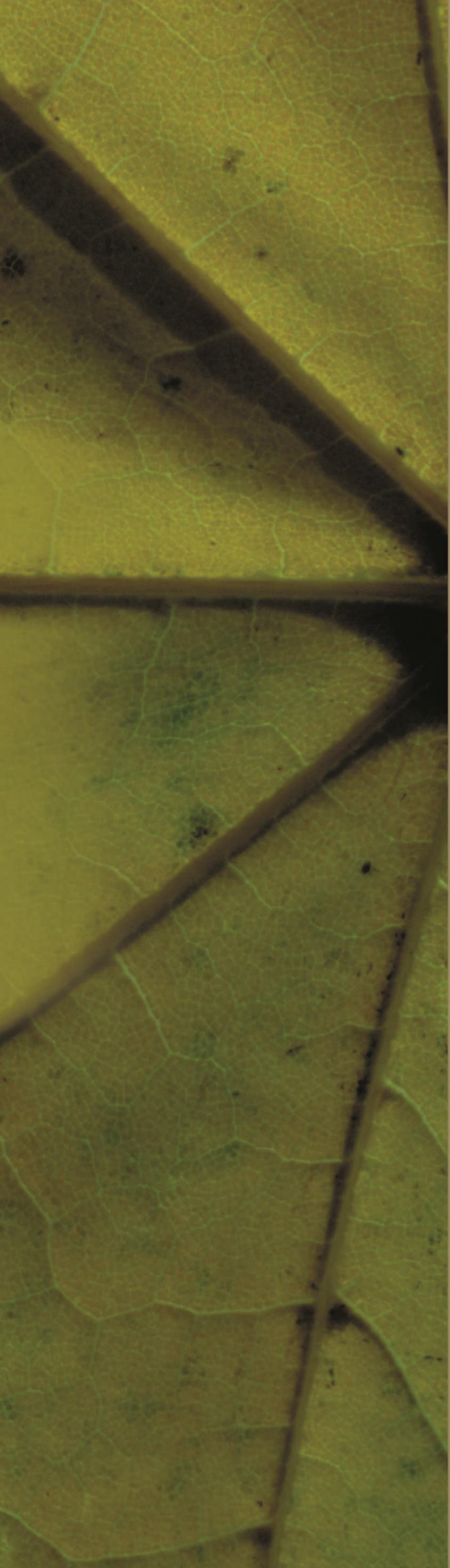

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Relationship of Tree Stand Heterogeneity and Forest Naturalness

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Abstract – The aim of our study was to investigate if compositional (tree species richness) and structural (vertical structure, age-structure, patterns of canopy closure) heterogeneity of the canopy layer is related to individual naturalness criteria and to overall forest naturalness at the stand scale. The naturalness values of the assessed criteria (tree species composition, tree stand structure, species composition and structure of shrub layer and forest floor vegetation, dead wood, effects of game, site characteristics) showed similar behaviour when groups of stands with different heterogeneity were compared, regardless of the studied aspect of canopy heterogeneity. The greatest difference was found for criteria describing the canopy layer. Composition and structure of canopy layer, dead wood and total naturalness of the stand differed significantly among the stand groups showing consistently higher values from homogeneous to the most heterogeneous group. Naturalness of the composition and structure of the shrub layer is slightly but significantly higher in stands with heterogeneous canopy layer. Regarding other criteria, significant differences were found only between the homogeneous and the most heterogeneous groups, while groups with intermediate level of heterogeneity did not differ significantly from one extreme. However, the criterion describing effects of game got lower naturalness values in more heterogeneous stands. Naturalness of site characteristics did not differ significantly among the groups except for when stands were grouped based on pattern of canopy closure. From the practical viewpoint it is shown that purposeful forestry operations affecting the canopy layer cause changes in compositional and structural characteristics of other layers as well as in overall stand scale forest naturalness.

forest naturalness / tree species richness / vertical canopy structure / age structure / canopy closure

Kivonat – A faállomány heterogenitása és az erdőtermészetesség kapcsolata. Vizsgálatunkban arra a kérdésre kerestük a választ, hogy a természetes fafajú erdők esetében a faállomány egyes összetételi (elegyesség) és szerkezeti (szintezettség, korszerkezet, záródás mintázata) jellemzőinek heterogenitása milyen összefüggést mutat az erdő egyes természetességi kritériumaival és állomány szintű természetességével. Az elemzett kritériumok (faállomány-összetétel, faállomány-szerkezet,

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cserjeszint-összetétel, cserjeszint-szerkezet, gyepszint-összetétel, gyepszint-szerkezet, holtfa, vadhatás, termőhely) természetességi értékei a különböző vizsgálati szempontokból a homogén és a heterogén csoportok esetében nagyon hasonló eredményeket mutattak. A legmarkánsabb elkülönülést a faállományt jellemző kritériumoknál lehetett tapasztalni. A faállomány-összetétel, a faállomány-szerkezet és a holtfa, valamint az erdőállomány természetessége esetében valamennyi csoport szignifikánsan különbözik, egyre magasabb természetességi értékeket mutatva a homogéntől a legheterogénebb csoportig. Ugyanebben az irányban a természetességi érték növekedése szintén e kritériumoknál a legnagyobb. A cserjeszint összetételének és szerkezetének természetessége csak kismértékben, de szignifikánsan nagyobb a heterogénebb faállományú csoportokban. A többi csoportosítási szempont során többnyire csak a homogén és a legheterogénebb csoport mutat szignifikáns különbséget, a köztes heterogenitású csoport általában valamelyiktől nem különül el. A vadhatás természetessége viszont mindegyik csoportosítási szempontnál szignifikánsan alacsonyabb a heterogénebb faállományok esetén, a termőhely természetességének értéke pedig nem különbözött a faállomány eltérő heterogenitású csoportjaiban – a záródás kivételével – egyik vizsgálati szempont esetében sem. Gyakorlati oldalról közelítve megállapítható, hogy a faállományt érintő tudatos erdészeti beavatkozások összefüggést mutatnak a többi állományszint összetételi és szerkezeti jellemzőinek, valamint az erdőállománynak a természetességével is.

erdőtermészetesség / elegyesség / szintezettség / korszerkezet / záródás

1 INTRODUCTION

In the multi-purpose evaluation of forests there is growing focus on forest naturalness and its temporal change as indicators of forest condition (e.g. Scherzinger 1996, Bergstedt 1997, Reif 1999/2000). Naturalness is the most important and widely used criterion for assessing conservation status and serves as a major tool for the analyses that support planning of conservation management (Hoerr 1993, Schmidt 1997). In the last decade a number of proposals were made on how forest naturalness should be evaluated in Hungary (e.g. Bartha et al. 1998, 2003, Mátyás 1996, 1998, Solymos 1998, 2004, Sódor – Madas 1998). However, only Bondor – Halász (1998) published country scale analyses based on the National Forest Database. No separate field measurements have been made for this purpose so far. Lately, some countries and regions managed to carry out the evaluation of forest naturalness using different protocols (e.g. Austria: Grabherr et al. 1998, Germany: Arbeitskreis Forstliche Landespflege 1996, Switzerland: Brassel – Lischke 2001, Baden-Württemberg: Schirmer 1999, Bradenburg: Steinmeyer 2003). These were taken into account when designing the methods for similar analyses of Hungarian forests.

By naturalness we mean the uncontrolled prevalence of natural processes and the occurrence of features shaped by them (Peterken 1996). In this interpretation naturalness is not equivalent to originality, which excludes human interference of any sort and thus can only be thought of in a historic context for the forests of Centre Europe (Kowarik 1999). Unfortunately, originality is not a measurable variable for large area and numerous stands. Available historical data are scarce to judge the compositional, structural and functional features of forest communities that could have developed in the absence of any human impact (Peterken 1996, Rose 1992). An alternative approach uses selected attributes (compositional, structural and functional characteristics) to estimate naturalness. This approach contains subjective elements as the measured indicator values depend partially on the judgement of professionals and estimation. It is likewise up to experts to decide which attributes to consider and how to weigh them. These decisions rose as the consensus of numerous researchers with various views (Delphi method, see Grabherr et al. 1998), and the methodology of the measurements and analyses was thoroughly documented. We set the reference forest as one shaped by natural forest dynamics. The attributes of the actual forest were compared to the corresponding development phase of the natural forest cycle (Leibundgut 1959, Korpel' 1995), and the differences were given in percent values. Naturalness was evaluated as a continuous variable ranging from totally artificial state (0 % naturalness) to natural state (100 % naturalness). Naturalness can be assessed at various spatial scales (stand – landscape – region), each calling for distinct methodology. In the present study we used stand (subcompartment) scale assessment of naturalness in a complex way, which provides data not only on general naturalness of a stand, but also enables independent analyses of different criteria of forest naturalness (composition and structure of canopy and shrub layers, of forest floor vegetation and of regeneration, site characteristics, dead wood and effects of games).

Several studies showed that the naturalness state of the tree stand greatly determines overall species composition, diversity and other community features of forest ecosystems (e.g. McComb – Lindenmayer 1999, Müller-Starck 1996, Peterken 1996, Scherzinger 1996, Frank 2000). Considering either traditional ways of forest use, or ongoing 'modern' forest management still prevalent in the major part of our forest landscape, it is the tree stand that has been mostly affected by human activities (Behre 1988, Bürgi 2003). Although forest management influence almost all components of forest ecosystems (site conditions, herbs, animal communities etc.), it is usually aimed at shaping the tree stand (and using timber).

This present study focuses on the relationships between the tree stand and naturalness criteria. To describe the tree stand we use one compositional (species mixture) and three structural (age structure, vertical and horizontal patterns of canopy) attributes that are both directly affected by and react sensitively to conscious forestry operations. The question at hand is whether the different values of these four stand attributes, and thus the different emerging stand types show correlation with the naturalness of compositional, structural and functional features of the forests stand. This knowledge is indispensable when one plans to improve the naturalness of our forests while still managing them. Our hypothesis is that in naturally heterogeneous tree stands (presence of associate tree species, mixed age structure, several canopy layers, patchy canopy closure) naturalness criteria describing other components and functional features have higher values than in the absence of this heterogeneity. We included only stands containing natural (native and site adapted) tree species. Stands with non-indigenous tree species can be very different in conditions from forests with natural tree species obscuring the features emerging from stand scale heterogeneity and horizontal and vertical structures (age structure, layers, canopy closure) potentially affecting naturalness.

2 MATERIALS AND METHODS

In the framework of our project titled „Assessing forest naturalness in Hungary" (2001-2004) a survey was completed in 3000 subcompartments selected by using stratified random sampling. The sample is representative for Hungarian forests in terms of main forest community types. Each selected subcompartments was in the size-range of 3 to 10 hectares. For the purpose of this analysis we only used those subcompartments, in which canopy trees are higher than 5 meters and are built of native tree species. A further constraint was set stating that the mixing ratio of dominating tree species had to exceed the minimum value established for the potential natural forest community. The minimum values are available in the detailed methodological documentation of the survey (http://ramet.elte.hu/~ramet/project/termerd/index.htm, Table A1b). 1074 subcompartments matched these conditions and thus became object for detailed analysis for this paper.

For assessing individual stands, we used 57 indicators of forest naturalness that were grouped into sets describing different criteria (tree species composition, tree stand structure, species composition of shrub layer, structure of shrub layer, composition of forest floor vegetation, structure of forest floor vegetation, dead wood, effects of game, site characteristics, see *Appendix*). These indicators describe mainly vegetation characteristics, even the effect of game is assessed by the impact on vegetation and site. Indicators describing site characteristics refer to human impacts. The reason for this bias is the need for indicators that can be estimated fast and reliably (giving robust results) during the field survey. This need resulted in the lack of – otherwise important – zoological indicators in our naturalness assessment.

Naturalness values are derived during a hierarchical process composed of three levels. At the first level, we evaluate the qualitative or quantitative indicators (observed in the field) by attaching a numerical value (on a ratio scale ranging from 0 to 100) based on how the status of the indicator in question corresponds to that of the hypothetical reference forest. The obtained value may depend on the potential natural forest community (PNFZ) of the stand. At the second level, the naturalness value of a criterion is derived as a weighed sum of the values of corresponding indicators. For each indicator, the applied weight is defined by estimating how important it is in determining the naturalness of the given criterion. To make naturalness values of different criteria comparable, for each criterion the obtained weighed sum is normalized by its possible theoretical maximum in the given PNFC. At the third level, the total naturalness value of the stand (a single number based on all assessed aspects) is calculated. It is derived as a weighed sum of the naturalness values of all the criteria used at the second level. Weight of a criterion may depend on PNFC. Detailed description of the methods used for the field survey and calculations can be found at http://ramet.elte.hu/~ramet/project/termerd/index.htm.

Since we aim to study the effects of four characteristics (tree species mixture, age structure, vertical and horizontal patterns) of the canopy layer on naturalness criteria, for each analysis we separated homogeneous stands from more heterogeneous ones based on the respective characteristic *(Table 1).* First we analysed the effects of these four characteristics separately, then we formed groups of stands based on different combinations of them. We distinguished three groups of stands based on three tree species composition indicators. We also formed three-level groupings based on age structure, vertical structure and horizontal patterns of canopy closure, respectively using a single indicator for each. Combined effects of canopy heterogeneity were studied by forming two stand-groups based on species mixture, age structure and vertical structuring: 1) pure, even-aged single-storeyed; 2) mixed, uneven-aged, multi-storeyed. We could not include horizontal pattern of canopy closure, since no stand could have been put into the heterogeneous group. Altogether 310 stands could be used for analysing the combined effects of these characteristics.

We compared average values of individual naturalness criteria and total naturalness among the distinguished stand-groups. The criterion on which we based stand grouping was excluded from each analysis, though the calculation of total naturalness was based on all 57 indicators in each case. Differences among groups were tested by ANOVA and Newman-Keuls multiple comparison, or by t-test when only two groups were formed. In cases where parametric tests could not be applied, we used non-parametric alternatives: Kruskal-Wallis test, non-parametric multiple comparison, Mann-Whitney U test (Zar 1999). We used Statistica for Windows 7.0 for our analyses (Statsoft 2004).

Table 1. Stand groups formed by different canopy characteristics (species composition, age structure, vertical structure, pattern of canopy closure) and their combinations

Canopy feature	Selection criteria
Species composition	
Pure	Tree stand is composed of a single tree species.
Mixed 1	Tree stands not belonging to 'Pure' or 'Mixed 2'.
Mixed 2	Numerical value of indicators '*Number of native tree species with cover > 5 %*' and '*Number of and mixing ratio of associate tree species with cover < 5 %*' ≥ 50.
Age structure	
Even-aged	Tree stand contains only a single age class.
Uneven-aged 1	Tree stand contains two age classes.
Uneven-aged 2	Tree stand contains three or more age classes.
Vertical structure	
Single-storeyed	Tree stand is single-storeyed.
Multi-storeyed 1	Tree stand is two-storeyed.
Multi-storeyed 2	Tree stand is three (or more)-storeyed.
Pattern of canopy closure	
Homogeneous	Canopy closure is uniform all over the stand.
Heterogeneous 1	There are a few larger patches with canopy closure different from the rest of the stand.
Heterogeneous 2	There are a several patches with canopy closure different from the rest of the stand.
Combined	
Homogeneous	Pure, even-aged, single-storeyed: tree stand is composed of a single species, of a single age class and is single-storeyed.
Heterogeneous	Mixed, uneven-aged, multi-storeyed: numerical value of indicators '*Number of native tree species with cover > 5 %*' and '*Number of and mixing ratio of associate tree species with cover < 5 %*' ≥ 50; tree stand contains at least two age classes, and is not single-storeyed.

3 RESULTS

3.1 Effects of tree species composition on naturalness criteria and on total naturalness of the stand

As *Table 2* shows, most criteria got higher naturalness values in mixed than in pure stands. There were two exceptions: 1) naturalness of site characteristics was independent form level of mixing; 2) naturalness values based on game effect were significantly higher in pure stands than in the other two mixed stand groups. All three stand groups had significantly different naturalness values for the following criteria: structure of the canopy layer, composition and structure of forest floor vegetation, dead wood. Total naturalness was also different among all three groups. The highest difference was observed for dead wood, where naturalness value of the most heterogeneous group (Mixed 2) was more than two times higher than that of group 'Pure'. Naturalness values of the shrub layer (both composition and structure) were less different among the stand groups, though mixed stands had higher values based on these criteria as well.

Naturalness values based on structure of regeneration were not significantly different between groups 'Mixed 1' and 'Mixed 2', but both had almost twice as high values as group 'Pure'. Tree species composition had even slighter effects on the naturalness based on the composition of regeneration. Multiple comparison could not differentiate the three stand groups.

Table 2. Naturalness values (mean ± standard error of the mean) of criteria in stand groups with different species richness

Criteria	Species richness type			ANOVA	Kruskal-Wallis-test
	Pure	Mixed 1	Mixed 2		
Sample size (n)→	*172*	*780*	*122*	*(F; p)*	*(H; p)*
Structure of canopy layer	29.61±0.52^{a}	38.06±0.36^{b}	43.61±1.15^{c}		144.41; $p<0.001$
Composition of shrub layer	82.98±1.89^{a}	85.14±0.82^{a}	91.22±1.84^{b}		13.79; $p<0.01$
Structure of shrub layer	73.67±1.69^{a}	78.30±0.74^{b}	78.20±1.68^{b}	3.58; $p<0.05$	
Composition of forest floor vegetation	56.75±1.71^{a}	68.36±0.84^{b}	74.08±2.13^{c}	23.62; $p<0.001$	
Structure of forest floor vegetation	53.38±2.36^{a}	64.17±0.99^{b}	72.10±2.46^{c}		32.53; $p<0.001$
Composition of regeneration	95.41±1.38^{a}	97.62±0.44^{a}	99.88±0.07^{a}		7.09; $p<0.05$
Structure of regeneration	18.45±1.87^{a}	33.19±1.07^{b}	34.09±2.70^{b}		47.21; $p<0.001$
Dead wood	10.22±1.19^{a}	16.76±0.75^{b}	26.25±2.30^{c}		52.32; $p<0.001$
Effect of game	70.62±1.70^{a}	63.45±0.89^{b}	57.44±2.57^{b}		16.82; $p<0.001$
Site characteristics	81.47±1.03	83.31±0.45	80.67±1.41		3.74; n.s.
Total naturalness of the stand	53.45±0.59^{a}	59.63±0.28^{b}	64.51±0.74^{c}	75.28; $p<0.001$	

Groups were compared by using ANOVA or Kruskal-Wallis test. Superscript letters indicate group membership by Newman-Keuls and non-parametric multiple comparisons using $p < 0.05$. 'n.s.' stands for not significant.

3.2 Effects of age-structure on naturalness criteria and on total naturalness of the stand

As *Table 3* shows, in uneven-aged stands several criteria (composition of the canopy layer and field layer vegetation, dead wood) and total naturalness of the stand got much higher naturalness values than in more even-aged stands. All three stand groups differed with high significance, and mean values also differed considerably, especially for dead wood. Significant, but only slight difference was found among the stand groups in the naturalness values based on composition and structure of the shrub layer, structure of regeneration. Naturalness based on the structure of the field layer vegetation only stand group 'Uneven-aged 2' had significantly higher naturalness value than the other two groups. In our investigation we did not find any statistical relationship between age-structure of the stand and naturalness of the composition of regeneration and of site characteristics. However, we found significant difference between 'Uneven-aged 2' and the other two stand groups when effects of game were considered, but this time, the most heterogeneous group had lower naturalness value than the other two stand groups.

Table 3. Naturalness values (mean ± standard error of the mean) of criteria in stand groups with different age structure

Criteria	Age structure type			ANOVA	Kruskal-Wallis-test
	Even-aged	Uneven-aged 1	Uneven-aged 2		
Sample size (n)→	*703*	*266*	*105*	*(F; p)*	*(H; p)*
Composition of canopy layer	67.69±0.32^{a}	71.10±0.55^{b}	74.45±0.88^{c}	36.37; p<0.001	
Composition of shrub layer	83.54±0.93^{a}	87.57±1.27^{ab}	93.27±1.48^{b}		13.52; p<0.01
Structure of shrub layer	76.42±0.80^{a}	79.18±1.25^{a}	80.92±1.70^{a}	3.24; p<0.05	
Composition of forest floor vegetation	63.81±0.90^{a}	71.36±1.35^{b}	78.86±2.20^{c}	24.89; p<0.001	
Structure of forest floor vegetation	61.84±1.08^{a}	64.10±1.75^{a}	71.47±2.66^{b}		12.23; p<0.01
Composition of regeneration	97.00±0.54	98.10±0.66	99.52±0.24		3.12; n.s.
Structure of regeneration	28.79±1.10^{a}	33.62±1.85^{ab}	38.47±2.91^{b}	6.38; p<0.01	
Dead wood	13.49±0.68^{a}	19.45±1.36^{b}	32.19±2.85^{c}		61.87; p<0.001
Effect of game	65.62±0.95^{a}	62.37±1.54^{a}	56.47±2.23^{b}	6.81; p<0.01	
Site characteristics	82.49±0.51	84.04±0.72	80.83±1.43		2.62; n.s.
Total naturalness of the stand	57.17±0.30^{a}	61.55±0.47^{b}	66.88±0.73^{c}	87.60; p<0.001	

Groups were compared by using ANOVA or Kruskal-Wallis test. Superscript letters indicate group membership by Newman-Keuls and non-parametric multiple comparisons using $p < 0.05$. 'n.s.' stands for not significant.

3.3 Effects of vertical structure of the canopy on naturalness criteria and on total naturalness of the stand

Vertical structure had similar effects on naturalness to that of age structure. It had no effects on the naturalness based on the composition of regeneration and on site characteristics, and a slight negative relationship was shown with effects of game. For all other criteria significantly higher naturalness values were found in stand groups with more complex vertical canopy structure (*Table 4*). Naturalness values differed greatly among the stand groups when composition of the canopy, dead wood and total naturalness were considered. For other criteria (composition and structure of the shrub layer and field layer vegetation, structure of regeneration) we found much slighter difference, and in several cases multiple comparison did not differentiate between stand groups 'Single-storeyed' and 'Multi-storeyed 2', mostly as a result of small sample size in the latter.

Table 4. Naturalness values (mean ± standard error of the mean) of criteria in stand groups with different vertical structure

Criteria	Vertical structure type Single-storeyed	 Multi-storeyed 1	 Multi-storeyed 2	ANOVA	Kruskal-Wallis-test
Sample size (n) →	*697*	*343*	*34*	*(F; p)*	*(H; p)*
Composition of canopy layer	66.89±0.31^{a}	73.24±0.46^{b}	75.55±1.58^{b}	75.77; p<0.001	
Composition of shrub layer	83.14±0.94^{a}	89.36±1.05^{b}	94.65±2.32^{ab}		15.52; p<0.001
Structure of shrub layer	76.36±0.81^{a}	79.20±1.04^{ab}	85.10±2.77^{b}	4.49; p<0.05	
Composition of forest floor vegetation	63.17±0.91^{a}	74.17±1.15^{b}	77.94±4.03^{b}	29.75; p<0.001	
Structure of forest floor vegetation	61.18±1.10^{a}	67.01±1.45^{b}	70.63±4.67^{ab}		10.26; p<0.01
Composition of regeneration	96.88±0.56	98.61±0.44	99.71±0.29		3.12; n.s.
Structure of regeneration	28.12±1.10^{a}	35.77±1.60^{ab}	39.66±5.64^{b}	9.31; p<0.001	
Dead wood	14.03±0.70^{a}	20.72±1.28^{b}	33.78±5.38^{c}		36.63; p<0.001
Effect of game	65.55±0.92^{a}	60.82±1.42^{a}	61.58±4.16^{a}	4.27; p<0.05	
Site characteristics	82.36±0.52	83.64±0.66	80.55±2.26	1.56; n.s.	
Total naturalness of the stand	57.03±0.30^{a}	62.67±0.38^{b}	68.68±1.57^{c}		141.78; p<0.001

Groups were compared by using ANOVA or Kruskal-Wallis test. Superscript letters indicate group membership by Newman-Keuls and non-parametric multiple comparisons using $p < 0.05$. 'n.s.' stands for not significant.

3.4 Effects of horizontal structure of canopy closure on naturalness criteria and on total naturalness of the stand

As *Table 5* shows, the three stand groups formed by horizontal canopy structure differed considerably in the naturalness values based on structure of the shrub layer, on dead wood and on total naturalness of the stand, by having much higher naturalness values in stands with heterogeneous canopy closure than in stands with more uniform canopy. The two heterogeneous stand groups got higher naturalness values than the uniform group when composition of the canopy, structure of regeneration and field layer vegetation layer were considered. Regarding the naturalness of composition of the field layer vegetation, stand group 'Heterogeneous 2' got higher values than the other two groups. Stand groups based on horizontal structure of canopy closure did not differ significantly in the composition of the shrub layer and regeneration. Similarly, only slight differences were found between these groups in naturalness values based on effects of game and site characteristics, but lower values were characteristic of stand groups with more heterogeneous canopy closure pattern.

Table 5. Naturalness values (mean ± standard error of the mean) of criteria in stand groups with different canopy closure patterns

Criteria	Canopy closure pattern type			ANOVA	Kruskal-Wallis-test
	Homogeneous	Heterogeneous 1	Heterogeneous 2		
Sample size (n) →	*650*	*295*	*129*	*(F; p)*	*(H; p)*
Composition of canopy layer	68.29±0.33^a	70.31±0.55^b	71.18±0.81^b	8.96; $p<0.001$	
Composition of shrub layer	85.21±0.92^a	84.34±1.35^a	89.53±1.86^a		6.99; $p<0.05$
Structure of shrub layer	75.37±0.81^a	78.23±1.29^b	86.90±1.32^c		42.83; $p<0.001$
Composition of forest floor vegetation	64.72±0.91^a	68.66±1.42^a	75.96±2.04^b	13.41; $p<0.001$	
Structure of forest floor vegetation	58.51±1.13^a	69.01±1.57^b	74.71±2.13^b		50.59; $p<0.001$
Composition of regeneration	97.26±0.53	97.81±0.65	98.18±1.09	0.38; n.s.	
Structure of regeneration	28.07±1.12^a	35.31±1.80b^b	35.36±2.64^b	7.78; $p<0.001$	
Dead wood	13.24±0.67^a	18.80±1.24^b	30.11±2.75^c		39.80; $p<0.001$
Effect of game	65.62±0.96^a	61.46±1.50^a	60.94±2.27^a	3.83; $p<0.05$	
Site characteristics	83.53±0.50^a	81.76±0.79^a	80.78±1.20^a		6.58; $p<0.05$
Total naturalness of the stand	57.24±0.30^a	60.78±0.46^b	65.40±0.76^c	65.17; $p<0.001$	

Groups were compared by using ANOVA or Kruskal-Wallis test. Superscript letters indicate group membership by Newman-Keuls and non-parametric multiple comparisons using $p < 0.05$. 'n.s.' stands for not significant.

3.5 Combined effects of canopy characteristics

As *Table 6* shows, when stand groups were formed by combinations of the studied stand characteristics, several criteria (composition and structure of forest floor vegetation, structure of regeneration, dead wood, total naturalness of the stand) got significantly and much higher naturalness values in stands that were heterogeneous regarding several canopy features (i.e. mixed, multi-aged, multi-storeyed). Similar trend but much less difference was shown when composition of the shrub layer was considered.

We found no difference between the two stand groups in the naturalness of the following criteria: composition of the shrub layer, composition of regeneration, site characteristics. Naturalness value based on the effects of game was significantly lower in the stands with more heterogeneous canopy.

Table 6. Naturalness values (mean ± standard error of the mean) of criteria describing the combined canopy types

Criteria	Combined stand type Homogeneous	 Heterogeneous 1	T-test	U-test
Sample size (n)→	*155*	*55*	*t; p*	*Z; p*
Composition of shrub layer	83.38±2.00	92.43±2.56		2.32; $p<0.05$
Structure of shrub layer	74.72±1.77	81.23±2.44	1.97; n.s.	
Composition of forest floor vegetation	55.52±1.79	77.94±3.21	6.29; $p<0.001$	
Structure of forest floor vegetation	53.34±2.51	74.43±3.45		4.31; $p<0.001$
Composition of regeneration	95.55±1.40	99.91±0.10		1.02; n.s.
Structure of regeneration	19.07±2.03	34.01±3.62	3.72; $p<0.001$	
Dead wood	10.24±1.28	29.26±3.87		5.58; $p<0.001$
Effect of game	70.91±1.83	57.58±3.98		2.81; $p<0.001$
Site characteristics	81.23±1.12	80.38±2.02	0.38; n.s.	
Total naturalness of the stand	53.43±0.62	66.74±1.14	10.74; $p<0.001$	

Groups were compared by using t-test and Mann-Whitney U-test. 'n.s.' stands for not significant.

3.6 Comparison of different groupings

As *Table 7* shows, the naturalness values of the assessed criteria showed similar behaviour when groups of stands with different heterogeneity were compared regardless from which of the 5 canopy characteristic was used for stand grouping. The greatest difference was found in the naturalness of criteria describing the canopy layer (composition, structure, dead wood) and of the total naturalness of the stand. For these criteria naturalness values increased significantly – and also in the highest degree – from homogeneous to more heterogeneous stand groups for all studied canopy characteristics. The greatest differences were found in dead wood, where the naturalness values obtained for the most heterogeneous groups were almost always twice as high as those for the homogeneous ones. Naturalness of the composition and structure of the shrub layer is slightly but significantly higher in stands with heterogeneous canopy layer. Regarding other criteria, significant differences were found only between the homogeneous and the most heterogeneous groups, while groups with intermediate level of heterogeneity did not differ significantly from one extreme. Between-group differences in naturalness values were higher for criteria describing composition and structure of the forest floor vegetation than those of shrub layer with higher values for the more heterogeneous stand groups. Naturalness values of forest floor vegetation differed among all three stand groups when species richness and age structure of the canopy served the basis for grouping, whereas stand groups of intermediate heterogeneity did not differ from one extreme. Naturalness of the composition of regeneration was insensitive for canopy characteristics except for species richness of the canopy, where more heterogeneous stand groups had slightly higher values. On the contrary, structure of regeneration got higher naturalness values in the most heterogeneous stand groups for all the five respects than in the homogeneous groups. Stand groups of intermediate heterogeneity either did not differ from others (age structure, vertical structure), or they only differed from the homogeneous groups (species richness, canopy closer). The criterion describing effect of game got lower naturalness values in more heterogeneous stands regardless from which canopy characteristics was used for stand grouping. This relationship was the strongest when groups based on combined canopy characteristics and on tree species composition. Naturalness of site characteristics did not differ significantly among the groups except for when stands were grouped based on pattern of canopy closure, where it slightly decreased with increasing heterogeneity.

Table 7. Effects of different canopy characteristics on naturalness

Criteria	Studied aspect of canopy heterogeneity				
	Species richness	Age structure	Vertical structure	Pattern of canopy closure	Combined
Composition of canopy layer	n.e.	⇒	⇒	⇒	n.e.
Structure of canopy layer	⇒	n.e.	n.e.	n.e.	n.e.
Composition of shrub layer	→	→	⇒	→	→
Structure of shrub layer	→	→	→	⇒	n.s.
Composition of forest floor vegetation	⇒	→	⇒	⇒	⇒
Structure of forest floor vegetation	⇒	⇒	→	⇒	⇒
Composition of regeneration	→	n.s.	n.s.	n.s.	n.s.
Structure of regeneration	⇒	→	⇒	⇒	⇒
Dead wood	⇒	⇒	⇒	⇒	⇒
Effect of game	⇐	←	←	←	⇐
Site characteristics	n.s.	n.s.	n.s.	←	n.s.
Total naturalness of the stand	⇒	⇒	⇒	⇒	⇒

Legend:
n.e. = not evaluated,
n.s. = not significant,
⇒ = considerable increase from homogeneous to heterogeneous,
→ = slight increase from homogeneous to heterogeneous
⇐ = considerable decrease from homogeneous to heterogeneous,
← = slight decrease from homogeneous to heterogeneous.

We found more pronounced between-group differences in naturalness when tree species composition, age structure and canopy closure were used for grouping, whereas differences among groups based on vertical structure and combined canopy characteristics – having only limited number of stands in the most heterogeneous group – were less noticeable.

