIONS

- According to the results of the investigation, turned elements can be successfully connected longitudinally with dowels by the rotational welding technique. The use of rotational welding is possible for connecting turning elements longitudinally to create rods of unlimited length that can be used to manufacture furniture and furniture parts.
- Results obtained in this study show that the depth of welding of the dowel has an impact on the tensile force, respectively on bond strength.
- Between the samples with identical dowel lengths, but with either cylindrical or tapered holes (samples 2_8 and 2_9/7 and samples 3_8 and 3_9/7) there is no statistically significant difference in the values of tensile force, but the application of tapered holes is justified because it reduces weld defects (cracking of the dowels).

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