4 DISCUSSION

While interpreting the findings of this work one has to consider that significant relationships between grouping variables (this time canopy characteristics) and naturalness criteria do not necessarily indicate causal relationship. An illustrative example is the naturalness based on dead wood, which shows strong positive relationship with tree species composition, age structure, vertical structure and horizontal patterns of canopy closure. It is obvious that naturalness of dead wood is not affected by canopy heterogeneity, rather, both are affected by the intensity (or lack) of forest management. On the contrary, naturalness of criteria describing sub-canopy layers (shrub, forest floor, regeneration) is more directly affected by the heterogeneity of the canopy layer, which is the target of purposeful forestry operations. Shrub layer might be an exception since it is often the object of direct forestry operations (e.g. complete removal), however, in such cases canopy layer also bears the signs (homogeneous character) of intensive management.

Forest floor vegetation has a much more stronger reaction (both in composition and structure) to changes in canopy heterogeneity than shrub layer and regeneration. The reason for this lies in the fact that forest floor species can react much faster to changes in canopy closure than woody species, resulting in a much stronger relationship with structural characteristics of the canopy layer. Based on this, we assume that effects of forest management (either increasing or decreasing heterogeneity) get manifest faster in the composition and structure of forest floor vegetation than those of the shrub layer and regeneration. We found that the naturalness of shrub layer composition showed more direct relationship with canopy heterogeneity than that of shrub layer structure. As a possible explanation, we assume that management-induced changes in the canopy layer have a more pronounced manifestation in composition (appearance of non-indigenous or nitrophilous species) than in changes of horizontal patterns of cover.

There is no straightforward explanation of our findings regarding the effects of game (i.e. stands with more heterogeneous canopy tended to have lower naturalness value). We assume no direct relationship between canopy structure and naturalness based on game effects. Instead, more heterogeneous stands tend to occur at such places (under special site conditions), where game density is generally higher because the these sites are difficult to access, have lower economic importance hence receive less intensive human impact. Examples include forests of rocky spots, riverine willow–poplar galleries and calciphile, thermophilous oak thickets and forests. In our naturalness assessment this criterion has the least representative data, since its evaluation in the field is rather difficult and suffers the most from subjectivity. Of the indicators we used, extent of damage in the litter layer (cf. *Appendix*) can be estimated relatively reliably, whereas it is hard to decide if the complete lack of a layer (shrub, regeneration or herbs) is caused by browsing game, or by site conditions (e.g. lack of light). Complete lack of certain layer is a typical phenomenon in stands with extremely homogeneous canopy.

While interpreting our findings, it is important to emphasize that – mainly as an effect of varying intensity of their use – potential natural forest communities are not equally represented within the stand groups formed by different aspects canopy structure. Although we made serious efforts to make our full sample (almost 2900 subcompartments) representative of Hungarian forests, the obtained ratios have changed while we selected stands for this study. However, naturalness values of different forest communities are comparable, since their different characteristics were taken into consideration during the assessment.

Complexity and hierarchical nature of our scheme for naturalness assessment is exemplified by the fact that stand groups formed by different levels of canopy heterogeneity differed the most in the total naturalness of the stand, while naturalness of individual criteria behaved individually among the stand groups. Total naturalness of the stand – based on evaluation of many indicators – proved to be a sensitive indicator of changes in the forest canopy. As a result, it can also be used for studying ecological, economic or other aspects of forest management, as an overall indicator of management intensity and for assessing if management follows close to nature principles.

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Appendix. Criteria and indicators used for assessing forest naturalness

Criteria	Indicators	Scale type	Potential values
A. Composition of canopy layer	Number of natural tree species with cover > 5%	ratio	Positive integers
	Presence of natural dominants*	binary	yes; no
	Number of associate tree species with cover < 5%	ratio	positive integers
	Proportion of associate tree species with cover < 5%	ratio	positive integers
	Proportion of non-indigenous tree species	ratio	positive integers
	Proportion of cultivars of native tree species	ratio	positive integers
	Proportion of native tree species, not suited to the site	ratio	positive integers
B. Structure of canopy layer	Age-structure of the canopy layer*	ordinal	1; 2 ;3 or more age classes
	Difference between maximum and minimum canopy closure	ratio	positive integers
	Mean canopy closure*	ratio	positive integers
	Cover of clearings (non-wooded areas)*	ordinal	0; <u><</u>20; >20
	Cover of patches with canopy closure < 50%*	ordinal	0; <u><</u>20; >20
	Cause of canopy openness	nominal	forestry; natural
	Pattern of canopy closure	nominal	several patches with different canopy closure; a few larger patches with different canopy closure; uniform canopy closure
	Vertical structure of the canopy	ordinal	1; 2; <u>></u>3
	Transition between the canopy and shrub layers	ordinal	continuous; locally continuous; non-continuous
	Number of old/veteran trees	ratio	positive integers (no/ha)
	Pattern of old/veteran trees	nominal	not present; large patches; small patches; random; uniform
	Relative abundance of trees with unusual crown or stem shape	ordinal	0; <u><</u>10; >10
C. Composition of shrub layer	Authenticity of species composition	binary	yes; no
	Proportion of non-indigenous and/or aggressive tree and shrub species in the shrub layer	ordinal	0 - <10; 10-50; >50
	Proportion of nitrophilous tree and shrub species in the shrub layer*	ordinal	0 - <10; 10-50; >50
D. Structure of shrub layer	Cause of the absence of shrub layer	nominal	Not absent; human impact; natural
	Signs of shrub removal	binary	visible, not visible;
	Difference between maximum and minimum cover of shrub layer	ratio	positive integers
	Mean cover in the shrub layer*	ratio	positive integers
	Spatial pattern of shrubs	nominal	small patches; large patches; random; uniform or missing
E. Composition of forest floor vegetation	Proportion of weeds and/or nitrophilous herb species	ratio	positive integers
	Presence of subordinate associate herbs	ordinal	present in great numbers, present, sparse, missing

Criteria	Indicators	Scale type	Potential values
F. Structure of forest floor vegetation	Difference between maximum and minimum cover of herbaceous species*	ratio	positive integers
	Mean cover in the herb layer*	ratio	positive integers
	Spatial pattern of herbs	nominal	small patches; large patches; random; uniform or missing
	Mean cover of bryophytes*	ratio	positive integers
G. Composition of regeneration	Proportion of non-indigenous and/or aggressive species in the regeneration	ratio	positive integers
H. Structure of regeneration	Difference between maximum and minimum cover of regeneration	ratio	positive integers
	Mean cover of regeneration of native trees	ratio	positive integers
	Proportion of viable, several-years-old regeneration	ratio	positive integers
I. Dead wood characteristics	Relative abundance of standing dead trees and snags	ratio	positive integers
	Number of large standing dead trees and snags	ratio	positive integers (no/ha)
	Cover of lying dead wood (∅ > 5 cm)	ordinal	<1; 1-5; >5
	Decay status of dead wood	nominal	Not present; all decay classes are evenly represented; mostly soft, well-decayed; mostly solid, less decayed
	Number of large lying dead logs (∅ >30 cm)	ratio	positive integers (no/ha)
K. Effects of game	Extent of stripping damage (%)	ordinal	0 - <10; 10-50; >50
	Extent of browsing in the shrub layer	ordinal	none, rare, abundant, on all individuals
	Extent of browsing in the herb layer	ordinal	none, rare, abundant, on all individuals
	Extent of damage in the litter layer (%)	ratio	positive integers
	Shrub layer completely eliminated by game	binary	yes; no
	Herb layer completely eliminated by game	binary	yes; no
	Regeneration completely eliminated by game	binary	yes; no
J. Site characteristics	Signs of secondary erosion*	binary	visible; not visible
	Extent of erosion	ordinal	0; <10; 10-50; >50
	Type of erosion*	nominal	gully, rill, sheet, partial, none
	Humus form*	nominal	mor; moder; mull
	Proportion of area with compacted soil	ordinal	0; ≤10; >10
	Mixing soil horizons*	binary	present; missing
	Damage to the soil surface	binary	present; missing
	Presence of microhabitats	ordinal	none; few; many

Detailed description of field sampling and calculation is available at http://ramet.elte.hu/~ramet/project/termerd/index.htm.

* – Applied rules of evaluation (attaching numerical value) depend on potential natural forest community dependent

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Stand structure and growth of mixed white poplar (*Populus alba* L.) and black locust (*Robinia pseudoacacia* L.) plantations in Hungary

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Abstract – The paper deals with the stand structure and yield of black locust (*Robinia pseudoacacia* L.) plantations mixed with white poplar (*Populus alba* L.) in various proportions, partly applying a new methodological approach. The main stand structure and yield factors were determined separately for each species, measured stem by stem, using volume functions prepared for each species. To demonstrate the advantage of white poplar - black locust mixed plantations over monocultures, a set of models expressing single-tree growth was elaborated. The models were applied to simulated stands with different proportions of *P. alba* and *R. pseudoacacia*. The estimated growth indicated that the advantage of mixing the two species peaked at about 40-50% *P. alba* (basal area percentage) between age 16 and 21. The trial may indicate that if two species have fast initial growth rates and similar rotation ages, planting them in mixed stands might lead to increased yield.

Forest yield / *P. alba* and *R. pseudoacacia* mixed stands / single-tree growth model

Kivonat – Fehér nyárral (*Populus alba* L.) **elegyes akácosok** (*Robinia pseudoacacia* L.) **faállomány-szerkezete és fatermése Magyarországon.** A tanulmány a fehér nyárral (*Populus alba* L.) elegyes akácosok (*Robinia pseudoacacia* L.) faállomány-szerkezetét és fatermését vizsgálja különböző elegyvariációkban részben új módszertani megközelítéssel. A főbb állományszerkezeti és fatermési tényezőket fafajonként külön-külön, törzsenkénti felvétellel, az egyes fafajokra kidolgozott fatérfogat-függvény alapján határoztuk meg. A fehér nyárral elegyes akácosok termesztése előnyös voltának bemutatására egyes fa növekedési modelleket dolgoztunk ki, amelyek segítségével a fehér nyár és az akác különböző elegyvariációit vizsgáltuk. A növekedés vizsgálatok azt jelezték, hogy az említett fafajok elegyes termesztése a fehér nyár 40–50%-os körlapösszeg szerinti elegyaránya mellett a legelőnyösebb 16–21 éves kor között. A kísérlet azt is bizonyítja, hogy ha két fafajnak gyors kezdeti növekedési erélye van és hasonló a vágásérettségi koruk, akkor elegyben telepítésük esetén nagyobb fatermés érhető el.

Fatermés / fehér nyár elegyes akácosok / egyes fa növekedési modell

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1 INTRODUCTION

Technical guidelines of primary forest production are usually aimed at the establishment and management of pure stands. However, mixed stands may provide advantages that justify mixed cultivation of two or three species, provided that the site conditions are suitable. Mixing has mainly biological and ecological advantages, but it may also have a positive effect on yield. In addition, non-material benefits of mixed forests, e.g. improvement of the environment and satisfaction of social expectations, are increasingly acknowledged. The scientific study of mixed forests is a more complex task than the study of pure stands. This partly explains why only limited efforts have been made so far to quantify the growth and yield of mixed stands and to compare the results with pure stands.

Forestry professionals started the description of the structure and species composition of mixed forests by the end of the 18th century. Oak was studied first, followed by the admixed tree species. Later other mixed forest types were studied. In the beginning of the 19th century mainly monoculture forests were established but from the middle of the century there was a shift back to mixed forests (Heyer 1854).

Early in the 20th century analyses made in Central Europe showed that the volume production of mixed spruce and Scots pine stands exceeded that of pure stands (Schilling 1925, Busse 1931). Similarly, it has been observed that the admixing of birch in spruce forests does not reduce the yield of spruce (Fiedler 1966). For instance, a mixture of 40% birch and 60% spruce provided a greater total yield than the same proportions of these species when grown in pure stands (Lappi-Seppala 1930). Furthermore, at fertile sites Wiedemann (1943) reported that the yield of mixed beech and spruce forests was higher than that of pure spruce stands. By contrast, at poor sites the yield of mixed stands was lower than that of pure spruce stands.

Assmann (1970) paid great attention to the study of mixed stands in his book, 'The Principles of Forest Yield Study'. Although it is almost impossible to define comparable pure and mixed experimental plots (for a given set of species), the main finding of the author is that mixing generally results in a greater total yield.

In practice the choice between mixed or pure stands is a complex issue. Mixed stands are often more resistant to pests and have a higher production level than pure ones. In most cases, the total yield of mixed stands exceeds that of light-demanding tree species grown in monoculture (Smith 1986). On the other hand, a balanced development of mixed stands is only obtained when the competition between the species involved is not too asymmetric. This implies that the species composition of mixed stands and the thinning regime should be adjusted to the site conditions but, as attempts to do this are not always successful, mixed stands are frequently claimed by foresters to be more difficult to control than pure stands.

Traditionally, simple stand growth models (growth and yield tables) have been used to predict the development of pure, even-aged stands. However, due to the higher complexity of mixed stands this approach is not generally applicable in this case. Instead the development of mixed stands is usually modelled at the diameter-class or single-tree level. For instance, single-tree growth models have been developed for mixed broad-leaved forests of the Appalachian mountains (Harrison et al. 1986), for coniferous forests in the North Western United States (Wykoff 1990), for mixed stands of spruce and pine in Finland (Pukkala et al. 1994,1998), and for yield forecasting in thinned birch-spruce stands in Sweden (Tham 1988,1989). Application of spatially explicit models like these implies that the stand growth simulation is based on the spatial location and initial diameter of the trees. The models include relationships between diameter and height and competition indices describing the specific growth conditions of each individual tree.

Two recent volumes summarise the latest research work including results on modelling the structure and yield of mixed stands (Robertson, Cannell and Malcolm 1992; Costa and Preuhsler 1994). Based on the literature it appears that two distinct directions of research can be identified. One direction is concerned with the extension of empirical growth and yield models already prepared for pure stands to mixed ones. The other direction focuses on dynamic models based on the physiology of individual trees. In the present context simple empirical models are applied.

The objective of this study was to examine the stand structure and growth in an experiment with mixed white poplar and black locust plantations in Hungary. Particularly, the observations from the experiment are used as a basis of estimating the potential advantage of mixed stands and the optimal basal area share of each of the two species. In this respect we considered also some methodological tools improved by Hungarian researchers (Béky – Somogyi 1995, 1999, Solymos – Béky 1995, Rédei 1999).

2 MATERIAL

Black locust is frequently planted together with white poplar on the sandy ridges between the Danube and Tisza rivers in Central Hungary. In forests covering more than 14,000 ha in this region the joint share of black locust and white poplar exceeds 80%, and 70% of the stands are less than 20 years old.

The experiment examined in this paper is located in the Danube-Tisza Interflow region, in the central part of Hungary (location: Ballószög, altitude: less than 80 m; latitude: N 46o 42'; longitude: E 19o 40'). The trial was established in 1995 in a 16-year-old stand that was planted in spring 1979 in an agricultural field with one-year old seedlings after shallow ploughing. The initial proportions of the tree species in scattered mixture were 70% black locust and 30% white poplar. According to the Hungarian classification of forest site types, the study area is located in the forest steppe climate zone with a relative air humidity of less than 50% in July at 2 pm and an annual precipitation of less than 550 mm. The soil is humic sand with a very shallow rootable depth (<20 cm).

Five plots were established within sub-compartment Kecskemét-Ballószög 20 C, in which black locust and white poplar occurred in various proportions. The area of plots 1–4 was 0.1 ha each, whereas that of plot 5 was only 0.035 ha. The breast height diameter and x,y coordinates of all trees were measured. The crown diameters were measured in four directions corresponding to the four points of the compass. Finally, height was measured for 20 per cent of the trees in plots 1–4 and 30 per cent of the trees in plot 5. All trees in the five plots were classified according to the tree height classification system generally used in Hungarian silvicultural practice: 1 = dominant tree, 2 = co-dominant tree, 3 = intermediate (partly dominated) tree, 4 = suppressed tree. The plots were measured again in 2000 at age 21.

The spatial structure and diameter distributions of the plots are shown in *Figure 1.* As visible in the Figure the experiment includes plots with very different shares of the two species as well as plots with more even shares.

3 METHODS

The main stand structure and yield statistics were determined separately for each species at ages 16 and 21 years (1995 and 2000). Volumes were calculated on the basis of stem-by-stem estimates. First, semi-logarithmic diameter-height regressions for each species were prepared.

Subsequently, these regressions were used for estimating the height of each tree. Finally, volumes were estimated using the volume functions developed by Sopp (1974):

for white poplar:

$$v = 10^{-8} d^2 h^1 \left(h/[h-1.3]\right)^2 \left(-0.4236\, d\, h + 12.43\, d + 4.6\, h + 3298\right),$$

for black locust:

$$v = 10^{-8} d^2 h^1 \left(h/[h-1.3]\right)^2 \left(-0.6326\, d\, h + 20.23\, d + 3034\right),$$

where v is stem volume (m^3),
d is diameter at breast height (cm), and
h is tree height (m).

The experiment does not include replications and is poorly balanced (cf. *Figure 1*). Therefore, we cannot evaluate the advantage of mixed plantations by analysis of variance. However, as will appear from *Figure 1* the plots include a wide range of competition states for both species and, hence, the advantage of mixed plantations with white poplar and black locust can perhaps be evaluated on the basis of the variation of growth observed for individual trees. The procedure includes the following steps: (i) elaborate a set of single-tree growth equations utilising the spatial structure of the plots and taking site-quality variation into account; (ii) hypothesize various stem numbers and species compositions and create hypothetical stands; (iii) use the growth models to evaluate the development of the hypothetical stands assuming homogeneous site quality; (iv) for each hypothetical stand and species calculate the deviation of the predicted volume production from that of a pure stand with the same stem number and share of the area; (v) use the results as a basis of estimating the optimal species composition at the particular site for the age interval 16–21.

The single-tree model should include one or more variables describing the competition experienced by each tree. One such variable is the current diameter of the tree, but including additional variables that describe the immediate neighbourhood of the tree may improve the model. A wide variety of such competition indices have been tried out and in unthinned stands it appears that, no matter which competition index is used, the explanatory power of such indices remains relatively low when the present size of the tree is also included in the model (e.g. Wichmann 2002).

To simplify matters it was decided to use the local basal area (including the tree itself) within a circle with radius 5 metres as the basic competition index. The index was calculated for each of the two species (*P. alba*: G_P; *R. pseudoacacia*: G_R) and in total for both species (G_T) and, as it appeared unlikely that the competition effects of *P. alba* and *R. pseudoacacia* were identical, the percentages of the total, local basal area were also calculated for each species (*P. alba*: P_P; *R. pseudoacacia*: P_R).

A range of different models including the above competition indices were tested and on the basis of the standard deviation and distribution of the residuals the following two models were chosen to be applied for growth prediction (iii):

$$\Delta d_{ijk} = \alpha_0 + \alpha_{1i} + \alpha_{2j} + (\beta_0 + \beta_{1j}) d_{ijk} + (\gamma_0 + \gamma_{1i}) G_{T,ijk} + (\delta_0 + \delta_{1j}) P_{P,ijk} + \varepsilon_{ijk} \qquad (1)$$

$$\Delta v_{ijk} = \alpha_0 + \alpha_{1i} + \alpha_{2j} + (\beta_0 + \beta_{1i}) d_{ijk} + (\gamma_0 + \gamma_{1j}) d_{ijk}^2 + \delta_0\, G_{T,ijk} + (\eta_0 + \eta_{1j}) P_{P,ijk} + \varepsilon_{ijk} \qquad (2)$$

where: G_T is local basal area (both species) within a circle with radius 5 metres (m^2/ha), $G_T = G_P + G_R$;
P_P is contribution of *P. alba* to the local basal area (%), $P_P = 100\% \times G_P / G_T$;
i is the plot number, $i = 1...5$;
j is the species, [*P. alba; R. pseudoacacia*];
k is the tree, $k = 1...n$;
Δd_{ijk} is diameter growth (cm/year);
Δv_{ijk} is volume growth (m^3/year); and
ε_{ijk} are independent and normally distributed error terms.

Diameters and competition indices were measured in 1995.

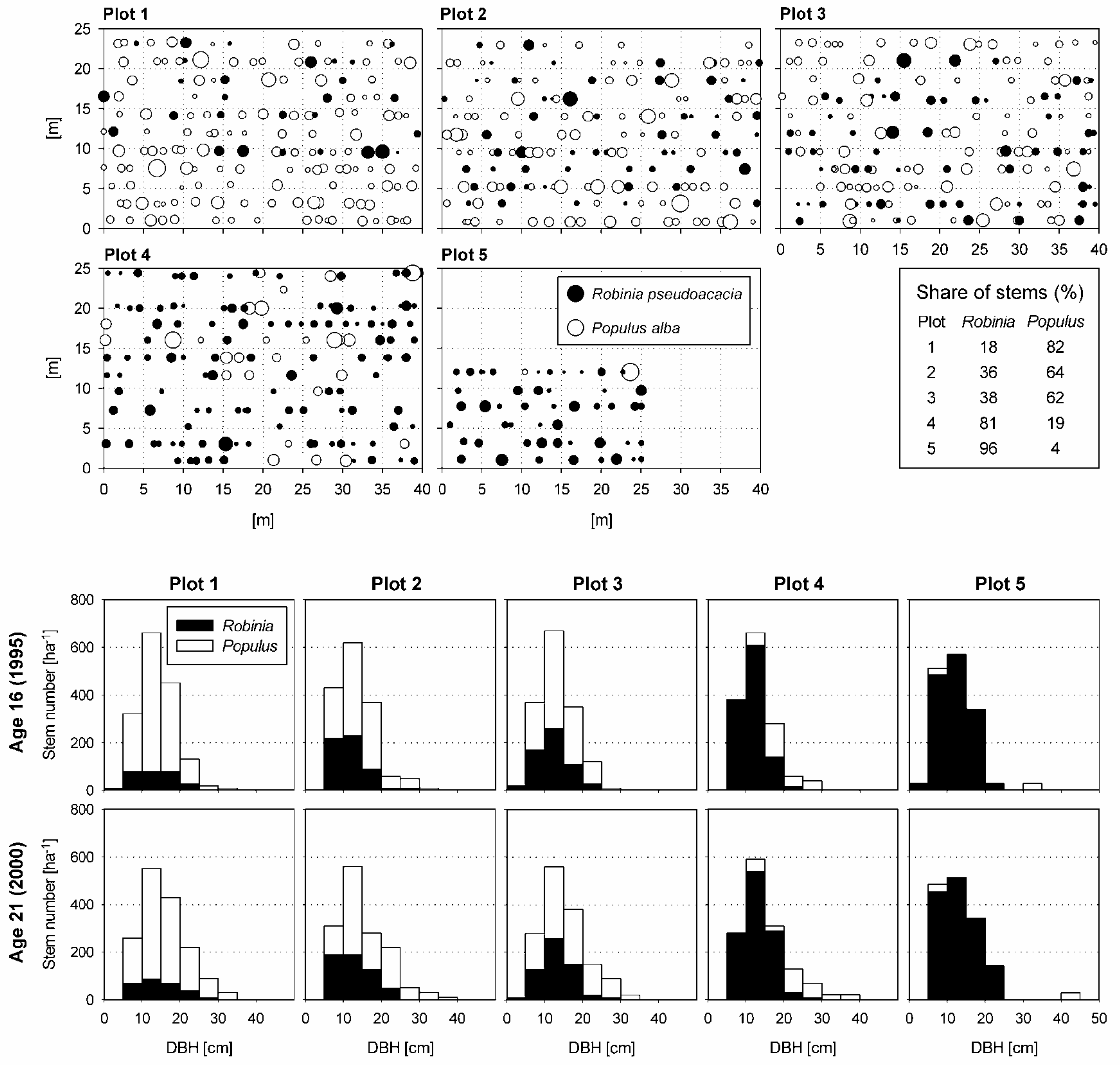

Figure 1. TOP: Stem maps of the experimental plots (Kecskemét-Ballószög 20 C). Symbol diameter is proportional to breast height diameter in 1995 (age 16). BOTTOM: Diameter distributions at ages 16 (1995) and 21 (2000)

4 RESULTS

We started by testing the effects of plot and species on the relationship between diameter (cm) at breast height and height (m) in each of the years, 1995 and 2000. In 1995 it turned out that there was an almost significant effect of plot (P=0.06), and in 2000 there was a significant effect of species (P=0.01). We therefore decided to continue with separate models for each year and species, testing whether significant effects of plot remained. Except for *Robinia pseudoacacia* in 1995 (P=0.06) it emerged that this was not the case. Accordingly, we used the following four models to estimate tree height:

P. alba, 1995:	$h = -3.29 + 6.81 \ln(d)$	RMSE = 1.16 m
R. pseudoacacia, 1995:	$h = -3.26 + 6.94 \ln(d)$	RMSE = 1.57 m
P. alba, 2000:	$h = -5.44 + 8.72 \ln(d)$	RMSE = 1.96 m
R. pseudoacacia, 2000:	$h = -5.58 + 8.28 \ln(d)$	RMSE = 2.02 m

Summary statistics regarding the stand structure and increment in the period 1995–2000 are shown in Table 1 for each species and plot, and in total for each plot. It appears that the initial stem number per hectare (1995) is almost similar for all plots (1420–1600 /ha). The share of *P. alba* stems ranges from 4 to 82 percent (cf. Fig. 1). As for the stand diameter (expressed as D_g) it immediately appears that for *R. pseudoacacia* D_g is 12–13 cm on plots 2–5 where the number of *R. pseudoacacia* stems is relatively high, whereas on plot 1 it is 14.2 cm. Similarly, the D_g of *P. alba* is 14–15 cm on plots 1–3, whereas it is 19–23 cm on plots 4–5. Similar observations can be done as regards the variation of stand height (H_g). Thus, it appears that when the share of a species is sufficiently low the trees are generally larger, both as regards diameter and height. The diameter increment of *P. alba* is almost twice that of *R. pseudoacacia* on plots 1–3, and on plots 4–5 the difference becomes even greater as the few *P. alba* trees are mostly large-diameter trees. On plots 4–5 the diameter increment of the *R. pseudoacacia* trees appears slightly reduced.

As regards the volume in 1995, plots 3–5 are almost similar whereas the volume of plots 1 and 2 is slightly greater. As expected the volume increment of *P. alba* is generally higher than that of *R. pseudoacacia* and, therefore, the total volume increment of a plot appears to increase with increasing share of *P. alba*. However, the volume increments of plots 3 and 4 are similar although their shares of *P. alba* and *R. pseudoacacia* differ markedly. Accordingly, the variation of volume increment between plots cannot be explained as a consequence of species composition alone. There was no possibility to include effects of potential microsite differences. Random variation due to the small plots, variation of growth conditions between plots, and variation as regards diameter class distribution and spatial distribution of trees must be involved as well. Obviously this would not be a problem had the experiment included a sufficient number of replications. Therefore an analysis at the single-tree (or sub-plot) level is needed.

Table 1. Summary statistics regarding stand structure and increment in the five experimental plots of subcompartment Kecskemét-Ballószög 20 C.

Plot	Species	D_g 1995	D_g 2000	$\dot{i}_{Dg}$	H_g 1995	H_g 2000	$\dot{i}_{Hg}$	N 1995	N 2000	$\dot{i}_N$	G 1995	G 2000	$\dot{i}_G$	V 1995	V 2000	$\dot{i}_V$
		cm		cm/yr	m		m/yr	/ha		/ha/yr	m^2/ha		m^2/ha/yr	m^3/ha		m^3/ha/yr
1	*Populus*	14.8	17.0	0.45	15.1	19.3	0.85	1320	1300	-4	22.60	29.56	1.390	185.9	302.6	23.33
1	*Robinia*	14.2	15.6	0.27	15.2	17.2	0.40	280	280	0	4.46	5.35	0.179	41.0	53.3	2.48
1								*1600*	*1580*	*-4*	*27.06*	*34.91*	*1.569*	*226.9*	*355.9*	*25.81*
2	*Populus*	15.0	17.8	0.56	15.2	19.7	0.90	980	900	-16	17.38	22.40	1.004	145.1	234.6	17.89
2	*Robinia*	12.2	13.7	0.30	14.1	16.1	0.40	560	560	0	6.58	8.28	0.340	57.5	78.7	4.23
2								*1540*	*1460*	*-16*	*23.96*	*30.68*	*1.344*	*202.6*	*313.2*	*22.12*
3	*Populus*	14.5	17.1	0.51	14.9	19.3	0.88	950	910	-8	15.70	20.77	1.014	128.3	213.3	16.99
3	*Robinia*	12.6	14.1	0.30	14.3	16.3	0.40	590	580	-2	7.36	9.04	0.336	64.7	86.3	4.32
3								*1540*	*1490*	*-10*	*23.05*	*29.80*	*1.350*	*193.0*	*299.6*	*21.31*
4	*Populus*	19.2	24.2	0.99	16.8	22.3	1.10	270	270	0	7.81	12.37	0.912	70.0	141.6	14.32
4	*Robinia*	12.2	13.4	0.24	14.1	15.9	0.36	1150	1150	0	13.47	16.19	0.543	115.9	150.2	6.87
4								*1420*	*1420*	*0*	*21.28*	*28.56*	*1.455*	*185.9*	*291.8*	*21.19*
5	*Populus*	23.0	29.8	1.37	18.1	24.2	1.22	57	57	0	2.36	3.97	0.322	23.5	50.9	5.49
5	*Robinia*	12.6	13.8	0.23	14.3	16.1	0.36	1453	1453	0	18.15	21.63	0.697	159.9	205.8	9.17
5								*1510*	*1510*	*0*	*20.51*	*25.60*	1.019	*183.4*	*256.7*	*14.65*

As a first attempt to estimate the advantage of mixed plantations of white poplar and black locust over pure plantations of these species, the volume increments were calculated for 250 m^2 sub-plots (12.5 × 20 m), i.e. one fourth of the plots (25×40 m). The volume increment of each species ($i_{V,P}$, $i_{V,R}$) was plotted against its contribution to the basal area of the sub-plot (P_P, P_R). If growth in mixed populations is greater than in pure stands of the same species, a non-linear (concave) variation would be expected. For *P. alba* no deviation from linearity could be observed but for *R. pseudoacacia* a concave relationship was detected and the power

$(\theta = 0.70)$ of the relationship $i_{VR} = \phi P_R^{\theta} \Leftrightarrow ln(i_{VR}) = ln(\phi) + \theta \; ln(P_R)$ was significantly different from 1 (P>F = 0.004).

Growth models and simulation

As the next step towards determination of the advantage of mixing the two species we estimated the parameters of the single-tree models, (1) and (2). The results are presented in *Table 2*. The differences between plots are considerable. Moreover, it appears that the growth of white poplar varies much more with tree diameter than that of black locust. Finally, the fact that δ_{1j} and η_{1j} are negative for white poplar, and numerically greater than the positive δ_0 and η_0 parameters, implies that an increasing basal area share of white poplar leads to reduced growth of this species. On the other hand, the growth of black locust is enhanced. Similarly, a reduced basal area share of white poplar (increased share of black locust) leads to increased growth of white poplar and reduced growth of black locust. Accordingly, for both species the observed increment of trees growing in mixed neighbourhoods was greater than that of trees growing in pure neighbourhoods.

Table 2. Estimated parameters of the two single-tree models applied for growth prediction. Standard errors are given in parentheses. Units of measurement: d: cm, G_T: m^2/ha, P_p: per cent, Δd: cm/year, Δv: m^3/year.

Diameter increment model (1)
RMSE = 0.1964 $R^2 = 0.6620$

		Plot	α_{1i}	γ_{1i}
α_0	0.117162 (0.0965)	1	-0.177632 (0.1180)	0.005790 (0.0048)
β_0	0.014464 (0.0028)	2	0.076948 (0.1122)	-0.004714 (0.0047)
γ_0	-0.003970 (0.0043)	3	-0.067341 (0.1116)	0.001677 (0.0047)
δ_0	0.001258 (0.0006)	4	0.016709 (0.1007)	-0.000347 (0.0046)
		5	0 (-)	0 (-)

Species	α_{2j}	β_{1j}	δ_{1j}
P. alba	-0.370410 (0.0747)	0.054722 (0.0037)	-0.004120 (0.0008)
R. pseudoacacia	0 (-)	0 (-)	0 (-)

Volume increment model (2)
RMSE = 0.007568 $R^2 = 0.8836$

		Plot	α_{1i}	β_{1i}
α_0	-0.000823 (0.0035)	1	0.016758 (0.0038)	-0.001426 (0.0003)
β_0	-0.000305 (0.0004)	2	0.012030 (0.0037)	-0.001167 (0.0003)
γ_0	0.000082 (0.00001)	3	0.009232 (0.0037)	-0.000887 (0.0003)
δ_0	-0.000109 (0.00004)	4	0.001631 (0.0034)	-0.000154 (0.0003)
η_0	0.000035 (0.00002)	5	0 (-)	0 (-)

Species	α_{2j}	γ_{1j}	η_{1j}
P. alba	-0.003759 (0.0025)	0.000109 (0.000006)	-0.000137 (0.00003)
R. pseudoacacia	0 (-)	0 (-)	0 (-)

To get a basic idea about the effect of mixing the two species model (2) can be applied for particular values of diameter, total basal area (G_T) and percentage of *P. alba* (P_P). The resulting volume growth can be compared with predicted growth for pure stands. Not surprisingly, it emerges that the estimated advantage of mixing the species depends on the chosen values of diameter and stand basal area. Therefore, to quantify the apparent advantage of mixed stands in Kecskemét-Ballószög 20 C (1995–2000) it is necessary to consider the growth of stand structures with properties similar to those observed in the plots, i.e. structures with similar diameter distributions, densities, and spatial distributions of trees. Therefore, models (1) and (2) were incorporated into a simulation program and used to evaluate the growth of mixed stands for a range of stem numbers and species compositions. For each combination of stem number and species composition the program generated a stand with diameter distribution and tree heights similar to those observed within the five plots in 1995. Thus, for white poplar the applied mean and standard deviation of diameter were 14.43 and

4.82 cm respectively, and for black locust these were 11.91 and 3.98 cm, respectively. The simulated tree growth was stochastic with mean corresponding to the predictions of models (1) and (2) for plot 5 and variance corresponding to the calculated RMSE (*Table 2*). The spatial distribution of trees was adjusted such that it resembled that of the experimental plots. The area of the simulated stands was 4 ha, i.e. 40 times the area of each of the experimental plots (1–4). Due to the uncertainty of growth caused by stochastic tree growth, variation of tree diameter and height, and variation of the spatial distribution of trees, this was necessary to obtain stable results.

Simulated stands were prepared for stem numbers ranging from 1000 to 2000 per ha and for species mixtures ranging from 0% to 100% white poplar (basal area shares). For each combination of stem number and species composition the volume increments were calculated for each of the species. Based on these results the apparent advantage of mixed stands over single-species stands with same stem number and basal area was estimated for the period from age 16 to 21. The results are shown in *Figure 2* and as will appear from the Figure, the extra volume increment obtained when mixing the two species reached a maximum for both species at 40-50% basal area share of white poplar.

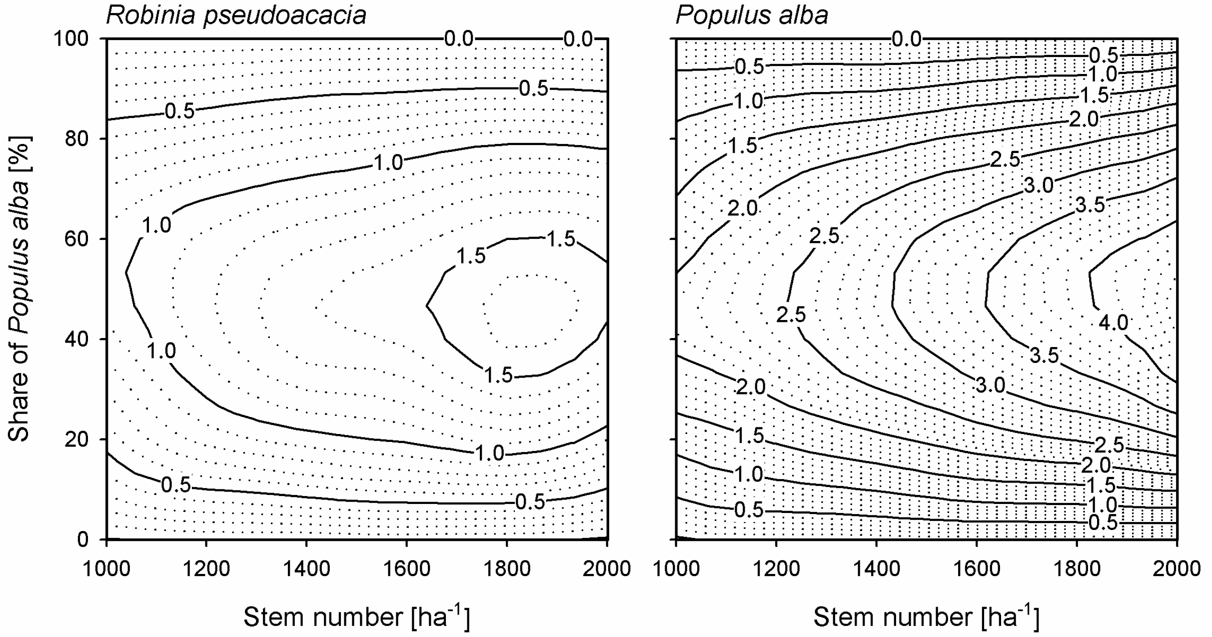

Figure 2. Estimated advantage ($m^3ha^{-1}yr^{-1}$) of mixing white poplar and black locust in various proportions and at different densities. Share of Populus alba: contribution of P. alba to the basal area in 1995.

5 DISCUSSION

When creating the simulated stands considerable effort was made to ascertain that the structural properties of the stands were similar to those of the experimental plots. In addition the simulations were based on plots with an area of 4 hectares. Still, it was observed that the results varied somewhat between simulation runs. Therefore, one should be cautious when interpreting the results in *Figure 2.*

The advantage of mixed stands appeared to increase when the stem number increased from 1000 to 2000 stems per hectare. However, it should be noted that this increase is likely to be a consequence of the fact that the simulation model did not include a mortality component. This implies that the model would potentially allow us to increase the stem number at age 16 to, e.g. 10,000 ha^{-1} and still produce an increased volume production. Therefore, the main result of the simulation is that for both species the advantage of mixed stands over single-species stands appeared to peak at about 40–50 per cent *P. alba*. Moreover, in the current case the maximum advantage of mixed stands appeared to correspond to roughly 12–14 percent for *P. alba* and 14–18 percent for *R. pseudoacacia*. However, as the volume production of *R. pseudoacacia* was lower than that of *P. alba* the absolute advantage was highest for *P. alba* (cf. *Table 1*).

The height growth of white poplar is faster than that of black locust when these two species are planted together (cf. *Table 1*) and black locust could never overgrow white poplar in mixed stands. Due to its nitrogen-fixing ability black locust has a stimulating effect also on growth of other tree species growing in the same stand. The difference is particularly impressive when white poplar trees are scattered in a stand and their share of the stems does not exceed 20% (plots 4 and 5). A similar pattern is observed for radial growth.

The trial appears to indicate that if both species have fast initial growth rates and similar rotation ages, planting them in mixed stands may lead to increased yield. However, planting (mixing) schemes have to be chosen in such a way that they support the compatibility of the two species. In addition, one must realise that the mixing scheme influences the character of intermediate thinnings. For example, if a site is suitable for both black locust and white poplar and they are mixed at the single-tree level, the dominating species with the larger number of stems should be preferred for removals in course of intermediate thinnings. If the two species are planted in groups, the growth rates and the proportion of each species within the groups will determine which species should be favoured in the thinnings.

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Migratory, Genetic and Phenetic Response Potential of Forest Tree Populations Facing Climate Change

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Abstract – Forest trees are especially vulnerable to climatic oscillations due to their long lifespan. Out of the possible mechanisms of acclimation and adaptation, natural selection and migration will play a subordinate role because of the relatively high speed of expected changes. Phenotypic plasticity retains on the other hand primary importance. Analysis of common garden experiments and of health monitoring data indicate that response across the distribution area will be differentiated. The low-latitude, low elevation periphery is especially threatened, while growth in the northern part of ranges will accelerate (in case moisture conditions will remain favourable). Comparing the velocity of predicted changes and the constraints of the buffering mechanisms of species for adaptation, it is obvious that *human interference will be essential for the maintenance of ecosystem stability*. Forest genetic and ecology research results have to be synthesised to better elucidate the requirements of stability and response of forest ecosystems under predicted climatic conditions.

Adaptation / ecological genetics / phenotypic plasticity / migration / natural selection / tolerance

Kivonat – Klímaváltozás és az erdei fás populációk migrációs, genetikai és fenetikai alkalmazkodási potenciálja. A hosszú életű fás növények különösen kiszolgáltatottak a környezeti változásoknak. Ennek megfelelően széleskörű az az eszköztár, amely lehetővé teszi a gyors alkalmazkodást. A természetes szelekció és a migráció – habár az előrejelzésekben szinte kizárólagos jelleggel szerepelnek – a klímaváltozáshoz alkalmazkodásban alárendelt szerepet kapnak a változás gyorsasága miatt. A fenetikai (fenotípusos) alkalmazkodásnak ezzel szemben nagy a jelentősége. Az elemzések szerint a fenetikai reakció az elterjedési területen belül eltérő: a melegedés az északi árearészben növedékgyorsulást, míg az área déli szegélyén vitalitás-gyengülést és mortalitást vált ki. A peremhelyzetű populációk veszélyeztetettségét alátámasztják az országos EVH háló adataiból készített elemzések is. Az eredmények megerősítik, hogy a klimatikus változást a peremhelyzetű populációk természetes szabályozási mechanizmusai nem lesznek képesek kompenzálni, hanem ehhez *emberi segítségre, gondosan tervezett beavatkozásra van szükség.*

Adaptáció / ökológiai genetika / fenotípusos plaszticitás / migráció / természetes szelekció / tolerancia

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1 INTRODUCTION: THE NEED FOR SYNTHESIS

Climate change mitigation, the maintenance of stability of forest ecosystems are serious challenges for both research, forest management and forest policy in the 21st century. In this respect, adaptability and adaptedness appears to become a crucial problem. The longevity of trees makes a fast adjustment to changing conditions more difficult than in agriculture. Long-term adaptedness and stability should therefore be of higher concern in forestry than possible gains in timber or fibre yield. The fundamental question is how tree populations and species will react and what the means are to maintain and enhance their adaptability.

Studies analysing the expected response of forest ecosystems to changing environmental conditions are either predicting spontaneous migration of forest tree populations (ecologically oriented studies) or investigating the prospects of adaptation through natural selection or random processes, such as gene flow (genetic studies). A proper synthesis of ecological and genetic information is seldom done, genetic and functional ecological aspects are investigated independently from each other.

Efforts to clarify the genetic background of adaptive traits and adaptation have progressed considerably and have yielded meaningful results. It is no surprise however that the molecular revolution of the recent decades has contributed relatively little yet to the synthesis with ecology. This is partially due to the fact that molecular genetic investigations in biology are concentrated on model organisms (often genetically screened) in artificial environments. Also, majority of species selected for such studies are either micro organisms, annual plants or animals (e.g. *Drosophila, Arabidopsis* sp., snails etc.).

There is a widely accepted opinion to exclusively judge adaptability based on genetic diversity on the biochemical-molecular level, often at loci of no or questionable adaptive importance. Quantitative response (growth, phenology) to ecological cues are insufficiently investigated, although their practical value for climate change effect mitigation and for selecting of suitable reproductive material is high. Out of the main genetic forces shaping the genetic structure of species, the random effects get too much attention as compared to ecologically interpretable, directed processes. To study adaptively important, quantitative traits in field tests is however indispensable not only for validation of genetic markers, but also to assess “nongenetic” regulatory effects such as phenotypic plasticity and ecological interactions – in order to put genetic results into a meaningful ecological context.

On the other hand little of the genetic results have penetrated ecology. Most ecological studies treat species as monolithic units, not counting with the intraspecific genetic variation pattern. Also, many functional ecological studies are confined to investigate traits in a single environment. Testing across multiple environments is however important, as reaction to ecological factors, relevance for competition and selection may drastically change. Finally, strong practical constraints on both migration and natural selection are seldom considered.

To achieve a more balanced approach, comprehensive studies are necessary for a deeper understanding of the functioning of ecosystems, of evolutionary diversification on genetic and species level and of the real value of biodiversity in stability and resilience of living systems.

1.1 Interpretation of ecology, genetics and evolution of observed wealth of variation in fitness

Contemplating the wealth of hereditary and phenetic variation in fitness on all scales and levels (qualitative and quantitative, geographic or within population), the famous question of Hutchinson (1959) about the reasons for existence of so many species, could be raised on within-species level as well; why is genetic variation so excessive not only in obviously neutral but also in strongly adaptive traits, such as length of growing cycle, phenotypic behaviour etc.

There are three possible approaches to answer this question: a historic-evolutionary, a genetic and an ecological one; all three are needed to correctly understand processes in natural populations and ecosystems.

According to the *ecological interpretation*, variation between individuals of a species is maintained by the temporal and spatial heterogeneity of environmental conditions, differences in age, in habitat conditions, in density etc. It seems that both on within-species and on between-species level, i.e. in genetic and also in species diversity, correlations with environmental (ecological) heterogeneity exist.

The *genetic* explanation of existing variation is based on the simultaneous dynamics of different directed and random genetic processes (natural selection, mutation, gene flow, drift, introgression, inbreeding etc.) and on existing constraints in the genetic system of the species (e.g. trade-off effects, genetic correlations).

Historic processes of evolution are random*:* speciation and extinction events, withdrawals to refugia and migrations in connection with glaciations and smaller-scale climatic oscillations. All these events leave marked genetic footprints.

Depending on historic, ecological and genetic circumstances, the generated diversity (both on species and genetic level) can be manifold. Members of the population will consequently utilize the given environment in multiple, alternative ways. Therefore it is important to realize that variation within a population (and in the ecosystem) in itself represents an adaptive value. The question however remains, *how and to which extent this diversity plays a role to counterbalance climatic oscillations*.

1.2 Options for balancing environmental changes

There are various genetic and non-genetic mechanisms on both individual, population, species and ecosystem level, balancing changes in environmental conditions. On *species and ecosystem/landscape level*, a possibility of responding to large-scale changes in the environment is migration through seed (and pollen) dispersal. Paleoecological evidence on migration during the epochs of glacial periods and interglacials is abundant – and this is the option generally described by most ecologically-oriented future scenarios as well.

On the *level of* populations, natural selection adjusts the average fitness of the population to changing conditions through genetic adaptation. Fisher's well known fundamental theorem on fitness change illustrates that the precondition for fast and effective genetic adaptation is provided by sufficiently large genetic diversity. *The maintenance of long-term genetic adaptability is therefore directly depending on the conservation or even reconstruction of adaptive genetic variance.* This is not to say that natural selection is able to follow and buffer environmental oscillations (Savolainen et al. 2004).

On *individual genotype level,* environmentally induced phenotypic plasticity and genetic carryover effects (Jablonka et al. 1995, for review see Martienssen - Colot 2001) provide the ability to survive in a wider range of environments without genetic change in the classic sense. Phenotypic plasticity will set the limits of environmental heterogeneity in time and space, a genotype or population can endure within its lifetime (*Figure 1*). Limits of distribution and cultivation are set by the decline of fitness across the environmental cline (in the figure: from left to right). If ecological interactions (i.e. competition) or certain biological constraints (e.g. failing natural regeneration) are counterbalanced by cultivation, limits can be extended beyond natural distribution limits. The genetically set tolerance limit varies on individual level, provoking selection. Weather extremes and disease outbreaks push the population toward mass mortality on off-limit sites.

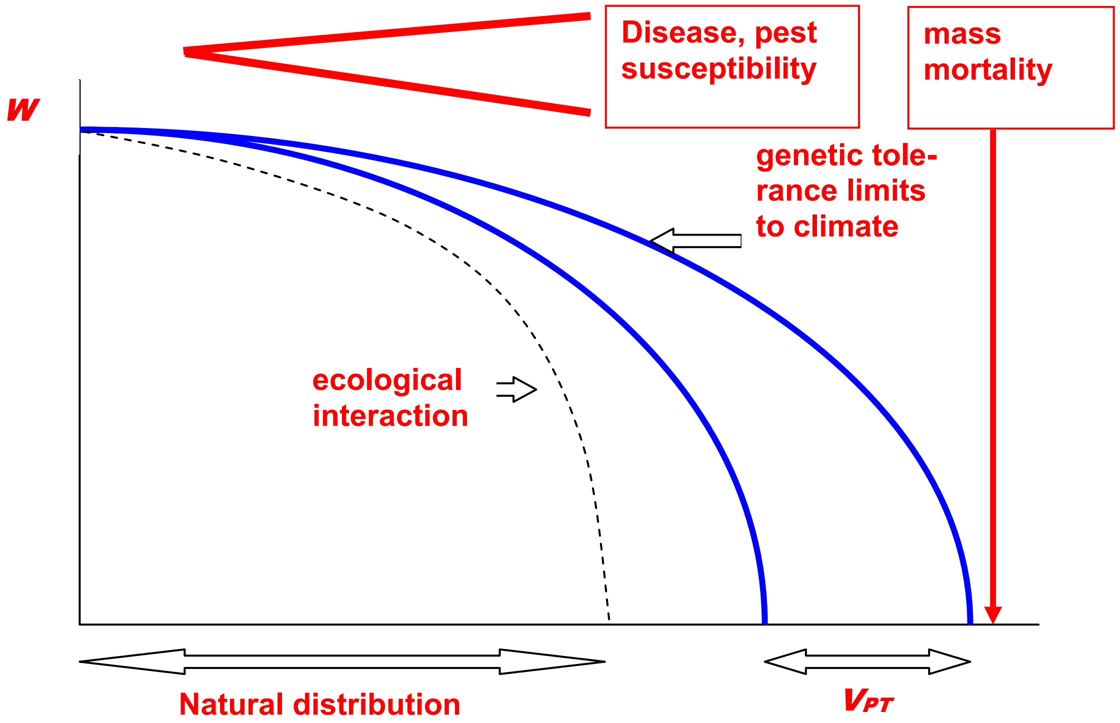

Figure 1. Ecological-genetic model of fitness decline and mortality triggered by worsening of climatic (site) conditions. The phenotypic variance of limits of tolerance (V_{PT}) represents the basis of natural selection. Due to interactions in the ecosystem, the natural distribution is usually stronger limited, than the genetically set critical tolerance (dashed line.)

With changing conditions, the fitness value of a trait will change as well. For instance, wide crown shape in conifers facilitates to utilize available resources and to keep away competitors; narrow crown shape helps to avoid snow brake; both are adaptively important values. While the former is especially vital in strongly competitive ecosystems with high species diversity, narrow crown shape is selectively preferred in rather monospecific, higher altitude environments. The fitness of the two types are inversely related to each other, representing a *functional trade-off.* It can be expected that divergent adaptive forces will determine the distribution of phenotypes. The observed distribution of crown types shown in *Figure 2* may have been generated – apart from random effects - either by gradient-dependent distribution of different alleles responding natural selection, by carryover effects (female parental effects) or by a perfectly functioning plasticity with no genetic change in the populations, but with highest probability *by the simultaneous effect of all mentioned mechanisms*.

2 RESPONSE POTENTIAL AND CONSTRAINTS

From the viewpoint of long-living sessile organisms, such as trees, environments are temporarily and spatially extremely heterogeneous, as compared to the lifecycle and dimension of occupied space. This fact requires special strategies and may pose also specific constraints. Long-living forest trees are therefore especially threatened by fast changing climatic conditions and are ideal organisms to study the parallel evolution of phenetic and genetic adaptation mechanisms. The necessity of efficient adjustment arises not only if progenies of trees migrate into new environments, but also if populations stay in their habitat but climate conditions change. In the followings some genetic and ecological considerations are briefly discussed.

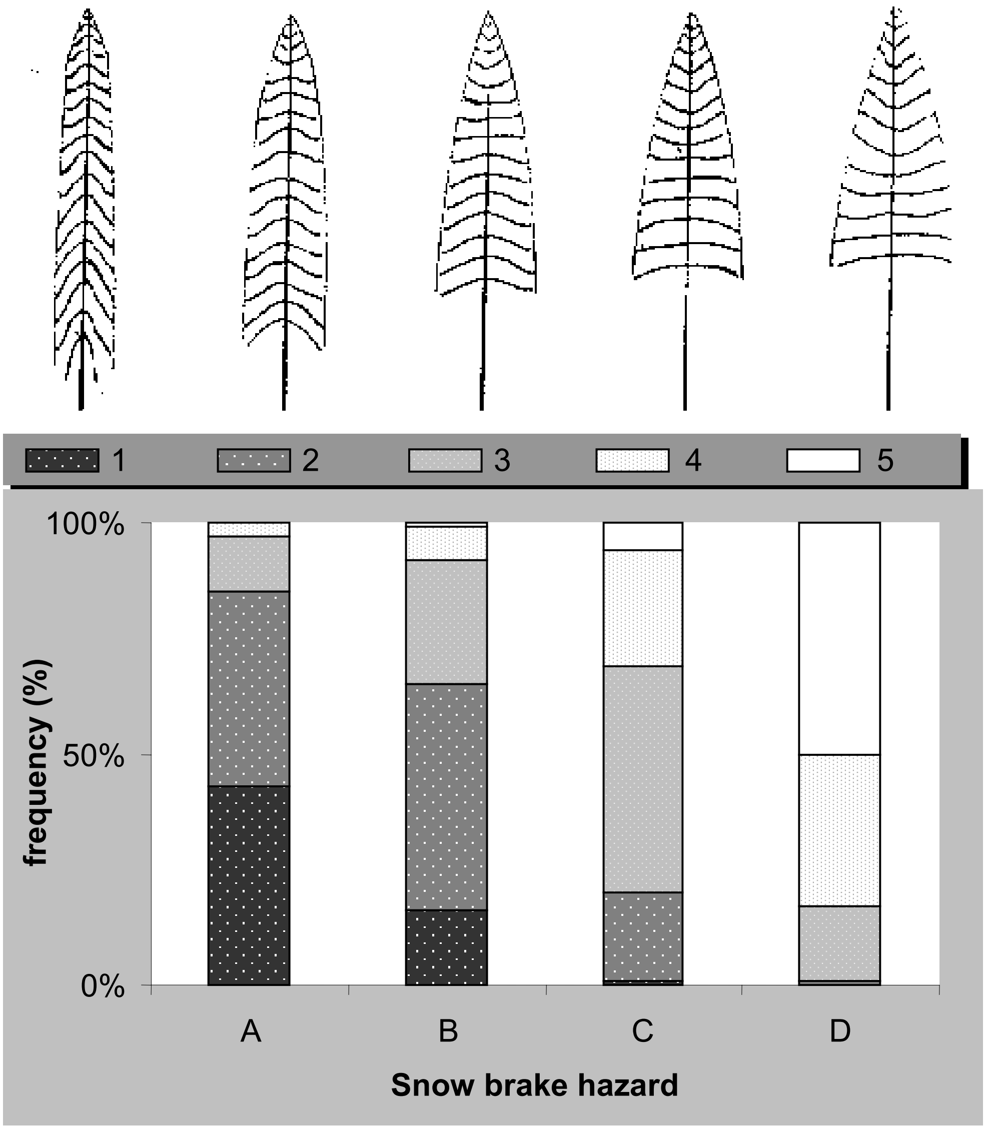

Figure 2. Frequency of spruce crown phenotypes in the Slovenian Alps: an example of interaction of natural selection, phenotypic plasticity, carryover and/or random effects. The columns represent different categories of snow break hazard: A: extreme cold, hazardous sites, B: exposed sites on a plateau, C: transitory sites, and D: low-hazard sites. Percentage of crown types are marked by shading (Mátyás 2004, data from Z. Grec)

2.1 Natural selection: constraints in a changing climate

Natural, autochthonous tree populations harbour an unusually high level of genetic variation compared to annual plants, offering ideal preconditions for genetic adaptation, i.e. selection of the fittest phenotypes in changing environments. However, both field observations and theoretical models support the view, that contrary to the general belief, that the population adapts its gene pool to temporal changes by fitness selection, these changes can be expected to be small and the selection process slow and ineffective. Reasons are inherent constraints of the genetic system of species, balancing even extreme selective forces. Some authors suggest that an appropriate genetic adjustment to climatic changes of the predicted magnitude (e.g. in the boreal: 2-4 ºC temperature increase) requires numerous, up to 10 or more generations (Tchebakova et al. 2005, Savolainen et al. 2004). Presuming at least 100 years per generation, this adds up to a millennium – the predicted change however might take place in less than a century. Thus, the *magnitude and speed of expected changes may neutralize* the natural balancing effect of selection.

In the following example basic ecological factors determining zonal forest ecosystems in Hungary are compared to climate scenarios. *Table 1* shows temperature and precipitation data for the main forest zones in Hungary. In spite of relatively large climatic heterogeneity within zones, the average difference between means of zones is very small – especially if the value is compared with the downscaled temperature and rainfall data of climate scenarios for the next quarter of century (*Table 1*). It seems that, theoretically within one tree generation time, the extent of climatic shift may surpass the difference between zonal forest belts. Consequently, present populations of dominant tree species might not be able to keep their present habitat. Due to the persistence of forest ecosystems, the described scenarios do not necessarily lead to a gradual shift of species composition, rather to sudden large-scale mortality events following extreme weather anomalies. Under these conditions the effective functioning of natural selection will be restricted. Such events have been already observed for Norway spruce a decade ago (Mátyás 1997), as well as for oak and more recently also for beech in Hungary,

Table 1. Average temperature and precipitation data of zonal forest belts in the lowlands of the Carpathian Basin and the magnitude of expected changes (Mátyás - Czimber 2000)

	Annual precipitation (mm)	July temperature (C^{o})
Beech zone	734 ± 65.2	19.1 ± 0.95
Hornbeam-oak zone	702 ± 70.3	20.0 ± 0.79
Turkey- sessile oak zone	616 ± 49.0	20.2 ± 0.70
Forest steppe zone	563 ± 49.0	21.5 ± 0.56
Average difference between zones	57	0.80
Climate change prediction, medium scenario for Central Europe	decrease by 40-60 mm	increase by 1.0-1.5 C^{o}

2.2 Species and allelic migration constraints

It could be argued that similar to the past, species and communities will keep pace with changes and counterbalance climatic shifts by colonising new habitats. Migration is frequently modelled by ecologists, by projecting climatic envelopes of present distributional ranges into future scenarios of changed climates.

Effective species migration has to match, however, the pace of expected changes as well. It has been shown that forecast climate changes are simply too fast be followed by tree populations (Mátyás cited in: Davis - Shaw 2001). In Central Europe, according to a more pessimistic scenario of a temperature increase of 2°C in 35 years, isotherms would wander horizontally in northerly direction with an average speed of 3 km/year and 12 m/year in altitude (*Table 2*). This has to be compared to the natural migration speed of species. It is known from paleobotanical studies (Davis 1981) that tree populations migrate - depending on migratory abilities - at rates of 0.1-0.4 km/year. The difference between the expected climatic shift and the potential migration speed is roughly one magnitude. This means that even in case if migration routes were available and environmental, geographical conditions would not provide obstacles, horizontal migration velocities do not keep up with the expected changes.

Table 2. Comparison of migration speed and predicted isotherm shift (Mátyás 2005)

Natural migration velocities through seed dispersal (from paleobotanical data, from Davis 1981):
Quercus, Fagus: 100-250 m/yr
Betula, Pinus: 200-400 m/yr
Velocity of isotherm shift (scenario: 2.0 °C in 35 years)

Direction	Gradient	Velocity
S ⇒ N horizontal	50 km/°C	3000 m/yr
Vertical (altitudinal)	200 m/°C	11.5 m alt./yr

There are other, more direct reasons which will prohibit the spontaneous mass migration of trees, such as the fragmentedness of man-dominated landscapes, and the comparably very slow development of soil conditions – a constraint in subpolar and alpine environments. In the north boreal and alpine tundra zone the theoretical possibility of a colonisation advance of forest trees exists according to climatic forecasts. It has to be considered, however, that apart from the fact that natural migration speed of forest trees is relatively low, even on the long run the utilisation of climatically improved zones off the present distribution range will be limited by soil conditions. The development of soil profiles takes millennia and the usually shallow, less developed soils of high altitudes and high latitudes will not change fast enough.

Another constraint for colonisation of new habitats is the limited availability due to geomorphological-distributional preconditions. Typical examples are populations restricted to mountain tops such as *Abies pinsapo* in Northern Africa or *A. fraseri* in the Appalachians which have simply nowhere to migrate (Eriksson - Ekberg 2001). In general, any species settled in a habitat which does not provide a geographically contiguous escape route will be affected. In addition to high–altitude species, coastal Mediterranean species may be exposed to this threat as well.

There is, on the other hand, not enough information on the effectivity of *migration through gene flow* within a contiguous distribution area. For many widely distributed species long distance gene flow might influence the gene pool of filial generations. There are indications that distant pollen sources, usually of southern origin, may significantly contribute to pollination in the north (Lindgren et al. 1995). The effect of adaptation of gene pool through gene immigration might be assumed as higher than the migration by dispersed seed. Preconditions are: a relatively unfragmented distribution of the species, the close to undisturbed state of populations (i.e. low frequency of stands planted with uncontrolled, less adapted plants) and the general application of natural regeneration techniques. Neither of these can be taken for granted, except possibly in certain regions of the boreal zone.

2.3 Phenotypic plasticity

2.3.1 Evolution of phenotypic plasticity

A common definition for phenotypic plasticity[*] is the *environmentally sensitive production of alternative phenotypes by given genotypes* (DeWitt - Scheiner 2004). The term has been coined in zoology, where it has been applied in a relatively restricted manner for certain environmentally induced developmental or morphological phenomena. For plants, plasticity has to be interpreted relatively broadly. In our interpretation, derived from the practice of forest tree breeding, the ability of the genotype (clone), or of the population to maintain relative (usually superior) fitness across a series of environments is regarded as phenotypic plasticity or stability.

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[*] Phenotypic stability is a synonimous term

According to this approach, stable genotypes or populations are better fit to utilise diverse environments than others. Similar to fitness, plasticity can be measured and analysed on vegetative growth and organic matter production. Phenotypically plastic genotypes should exhibit less morphological, vitality and growth variation across environments than others. Naturally, this relatively constant performance is expected to be in the upper or above-mean range; a genotype with generally bad performance could not be regarded as “plastic” or “stable”.

Although seen by many as “nongenetic”, plasticity is doubtless a genetic trait and certainly influences evolution: individuals carrying more plasticity will show fitness in more environments – on the other hand plasticity will also put a constraint on genetic adaptation of the population by concealing the “true” genotypes.

Statistical evidence for plasticity in plants is supplied by multiple-test comparative trials, where the variance component for genotype × environment interaction ($V_{G \times E}$) indicates that the response of test entries (clones or populations) to changing test conditions is different.

According to field tests of numerous species, exclusivity of phenotypic plasticity is certainly not the evolutionary strategy of forest trees as proposed by certain studies (e.g. Maherali et al. 2002). There are obviously trade-off limitations to develop a high level a plasticity and the availability of high genetic variation in itself may put limitations to the further development of plasticity. Although plasticity appears to be highly adaptive, it has to be cautioned, however, against supposing that plasticity as a trait is always a product of natural selection. As shown in the review of van Kleunen and Fisher (2005), there are certain constraints on the development of phenotypic plasticity, which *per se* needs not even be adaptive.

2.3.2 Plasticity and climatic oscillations

A major factor in supporting the evolution of plasticity is the unpredictable nature of main ecological factors. The first factor which offers itself for examination is weather and climate. *Could it be that different levels of climatic stability might be linked to differences in plasticity?* Such connections may be found for example when comparing reaction norms of populations adapted either to stable, typical climates or to transitory zones toward other climate types. Due to the difficulties of collecting relevant climatic information, very few hints can be traced.

Riley and Spolton (1974) analysed the conformity of annual weather types with the actual climate zone and delineated zones of lower stability for Europe (out of 30 years at least 5 years of untypical weather). They found that a zone of relatively high instability divides in East-Central Europe the maritime and continental climate. If the hypothesis of links between plasticity and environmental (climatic) fluctuation holds, phenotypically plastic populations should have evolved in more than one species in this region. As a matter of fact, comparing this zone with East European provenance regions of higher plasticity both in Norway spruce and Scots pine, the author has found surprising similarities (Mátyás 1986). For jack pine (*Pinus banksiana*) a zone of elevated plasticity could be identified in the Ottawa Valley, being climatically a transitory zone as well (Mátyás 1986). A similar zone presumably supporting the evolution of plasticity of Douglas fir is suspected in inland British Columbia, Washington and Oregon, which seems to be substantiated by recent research results (S. Aitken, pers. comm.).

2.3.3 Assessment of phenotypic response

Phenotypic response of populations in changed environments may be predicted from data of provenance (common garden) tests, as has been proposed by the author (Mátyás 1996). As an example, in *Figure 3* we show the prediction for height growth response across the distributional range for Scots pine (details may be found in Mátyás - Nagy 2005). Using transfer analysis techniques, a response curve for maximum height performance (Y2) was calculated from data of provenances representing a transect of the European distribution area, from north to south, i.e. with temperature sums from 810 to 2310 average degree-days above 5°C. Through the lowering of the regression line by 200 degree-days, that is by approx. 1°C temperature rise in the vegetation period (Y3 in *Figure 3*) we have simulated a virtual climate change scenario. The shaded areas below the curve stand for increment responses of populations in different parts of the range. These indicate that in the northern half of distribution (left side of the graph) an increment acceleration can be expected, while on the southern limits (right side) Scots pine populations will perform much below their original potential, which may mean also mortality.

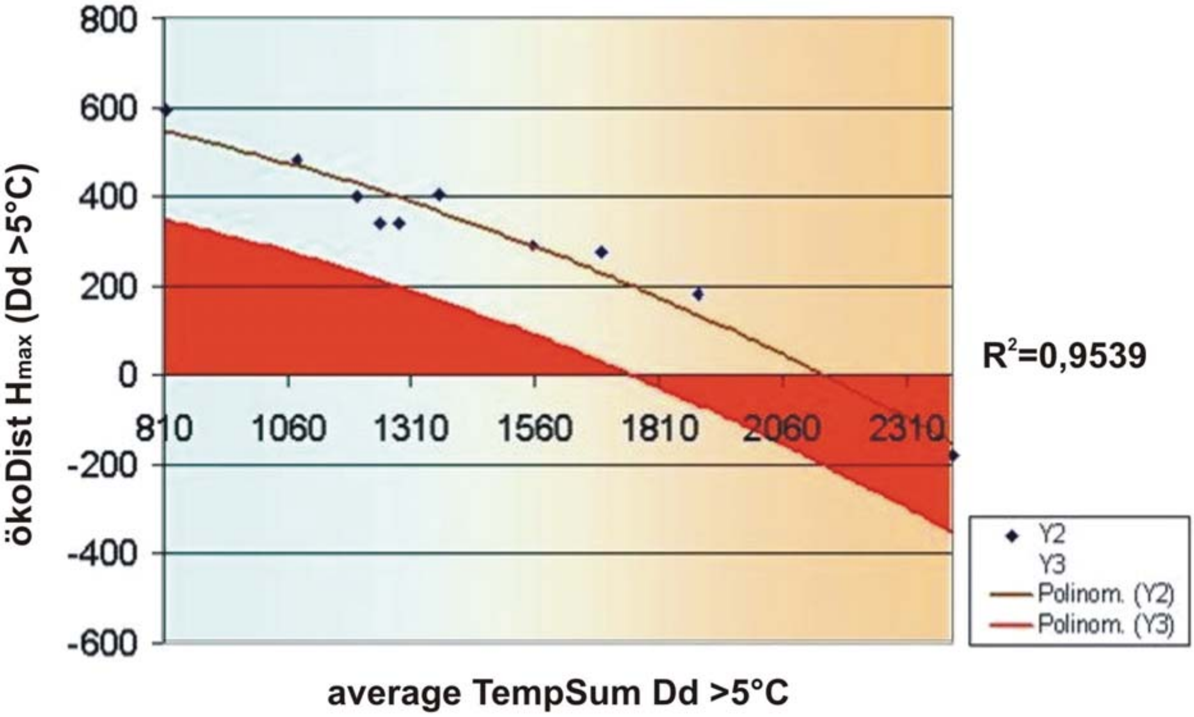
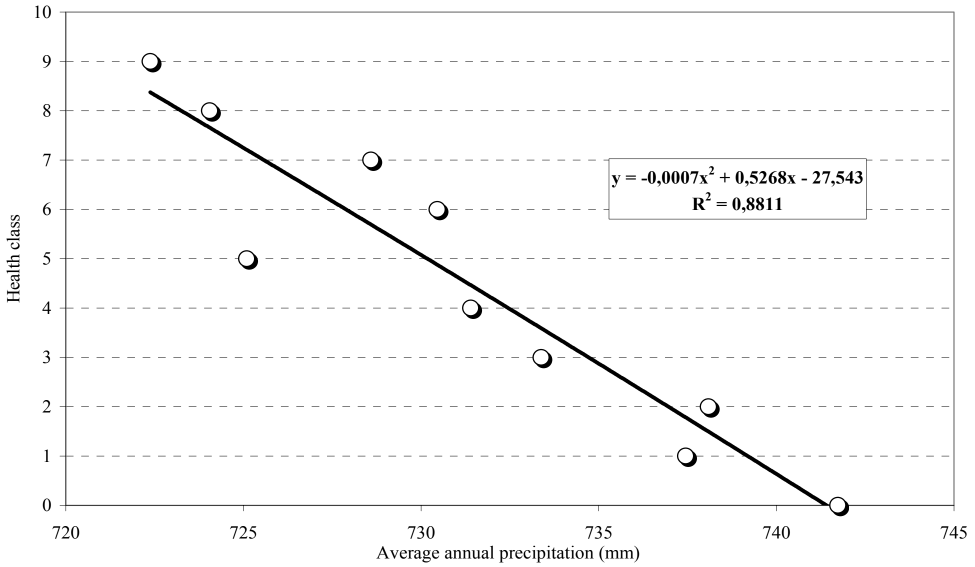


Figure 3. Increment response prediction (vertical axis) of differently adapted Scots pine (Pinus sylvestris) populations for an annual temperature rise of +200 degree-days change scenario. The model was constructed for a cross-section of the Eurasian distribution area of Scots pine from North to South, i.e. from low to high temperature sum climates, utilising calculations of Rehfeldt et al. (2003) (from Mátyás - Nagy 2005, see explanation in text)

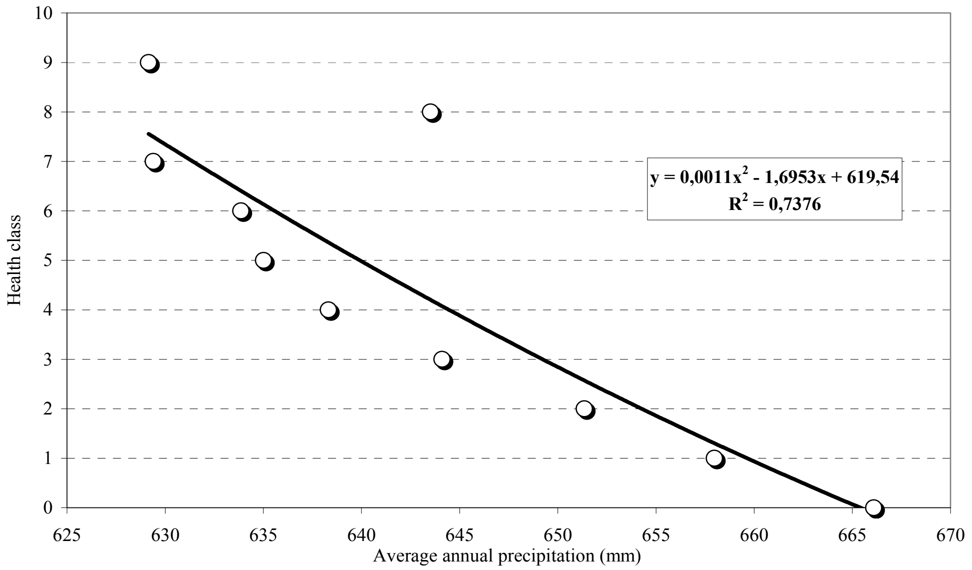
The model illustrates that phenotypic response to changes will be differentiated. While species-specific reactions, and other ecological effects (synchrony changes with competitors or consumers etc.) may diversify the overall picture; it may be assumed, that in general at the upper/northern limits, temperature increase will bring an improvement of site conditions, resulting in increment acceleration in forest tree populations. At low elevations and in the southern outliers of the distribution, close to the present lower limit of the area, temperature increase and lower humidity certainly will lead to the thinning out and disappearance of the species, loosing its competitive ability against other species.

2.3.4 Limits of tolerance

Although ecologically set limits of tolerance are integral parts of modelling considerations, it is rather difficult to concretely define such limits as shown in *Figure 1*. One reason is the lack of relevant experiments. For obvious reasons (little interest in low-yield, risky sites) there are few trials where quantitative responses can be studied under extreme conditions in forestry. In addition, correlation between climatic parameters and vitality are usually sought on basis of weather conditions for an anteceding period triggering disease symptoms or pest outbreaks.



BEECH (*Fagus silvatica*)



SESSILE OAK (*Quercus petraea*)

Figure 4. Climatic limits of tolerance and plasticity on species level, set by recent deterioration of health condition of forest trees: correlation of leaf loss of beech and of sessile oak vs. average annual precipitation. Rainfall data refer to the past climate of analysed network points, for the years 1960-1990. Health classes have been assessed in 10 percentiles of leaf loss; 0 = healthy, 9 = 90% leaf loss. Evaluated from Hungarian data of the European Forest Health Monitoring Network by G. Veperdi (2005). Data source: State Forest Service, average of assessments between 1989 and 2002

To test the hypothesis that worsening of climatic conditions lead to health decline and finally to death, data of the Forest Health Monitoring Network have been analysed. In this study climate data were set against health condition of sample trees at observation network points over a prolonged period. Climate parameters were determined from digital surfaces.

The parameters of trees with similar health score were averaged. In *Figure 4*, precipitation averages calculated according to this method are shown for leaf loss classes 1 to 9 (10, mortality could not be included because of low number of data and random effects). As the lower limit of distribution is defined by moisture supply as minimum factor, precipitation means may be interpreted as the ecological position of the sample point in the zone of distribution, i.e. as the distance from the xeric tolerance limit (Veperdi 2005).

The graphs indicate very close relationship between health and precipitation at the xeric (lower) limit of the distribution range of both sessile oak and beech (it has to be stressed that the precipitation data refer to climate, i.e. 30-year averages!). The nearly linear, highly significant correlation depicts the loss of vitality towards the xeric end of the distributional niche of the species without regard of actual extreme weather conditions. Comparing the two species, a difference of 80 to 90 mm annual rainfall[†] can be observed between the response of beech and the more drought-tolerant sessile oak. The result shows that the assessment of species-specific tolerance limits on climatic basis is possible. Its usefulness for strategy planning is self-evident. However, *climatically defined critical limits* are not necessarily the exclusive constraints for the species. Pests and diseases may strike much earlier, depending on weather extremes (droughts) and their frequency.

2.4 Carryover effects

Parallel to phenotypic plasticity, environmentally induced carryover (epigenetic) effects are relatively common in plants and seem to represent an adaptive advantage in changing environments (Jablonka et al. 1995). Investigations on some forest trees (e.g. Skroppa and Johnsen 2000) have proven that, for instance, parental effects may also contribute to the effective adjustment to spatially or temporally changing conditions. It need not be a chance that – although observed on a number of species – most striking effects have been observed on conifers in boreal environment. Especially in both topographically and climatically variable conditions (Norway!) the maintenance of proper adaptedness needs small-scale adjustment which is obviously more "costly" by genetic adaptation through selection alone. The observation that parental effects in Norway spruce were more explicit in northern populations than toward the south, supports this hypothesis. Due to the unknown importance and extent of carryover effects in forest trees in general, it is however advisable not to count too heavily with carryover effects in buffering climatic oscillations.

3 PREPARING FOR THE FUTURE

3.1 Importance of plasticity studies

More synthesis between genetics, evolution and ecology, as well as between qualitative (molecular) and quantitative aspects of genetics is needed. To avoid isolation, geneticists should endeavour to improve communication towards related fields where their results may find practical application.

Phenotypic plasticity and tolerance will play in the adaptation of forest stands to changing environmental conditions an increasing role (*Figure 3*). Genetic background of respective QTL-s should be investigated as priorities. New field tests are indispensable to collect more

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[†] note that closely matching average rainfall difference between beech and sessile oak is presented in *Table 1!*

evidence. Existing field trials should be evaluated for these purposes even if considered statistically less valuable, and new comparative tests be established. Locations at lower limits of distribution are of special interest. In addition to ecological and genetic modelling, data from comparative test series are essential to bring assessments and forecasts closer to reality.

The importance of phenotypic plasticity for "standard" forest management, for use of forest reproductive material and for mitigation strategies of expected environmental changes is self-evident. The understanding of the balance between natural selection, genetic constraints and other strategies as plasticity and carryover effects is essential for predicting responses and tolerance limits for dominant species in forest ecosystems.

The fact that mitigation of climate change effects has a very strong genetic component, has not yet penetrated forest and nature conservation strategies. It has to be made clear that implications to yield and profitability and ecological processes (succession, degradation and structural changes) are serious and significant.

3.2 Preparing for mitigation - need for human interference

Climate change research results indicate that because of the conservative nature of the genetic adaptation process, and of the relative speed of expected changes, even agricultural crops will demand a strategy to facilitate adaptation. Long-lived, immobile organisms, such as trees will especially need human interference in order to enhance adaptation to altered conditions, in spite of an impressing adaptive capacity. National forest policies have to incorporate this task into the agenda of the next decades.

More attention should be paid to alternatives of genetic adaptation, which seem to act faster and without the diversion of sexual reproduction. *Phenotypic plasticity is the adaptive answer to fast changes of the environment*, within the generation time of present-day forest genetic resources. This trait has been undervalued as priority in selecting forest reproductive material sources and also in gene conservation.

The need for active measures is the most pressing in the southern peripheries of the distribution areas. Because of grave environmental changes, human interference and mitigation is especially urgent in regions lying in the transitory zone of closed forests toward open woodlands and steppe, such as in continental Southeast Europe and low elevation areas of the Mediterranean. In these regions water supply is already now a minimum factor and presently native tree species have few sensible alternatives. Deteriorating climate parameters trigger pandemics and uncontrollable mortality already now, leading to loss of crown closure, spontaneous change in species composition rates and yield decline, which will affect profitability of forest operations.

As a consequence, *human interference will be essential for the maintenance of adaptability of forest trees under changed conditions in the present areas of distribution*. Due to the long-term impact and high risk of necessary measures and the low reliability of forecasts, it is imperative that forest genetic and ecology research join forces to better elucidate the discussed issues of predicted stability and response of forest ecosystems.

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Adaptation of Progenies of a Norway Spruce Provenance Test (IUFRO 1964/68) to Local Environment

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Abstract – Adaptability of open pollinated offspring of different Norway spruce provenances has been studied in a progeny test. 38 superior and 10 inferior mother trees were selected in the Inventory Provenance Test with Norway Spruce (IUFRO 1964/68). The mother trees originated from different European regions from different geographical distances. Local sources were introduced as controls both in the provenance test and in the progeny test. Survival and height growth of 13 years old half-sib families were used for assessing the adaptability. Survival of families has shown small differences, the average amounted to 91 %. The family mean heights were more equalized than expected but significant differences could be shown among the families. Offspring of the superior mother trees performed well, most of them exceed the local control. The offspring of inferior mother trees showed reduced growth. A highly significant correlation (P = 1 %) was found between the height of mother trees and mean height of their progenies. Correlation between provenance mean of mother trees and the family mean was also significant.

***Picea abies* / mother tree / open pollinated offspring / progeny test / half-sib family**

Kivonat – A nyírjesi IUFRO lucfenyő származási kísérlet utódnemzedékeinek alkalmazkodása a helyi környezethez. A tanulmányban különböző származású lucfenyő anyafák szabad beporzású utódnemzedékeinek alkalmazkodó képességét vizsgáltuk egy mátrai utódvizsgálati területen. A Leltározó Lucfenyő Származási Kísérletben (IUFRO 1964/68) 38 kiváló növekedésű és 10 növekedésben elmaradt anyafát jelöltünk ki. Az anyanövények eltérő földrajzi távolságból, különböző európai régiókból érkezetek, kontrollként helyi – észak-középhegységi – populáció szolgált. Az alkalmazkodó képesség meghatározásához az utódok megmaradását, valamint 13. évben elért magassági növekedésüket vettük alapul. Az utódnemzedékek átlagos megmaradása 91% volt. Magassági növekedésüket tekintve a családok között bizonyos kiegyenlítődés mutatkozott, de a varianciaanalízis szignifikáns különbségeket igazolt. A helyi populációhoz viszonyítva 3 család szignifikánsan jobb növekedésű, 5 pedig szignifikánsan gyengébb volt. A jó növekedésű anyafák utódnemzedékeinek többsége megtartotta fölényét, az anyafák és utódok között szoros, P = 1%-os szinten szignifikáns korrelációt mutattunk ki. Ugyancsak szoros korrelációt találtunk a szülői származásátlag és az utódnemzedék átlagmagassága között.

***Picea abies* / anyafa / utódnemzedék / utódvizsgálat / féltestvér populáció**

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1 INTRODUCTION, BACKGROUND OF THE RESEARCH

Hungary has participated in numerous provenance tests organized by IUFRO (International Union of Forest Research Organisations). One set of a large-scale, international project, the Inventory Provenance Test with Norway Spruce (IUFRO 1964/68) was established in Hungary in 1968 (Szőnyi – Ujvári 1970). That time the main objective of the research was the selection of the best suitable populations and seed import sources to increase growth and yield (Szőnyi – Ujvári 1975).

During the study of the provenance test not only the provenances but also the individuals within the provenance showed a high phenotypical variation mainly in growth. The outstanding phenotypic and genetic variation of the Norway spruce can be explained with its wide natural range.

Having observed the first cone yield in the IUFRO provenance test, we selected mother trees and in 1985, out of the 13 participant countries, we were the first to introduce a progeny test. The offspring originated from open pollination. We therefore assumed that the adaptability of the progenies would show a great variation also within family.

The main objectives of this study were to study the implications of selection in a provenance trial and compare the performance of the progenies of selected mother trees that originate from geographically distant sites and from different ecologic environments with that of the local control. As the selection was done for both superior and inferior phenotypes in the provenance test, it was also of interest to see how well these characteristics were inherited by the progeny.

2 MATERIALS AND METHODS

Having started in 1968, the Inventory Provenance Test with Norway Spruce (IUFRO 1964/68) in Mátra mountains, Hungary, is part of a series that consists of 20 experiments with the participation of 13 countries. The 1 100 geographical provenances were collected from 96 regions (Krutzsch 1974). The trial layout followed the internationally recommended design. These 1 100 sources were grouped into 11 groups (blocks) of 100 provenances each, which have been planted in a 1 ha block. Each provenance was represented by 25 plants. For the experimental layout single tree plots with 2 meter by 2 meter spacing was applied. The whole experiment extends over 11 hectares (Szőnyi – Ujvári 1970). Each block of 100 sources is a complete trial. Due to stratified sampling, the blocks are estimated to be equal in mean and variance, thus easily comparable (Krutzsch 1992).

Having observed the first cone yield we have selected a number of the tallest, superior, vigorous mother trees based on their phenotypic performance in the provenances that showed a good or average performance. This first, sporadic seed yield enabled only the selection of few mother trees and because of the high ratio of empty seed the number of offspring was less than expected. The mother trees that produced enough seedlings to be included in a progeny test significantly exceeded the provenance and block means. The selection intensity varied between 2.2 – 2.8. For the sake of comparison we also selected 10 short, inferior but healthy mother trees, mostly from the poorer provenances. In *Table 1* we indicate the origin of the mother trees in the IUFRO experiment, and the growth in decreasing order of the height of the mother trees (we used a darker background to mark the mother trees that showed an inferior performance). The data of the local population (no. 796. Bükkszentkereszt, K1) is also included.

Table 1. Geographic origin and height performance of mother trees, block means, provenance means and control (K1) in the provenance trial IUFRO 1964/68.

No. and location of mother trees		Geographic origin					Height at 10 year			Rank[1]
No.	block	prov. no.	country	lat.	long.	alt. m	mother tree	block mean cm	prov. mean	
1	8	835	DEN	54º 50'	9º 19'	70	680	441	482	26
2	8	870	GER	47º 52'	10º 38'	800	680	441	477	33
3	7	781	POL	50º 30'	16º 40'	400	670	450	470	40
4	10	1075	BEL	49º 46'	5º 28'	400	670	417	444	32
5	6	675	GER	49º 06'	13º 28'	600	640	396	422	31
6	6	691	POL	54º 17'	20º 30'	150	640	396	416	35
7	7	742	GER	48º 53'	13º 36'	1000	640	450	442	60
8	7	791	CZE	49º 47'	14º 10'	450	640	450	500	15
9	8	877	CZE	50º 30'	16º 30'	550	640	441	502	6
10	4	471	GER	50º 56'	10º 36'	200	630	360	386	35
11	6	648	GER	51º 47'	10º 09'	300	630	396	513	2
12	7	736	CZE	49º 20'	18º 15'	800	630	450	478	29
13	7	741	GER	47º 44'	10º 24'	1000	630	450	453	52
14	7	751	CZE	50º 37'	15º 37'	750	630	450	472	38
15	7	755	ROM	47º 45'	25º 45'	670	630	450	516	4
16	7	755	ROM	47º 45'	25º 45'	670	630	450	516	4
17	7	786	POL	49º 38'	19º 08'	700	630	450	501	16
18	8	815	AUT	47º 05'	14º 09'	1200	630	441	478	32
19	8	830	AUT	47º 05'	14º 09'	1150	630	441	442	59
20	9	928	POL	49º 35'	18º 55'	650	630	420	497	3
21	6	695	GER	50º 41'	10º 50'	800	620	396	437	18
22	8	859	CZE	49º 35'	16º 05'	580	620	441	502	7
23	9	976	SVK	49º 08'	20º 30'	800	620	420	456	17
24	10	1048	GER	48º 04'	11º 53'	620	620	417	449	29
25	10	1079	CZE	49º 33'	17º 43'	500	620	417	482	7
26	3	331	POL	52º 40'	23º 50'	130	610	362	405	15
27	6	600	CZE	49º 15'	15º 50'	550	610	396	432	23
28	6	606	BLR	54º 05'	26º 30'	230	610	396	451	9
29	6	691	POL	54º 17'	20º 30'	150	610	396	416	35
30	10	1030	GER	54º 10'	12º 30'	100	610	417	423	49
31	10	1061	GER	49º 54'	11º 20'	500	610	417	428	45
32	2	252	POL	53º 40'	16º 45'	100	580	336	354	33
33	2	273	CZE	49º 15'	15º 50'	550	580	336	377	16
34	11	1147	BLR	53º 40'	30º 00'	150	580	381	418	23
35	11	1198	POL	49º 35'	18º 55'	500	580	381	432	12
36	11	1199	GER	50º 47'	10º 44'	650	580	381	375	63
37	11	1160	GER	50º 26'	12º 54'	980	570	381	377	60
38	2	230	LAT	56º 40'	26º 40'	90	550	336	397	5
39	3	310	GER	47º 41'	7º 57'	850	400	362	353	64
40	8	838	SWE	58º 12'	12º 55'	90	380	441	373	91
41	8	820	SWE	59º 18'	14º 41'	100	350	441	367	92
42	8	873	GER	48º 20'	9º 30'	800	350	441	465	43
43	9	927	NOR	58º 20'	8º 20'	100	320	420	323	93
44	10	1083	SWE	59º 05'	16º 21'	75	310	417	337	94
45	8	897	RUS	58º 00'	39º 00'	100	290	441	361	93
46	8	875	SWE	62º 47'	14º 23'	350	280	441	282	99
47	9	981	FIN	61º 41'	27º 15'	100	250	420	292	97
48	8	876	SWE	57º 22'	13º 12'	180	200	441	402	81
K1	**7**	**796**	**HUN**	**48º 04'**	**20º 38'**	**615**		**450**	**474**	**35**
K2			**HUN**	**48° 20'**	**20° 50'**	**700**				

[1] Rank of the provenance within the block (1 – 99; 1. = the best)

▨ Selected slow growing mother trees (no. 39 – 48)

K1 Local control for mother trees (provenance in IUFRO provenance trial)

K2 Local control for progenies (commercial seed lot from Telkibánya)

We selected the mother trees in an area of large extension, in 9 blocks of the provenance test. Since there were great differences in the site conditions (e.g. exposure, slope and mainly the depth of the soil), the block effect could significantly influence the performance of the mother trees. To eliminate this, for the analysis of the correlations of the height performance between the mother trees and their progenies we chose 12 mother trees in block 8located in a nearly flat area, where site conditions could be regarded as more or less homogenous.

To analyse the performance of the offspring, we used a commercial seed lot from a domestic seed extractory (Telkibánya, K2) as control. The lot was collected in Norway spruce stands in the Zemplén mountains in the Northern mountain range. *Table 1* contains the provenance data of the control populations.

The cone collection and the growing of the seedlings took place separately for each tree. We established a progeny test with the half-sib progenies of 48 mother trees and the control lot. In each plot we planted out 24 seedlings in 7 x 7 simple lattice design, with 2 replications. The 2 ha experiment is located in forest sub-compartment Nagybátony 8 E in the Mátra mountains, at an altitude of 400 m above sea level. In the experiment located on a slope, the depth of the soil is unfortunately uneven. Some plots are therefore located on shallow soil.

The field assessment was carried out at the age of 13 after planting. The assessment included the measurement of the diameter at the breast height (DBH), the total height, the survival and the recording of damages.

The statistical analysis was based on plot means. A weighting factor was used to obtain the adjusted treatment totals. For the testing of significance an *F*-test of the adjusted treatment totals was completed (Cochran – Cox 1956),

3 RESULTS

3.1 Evaluation of progenies

Numerous scholars recommended the analysis of the biomass (dendromass) for the evaluation of adaptation to the climate (e.g. Callaham 1964). Adaptedness can be characterized well by growth traits over a longer period (height, tree volume, etc.) because they combine the effects of several factors. The height growth is an eminent component of tree production capacity, which is best determined genetically (Mátyás 2002). In our investigations we gave preference to the method of Mátyás – Yeatman (1987) applied for jack pine. For the characterization of adaptive variation we used the height data measured at the age of 13.

The analysis of variance showed significant differences among the families at P=0.1% level (*Table 2*). The adjusted F-value$_2$ showed a greater accuracy so we used the adjusted family means for the further calculations.

During the analysis of the adjusted family means we found that the height growth of the progenies was more equalized than expected. Surprisingly, the test mean (637.2 cm) was nearly the same as the mean of the local population – K2, Telkibánya (636.4 cm) – that was used as control. In *Table 3* the ranking follows the decreasing order of the family mean heights. Comparing it to the original rank according to the height of the mother trees, it can be stated that ranks are somewhat modified. It can be, nevertheless, said that the overwhelming majority of the progenies of the superior mother trees also showed a performance above the average. In the first third of the rank according to height we can find only progenies of the superior mother trees. The families of the inferior mother trees – with two exceptions – failed to reach the average of the local population. Further, in the last third of the table we can mainly find the progenies of the inferior mother trees.

Table 2. Analysis of variance of family mean heights at the age of 13 in the 7 x 7 simple lattice experiment

Source of variance	DF	MS	F-value$_1$	F-value$_2$
Replications	1	3.30		
Families	48	35.06	3.27***	3.55***
Block within replication (adj)	12	12.71		
Intra-block error	36	10.04		
Total	97			

F-value$_1$ = of originally measured and calculated family means
F-value$_2$ = of adjusted family means
*** significance level P = 0.1 %

Three families – all of them progenies of the selected mother trees – were significantly higher (P = 5%) than the local population (SD = 66.0 cm). Five families – mostly the progenies of the inferior mother trees – performed significantly worse than average.

In the evaluation of the progenies we have to take into account the survival too. In spite of the droughty weather that preceded the field assessment the vitality of the progenies was also impressive besides their good height performance. We did not experience significant damages apart from game damage. As compared to our other field tests, the survival was excellent, 91% on average. Only few families were exceptions (e.g. number **2**) where severe game damage caused the loss of several seedlings (*Table 3*).

3.2 Relationship between growth characteristics

For the comparison of the performance of the provenances, mother trees and their progenies we chose block 8 of the IUFRO experiment. We tested 12 – 6 superior and 6 inferior – mother trees out of the examined 48 trees in this block. The assessment of the height of the mother trees and of the progenies took place at different ages (at the age of 10 and 13, respectively). Therefore we compared relative heights (*Figure 1*). The height of the local control population in the Northern mountain range represented 100%. For the mother trees, the mean of the Bükkszentkereszt provenance was used (K1 = 474.0 cm), while the mean of the Telkibánya seed lot served for comparison of progenies (K2 = 636.4 cm).

Figure 1 illustrates the large differences among the mother trees. At the same time the performance of the open pollinated progenies were rather equalized. As already discussed, the progenies of the vigorous mother trees had the best performance, all of them exceeding the control. In case of the families marked **2** and **18** the difference is statistically significant. The progenies of the inferior mother trees showed results that were better than expected but with one exception (St. Johann marked **42**, from the Swabian Alb region) they failed to surpass the control. This provenance also exceeded the block mean in the IUFRO experiment. The families marked **40**, **45** and **48** were the shortest. All of them significantly differed from the control.

The correlation analysis (*Table 4*) showed a significant correlation at P = 1 % level between the mean heights of the mother trees and of the progenies (R = 0.81).

We examined the relationship between the provenances and their progenies, too. We also found a significant correlation at P = 1 % level between the mean heights of the provenances and of the progenies (R = 0.73).

Table 3 Results of the half-sib progeny test (Nagybátony 8 E) at the age of 13. Family mean heights (ranking trait), coefficient of variation (CV) and survival

Rank	Mother tree (family)	Provenance		Family mean height	Sign. diff.[1]	CV	Survival
		no.	name	cm		%	%
1	**21**	695	ELGERSBURG	723.2	*	10.0	91.7
2	**2**	870	KAUFBEUREN	717.0	*	12.8	77.1
3	**18**	815	EMMACH/MURAU	708.0	*	9.7	91.7
4	**9**	877	ZAMBERK	686.9		10.3	95.8
5	**16**	755	MARGINEA	679.0		10.6	91.7
6	**36**	1199	CRAWINKEL	677.3		12.1	93.8
7	**26**	331	BIALOWIEZA	676.2		11.2	93.8
8	**1**	835	GRAASTEN	674.0		14.7	95.8
9	**12**	736	VELKE KARLOVICE	673.3		10.0	93.8
10	**31**	1061	NEUWIRTSHAUS	672.9		10.7	89.6
11	**35**	1198	ISTEBNA	672.9		12.7	87.5
12	**28**	606	WOLOZIN	672.3		9.2	85.4
13	**5**	675	ZWIESEL OST VI/11	668.0		12.9	93.8
14	**4**	1075	MELLIER	666.8		11.6	89.6
15	**3**	781	KLODZKO	663.8		11.9	89.6
16	**10**	471	MECHTERSTAEDT	662.0		12.3	91.7
17	**22**	859	MORAVEC	656.3		11.6	87.5
18	**11**	648	WESTERHOF 50/58	655.2		11.2	93.8
19	**24**	1048	LANDSBERG	654.9		13.8	93.8
20	**42**	873	ST. JOHANN	654.6		11.7	91.7
21	**38**	230	VARAKALANI REV.	651.9		10.2	91.7
22	**17**	786	WEGIERSKA GOR.	647.3		11.0	85.4
23	**27**	600	TREBIC	642.6		17.7	83.3
24	**19**	830	EMMACH/MURAU	639.8		11.2	95.8
25	**37**	1160	TELLERHAEUSER	638.5		10.3	95.8
26	**44**	1083	FLODA	636.6		12.7	93.8
27	**K2**		*TELKIBÁNYA*	**636.4**		**11.5**	**97.9**
28	**15**	755	MARGINEA	635.5		11.7	95.8
29	**25**	1079	HRANICE	632.4		10.4	100.0
30	**41**	820	VILLINGSBERG	632.2		11.6	91.7
31	**34**	1147	MOGILEVSK. OBL.	631.3		12.2	79.2
32	**8**	791	DOBRIS	621.3		14.4	93.8
33	**6**	691	GOROWO	618.2		13.1	91.7
34	**7**	742	MAUTH OST	618.1		12.1	93.8
35	**30**	1030	ROSTOCK	616.5		12.4	95.8
36	**14**	751	VRCHLABI	611.8		15.2	79.2
37	**39**	310	TODTMOOS	611.2		12.3	95.8
38	**13**	741	BETZIGAU	609.2		12.7	83.3
39	**46**	875	BERG BEV.	606.0		13.1	91.7
40	**32**	252	SZCZECINEK	605.0		14.2	87.5
41	**33**	273	TREBIC	598.0		14.2	93.8
42	**29**	691	GOROWO	597.4		15.7	77.1
43	**47**	981	MIKKELIN	593.2		12.9	97.9
44	**23**	976	PODOLINEC	588.0		15.8	89.6
45	**20**	928	ISTEBNA	570.7	*	19.2	95.8
46	**48**	876	BJOERLIDA	566.9	*	13.9	89.6
47	**40**	838	HILLET	557.4	*	18.2	85.4
48	**43**	927	AUSTAGDER	550.7	*	16.4	93.8
49	**45**	897	JAROSLAWL	543.2	*	15.5	95.8
			TEST MEAN	**637.2**			**91.0**

* Families that significantly differ from the average mean height of the local populations (P = 5%)

▨ Inferior mother trees and their progenies (**39 – 48**)

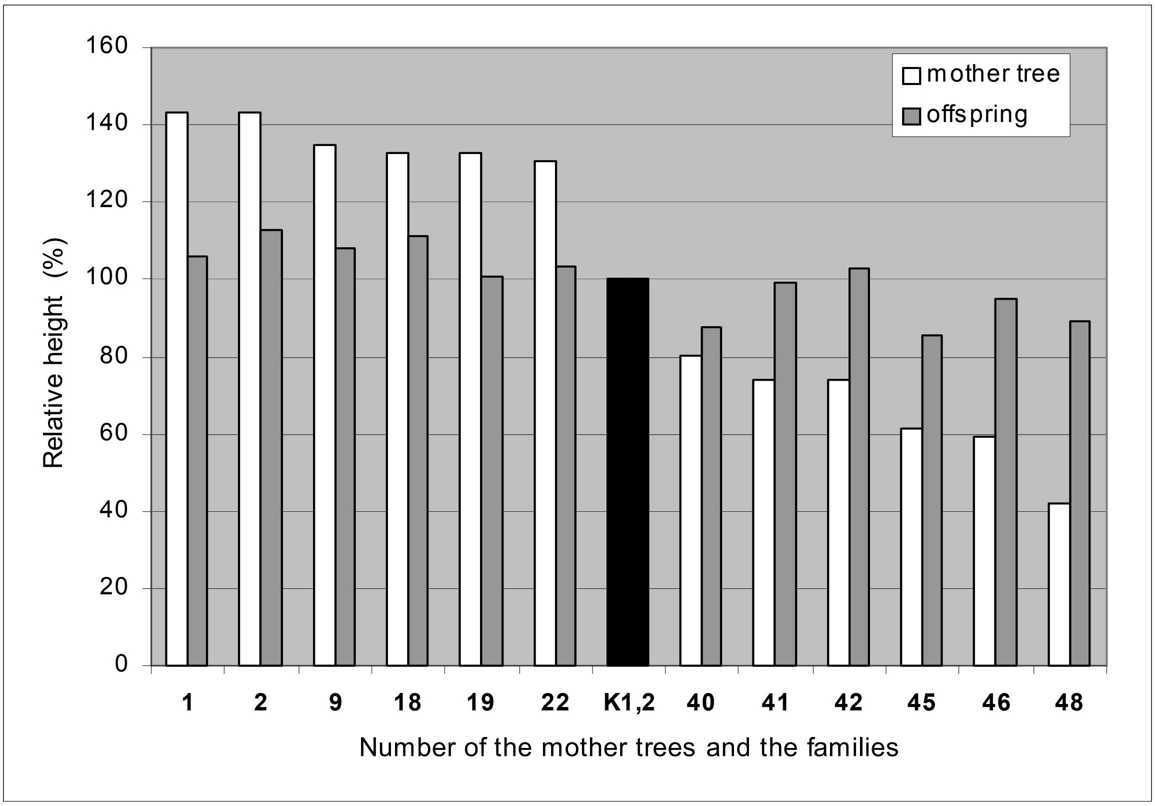

Figure 1. Relative height of mother trees and their half-sib progenies. Identification numbers are the same as in tables 1 and 3. (K1 and K2 represent the local sources for the mother trees and the progenies, respectively)

Table 4. Results of correlation analysis on height increment (provenance means, mother trees and their progenies)

Generation	Provenance	Mother tree
Provenance	1	
Mother tree	0.79**	1
Open pollinated progeny	0.73**	0.81**

** Correlation is significant at the P=1% level

4 DISCUSSION

The results of the progeny tests confirmed the general impression that Norway spruce has an outstanding adaptability and plasticity. The progenies originating from very different ecological environments had shownlow mortality, which did not significantly differ from the mortality of the control. This is perhaps not surprising because the populations of the mother trees already went through a selection for fitness in the Hungarian IUFRO experiment. We can mention here the example of a provenance from the West Siberian Plain (Timirjas), which disappeared from the experiment within 30 years. The selected mother trees can already be regarded as "survivors" of juvenile fitness selection

There was no opportunity to examine the tolerance to biotic and abiotic damages because fortunately, there was no significant damage in the experiment apart from the game damage.

We found that height growth of several progenies significantly exceeded the local (control) population. This is a well known phenomenon. In the IUFRO provenance test we could show that the 11 Hungarian provenances had a performance above the average (Ujvári – Ujvári 1980), but the best originated from relatively distant locations, e.g. from the Eastern Carpathians, from the region of the Beskids (Ujvári – Ujvári 1979). Namkoong (1969) and many other researchers formulated the opinion that at a given site it may not be the local population that grows best. For example, for jack pine (*Pinus banksiana*) Mátyás – Yeatman (1987) could statistically prove, that autochtonous populations are not necessarily the best growers at a given site.

The relatively low number of the Norway spruce progenies did not allow to identify general relationships. We could, nevertheless, show a strong correlation (R = 0.81) between the mother trees and their offspring when selection was made both for good and poor height growth. The experiment supported earlier information that the mother trees of the best progenies originate from Swabia, Thuringian Forest, Sudeten, Eastern Carpathians, Western Beskids, etc.

We included intentionally the mother trees of provenances showing extreme performance in our experiment. Therefore we had an opportunity to identify further relationships. In the progeny tests we also have shown that there is a highly significant correlation (P = 1%) between the mean heights of the provenances and their open pollinated progenies.

The analysis of growth traits has proven that even though the differences among the families were smaller than expected, the phenotypic variation of the individuals within a family was large. Particularly the coefficient of variation (CV) of the inferior progenies was higher than the control (*Table 3).*

We have found also some remarkable correlation breakers. While very distant provenances, e.g. Floda and Villingsberg (Southern Sweden) originating from the 59th degree of latitude were among the poorest growers in the IUFRO experiment, the height growth of the progenies from these provenances approached or even reached the performance of the local population. Thus the differences between the two groups of selected provenances were considerably larger in the original provenance trial than they were in the progeny test.

Two factors may have contributed to these results. The first relates to the pollination in the provenance trial. Different trees may have contributed in varying degrees and random mating can therefore not be expected to have taken place. Most likely trees from the best growing, and more southern provenances contributed more to the pollen cloud and thus became the pollen parents of the open pollinated families. Inferior trees from inferior provenances may have contributed to a less extent as their flowering was presumably less abundant due to their position among better growing trees. In addition, there could be background pollination from local spruce stands. Thus, the contribution from the pollen parent may be one factor that caused the unexpectedly good performance of families from poorly growing provenances (Skrøppa pers. comm.).

Another important factor may be the effect of the climatic conditions at the site where the seeds were produced. Studies with Norway spruce in Northern Europe have shown that both day length and temperature during seed production can affect the annual growth rhythm and growth of the progenies (Skrøppa – Johnsen 1999; Johnsen et al. 2005a, b). It has also been demonstrated that seedlings from seeds collected in stands of transferred provenances have changed their annual growth rhythm towards that of the local provenance (Tollefsrud et al. in prep.). Such effects could have a common influence in particular on provenances that have been transferred from northern latitudes and may explain that some of the Nordic provenances perform surprisingly well and better than they do in the original provenance trial (Skrøppa pers. comm.).

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Direct Effects of Carpophagous Insects on the Germination Ability and Early Abscission of Oak Acorns

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Abstract – Carpophagous insects play an important role in decreasing the viability of acorns in both direct and indirect ways. Therefore they significantly influence the reproductive potential of oaks. As a direct effect, their feeding on the embryo and on the cotyledons may prevent the germination of the acorn and on the other hand, their damage causes premature acorn abscission. During 3 years, 60 acorn samples from five oak species (Turkey oak – *Quercus cerris*, pedunculate oak – *Quercus robur*, sessile oak – *Quercus petraea*, downy oak – *Quercus pubescens*, red oak – *Quercus rubra*) have been investigated. The average rate of damage varied a lot between years, but was always significant (2000: 36%, 2001: 61%, 2002: 51%). The insects' influence causing premature acorn abscission was significant both for pedunculate and Turkey oaks. The premature acorn abscission was 34% of the total crop in 2000 for pedunculate oak (*Curculio* spp. 26%, *Cydia* spp. 2% and *Andricus quercuscalicis* 6%) and 39% in 2001 (*Curculio* spp. 14%, *Cydia* spp. 2%, *Andricus quercuscalicis* 13%, *Callirhytis glandium* 10%). In case of Turkey oak it was 29% in 2001 (*C. glandium* 16%, *Neuroterus saliens* 13%, and 12% in 2002 (*C. glandium* 10%, *N. saliens* 2%).

oaks / *Quercus*, / acorn / carpophagous insects / germination ability/ early abscission

Kivonat – A karpofág rovarok közvetlen hatása tölgymakkok csíraképességére és korai hullására. A karpofág rovarok közvetlenül és közvetve is egyaránt jelentős szerepet játszanak a tölgymakkok csíraképességének csökkenésében, ezáltal a tölgyek reprodukciós képességében. Közvetlen szerepük kettős, egyrészről a lárvák a makkokban a csíra és a sziklevelek megrágásával megakadályozzák a makkok kicsírázását, másrészt jelenlétük, a korai makkhullás révén lehetetlenné teszi a makkok teljes kifejlődését. 5 fafaj (cser, kocsányos tölgy, kocsánytalan tölgy, molyhos tölgy, vörös tölgy), összesen 60 mintájának vizsgálata alapján megállapítható, hogy 3 vizsgálati év alatt a rovarok által elpusztított makkok aránya változó, de jelentős volt (2000: 36%, 2001: 61%, 2002: 51%). Két év vizsgálatai alapján megállapítható, hogy a fejletlen makkok lehullását előidéző rovarfertőzés kocsányos tölgy és cser esetében is egyaránt jelentős lehet. Kocsányos tölgynél 2000-ben a teljes makktermés 34%-ában, 2001-ben pedig 39%-ában okoztak idő előtti makkhullást a karpofág rovarok. Cser esetében ez az arány 2001-ben 29%, 2002-ben pedig a 12% volt.

tölgyek / *Quercus* / tölgymakk / karpofág rovarok / csíraképesség / korai makkhullás

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1 INTRODUCTION

Oaks cover 32.4% (547, 547 ha) of the total forested area in Hungary and their share from the standing tree volume (38%) is even higher (ÁESZ 2002). Although the percentage of natural regeneration is increasing in some regions of the country, artificial regeneration still remains dominant.

To fulfil the acorn demand for artificial regeneration, collecting of at least 1,000 tons of acorns per year are needed in Hungary (Hirka 2003). The acorn crop of oaks (with exception of Turkey oak) fluctuates significantly from year to year with good crops only every 5-6 years and 1-2 medium crops within these periods. Based on these facts, each biotic and abiotic factor influencing the survival and germination ability of the acorn crop (e.g. carpophagous insects) has outstanding importance.

Only the specialist herbivore insects connected directly to acorns are considered as carpophagous in this study. According to recent studies, 19 species of carpophagous insects (6 acorn weevils, 4 acorn moths and 9 gall wasps) are recorded from acorns of oaks in Hungary. Only 5 of them (*Curculio glandium, Cydia splendana, Andricus quercuscalicis*, *Callirhytis glandium*, *Neuroterus saliens*) are widespread and abundant enough to have a significant influence on acorn viability, the other species being rather sporadic and less abundant (Hirka 2003). Their influence can either be direct or indirect. This study considers the direct effects only.

2 LITERATURE REVIEW

Numerous authors have dealt with carpophagous insects of oaks in Hungary during the 20th century concerning both their direct and indirect effects. Ujházy (1950) discussed the life history of several acorn insects and the possible methods of winter storage of acorns. Győrfi (1954) listed the insects damaging acorns with special regard to their life history and importance. Beginning from the 1950s Mátyás (1963, 1965) studied the abiotic factors influencing the acorn crop, but also paid attention to the biotic factors including all three main groups of carpophagous insects. Vicze (1965, 1966) studied the development of acorn weevils and the abscission periods of acorns infested by them. Bürgés (1973, 1990) dealt with the pests of sweet chestnut including several species damaging both chestnuts and acorns (acorn weevils and acorn moths). Later he published data concerning the damage by acorn insects specifically (Szemes - Bürgés 1999). Fodor (1986) reported on the experimental control methods applied in order to reduce the loss due to the acorn insects. Hirka - Csóka (2000, 2001, 2002a,b) studied in detail the direct, and more intensively, the indirect effects of carpophagous insects on germination ability of acorns. These investigations raised several new questions and unsolved problems.

3 AIM OF THE STUDY

One of the direct effects of carpophagous insects is the consumption of the embryo by the larvae or the damaging the cotyledons to such an extent which makes the germination and the development of the seedling impossible. The aim of our investigation was to asses the rate of damaged acorns in storage and to quantify the probability of the germination of damaged acorns. According to both Hungarian and foreign authors (Kiss 1928, Magyar 1931, Roth 1941, Oliver - Chapin 1984, Forrester 1990, Rolfs 1999, Branco et al 2002, Hirka 2003) acorns infested by carpophagous insects do not always lose their germination ability. A considerable percentage can keep germination ability and still be able to produce viable seedlings.

Another of direct effect is the premature abscission of the infested young acorns, however less apparent because the result is often hardly visible and certainly less spectacular than the emergence holes on the infested fully-grown acorns. Therefore this damage was often overlooked even if its impact was not negligible. In our investigation we also aimed to quantify the effect of different carpophagous insects on early acorn abscission and to obtain a temporal pattern of process of acorn falling within a year.

4 METHODS

4.1 Embryo damage assessment

Samples were taken in 3 years (2000-2001-2002) in late February, after ca. 4 months storage from acorns of 5 species of oaks (*Quercus cerris*, *Q. robur*, *Q. petraea*, *Q. pubescens*, *Q. rubra – Table 1*). The acorns were originally collected at different locations in Hungary (*Table 2*). The average number of acorns in the samples was 554, 535, 859 respectively in the consecutive years (2000, 2001, 2002). The acorns in the samples were divided into two groups, „intact” and „damaged” (acorns with emergence holes) and the ratio of insect damaged acorns was calculated. 100 randomly selected damaged acorns were taken from each sample and cut in order to record the embryo’s condition (dead/alive).

Table 1. Distribution of acorn samples by species and year

Species/Year	2000	2001	2002
Q. cerris	10	0	9
Q. robur	2	13	8
Q. petraea	3	5	1
Q. pubescens	1	3	0
Q. rubra	1	2	2
Total:	17	23	20

4.2 Premature acorn abscission assessment

The role of different carpophagous insect species in early acorn abscission was investigated in 2000 and 2001 at Püspökladány on *Quercus robur* and in 2001 and 2002 at Mátrafüred on *Quercus cerris*. The falling acorns were collected using 1x1 m collecting baskets (2 baskets under each of 2 *Q. robur* trees at Püspökladány and 3 baskets under 1 *Q. cerris* at Mátrafüred). The baskets were emptied weekly. The acorns caught in the baskets were examined and dissected to detect the presence of the different carpophagous species. The different species could be distinguished with high accuracy. The typical asexual galls of *Andricus quercuscalicis* on the acorns can be identified easily. The grouped galls of *Callirhytis glandium* and *Neuroterus saliens* could be identified based on size of the chambers inside the acorns. Larvae of *Curculio* and *Cydia* can also be distinguished easily. If larvae were not present, their faeces and emergence holes helped the identification. Faeces of *Curculio* larvae are dust-like and their emergence holes are circular. Faeces of *Cydia* larvae are grainy and they leave the acorns through a flattened oval emergence hole.

Table 2. Geographical origin of the acorn samples

Origin/Year	2000	2001	2002
Great Plain			
Baktalórántháza	–	QR, QRU	QR, QRU
Fehérgyarmat	–	QR (2)	QR
Gyula	–	–	QR, QRU
Valkó	QC	QR	QC
Northern Medium Mountains			
Buják	-	–	QC
Dejtár	QC, QP	–	QC
Felsőtárkány	QP	–	–
Kál	QR	–	–
Kálló	–	–	QC
Mátrafüred	QC	QP	QC
Szokolya	–	QP	–
South Transdanubia			
Iharosberény	–	–	QR
Sellye	QR	QR (2)	–
Tarany	–	–	QC
Transdanubian Medium Mountains			
Bakonyszentlászló	QC	–	–
Balatonfüred	QPU	–	–
Budaörs	–	QPU	–
Devecser	QC	QR (4)	QR
Leányfalu	QP	–	–
Olaszfalu	QC	–	–
Pápa	QC, QRU	QR	–
Pilismarót	–	QP	QC
Süttő	QC	–	–
Szentendre	–	QP	–
Veszprém	–	QR, QP, QPU (2), QRU	QC, QR
West Transdanubia			
Ravazd	QC	–	–
Röjtökmuzsaj	–	–	QC, QR, QP
Sopron	QC	–	–
Szentgotthárd	–	QR	–
Szombathely	–	–	QR

Abbreviation of oak species:
QC = Q. cerris,
QR = Q. robur,
QP = Q. petraea,
QPU = Q. pubescens,
QRU = Q. rubra

5 RESULTS AND DISCUSSION

5.1 Embryo viability in infested acorns

The infestation rate varied greatly between years, tree species, and locations. The average infestation rate for all investigated oak species was 23% in 2000 (17 samples - ranging from 8% to 47%), 11% in 2001 (23 samples - ranging from 4% to 24%) and 25% in 2002 (20 samples - ranging from 3% to 55%). For the year 2000, 64% of insect-infested acorns had still viable embryos. The ratio was 39% in 2001 and 49% in 2002 (*Figure 1*).

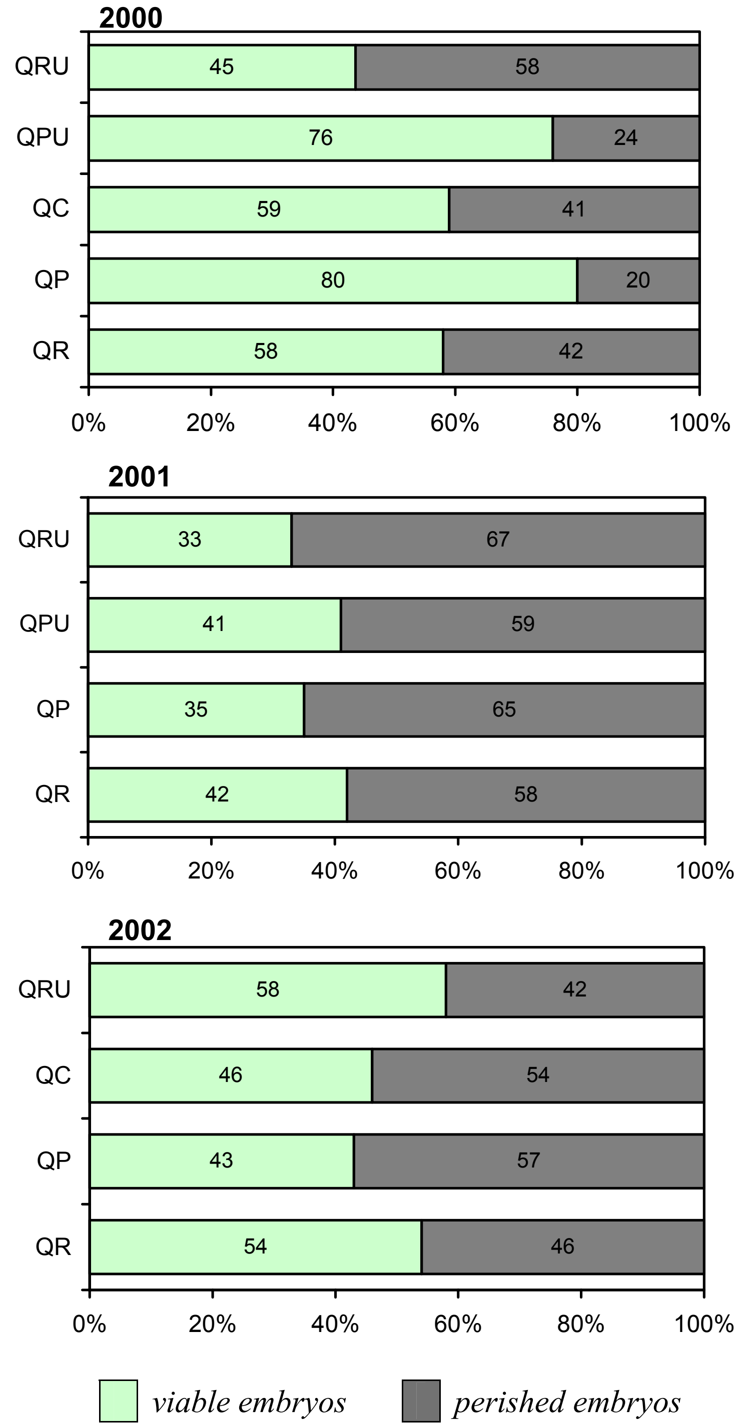

Figure 1. Ratio of viable and perished embryos in insect-infested acorns by different oak species in 2000-2001-2002 (for explanation of species abbreviations see Table 2)

In theory, the acorns with intact embryos could have been able to germinate. However, according to our other investigations, embryo mortality in infested acorns is more often caused by fungus penetrating the acorns via the emergence holes (to a lesser extent via the oviposition holes). So the acorns with intact embryos often loose their viability due to fungal infection (Hirka 2003). As this is not considered as a direct effect of carpophagous insects, it is not discussed further in this paper.

The ratio of acorns with perished embryos varied considerably between years: 36% in 2000, 61% in 2001 and 51% in 2002 (as an average of all oak species and all locations for the given year). Embryos of acorns with 2 or 3 emergence holes were mostly killed directly by feeding of larvae. However even in acorns with 3 emergence holes, embryos could sometimes survive. This does not mean of course that these acorns could produce vigorous seedlings, because the quantity of available nutrients of the wholly or partially consumed cotyledons is insufficient for the first period of the seedling's development.

It is worth mentioning that the number of emergence holes on an acorn is not a good indicator for the number of larvae that developed in the acorn (Hirka - Csóka 2004). During our investigations we found even an acorn from which 11 weevil larvae emerged through one single emergence hole.

It can be concluded that the feeding of carpophagous insect larvae does not necessarily destroy the embryo, and that insect infested acorns often retain their germination ability. Oliver - Chapin (1984) found that 24% of *Quercus virgiliana* acorns with emergence holes germinated. According to Forrester (1990) the intact acorns germinated at a twice higher ratio than the infested ones. In our other studies we found that the germination rate of intact *Quercus cerris* acorns was only 17% higher than that of the insect infested ones (Hirka 2003). Of course the viability of infested but still viable acorns strongly depends on acorn size and the number of larvae developed in it.

5.2 Early abscission of premature acorns

5.2.1 Quercus robur

Carpophagous insects damaged 59 % of the total crop in 2000 and 48% in 2001 (*Table 3*).

Table 3. Abscission of Q. robur acorns grouped by damaging factors at Püspökladány in the years 2000 and 2001

Damaging factors	*Q. robur* at Püspökladány 2000	 2001
	%	
Callirhytis glandium	*0*	*10*
Andricus quercuscalicis	*6*	*13*
Curculio spp.	*49*	*19*
Cydia spp.	*4*	*6*
Carpophagous insects together	59	48
Fungal infection	4	4
Other abiotic factors	33	47
Intact, healthy acorns	4	1
Total (acorns/m^2)	261	175

The most significant change between 2000 and 2001 is the spectacular increase in the ratio of acorns infested by gall wasps. Two species (*Andricus quercuscalicis* and *Callirhytis glandium*) together infested 23% of the acorns, and in particular, the increase in the case of

Callirhytis is dramatic (from 0% to 10%). The ratio of acorns infested by *Curculio* decreased from 49% in 2000 to 19% in 2001.

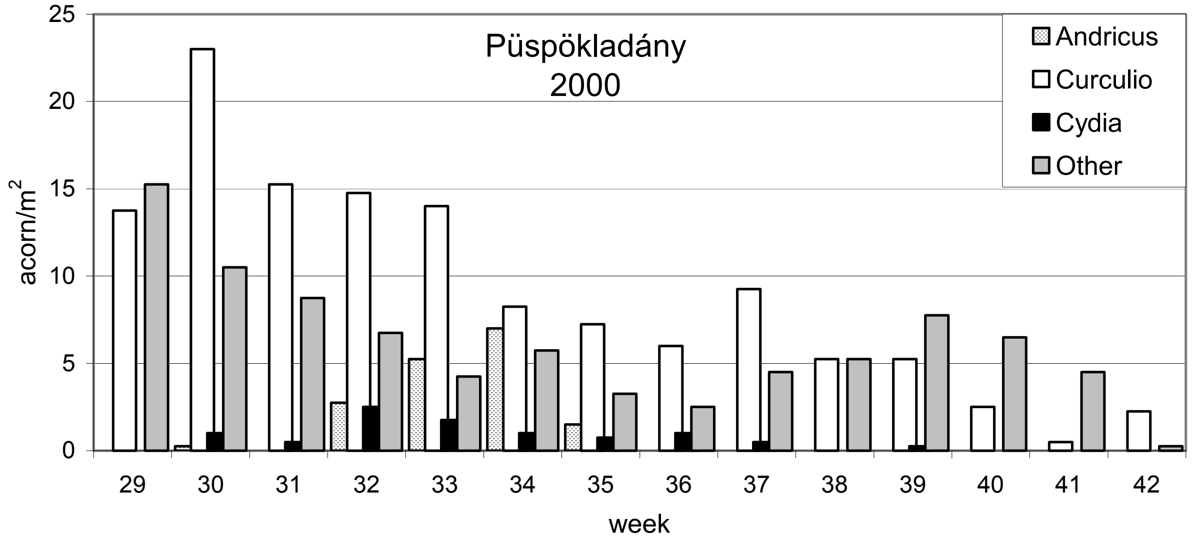

Figure 2. Abscission process of Quercus robur acorns at Püspökladány in 2000

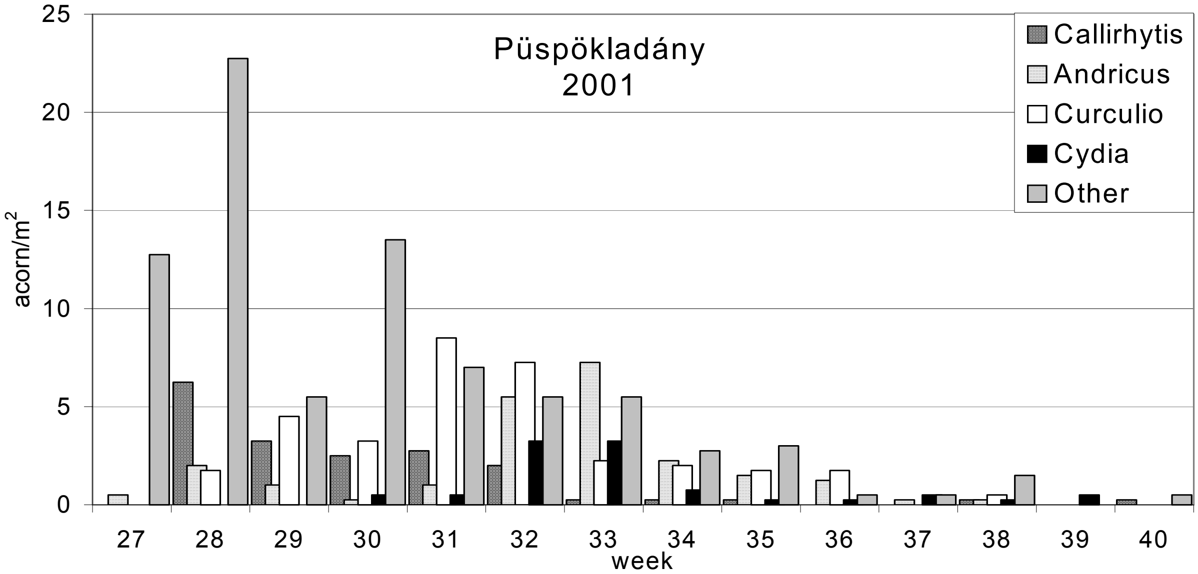

Figure 3. Abscission process of Quercus robur acorns at Püspökladány in 2001

Acorns falling until mid August were of small size (ca. half of the normal size) and these were not developed enough to be able to germinate. Acorns galled by *Andricus quercuscalicis* (6% in 2000 and 13% in 2001 of the total acorn crop) fell down within a relatively short period (a few weeks in August) in both years (*Figure 2,3*). Although these acorns were not small, the majority of them did not germinate. Acorns which fell due to the drought (33% in 2000 and 47% in 2001of the total crop) were small and not viable.

Vicze (1965) and Leskó (1991) found that insects play an important role in the early acorn abscission in the period from June to August. These observations were supported by the results of our investigations with the remark that drought played an outstanding role in both years by triggering premature acorn abscission.

5.2.2 Quercus cerris

Carpophagous insects in 2001 together infested 46% of the total crop in 2001 and 38% in 2002 (*Table 4*).

Table 4. Abscission of Q. cerris acorns grouped by damaging factors at Mátrafüred in the years 2001 and 2002

Damaging factors	*Q. cerris* at Mátrafüred 2001	 2002
	%	
Neuroterus saliens	13	2
Callirhytis glandium	27	11 (9)*
Curculio spp.	3	18
Cydia spp.	1	6
Curculio spp.+ *Cydia* spp. **	0	1
Callirhytis gl.+ other larvae**	2	0
Carpophagous insects together	46	38
Fungal infection	4	8
Other abiotic factors	47	49
Intact, healthy acorns	3	5
Total (acorns/m^2)	888	749

(*previous year's *Callirhytis glandium,* **together in one acorn)

Two gall wasps, *Neuroterus saliens* and *Callirhytis glandium,* played a major role in the premature acorn abscission in 2001. While *Neuroterus* infested 13%, *Callirhytis* infested 27% of the total acorn crop, *Curculio* and *Cydia* played a relatively minor role in this year with 3% and 1% infestation rate. Their low prevalence is partially explained by the fact that the major early acorn abscission caused by the drought and the gall wasp species mentioned above decreased the number of available acorns dramatically, so *Curculio* and *Cydia* already did not have enough acorns in order to lay eggs and develop. In 2001 76% of the *Q. cerris* acorns fell down as small undeveloped acorns, unable to germinate.

These two gall wasp species damaged significantly decreased ratio of the crop in 2002. Contrary to this *Curculio* and *Cydia* larvae damaged an increased ratio of the acorns.

There were two distinct peaks in the abscission of acorns infested by *Callirhytis* in 2001 (*Figure 4*). The small undeveloped acorns fell first (16% of the total acorn crop and 60% of the *Callirhytis* infested acorns) in August-September. The fully grown *Callirhytis* infested acorns started to fall in late September and continued falling until the end of the falling period.

The temporal pattern of the abscission caused by the different factors in 2002 (*Figure 5*) differed slightly from the patterns of the previous year. The acorn abscission due to the drought (49% of the total acorn crop) peaked in July but continued with changing intensity until the end of the acorn falling period.

Acorns infested by *Neuroterus saliens* (2%) fell in June and July. The abscission of *Callirhytis* infested acorns can be divided in two periods. From late June to early August previous year's small acorns fell. These acorns remained on the tree until the following spring/early summer and were predated by birds (larvae were removed from the acorn leaving empty larval chambers in the cotyledons). Half of the current year's two year old acorns infested by *Callirhytis* fell as "half-size" acorns from mid August to late September and the fully grown infested acorns fell from mid September to mid October. 9/10 of the *Callirhytis* infested acorns did not develop to full size. 61% of the total acorn crop remained half-size or even smaller in 2002. 12% of the total acorn crop remained undeveloped due to some insect infestation (mainly the two gall wasp species).

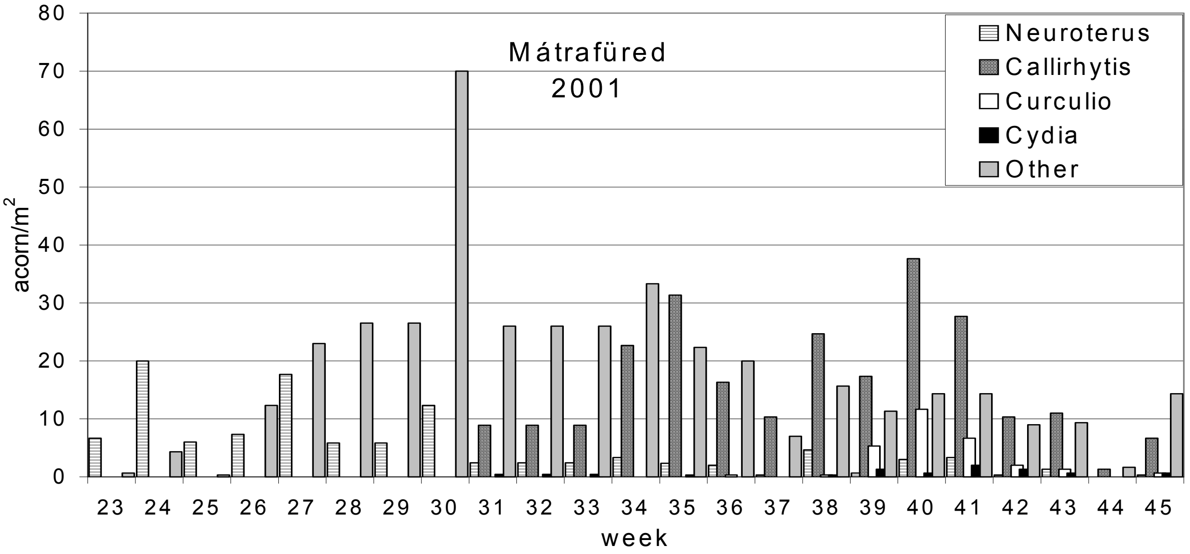

Figure 4. Abscission process of Quercus cerris acorns at Mátrafüred in 2001

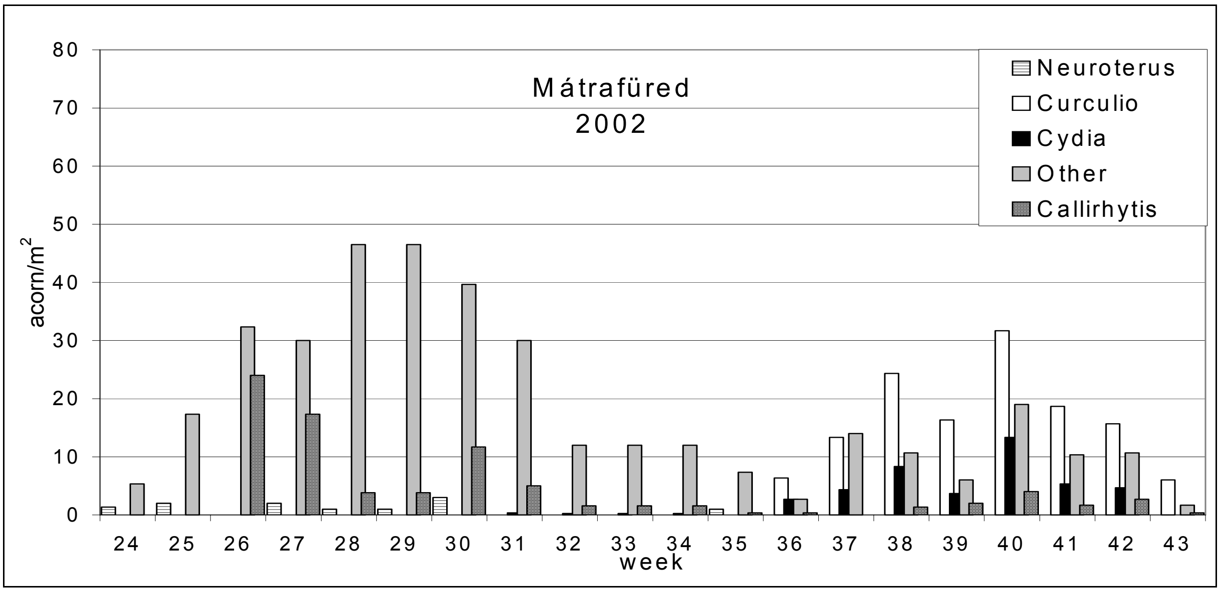

Figure 5. Abscission process of Quercus cerris acorns at Mátrafüred in 2002

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Collembola Diversity of Moss Habitats in the Sopron Region, NW-Hungary

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Abstract – The *Collembola* fauna of the moss flora in the Sopron region was studied. 18 moss species as well as 3.451 *Collembola* specimens (belonging to 60 species) were collected in 2003/04 in moss samples of three habitats. The highest *Collembola* diversity was found in Tómalom (a reed bed habitat) where very low abundance and relatively high species richness were characteristic. The *Collembola* diversity of the other two habitats (Sopron, Botanic Garden; Fertőrákos – a dry xerophile grass habitat) was lower. The results have shown a relatively high similarity between the *Collembola* communities in Sopron and Fertőrákos while just the opposite was observed between the Sopron and Tómalom samples.

bryofauna / Collembola diversity / dominance structure

Kivonat – Sopron környéki mohás élőhelyek Collembola-diverzitása. A Sopron környéki mohaflóra feltárása során vizsgáltuk a mohapárnákban élő ugróvillás közösségek diverzitását. 2003/2004-ben három vizsgálati területen gyűjtve 18 mohafaj mintáiban összesen 60 faj 3451 egyede került elő. A legmagasabb diverzitást a Tómalomnál, egy nádas-vizes habitatban találtuk. A két másik területen (Sopron, Botanikus kert; Fertőrákos, száraz sziklagyep) az egyedszám magasabb volt, a diverzitás azonban alacsonyabbnak adódott. Az eredmények a *Collembola* közösségek viszonylag nagy hasonlóságát mutatták Sopron és Fertőrákos viszonylatában, míg ennek ellenkezője igaz Sopron és Tómalom között.

bryofauna / Collembola-diverzitás / dominancia-viszonyok

1 INTRODUCTION

The *Collembola* (springtails) are the most abundant *Apterygota Entognatha* insects in the world, found in vast numbers from the tropics to the poles. The *Collembola* are mostly connected to forest habitats. They are chiefly soil dwellers, but we can also find springtails living in the canopy of tropical rain forests and they are also characteristic members of the bryofauna (Varga – Vargha 1992, Varga – Oldal 1998, Palacios-Vargas et al. 1998, 1999). In individual cases *Collembola* density can reach 98% proportion of the total density of *Arhtropoda* collected. An average square metre of soil in a temperate woodland can yield up to 50.000 individuals (Dunger 1983). Moreover, Dunger (1983) reveals that the optimal *Collembola* density would be tenfold of the mentioned value.

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The ecological importance of Collembola is indispensable in the decomposition of litter. They have an important role also in the food chain since they often form an important food source for predator Arthropods (e.g. for ground beetles). Most Collembola species prefer humid habitats. Their occurrence is furthermore determined by vegetation types, so springtails are important ecological indicator species for habitats and microhabitats. Although a paper on this region's Collembola fauna has already been published (Traser 2002), it doesn't treat the aspect of the springtail-moss connection.

The aim of this study was to determine the relationship between Collembola community composition, species richness, density, diversity in three different moss habitats in the Sopron region. Further investigations were related to the comparison of structural properties of Collembola communities between the moss habitats.

2 MATERIAL AND METHODS

2.1 Study area

The heart of the Sopron region is formed by the valley of the Ikva streamlet between the Sopron Mountains and the Szárhalmi Hillocks. The three study areas are the following: the Botanic Garden (Sopron), a wooded area with grass mosaic; Tómalom, a reed bed habitat and Fertőrákos, a dry limestone/grass habitat. *Table 1* shows further details on the study sites.

Table 1. Moss samples data and locality

	Moss samples in 2003 / 2004		
Location	Date	GPS coordinate	Habitat
Sopron – Botanic Garden	06. 03. 2003. 09. 10. 2003. 02. 03. 2004.	47.68056°N 16.58222°E	wooded area with grass mosaic
Tómalom – reed bed	10. 09. 2003.	47.70965°N 16.62362°E	*Caricion davallianae* reed, wet area
Fertőrákos – dry grass	06. 05. 2004.	47.72844°N 16.64010°E	*Festucetalia valesiacae* limestone grassland

2.2 Data collection and analysis

Samples of 100 cm^3 of moss were collected. A total of 43 samples were obtained from the three different habitats ranging from 10 to 19 samples per site (Tómalom:10; Sopron: 14; Fertőrákos: 19).

Extraction of *Collembola* specimens from the moss was carried with the help of a modified Tullgren's apparatus at room temperature (Balogh 1958). The *Collembola* and moss species have been stored in the archives of the authors. For identification of the *Collembola* fauna we used the keys of Gisin (1960), Bretfeld (1999), Jordana et al. (1997), Babenko et al.(1994), Deharveng (1982), Fjellberg (1980, 1998), Massoud (1967), Potapow (2001), Pomorski (1998), Thibaud et al. (2004), Zimdars & Dunger (1994), Stach (1960, 1963), Weiner (1996) and several other papers, while for the moss flora we used the keys of Orbán – Vajda (1983), Smith (1978, 1990) and Hedenas (1993).

Graphical methods (dominance curves) were employed to allow direct comparison of *Collembola* species diversity characteristics between the sites.

To measure *Collembola* similarity (based on dominance) between the habitats the Renkonen coefficient (Re %) was used:

$$\text{Re}\ \% = \sum \min D_{A;B}$$

where “D_A“ and “D_B”: dominance % of the common species in habitat “A” and “B”

Another similarity coefficients such as the Sörensen quotient ($QS\% = 2G/(S_A+S_B)*100$), the Jaccard’s species identity index [$J_N\% = G*100/(S_A+S_B-G)$] and the similarity index of Weinstein ($K_W = Re*J_N$) were calculated to determine the similarities/differences between the habitats and their collembolan communities. (Symbols are: “G”= number of the common species in the paired habitats; “S_A“ and “S_B“ are the species numbers in habitat “A” and habitat “B”).

To compare *Collembola* diversity values of two different habitats a *t* test was used.

3 RESULTS AND DISCUSSION

Table 2 shows the distribution and quantity of the moss samples in the three different habitats. There are no common moss species in these habitats except for two species that are present in both Sopron and Tómalom and one species found both in Sopron and Fertőrákos.

Table 2. Moss species and the number of samples taken

Moss species	Sopron	Tómalom	Fertőrákos
Tortella tortuosa (HEDW.) LIMPR.			3
Pleurochaete squarrosa (BRID.) LINDB.			4
Plagiomnium elatum (BRUCH et SCHIMP.) T. J. KOP.		1	
Plagiomnium undulatum (HEDW.) T. J. KOP.	2		
Climacium dendroides (HEDW.) F. WEBER et D. MOHR	1		
Thuidium philibertii LIMPR.	1		
Thuidium abietinum (HEDW.) SCHIMP.			4
Campylium chrysophyllum (BRID.) LANGE			1
Amblystegium varium (HEDW.) LINDB.		2	
Drepanocladus cossonii (SCHIMP.) LOESKE		2	
Calliergonella cuspidata (HEDW.) LOESKE	3	4	
Homalothecium lutescens (HEDW.) H. ROB			3
Brachythecium rutabulum (HEDW.) SCHIMP.	1	1	
Scleropodium purum (HEDW.) LIMPR.	2		
Eurhynchium hians (HEDW.) SANDLE LAC.	1		
Hypnum cupressiforme HEDW.	2		3
Rhytidium rugosum (HEDW.) KINDB.			1
Rhytidiadelphus triquetrus (HEDW.) WARNST.	1		
number of moss samples	14	10	19
moss species number	9	5	7

The moss species *Calliergonella cuspidata* and *Brachythecium rutabulum* were present both in Sopron and Tómalom while *Hypnum cupressiforme* was found both in the Sopron and in the Fertőrákos samples. The common *Collembola* species in the mentioned moss cushions are the followings:

Moss sp.: ***Calliergonella cuspidata*** (HEDW.) LOESKE

In Tómalom 15 *Collembola* species were collected on September 10, 2003. Out of these species only two spp. (*Sphaeridia pumilis; Parisotoma notabilis*) were found common to both Tómalom and Sopron samples (in Sopron 16 *Collembola* spp. were found on the same moss species).

Moss sp.: ***Brachythecium rutabulum*** (HEDW.) SCHIMP.
This moss species was collected from monospecific cushions in Tómalom**,** but mixed with *Scleropodium purum* (HEDW.) LIMPR. and *Eurhynchium hians* (HEDW.) SANDLE LAC. in the Sopron samples. The *Collembola* species richness was 4 in the samples of Tómalom and 9 in Sopron, but no common species to both samples were found.

Moss sp.: ***Hypnum cupressiforme*** HEDW.
We collected 14 *Collembola* species in the Fertőrákos samples and 9 in the Sopron samples. The only *Collembola* species found common to both samples was *Entomobrya nivalis.*

Table 3 shows the number of *Collembola* individuals in the different habitats. Since the number of samples was not equal in the three habitats, these values can give approximate information on the volume only. The low number of individuals in the Tómalom samples is a very uncommon phenomenon.

Table 3 Number of Collembola individuals in the three habitats

	Sopron	Tómalom	Fertőrákos	Σ
Hypogastruridae				
Hypogastrura socialis (Uzel, 1891)	4	0	0	**4**
Hypogastrura vernalis (Carl, 1901)	0	0	284	**284**
Xenylla boerneri (Axelson, 1905)	400	0	145	**545**
Xenylla maritima (Tullberg, 1869)	1	0	0	**1**
Xenylla brevicauda (Tullberg, 1869)	1	0	120	**121**
Willemia virae (Kaprus, 1997)	0	0	1	**1**
Brachystomellidae				
Brachystomella parvula (Schaeffer 1896)	0	10	0	**10**
Neanuridae				
Friesea truncata (Cassagnau, 1958)	0	10	0	**10**
Micranurida pygmaea (Börner, 1901)	0	3	0	**3**
Neanura muscorum (Templeton, 1835)	0	1	0	**1**
Onychiuridae				
Supraphorura furcifera (Börner, 1901)	0	7	0	**7**
Protaphorura armata (Tullberg, 1869)	0	0	2	**2**
Doutnacia xerophila (Rusek, 1974)	4	0	0	**4**
Mesaphorura critica (Ellis, 1976)	0	0	4	**4**
Mesaphorura hylophila (Rusek, 1982)	14	0	0	**14**
Mesaphorura krausbaueri (Börner, 1901)	0	0	36	**36**
Mesaphorura macrochaeta (Rusek, 1976)	1	2	0	**3**
Metaphorura affinis (Börner, 1902)	1	0	0	**1**
Isotomidae				
Pachyotoma crassicauda (Tullberg, 1871)	0	10	0	**10**
Cryptopygus bipunctatus (Axelson, 1903)	311	0	319	**630**
Folsomia manolachei (Bagnall, 1939)	0	0	632	**632**
Folsomia penicula (Bagnall, 1939)	31	0	0	**31**
Folsomia quadrioculata (Tullberg, 1871)	0	4	0	**4**
Isotomiella minor (Schaeffer, 1896)	0	13	2	**15**
Parisotoma notabilis (Schäffer, 1896)	264	7	159	**430**
Isotoma viridis (Bourlet, 1839)	0	0	4	**4**
Isotoma riparia (Nicolet, 1842)	0	1	0	**1**
Isotomurus cf. palustris (Müller, 1776)	6	0	0	**6**
Isotomurus prasinus (Reuter, 1891)	0	21	0	**21**

Table 3 cont. Number of Collembola individuals in the three habitats

	Sopron	Tómalom	Fertőrákos	Σ
Entomobryidae				
Entomobrya corticalis (Nicolet, 1842)	2	0	0	**2**
Entomobrya handschini (Stach, 1922)	0	0	11	**11**
Entomobrya multifasciata (Tullberg, 1871)	0	0	4	**4**
Entomobrya nigriventris (Stach, 1929)	0	0	3	**3**
Entomobrya nivalis (Linnaeus, 1758)	1	0	11	**12**
Lepidocyrtus cyaneus (Tullberg, 1871)	0	3	0	**3**
Lepidocyrtus lanuginosus (Gmelin, 1788)	91	0	25	**116**
Lepidocyrtus lignorum (Fabricius, 1775)	0	0	2	**2**
Lepidocyrtus paradoxus (Uzel, 1890)	0	2	0	**2**
Lepidocyrtus peisonis (Traser et Christian, 1992)	0	15	0	**15**
Lepidocyrtus violaceus (Fourcroy, 1785)	1	0	0	**1**
Pseudosinella alba (Packard, 1873)	6	0	1	**7**
Pseudosinella octopunctata (Börner, 1901)	0	0	32	**32**
Orchesellidae				
Orchesella cincta (Linnaeus, 1758)	10	0	12	**22**
Orchesella bifasciata (Nicolet, 1842)	1	0	0	**1**
Orchesella xerothermica (Stach, 1960)	0	0	2	**2**
Heteromurus major (Moniez, 1889)	22	0	3	**25**
Heteromurus nitidus (Templeton, 1835)	11	0	0	**11**
Tomoceridae				
Tomocerus cf. baudoti (Denis, 1932)	3	0	0	**3**
Tomocerus minor (Lubbock, 1862)	3	0	0	**3**
Cyphoderidae				
Cyphoderus albinus (Nicolet, 1842)	1	0	1	**2**
Oncopoduridae				
Oncopodura crassicornis (Schoebotham, 1911)	0	0	1	**1**
Neelidae				
Megalothorax minimus (Willem, 1900)	16	13	4	**33**
Neelides minutus (Folsom, 1901)	0	3	0	**3**
Sminthuridida				
Sphaeridia pumilis (Krausbauer, 1898)	6	25	0	**31**
Katiannida				
Sminthurinus elegans (Fitch, 1863)	31	0	0	**31**
Sminthurinus aureus (Lubbock, 1862)	2	0	0	**2**
Dicyrtomida				
Dicyrtoma fusca (Lubbock, 1873)	0	2	0	**2**
Bourletiellida				
Deuterosminthurus bicinctus (Koch, 1840)	0	0	1	**1**
Fasciosminthurus strigatus (Stach, 1922)	0	1	6	**7**
Heterosminthurus bilineatus (Bourlet, 1842)	0	0	4	**4**
Σ	**1245**	**153**	**1831**	**3229**

Some of the data are interesting since species richness is much higher in the moss cushions of Sopron region than the one recorded in the Bükk Mountains in NE Hungary (Varga 1989, 1991, 1992, 1998).

Collembola dominance curves (*Figures 1-3*) of the three habitats show very different characteristics. The most abundant species in the samples are different for all three habitats. The dominant species primarily belong to taxa *Isotomidae* and *Hypogastruridae* (followed by taxa *Entomobryidae* and *Symphypleona*). There are only few species belonging to the family

Neanuridae. This proportion of species roughly corresponds to the one characteristic for the Central European *Collembola* fauna.

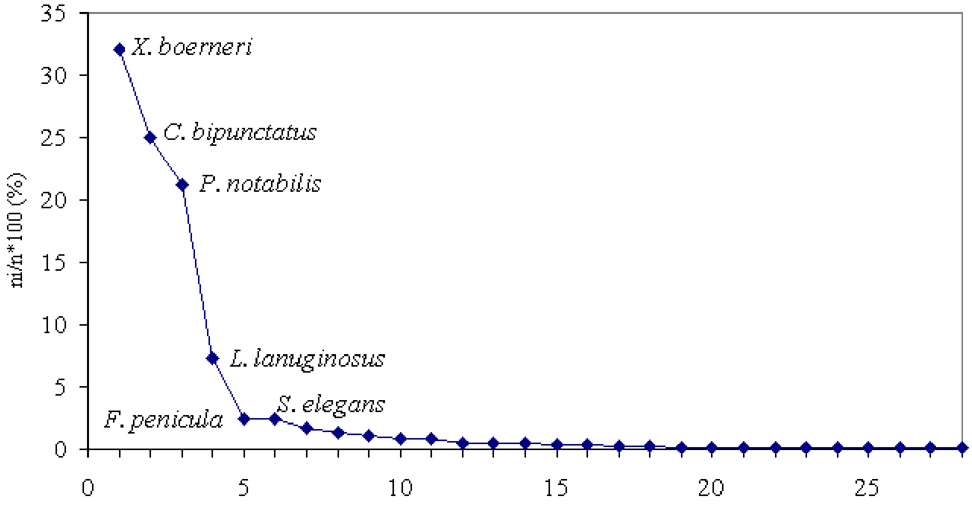

Figure 1. Collembola dominance in Sopron (n =1245 specimens)

The *Collembola* dominance curve of the Sopron sample shows three species with relatively high dominance rank. *Xenylla boerneri*, accounting for > 30 % of the total number of individuals, is a widely distributed species in Europe (including Ukraine and Latvia), occurring in litter, mosses and lichens on trunks and under the bark of trees (Thibaud et al. 2004). *Cryptopygus bipunctatus* (D = 25%) is rather common in Central Europe, rarer in Northern and Southern Europe. It is a xerothermic, ruderal species, mostly occurring in open and disturbed sites (Potapow 2001). *Parisotoma notabilis* (D = 21 %) is one of the most ubiquist *Collembola* of the Western Palaearctic. Its optimum is located in Central Europe and in the European part of Russia. It reaches high densities in both natural and disturbed sites (open grasslands, shelter belts, forests). Its presence in every kind of biotopes (excluding the too extreme ones) is a characteristic of this species (Potapow 2001).

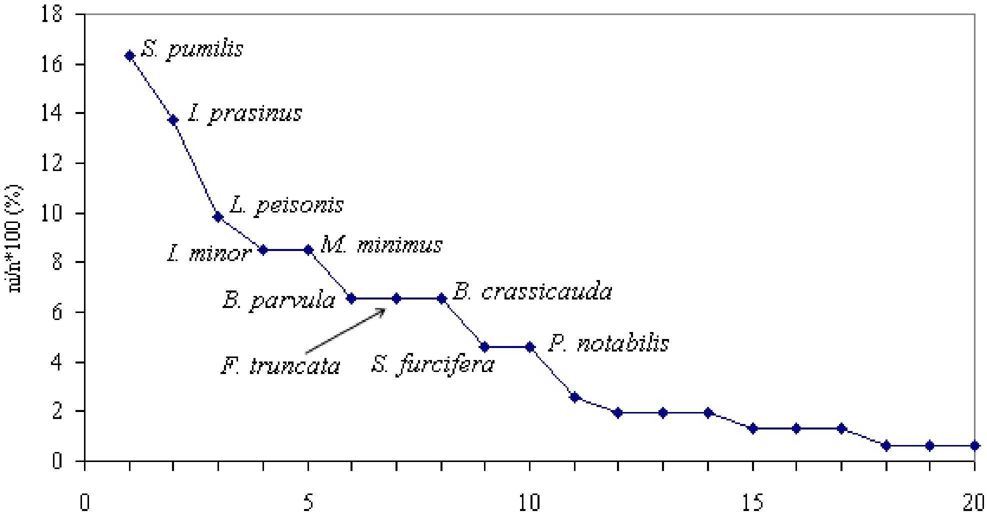

Figure 2. Collembola dominance in Tómalom (n =153 specimens)

The most dominant *Collembola* (D = 16,5%) in the Tómalom samples was *Sphaeridia pumilis*, a widespread species in Europe and North America (type locality: Germany, on *Rumex nemorosus* and *Glyceria* of a forest path), occurring on the surface and in upper layers of different moist soil types and in their low vegetation (Bretfeld 1999). Further dominant member (D =14 %) of this community is *Isotomurus prasinus*, a typical hydrophilous species, common and abundant in various moist sites, often occurring also in agricultural fields (especially in Central Europe). Its exact distribution has still to be determined. Type locality: Siberia, Yenisei River (Potapow 2001). The third most dominant collembola, *Lepidocyrtus peisonis* is a typical hydrophile species, occurring mostly on banks of stagnant eutrophic waters in the Kisalföld region. It has only been recorded in Hungary and Austria (Traser – Christian 1992). Type locality: Fertőrákos, in a humid sedge (*Carex riparia* and *Phragmites australis*) field.

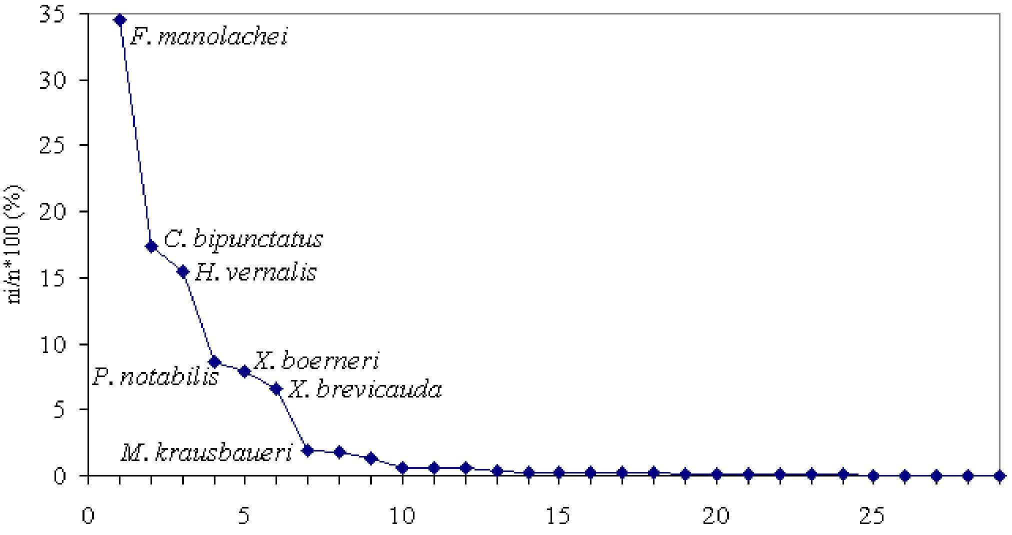

Figure 3. Collembola dominance in Fertőrákos (n =1831 specimens)

The species *Folsomia manolachei* was found the most dominant in the Fertőrákos sample (accounted for 35 % of the total number of individuals). It is a widespread springtail presumably all over the Palaearctic, recorded in almost all European countries (Potapow 2001). An eurytopic species, reaching high abundances in various biotopes (forests, open grasslands). It is also common but less abundant in strongly disturbed areas (intensively cultivated agricultural fields, recultivated sites etc.). Similarly to the Sopron samples, *Cryptopygus bipunctatus* was found among the most dominant species (D = 17%) also in the Fertőrákos sample. Dominant species also include the Palaearctic *Collembola Hypogastrura vernalis* (D = 15,5%), characteristic for seashore meadows with wide distribution along the Nordic coasts. Sporadic European inland records (mostly in continental sands) are also known (Thibaud et al. 2004).

The result of various similarity calculations is presented in *Tables 4-7.* Despite of the high *Collembola* species richness, the similarity between the Sopron-Tómalom-Fertőrákos samples is very low.

Table 4. Renkonen's similarity

	Sopron	Tómalom
Tómalom	6.4028	
Fertőrákos	36.6434	5.1819

Table 5 Sörensen's similarity

	Sopron	Tómalom
Tómalom	0.1276	
Fertőrákos	0.3509	0.1250

Table 6. Jaccard's similarity

	Sopron	Tómalom
Tómalom	6.8182	
Fertőrákos	21.2767	7.1429

Table 7. Wainstein's similarity

	Sopron	Tómalom
Tómalom	43.6557	
Fertőrákos	779.6476	37.0137

The Renkonen similarity index indicates a relatively high similarity between Sopron and Fertőrákos while just the opposite can be observed for the Sopron and Tómalom samples. The other similarity coefficients calculated (Sörensen quotient, Jaccard's species identity index, Weinstein similarity index) also show the "marginal" position of Tómalom.

Table 8 shows the most important structural properties of the *Collembola* communities.

Table 8. Structural properties of Collembola communities

	Sopron	Tómalom	Fertőrákos
Species richness *(S)*	28	20	29
Number of individuals	1245	153	1831
Shannon diversity *(H)*	1.883	2.628	2.01
Equitability *(J)*	0.5651	0.8771	0.597

Despite of the lower abundance in Tómalom the species diversity is relatively high, higher than for the other two habitats. The higher community equitability value for the Tómalom sample can be explained with the lower species richness with a relevant implication on the algorithm used.

Table 9 shows the results of *t* test based on Shannon diversity indices.

Table 9. Results (t-values) of comparison of Shannon diversity indices
(significant difference at P=0.05 level)*

	Sopron	Tómalom
Tómalom	5.0778*	
Fertőrákos	1.9089	4.0871*

Concerning the Sopron and Fertőrákos samples, there are no remarkable differences between diversity values of *Collembola* communities collected in these habitats. Significant difference can be observed between the Sopron - Tómalom and the Tómalom - Fertőrákos samples.

CONCLUSION

Knowing the ecology of the collected species a strong connection between them and the moss species cannot be proved. Their presence is supposedly determined by the surrounding habitats.

Typical bryobiont species – like e.g. *Hymenaphorura creatricis* (Traser – Salló 2003) – were not recorded, only some bryophile species (e.g. *Xenylla boerneri*) were found. Among the most dominant *Collembolas* there are no species living solely on moss. Most of the dominant species collected are eurytopic and less sensitive to anthropogenic disturbance.

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Appendix. Raw data of the Collembola specimens collected

Tortella tortuosa (HEDW.) LIMPR.
Fertőrákos, 06. 05. 2004: *Hypogastrura vernalis 35; Xenylla brevicauda 50; Lepidocyrtus lanuginosus 1; Pseudosinella octopunctata 12; Orchesella cincta 2; Orchesella xerothermica 2; Folsomia manolachei 5; Cryptopygus bipunctatus 5; Entomobrya multifasciata 4; Parisotoma notabilis 11; Protaphorura armata 2; Isotomiella minor 1;*

Pleurochaete squarrosa (BRID.) LINDB.
Fertőrákos, 06. 05. 2004: *Lepidocyrtus lanuginosus 4; Folsomia manolachei 237; Entomobrya handschini 7; Entomobrya nivalis 8; Fasciosminthurus strigatus 1; Parisotoma notabilis 9; Cryptopygus bipunctatus 5; Isotoma viridis 2; Pseudosinella octopunctata 13; Hypogastrura vernalis 24; Xenylla brevicauda 70; Orchesella cincta 2; Megalothorax minimus 1; Mesaphorura krausbaueri 1;*

Plagiomnium elatum (BRUCH et SCHIMP.) T. J. KOP.
Tómalom, 10. 09. 2003: *Lepidocyrtus cyaneus 1; Lepidocyrtus peisonis 2; Friesea truncata 1; Supraphorura furcifera 1;*

Plagiomnium undulatum (HEDW.) T. J. KOP.
Sopron, 27. 03. 2003: *Lepidocyrtus lanuginosus 8; Sminthurinus elegans 20; Mesaphorura macrochaeta 1; Parisotoma notabilis 5; Heteromurus major 5;* - **Sopron, 10. 09. 2003**: *Parisotoma notabilis 2; Lepidocyrtus lanuginosus 10;*

Climacium dendroides (HEDW.) F. WEBER et D. MOHR
Sopron, 10. 09. 2003: *Megalothorax minimus 4; Parisotoma notabilis 4; Folsomia penicula 12; Heteromurus nitidus 2; Lepidocyrtus lanuginosus 5; Cryptopygus bipunctatus 42; Pseudosinella alba 2;*

Thuidium philibertii LIMPR.
Sopron, 20. 03. 2003: *Heteromurus major 1; Tomocerus minor 1; Metaphorura affinis 1; Parisotoma notabilis 35; Orchesella cincta 2; Cryptopygus bipunctatus 20; Sminthurinus elegans 6; Megalothorax minimus 2; Pseudosinella alba 2;*

Thuidium abietinum (HEDW.) SCHIMP.
Fertőrákos, 06. 05. 2004: *Mesaphorura krausbaueri 2; Lepidocyrtus lanuginosus 9; Cryptopygus bipunctatus 1; Hypogastrura vernalis 48; Folsomia manolachei 41; Megalothorax minimus 1; Entomobrya nigriventris 3; Fasciosminthurus strigatus 3; Pseudosinella octopunctata 2; Isotoma viridis 2; Parisotoma notabilis 10; Heteromurus major 1; Willemia virae 1; Heterosminthurus bilineatus 2; Entomobrya handschini 4; Isotomiella minor 1;*

Campylium chrysophyllum (BRID.) LANGE
Fertőrákos, 06. 05. 2004: *Cryptopygus bipunctatus 1; Lepidocyrtus lanuginosus 2; Parisotoma notabilis 8; Hypogastrura vernalis 4;*

Amblystegium varium (HEDW.) LINDB.
Tómalom, 10. 09. 2003: *Lepidocyrtus cyaneus 1; Lepidocyrtus peisonis 5; Friesea truncata 3; Megalothorax minimus 5; Spaeridia pumilis 5; Isotomiella minor 2; Supraphorura furcifera 2; Parisotoma notabilis 2; Lepidocyrtus paradoxus 1; Neanura muscorum 1;*

Drepanocladus cossonii (SCHIMP.) LOESKE
Tómalom, 10. 09. 2003: *Lepidocyrtus peisonis 3; Lepidocyrtus paradoxus 1; Brachystomella parvula 2; Isotomurus prasinus 8; Supraphorura furcifera 1; Friesea truncata 2; Megalothorax minimus 2; Spaeridia pumilis 1; Isotomiella minor 1;*

Calliergonella cuspidata (HEDW.) LOESKE
Tómalom, 10. 09. 2003: *Lepidocyrtus cyaneus 1; Lepidocyrtus peisonis 1; Isotomurus prasinus 5; Friesea truncata 4; Megalothorax minimus 6; Spaeridia pumilis 18; Isotomiella minor 10; Supraphorura furcifera 3; Parisotoma notabilis 5; Pachyotoma crassicauda 2;*

Brachystomella parvula 1; Neelides minutus 2; Micranurida pygmaea 3; F. quadrioculata 4; Dicyrtoma fusca 2; - **Sopron, 06. 03. 2003:** *Heteromurus major 3; Lepidocyrtus lanuginosus 2; Parisotoma notabilis 5; Cryptopygus bipunctatus 220; Pseudosinella alba 1;* - **Sopron, 20. 03. 2003***:* *Lepidocyrtus lanuginosus 20; Heteromurus major 4; Tomocerus cf. baudoti 1; Cryptopygus bipunctatus 100; Parisotoma notabilis 200; Spaeridia pumilis 4; Mesaphorura hylophila 12; Doutnacia xerophila 6; Megalothorax minimus 2; Orchesella cincta 2; Heteromurus major 8; Sminthurinus elegans 2;* - **Sopron, 10. 09. 2003:** *Megalothorax minimus 1; Spaeridia pumilis 2; Parisotoma notabilis 5; Folsomia penicula 6; Sminthurinus aureus 2; Tomocerus minor 1; Heteromurus nitidus 1; Lepidocyrtus lanuginosus 6; Cryptopygus bipunctatus 2;*

Homalothecium lutescens (HEDW.) H. ROB

Fertőrákos, 06. 05. 2004: *Mesaphorura critica 4; Folsomia manolachei 73; Parisotoma notabilis 14; Heteromurus major 2; Hypogastrura vernalis 64; Fasciosminthurus strigatus 2; Oncopodura crassicornis 1; Orchesella cincta 8; Orchesella xerothermica 1; Cryptopygus bipunctatus 11; Mesaphorura krausbaueri 3; Parisotoma notabilis 4; Lepidocyrtus lignorum 2; Pseudosinella octopunctata 1;*

Brachythecium rutabulum (HEDW.) SCHIMP.

Tómalom, 10. 09. 2003: *Lepidocyrtus peisonis 4; Isotomurus prasinus 8; Spaeridia pumilis 1; Pachyotoma crassicauda 4;*

Scleropodium purum (HEDW.) LIMPR.

Sopron, 10. 09. 2003: *Parisotoma notabilis 8; Folsomia penicula 11; Lepidocyrtus lanuginosus 10;*

Eurhynchium hians (HEDW.) SANDLE LAC.

together with *Scleropodium purum* (HEDW.) LIMPR. and with *Brachythecium rutabulum* (HEDW.) SCHIMP. samples **Sopron, 06. 03. 2003:** *Mesaphorura macrochaeta 2; Lepidocyrtus lanuginosus 17; Heteromurus major 4; Orchesella cincta 6; Isotomurus cf. palustris 6; Parisotoma notabilis 35; Cryptopygus bipunctatus 47; Megalothorax minimus 2; Pseudosinella alba 1;*

Hypnum cupressiforme HEDW.

Fertőrákos, **06. 05. 2004:** *Pseudosinella alba 1; Pseudosinella octopunctata 3; Lepidocyrtus lanuginosus 7; Entomobrya nivalis 3; Folsomia manolachei 270; Parisotoma notabilis 93; Hypogastrura vernalis 32; Megalothorax minimus 2; Mesaphorura krausbaueri 23; Cryptopygus bipunctatus 58; Xenylla boerneri 145; Cryptopygus bipunctatus 88; Heterosminthurus bilineatus 2;* - **Sopron, 02. 03. 2004:** *Xenylla boerneri 400; Hypogastrura socialis 4; Entomobrya nivalis 1; Lepidocyrtus violaceus 1; Entomobrya corticalis 2; Orchesella bifasciata 1; Xenylla brevicauda 2; Xenylla maritima 1; Cyphoderus albinus 1;*

Rhytidium rugosum (HEDW.) KINDB.

Fertőrákos, 06. 05. 2004: *Cryptopygus bipunctatus 150; Hypogastrura vernalis 75; Lepidocyrtus lanuginosus 2; Mesaphorura krausbaueri 8; Parisotoma notabilis 10; Cyphoderus albinus 1; Folsomia manolachei 6; Fasciosminthurus strigatus 1;*

Rhytidiadelphus triquetrus (HEDW.) WARNST.

Sopron, 20. 03. 2003: *Tomocerus minor 1; Tomocerus cf. baudoti 2; Lepidocyrtus lanuginosus 8; Folsomia penicula 2; Heteromurus major 5; Parisotoma notabilis 10; Sminthurinus elegans 5*

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Streamflow Characteristics of Two Forested Catchments in the Sopron Hills

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Abstract – One of the central issues in hydrology is today to establish a relationship between the hydrological and biological processes in ecosystems. One question of this theme is the vegetation impact on the water budget of the catchment. Water use by vegetation can closely be linked to streamflow patterns on a variety of time scales. At present many details of these connections are poorly understood.

Investigation on small catchments is the best way of studying hydrological processes in headwater, forested watersheds. In this paper drainage basin morphology and streamflow characteristics (base flow and quick flow) have been analysed under conditions of forest management in two neighbouring small forested catchments (the Farkas Valley and Vadkan Valley located in the prealpine hills bordering to Austria) on the basis of streamflow data collected during 2001.

streamflow characteristics / small catchment / forest vegetation

Kivonat – A Soproni-hegység két erdősült vízgyűjtőjének lefolyási jellemzői. Napjainkban a hidrológia egyik központi kérdése az ökoszisztéma hidrológiai és biológiai folyamatai közötti kapcsolat megfogalmazása. Ennek a témának az egyik kérdése a vegetáció hatása a kisvízgyűjtők vízmérlegére. A vegetáció vízfelhasználása különböző időskálákon szoros kapcsolatban lehet a lefolyás mintázatával. Manapság azonban még ennek a kapcsolatnak a részletei tisztázatlanok.

A kisvízgyűjtők vizsgálata az egyik legjobb módszer a hidrológiai folyamatok tanulmányozására a felső, erdővel fedett vízgyűjtőkön. Ebben a cikkben két párba állított szomszédos kisvízgyűjtő (a Vadkan-árok és a Farkas-árok) morfológiáját és lefolyási jellemzőit (alapvízhozam és árhullámok szintjén) elemezzük az erdőgazdálkodási tevékenység hatásai alatt a 2001-es év lefolyási adatai alapján.

lefolyási jellemzők / kisvízgyűjtő / erdő vegetáció

1 INTRODUCTION

Rainfall concentration and runoff causing discharge fluctuations, is one of the central issues of hydrology. Another important question in hydrology is the impact of vegetation on the water budget of the catchment. Water use by vegetation can closely be linked to streamflow patterns on a variety of time scales (Bond et al. 2002). Several social-economic demands have a strong connection with small or bigger streamsregarding both quantity and quality of the water. Meeting or consideration of these demands is substantially complicated because knowledge about streamflow regimes is still insufficient.

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1.1 The experimental catchment

Physical and statistical features of hydrological processes have already been analysed in experimental catchments for a century. The most famous forestry projects, Hubbard Brook (Bormann – Likens, 1979) and the Coweeta Experimental Forest (Swank et al. 1988) in the USA, have been analysed using several forested watershed ecosystems. In Hungary establishment of experimental and regionally representative catchments in a wider scale and the development of their network was begun in the 1950s and 1960s , but unfortunately some of them had already been terminated in the 1970s (Szesztay 1965, Domokos 1980).

In 1954 the first forested experimental catchment was chosen and equipped with recording instruments in the Dolina Valley near the village of Kisnána by the Forest Research Institute. The main purpose of this research was to study erosion and sediment movement processes. Not far from this catchment (also in the Mátra Hills) a forest hydrological research catchment was founded in the Szárazkesző Catchment (Bánky 1959, Szőnyi 1966, Újvári 1981). Later on the Forest Research Institute commenced to study the third generation of experimental catchments in the Mátra Hills, mainly from the point of view of environmental protection. This site was established at Nyírjes (Sitkey 1994).

The Faculty of Forestry has been studying the hydrological role of forests over a century. These research activities were generally intermittent, but some of them were based on long term data collection (Firbás 1963, Führer 1979). At the end of the 1970s, on the basis of earlier studies, József Rácz established an experimental catchment area in the Sopron Hills (Rácz, 1981). The location available for establishing a hydrological experimental catchment was the totally forest covered upper watershed of the Rák Stream (Hidegvíz Valley). The extension of the whole catchment is 6 km^2 and it has several favourable features (e.g. ephemeral streams, undisturbed environment, diverse forest vegetation types, easy accessibility etc.).

In this article we present streamflow patterns of two small catchments of the Hidegvíz Valley on the basis of one year's data. Both catchments are of a similar magnitude: 0.6 and 0.9 km2. We have analysed in detail some hydrological elements: Patterns of rainfall, discharge, rainfall-induced flood waves, and basic discharge in drought periods. Variances of these parameters have been analysed in relation to the surface of the catchments, vegetation coverage and forest management.

2 MATERIAL AND METHODS

2.1 Study area

The model catchments are placed in the Hidegvíz Valley, at the foothills of the Alps, (*Figure 1*) at following geographical coordinates:

ρ (latitude) = 47-40-24;
λ (longitude) = 16-27-49.

Figure 1. Location of model catchments

2.2 History of measurements of discharge and other parameters

Discharge measuring was started in 1992 in the the Farkas Valley stream (Kucsara – Vig 1993). The volumetric method was adopted. This measurement period was continued in 1993 and 1994 in both catchments. In these years we made expedition measurements when we tried to measure flood wave shapes on rainy days. Soon it became obvious that only continuous measuring can provide enough data for analysis of these phenomena.

In 1995 gauging stations were established at the catchment outlets (*Figure 2*). In the beginning the water level was measured by a float. These instruments operated with frequent mechanical breakdowns, resulting in a lot of missing periods.

In the year 2000, the water level measuring instruments were changed. We chose sensors functioning on the principle of water pressure. These sensors provided more reliable discharge time series data since 2001.

Figure 2. Gauging station

A data logger records water level values every second minute. In order to convert the water stages into discharge values we used an empirical stage-discharge relation (Kucsara et. al. 2000).

Besides the water gauge at catchment outlets, meteorological data (e.g. rainfall with 0.1 mm precision, air and soil temperature, air humidity, net radiation, wind direction, gusts, speed) and other hydrological parameters (e.g. interception) have been measured in an opening and in different forest sites in the catchments.

2.3 Morphology

Drainage basin morphology data (characteristic physical parameters calculated on the basis of works of Lee (1980) and Hewlett (1982)) are presented in *Table 1*.

Table 1. Characteristic physical parameters of the two catchments

Physical parameters	Farkas Valley	Vadkan Valley
Area of catchment (A) (km^2)	0.62	0.92
Length of catchment (L) (m)	1320	1340
Perimeter of catchment (m)	4680	5140
Shape		
Form factor [catchment area]/[catchment length]^2	0.36	0.51
Mean width (A/L) (m)	470	690
Greatest width (m)	602	880
Average length of overland flow (A/L*1/2) (m)	235	343
Mean height (m.a.s)	489.83	484.51
Lowest point (m.a.s.)	401.88	403.25
Highest point (m.a.s.)	549.00	555.80
Total relief (m)	147.12	152.55
Slope steepness (° and %)	20.3° (34.7%)	18.6° (31.9%)
Stream channel length [sum{main channel}] (m)	1170 {1170}	1685 {1418}
Channel slope (° and %)	4.4° (7.7%)	3.2° (5.5%)
Drainage density (length of cannel/surface area [km/km^2])	1.89	1.83
Average exposure of catchments	W-NW	N-NW

The table shows that the physical parameters of the two catchments are similar, but the Farkas Valley is a narrower watershed and has a steeper hillside than Vadkan Valley.

2.4 Geology and Soils

The geology of the two investigated catchments is crystalline bedrock deposited in the Tertiary (Miocene) period, and fluvial sediment, which is strongly unclassified. The fluvial sediment was deposited in five layers. The lowest layer is called the Brennberg Lignite Formation. Above it there is a thick fluvial sandy-gravel layer called the Ligeterdő Gravel Formation.

The lower beds (with prevailing metamorphic pebbles and conglomerates), are distinguished as the Alsóligeterdő Formation while the subsequent bundles of beds as the Felsőligeterdő Formation. The middle part of the formation with lignite strings and Congeria-bearing beds is called the Magasbérc Sand Formation. The letter formation is capped with gravel and conglomerate beds of the Felsőtödl Gravel formation. These formations of the Ottnangian and Carpathian ages are up to 500 meters thick.

Only the two upper layers appear on the surface. On the hilltop and hill-slope the Felsőtödl Gravel Formation can be found. The thickness is 10 - 50 meters. This contains coarser gravels and finest loam, and is therefore strongly unclassified. On the valley bottom, the finer material of the Magasbérc Sand Formation appears everywhere. These layers are a good aquifer, so both valleys have a perennial streamflow. Streams never dry out, not even in driest periods (Kisházi – Ivancsics 1981-85).

On the basis of fluvial sediment, podzolic brown forest soils, highly acidic non-podzolic brown forest soils and lessivated brown forest soils have evolved. To a small extent eroded skeletal soils and on the bottom of the slopes also colluvial soils can be found. All soils have a 70-80 cm deep and water retaining loamy layer producing subsurface flow.

2.5 Characteristics of the Vegetation Cover

Both catchments and their surroundings have been totally covered by forest for hundreds of years.

The catchments are basically similar from the point of view of forest coverage, but show some small differences:

In the Vadkan Valley 59.6% of the catchment's area is deciduous (mainly beech and oak) 37.7% coniferous (mainly spruce) forest in contrast to Farkas Valley, where 40.7% is deciduous, and 53.1% is coniferous forest. The main conifer species is spruce (*Picea abies*) and the main deciduous is beech (*Fagus sylvatica*). These species have different hydrological behaviours. Spruce has a higher interception capacity (more than 40% of the yearly precipitation), and a higher transpiration constant, and has therefore a dryer impact. Beech has more favourable features, smaller interception (20-25%) and is directing its streamflow along the root systems into the soil. These species also have different forest floor cover. In the bottom of the valleys another species, alder (*Alnus glutinosa*) is the dominant species.

For the last few years a lot of clear-cutting took place in this area. In the year 2001 clear-cutting areas were bigger and closer to the stream system in the Farkas Valley therefore it probably had an effect on the runoff.

There is a difference between the shares of road areas within the two catchments. The road area is more than twice as big in the Farkas Valley (6.2 %) than in the Vadkan Valley (2.7%). These roads can modify runoff processes: e.g. they can separate or even detach areas from the catchment and they can slow or accelerate surface runoff.

3 RESULTS AND DISCUSSION

3.1 Water Yield

In 2001 the annual runoff patterns of two small catchments showed both similarities and differences As a first comparison let us have a look at the daily water yield time series, mm/day. *Figure 4* shows unequivocally the similarity of the streamflow patterns. There is a similar tendency of the time series of base flow, and the impact of rainfall is similar to the two smaller catchments' runoff. Direct runoff values vary differently in the two catchments, but the base flow is always higher at the Vadkan Valley.

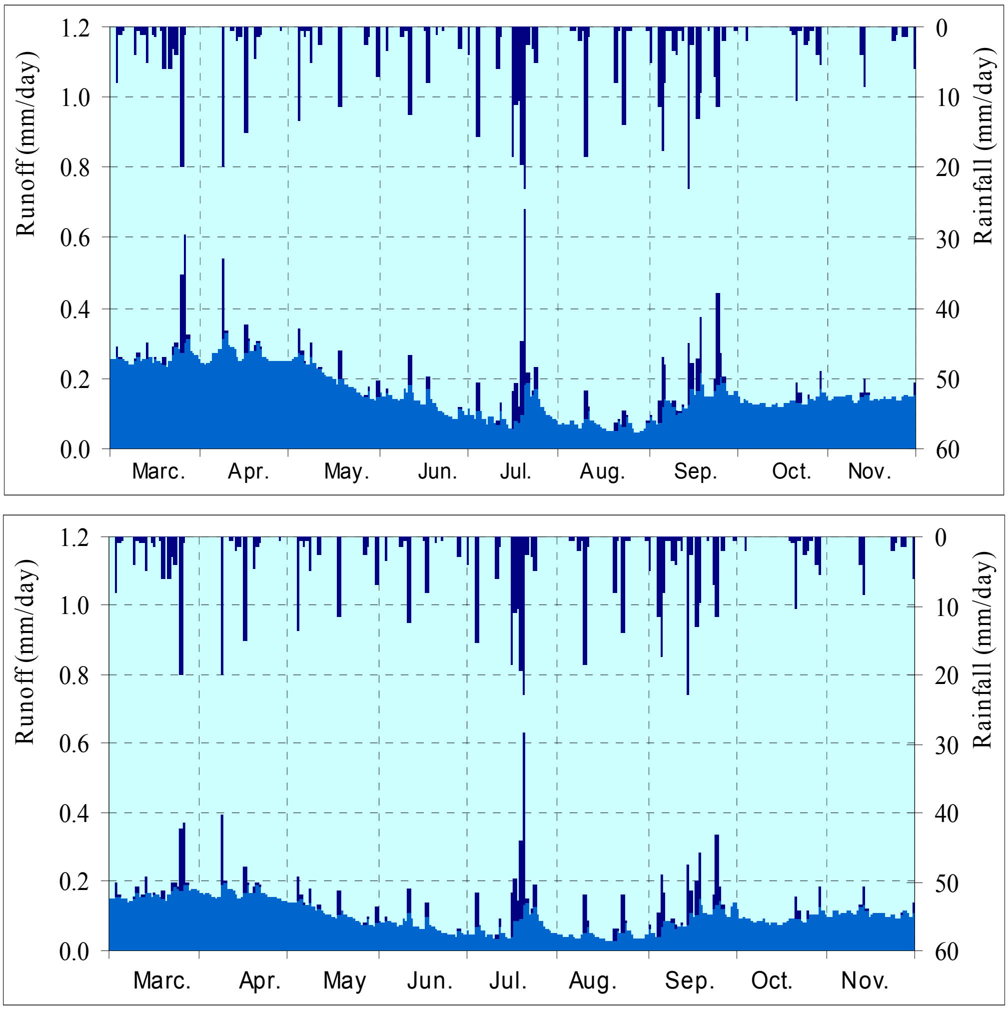


Figure 3. Streamflow patterns of Vadkan Valley (above) and Farkas Valley (below) in 2001

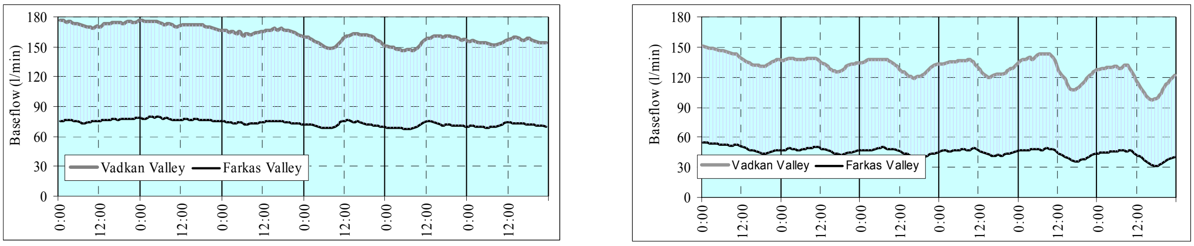
3.2 Base Flow

Originating from groundwater outflow the resultant base flow patterns show a characteristic annual rhythm. This rhythm is mainly influenced by longer rainfall periods filling up pores in the soil and seeping out.

Forested catchments have their own base flow diurnal fluctuation (Förtge 1996, Bond et al. 2002, Gribovszki 2002), which reflects the daily rhythm of other hydrological parameters.

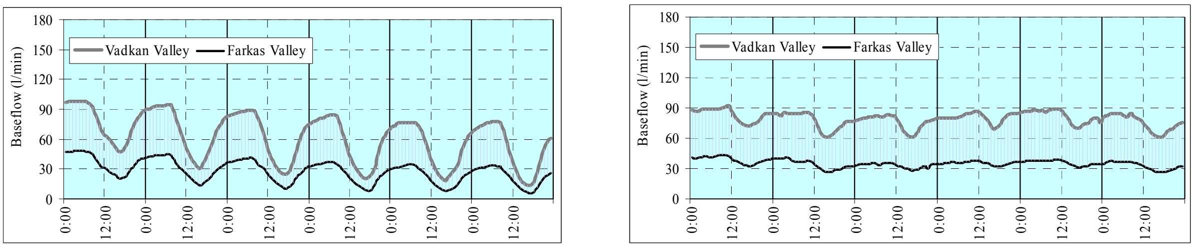
Diurnal fluctuation has different typical forms at different periods of the year. Four characteristic periods have been identified (*Figure 4*):

- Normally at the end of winter (2001 in March and at the beginning of April), when soil surface temperatures fluctuate around zero, streamflow discharge has its minimum in the early morning and its maximum early afternoon (*Figure 4 a*).
- After freezing stops (from May in 2001) the transpiration impact of vegetation becomes more and more relevant. Maximum discharge appears in the morning and the minimum in the afternoon (*Figure 4 b*).
- As the summer becomes warmer, water consumption of vegetation and its impact on the hydrological regime intensifies and the amplitude of the streamflow's daily increases significantly (*Figure 4 b-c*). This amplitude, in terms of per cent of base flow starts from 2-3% in early May and rises to 45-50% in July (*Figure 4 b-c*). The daily rhythm amplitude of temperature in winter is commonly much smaller than transpiration amplitude.
- In October the transpiration- (summer) and temperature- (winter) induced diurnal rhythms overlap (*Figure 4 d*). The transpiration-caused rhythm can be detected even at the end of October.



a) March 29. – April 3.

b) May 12 – 17.



c) July 26 – 31.

d) October 10 - 15

Figure 4. Typical shapes of the diurnal fluctuation in 2001

Table 2 shows some characteristic values (time of minimum, time of maximum, amplitude) of base flow diurnal rhythms in 2001 (Gribovszki et al. 2004). The data show the time of the minimum and maximum discharge and amplitude of the base flow through the year modified by the impact of vegetation and the effect of frost.

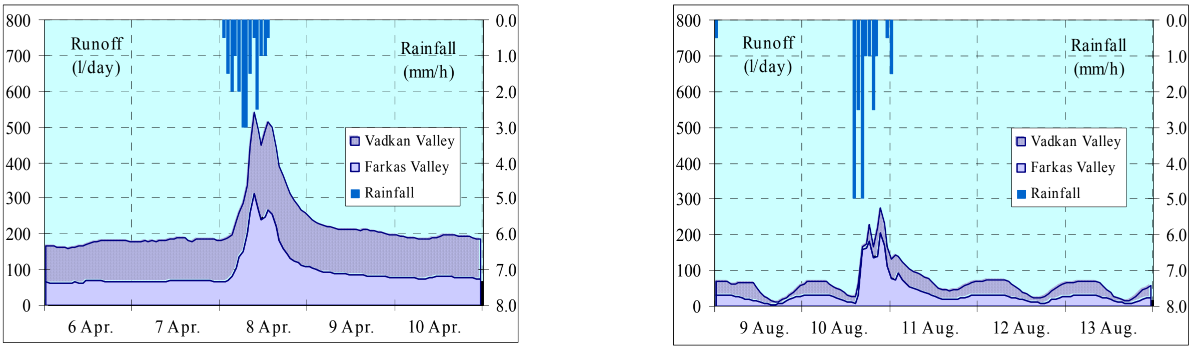
Table 2. Diurnal fluctuation features of the Vadkan Valley base flow in 2001

Date	Time of base flow minimum value (h)	Time of base flow maximum value (h)	Amplitude of diurnal fluctuation (l/min)
Mar. 14 – 20	8:00	14:00	19
Apr. 10 – 16	5:00	14:30	26
Jun. 03 – 09	15:00	5:30	50
Jul. 25 – 31	15:30	5:30	113
Aug. 13 – 19	16:00	7:00	110
Sep. 07 – 13	15:00	7:00	54
Oct. 10 – 16	15:00	8:30	38
Nov. 03 – 09	23:30	14:30	12

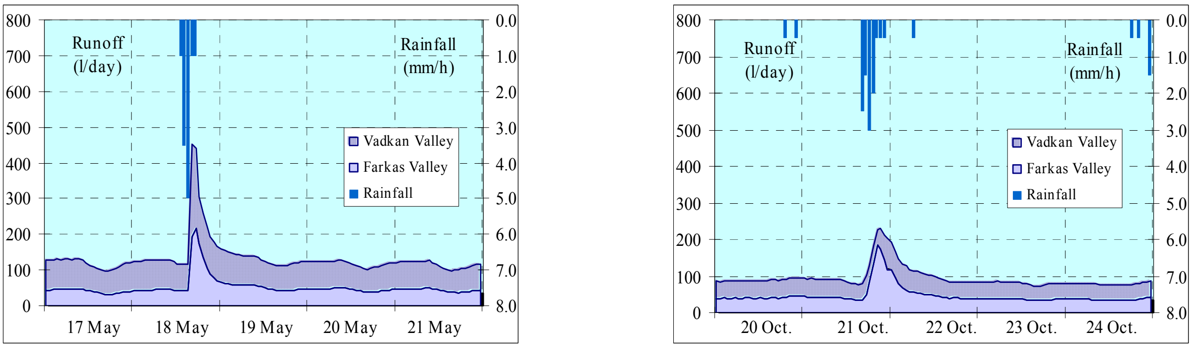
3.3 Stormflow

The runoff of catchments depended mainly on the various rainfall events during the year 2001:

- Even modest rainfalls increased the streamflow discharges. After rain begins, the discharge immediately rises. The reason for this phenomenon is that the less permeable surfaces have less infiltration and more overland flow (*Figure 5 d*).
- Short, high intensity rainfall (shower) causes significant surface runoff (*Figure 5 c*). Water concentration is very quick and peak discharge manifests itself in a few minutes in these small catchments.
- Longer, protracted rainfall causes a protracted flood wave, where the shape perfectly follows rainfall characteristics (*Figure 5 a and b)*
- In spring and autumn flood waves settle onto a non-periodic base flow. Separation of flood waves is simple (*Figure 5 d*). But on hot summer days, a shower-caused flood wave cannot be separated without taking the diurnal fluctuations into consideration (*Figure 5 b*).



a) April 6 – 10. b) August 9 – 13.



c) May 17 – 21. d) October 20 – 24.

Figure 5. Typical shapes of characteristics hydrographs in 2001

Table 3 shows characteristic rainfall-induced flood wave features. The data of *Table 3* show that only a small part of the big storm's rainfall was transformed into direct runoff. Hydrologic response variability is fairly big, because it depends on continuously changing environmental parameters. The first three rows show a seasonal tendency. At the end of the dormancy season, the runoff was bigger, because the soil's pore capacity was filled and sometimes frost appeared on the surface. As the weather became warmer and vegetation transpiration began, water storage capacity of catchments was reduced and not only the base flow but the same magnitude of rainfall-induced stormflows also decreased in volume (by July hydrologic response was reduced to less than one fifth of the original value in March).

Table 3. Some features of characteristic flood waves

		Vadkan Valley (93.3 ha)			Farkas Valley (62.2 ha)		
Period	P Precipitation (mm)	Volume of flood wave (m^3)	Q_s Storm discharge (mm)	$\alpha = Q_s/P$ Runoff coeff.	Volume of flood wave (m^3)	Q_s Storm discharge (mm)	$\alpha = Q_s/P$ Runoff coeff.
Mar. 25-26.	20.0	488	0.52	0.026	221	0.36	0.018
Apr. 08-09.	20.0	212	0.23	0.012	129	0.21	0.010
Aug. 10-11.	20.0	86	0.09	0.005	82	0.13	0.007
Jul. 19-20 .	40.0	654	0.70	0.018	447	0.72	0.018
Sep. 24-25.	11.5	309	0.33	0.029	151	0.24	0.021

Besides the drainage basin's morphology and instantaneous (actual) hydrological conditions (e.g. saturation, vegetation cover), the amount and intensity of rainfall has a dominant effect on runoff processes. In July 40 mm of rainfall recharged the subsurface storage capacity of catchments, and produced a significant stormflow. However a smaller rainfall had the biggest runoff coefficient in 2001. It was the 11.5 mm of precipitation (last row of Table 3.), which had induced a fairly big stormflow, because earlier rainfalls (until this time in September 108.5 mm) recharged the storage capacities of the catchments. Under these conditions the runoff coefficient in these forest covered catchments had not even reached 0.03 (3%) value.

Comparing the two catchments we can generally say that the volume of stormflows in the Farkas valley was generally smaller than in the Vadkan Valley (Table 3), but water concentration is faster and falling limbs of flood waves are steeper in the Farkas Valley. The reason for this must be that there is a bigger area of less permeable surfaces and steeper slopes of the Farkas Valley.

During the summer period both peak discharges and the volume of flood waves of the Farkas valley stream gradually reached and sometimes exceeded the same values in the Vadkan Valley stream (Table 3 and Figure 5). The reason for this change could be a clear cutting, which had been done along the stream banks, very close to the Farkas Valley outlet. This activity significantly increased the area of surface runoff.

4 SUMMARY AND CONCLUSIONS

Because of their high sensitivity, small catchments are very useful to investigate hydrological elements, their interactions and the impact of different human interferences (e.g. clear cutting) on them.

In 2001 the annual total of precipitation (607 mm) was under the long term annual mean (917 mm/a). Figure 6 shows precipitation, stormflow and baseflow annual pattern as specific values (in mm) for each month,illustrating that:

- In 2001 the annual runoff volume of the Vadkan Valley and the Farkas Valley catchments were only 10% and 7% respectively of the annual precipitation total;
- Streamflow mainly got its supply from baseflow (groundwater outflow) and only a small part of the streamflow (Vadkan Valley 11.0% and Farkas Valley 7.2%) was produced by direct runoff (stormflow);

- Annual streamflow (with its dominant component baseflow) has a standard regime in our climate, which shows a spring maximum and a summer recession, but these regular patterns can be modified a little by rainfall e. g. a rainy period in summer can also raise the base flow but can not fundamentally change the seasonal rhythm.
- While there were only minor differences between the annual stormflow volumes of the two investigated catchments (Vadkan Valley 4.4 mm/a and Farkas Valley 4.3 mm/a), the differences between their annual base flow volumes (their average ratio being 3:2) were caused by the geological, pedological, vegetation, etc. characteristics of the two catchments.

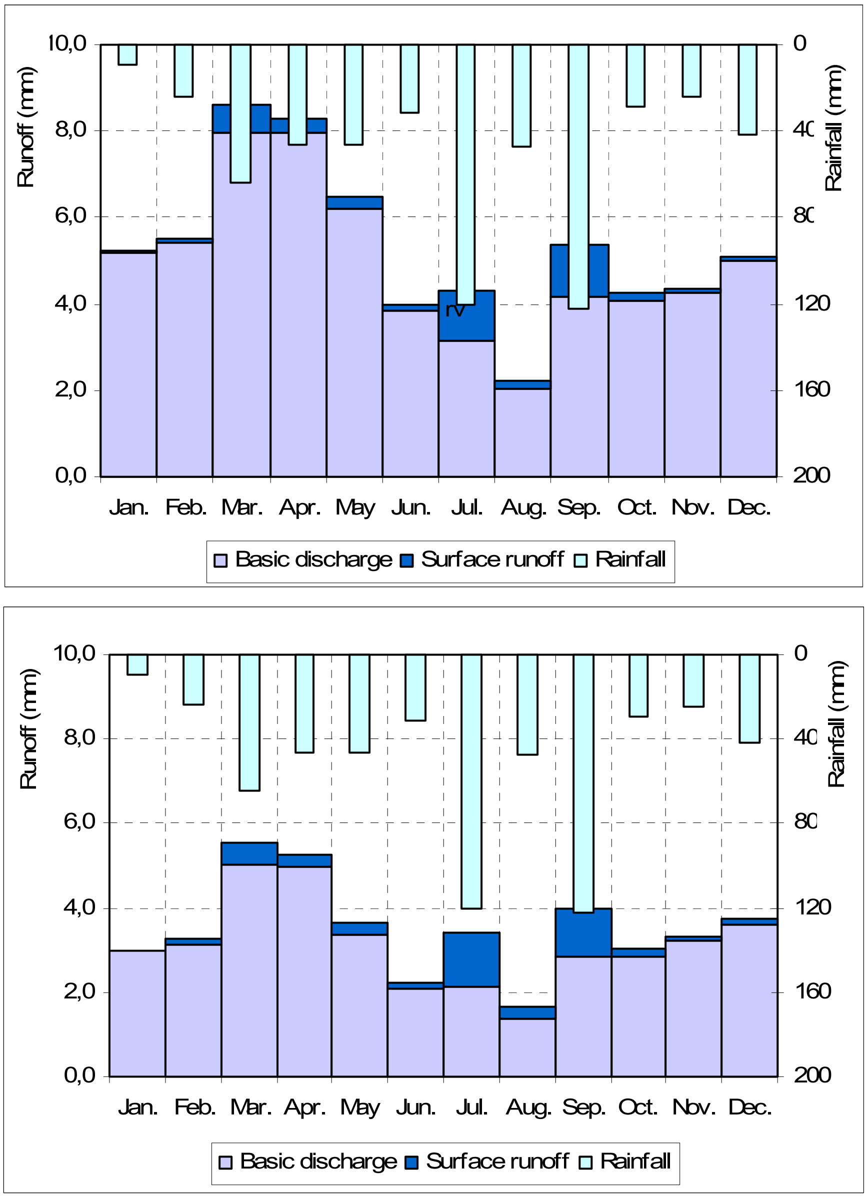


Figure 6. Monthly values of base flow and stormflow of Vadkan (above) and Farkas Valley (below)

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The Effect of Moisture Content on the Micro-damage Processes of Spruce Wood, Investigated by Acoustic Emission Method and Electron Microscopy

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Abstract – Spruce was investigated by acoustic emission during tensile tests. The examined moisture contents were 0%, 12%, and 26%. The fracture surfaces were photographed using electron-microscopy. The experiments showed, that micro-damage processes start near the ultimate strength, regardless of moisture content. This indicates the brittle behaviour of wood.

The analysis of detected acoustic events at different moisture contents indicated that the number and properties of events supposedly resulting from breaking do not change with increasing moisture content. Decrease occurs in the total number of events at higher moisture contents as a consequence of the increasing acoustic attenuation of wood and the elimination of friction type events. Electron microscopic analysis of fracture surfaces supports the result of acoustic emission experiments. The fracture surfaces showed characteristic brittle tension and shear across the cell wall of different cells. Based on both investigations we can say that wood has brittle fracture characteristics in the 0-30% moisture content range.

acoustic emission / wood / brittle fracture / damage process / moisture content

Kivonat – A nedvességtartalom hatása a lucfenyő mikro-tönkremeneteli folyamataira, vizsgálatok akusztikus emissziós módszerrel és elekron mikroszkóppal. Lucfenyő húzóvizsgálat során mutatott akusztikus emisszióját vizsgáltuk 0%, 12%, 26% nedvességtartalom mellett. A tönkremeneteli felületekről EM képeket készítettünk.

A vizsgálatok azt mutatták, hogy a nedvességtartalomtól függetlenül a tönkremeneteli folyamatok csak a törőterhelés közelében indulnak meg döntően. Ez a faanyag rideg törési természetére utal. A különböző nedvességtartalmi osztályokban kapott akusztikus események vizsgálata azt mutatta, hogy feltehetően törésből származó jelek száma és tulajdonságai nem változnak a nedvességtartalom növekedésével. A nagy nedvességtartalom mellett megfigyelhető eseményösszeg csökkenést feltehetően a faanyag növekvő akusztikus csillapítása és a súrlódásos jellegű események eltűnése okozza. A törési felületek elektronmikroszkópos vizsgálatai alátámasztották az akusztikus emissziós vizsgálatok eredményeit. A törési felületek jellemzően sejtfalon átmenő rideg szakadási és nyírási törési felületeket mutatnak. Mindezek megerősítik, hogy a faanyag nedvességtartalomtól függetlenül rideg törési természetű a 0-30% nedvességtartalmi tartományban.

akusztikus emisszió / fa / rideg törés / tönkremeneteli folyamat / nedvesség tartalom

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1 INTRODUCTION

The phenomenon of acoustic emission (AE) is related to elastic waves originating from the release of stored energy due to mechanical loading in solid materials. The source of these acoustic events in case of wood are fibre breakage, cracking, crack propagation and friction type events due to the movements of crack surfaces. The fracture of wood is accompanied by noise in the audible range. However, this phenomenon often starts just above the 90% of the ultimate strength. On the other hand, the damage process start earlier, at about the 40-50% of the ultimate strength. According to Hansel (1980), the frequency range of AE events is 50 kHz to 1.5 MHz. Most researchers typically use a much narrower range. In case of wood, piezoelectric transducer with 150-200 kHz resonant frequency were used (Rice 2001; Kowalski 2004). Based on our own frequency analysis of AE events we established that the analysis of 20-100 kHz frequency domain is also necessary, because wood shows significant AE activity in this range. This range was examined by other researcher too (Reiterer 2000). Because of this, our researches were also carried out with wideband transducers, sensitive between 20 and 250 kHz frequencies (Kánnár 2004).

The AE method was applied successfully in many fields of wood science and technology in the last 30 years. Porter (1972) used AE to predict failure in finger joints. The closer the load was to the ultimate strength, the more precise the predictions were. Ansell (1982) examined the effect of different proportion of earlywood to latewood in Parana pine and Douglas-fir. He established that the logarithmic sum of events as a function of strain shows a linear characteristic in case of Parana pine that has a narrow late wood, but is more irregular in case of Douglas-fir that has a more pronounced late wood.

Molinski (1994) examined the crack formation in wood due to cyclic moisture content changes. He observed partial damage in wood as early as in the first cycle of wood drying/wetting treatment. This decreases the resistance of wood to internal stresses created during wetting. Wood shows a kind of fatigue. Cracks created - like mechanical loads - cause increase in the AE activity, even at stress levels lower than the original.

Poliszko (1994) examined the relationship between water bonding energy in wood and its mechanical strength. He found it theoretically possible to determine the long term behavior and the structural fracture of wood based on short term tests. Reiterer (2000) investigated the AE of notched hardwood and softwood specimens during splitting test. He experienced that there are characteristic differences between the two groups. Conifers showed tenacious fracture and produced a high number of AE events, while hardwoods showed brittle fractures and created a lower number of events. Gozdecki (2005) used the method for detecting failures of adhesive-bonded joints. He found it possible to predict the development of the destruction of an adhesive joint on the basis of the increasing cumulative AE count combined with tangential stresses determined by the finite element method.

Based on the literature, the AE technology is applicable for testing wood and wood products. The presented investigation shows that the number and properties of detected AE events depend on the wood species, moisture content, applied stresses and the load history of the specimen. Research orientation is very diverse; each researcher used different AE apparatus and detectors, therefore results are hard to generalize. Most of the investigations are applied research projects. However, the underlying relationships between the measured AE signals, mechanical properties and fracture processes of wood are not very well known. Basic research is therefore needed to reveal these relationships.

2 MATERIAL AND METHODS

Spruce (*Picea abies*) species were tested in tension parallel-to-grain in RL plain, at three moisture contents (*Figure 1*). The weakening of the specimens' middle section caused the fracture to occur there or start from that location. The measurement setup allowed events that originated from locations other than the tension mid-region (the mid 30 mm) to be filtered out, based on time delay differences between the two transducers. This is important, because many events originated at the grips because of the combined stress state and events originated in the 8mm thick section too. Each series contained 25 specimens. The moisture content levels used were 0%, 12%, 26%. The applied acoustic emission (AE) apparatus was a Defectophone (KFKI Hungary) with two logarithmic amplifiers (*Annex*) and two wideband piezoelectric-transducers type SE1000-H (*Figure 2*). The examined frequency domain was 20-250 kHz. The applied threshold was 22 μV. The examination of 20-100 kHz range seemed to be essential due to the preliminary analysis, which showed ca. 30% of the total events are in this range (Kánnár 2004). The coupling material was silicon grease. The characteristic fracture surfaces were captured via electron microscopy (EM) (ETH Zürich).

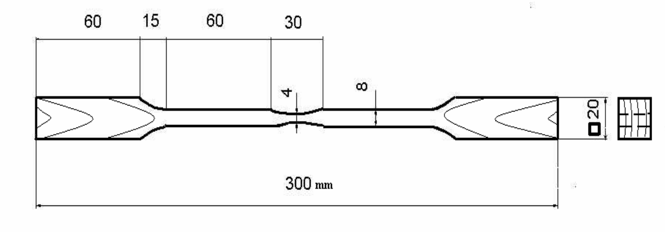

Figure1. Specimen detail (units: in mm)

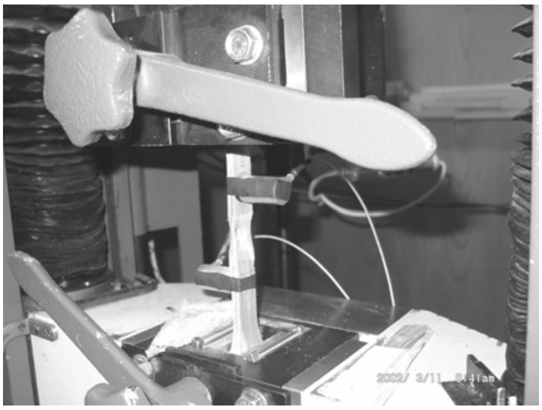

Figure 2. Fastening the transducers on the specimen with rubber bands

3 RESULTS

The experiments showed that the AE processes start at stress levels near the ultimate strength in most cases (*Figure 3 and 4*). Because the sources of AE are breaks, cracks and the friction of fracture surfaces, this implies brittle behaviour in wood. This behaviour did not change with increasing moisture content. At higher moisture content levels fewer events were detected, but the starting point of the micro-damage process did not vary. Drawing further conclusions concerning the relationship between AE processes and moisture content was difficult, because the investigation of AE processes of several specimens - made of the same wood species - did not give an unequivocal picture about the AE behaviour of wood. Some specimens broke producing a few events while in other cases several hundred events could be detected (*Figure 3 and 4*). The reason for this anomaly is that failures may be initiated at various points within the full volume of the stressed specimen, which progress randomly towards one another (Bariska 1985). Additionally, the advancement of micro-damage processes is a function of the particular specimen's biological and anatomical structure.

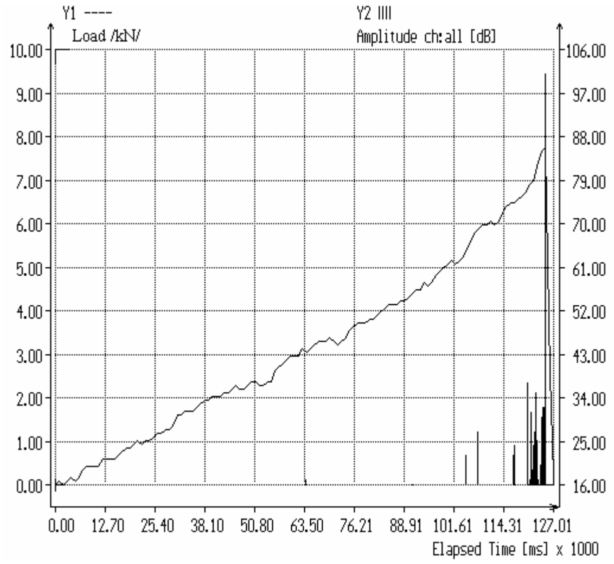

Figure 3. Acoustic activity of spruce specimen no. 6 at 12% MC

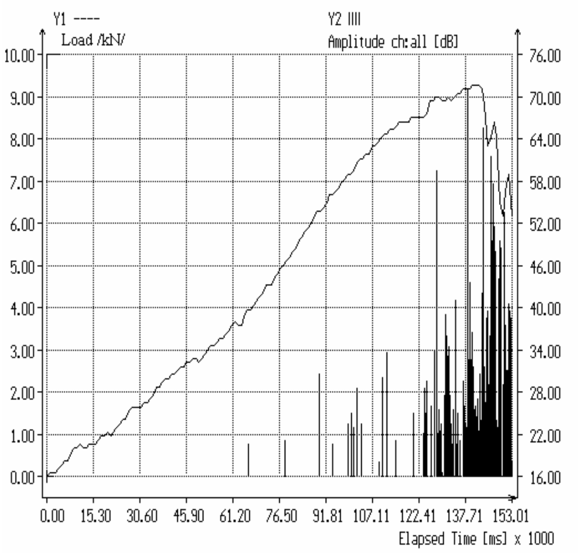

Figure 4. Acoustic activity of spruce specimen no. 10 at 12% MC

Based on the above considerations, the data resulting from specimens with equal moisture content were pooled and examined in clusters. These clusters consist of 3000-6000 acoustic events each, which are representative in terms of the AE properties of wood. Valuable conclusions can be drawn from the examination of the distribution of AE events concerning the fracture behavior of wood.

First the frequency curve of event amplitudes are presented for the three investigated moisture content (MC) classes (*Figure 5*).

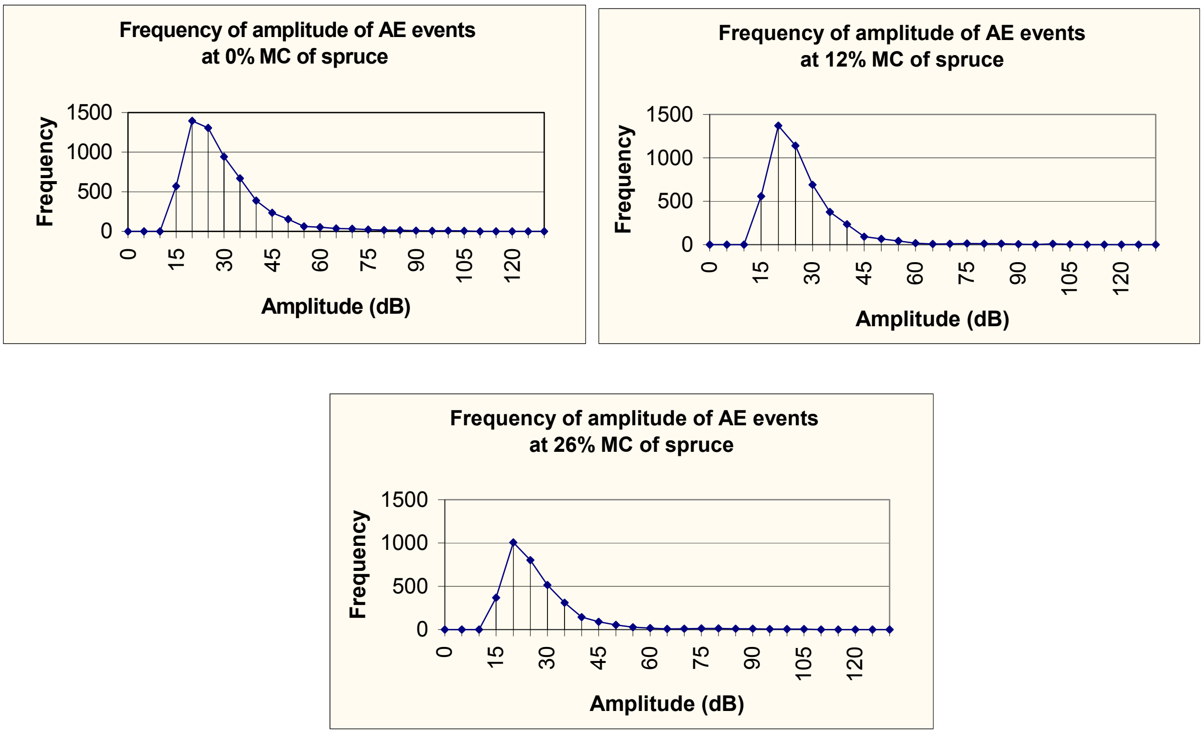

Figure 5. Frequency of amplitude of AE events at different MC of spruce

Comparing the three amplitude frequency functions, it is established that they are almost the same. Maximum frequencies are in the 20 dB range and the amplitude domain is 15-60 dB in all cases. (Amplitude values may be converted from dB to Voltage using the $U_{amp}(V) = 0.4x10^{(AMP\ (dB)-100)/20}$ relationship. Accordingly, 20 dB and 60dB correspond to 4μV and 4 mV, respectively). Let us compare the frequency functions with the total number of events detected in each moisture content class, which have an equivalent with the sample size. At 0%, 12% and 26% moisture content levels 5707, 4697 and 3180 events were registered, respectively. Comparing the frequency functions we can say that there is a considerable decrease mainly in the higher amplitude domain in case of 0% and 12% MC. The decrease did not influence the maximum frequency. The additional increase of MC affected the maximum frequency, and all other frequencies decreased proportionally. Based on the ditribution function the following conclusions can be drawn:

Despite the fact that most mechanical properties, e.g. strength, change considerably with increasing MC (Kollmann 1982), the most-frequently-experienced micro-damage event amplitude does not change. Accordingly, changes in the nature of the damage processes cause the frequency to decrease in the higher amplitude range. This due partly to the increased acoustic attenuation, which increase with 5-7% at the 0-30% MC range in a distance 0-30mm (Kánnár 2004).The other reason is the changes of deformation properties with increasing MC.

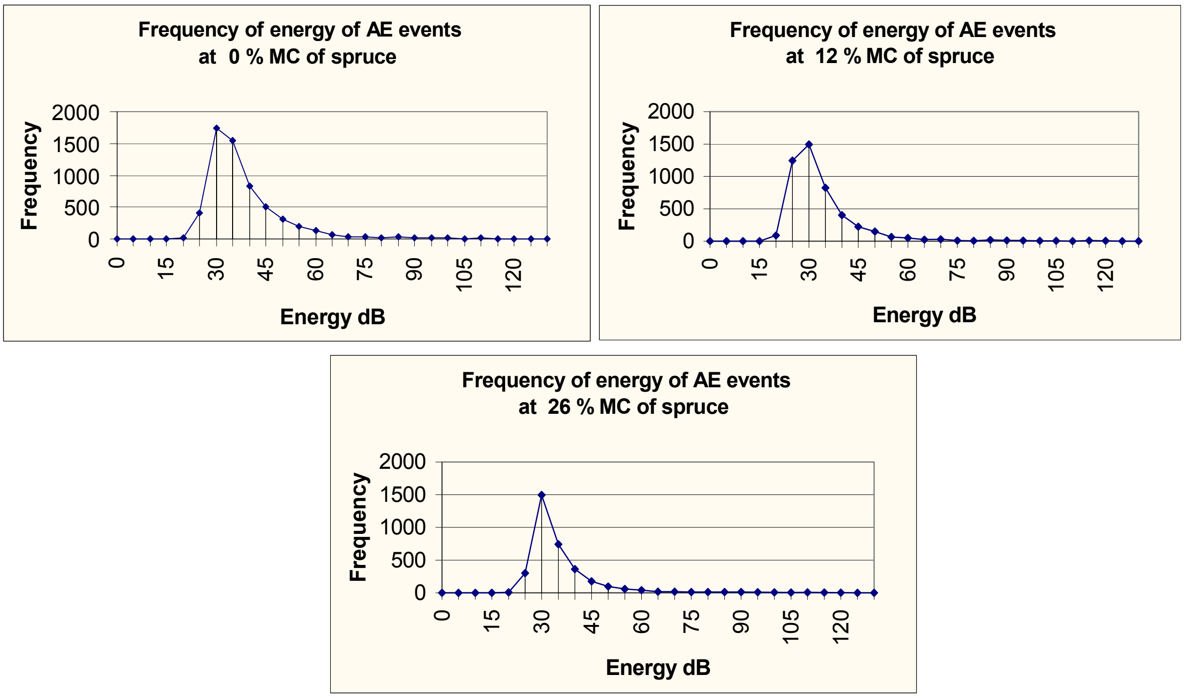

Figure 6. Frequency of energy of AE events at different MC of spruce

Further conclusions can be drawn based on the analysis of energy-frequency distribution functions (*Figure 6*). The energy-frequency curves show that the maximum frequency is given in the 30 dB energy domain in all cases. (The conversion of dB to picoJoule $E\ (pJ) = 2.75x10^{-6}x\ 10^{(E\ (dB)/10}$ accordingly, 30 dB and 60dB correspond to $2.75x10^{-3}$ pJ and 2.75 pJ, respectively.) The character of the curves is similar, but the second most frequent energy class varies, being at 35 dB ($8.69x10^{-3}$ pJ), 25 dB ($8.69x\ 10^{-4}$ pJ) and 35 dB, at 0%, 12% and 26%, respectively. Also, at 26% MC, the frequency in the second most frequent class is considerably smaller than at 0% MC. At 12% MC, the second highest frequency occurs at an energy level ten times lower than at 0%. The observable decrease in the sum of events with increasing MC causes the decrease of high-energy events. In the meantime, the event number is three time bigger in the 20 dB class at 12% MC as it is at 0% MC.

Further increase in MC causes event numbers to decrease at 20dB energy range, which falls back to the value detected at 0% MC. The energy domain is 20-60 dB in all cases. The following assumptions may explain the phenomena experienced:

- In case of 0% MC, the existing drying cracks generate a high number of friction type events, due to the friction of crack surfaces. Coupled with the smaller acoustic attenuation of dry wood, this gives rise to a large number of high energy events.
- At 12% MC, bound water between cellulose microfibrils and between cellulose and lignin allows bigger deformations without micro-damages. Wet wood contains fewer cracks, therefore there are fewer friction type events too. The measured event energy is lower due to the higher MC.
- In case of 26% MC the fibre walls are nearly saturated with water. The water molecules relax the hydrogen-bonds between the micro-fibrils and allow slipping without generation friction-type acoustic emission, or the energy level of friction-type events is below the threshold level. Accordingly the disappearance of small energy friction-type events causes less event frequency in the 20 dB energy range.

The number of events in the maximum frequency class was nearly the same in all three cases. This indicates that the number and character of fracture-type events do not change with changing MC. Any change in the frequency curve probably originates from changes in friction-type events and acoustic attenuation.

Next, event rise time functions were examined. The rise time is defined as the time elapsed until events reach their peak amplitude. The rise time characterizes how fast micro-damage process arises. With the use of rise time the approximate ratio between fracture- and friction-type events may be determined. The following figures show the rise time-frequency distribution function for the three MC ranges (*Figure 7*).

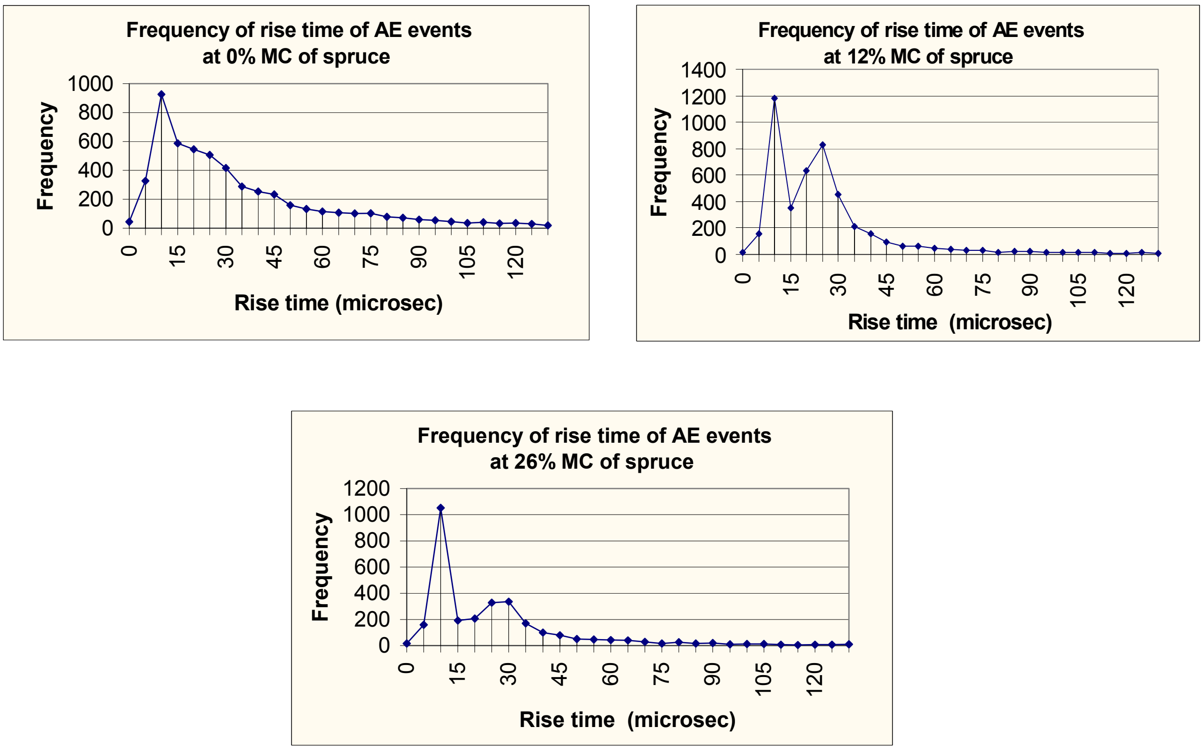

Figure 7. Frequency of rise time of AE events at different MC of spruce

The analysis of the three functions showed that they are similar, but observable differences can be found in the 15-100 µs rise time range. In all three cases, events with 10 µs rise time, presumably originating from fracture-type events, are dominant, and this does not change notably with MC. The characteristic rise time range is 0-100 µs at 0% MC. This range shrinks to 0-60 µs at 12% MC and shows no further change at 26% MC. However, there are differences between the latter two MC classes in terms of frequencies in the 20-50 µs range. At 26% MC, half as many events were detected in 20-50 µs range than at 12% MC. Comparing this phenomenon to the sample size of AE events at the three MC levels we can say that the decreasing event number detected at increasing MC's did not affect the number of events in the maximum frequency class. The decrease occurred in the higher rise time domain. If we accept the assumption, that shorter and longer rise times are related to fracture and friction, respectively, we can make the following statements:

- At 0% MC friction-type events, generated at drying crack surfaces, cause higher frequencies in the 15-60 µs rise time range.
- In case of 12% MC the frequency of the 10 µs class slightly increases. This supposedly indicates an increase in the number of fracture-type events. The characteristic rise time range shrinks from 0-100 µs to 0-60 µs. The total number of events in this smaller range is approximately the same as at 0% MC. Increasing MC causes long rise time events to disappear.
- Increasing MC to 26% MC does not change the typical15-60 µs rise time range. The number of events in the 15-60 µs range, however, decreases to one half, however it remains unchanged at its maximum of 10 □s.

In summary, we can say that increasing the MC causes decrease in the number of friction type events. The number of fracture type events does not change considerably with changing MC. Thus, analysis of the rise time function supports the results of energy function analysis.

To verify the conclusions of AE experiments, SEM images were taken of the fracture surfaces at each MC level. The characteristic fracture modes were tension and shear at all MC content levels, so these two types were analysed in all cases (*Figure 8*).

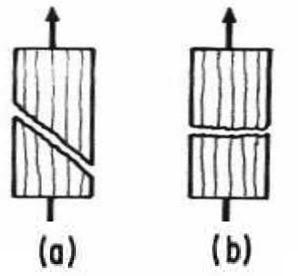

Figure 8. Fracture modes of spruce specimens (a.) shear, (b.) tension

Figure 9 shows the fracture surface of spruce at 0% MC. The left-hand picture shows a view of the fracture surface. It demonstrates that most tracheids showed brittle transwall failure, but at certain points, bundles of tracheids were pulled out. The right-hand picture shows one of the extracted tracheids packets, along with brittle shear fracture on their lateral surfaces.

Shear failure is actuated along ray parenchyma cells, that constitute critical cross-sections in terms of shear.

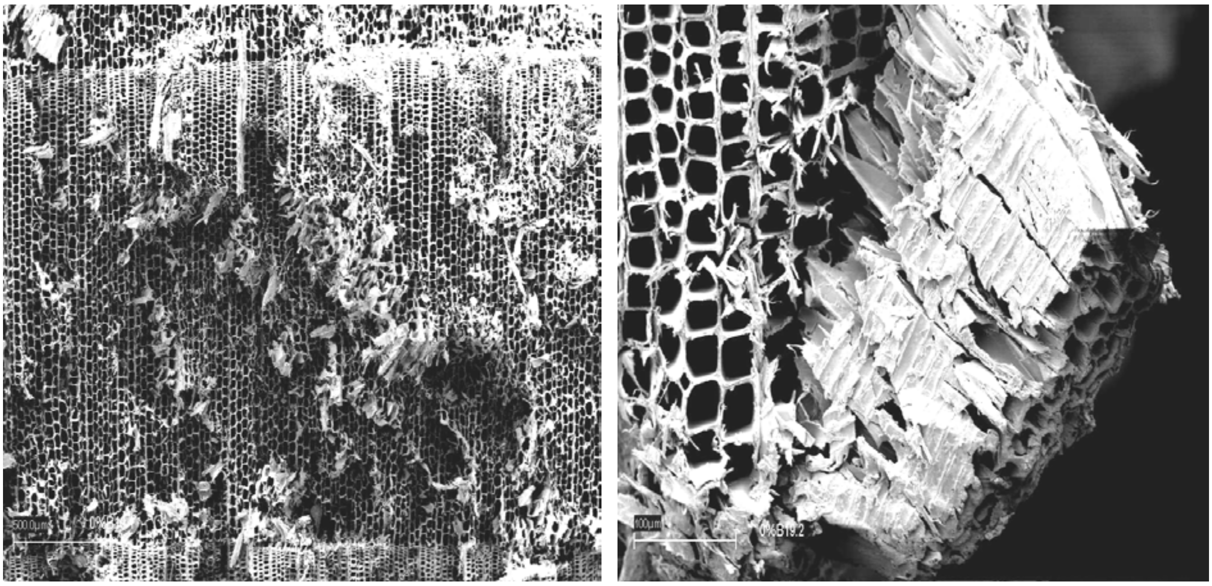

Figure 9. Tension fracture surface of spruce at 0% MC after tensile test

If the fracture mode is shear (*Figure 10*) then tracheids shear longitudinally. The fracture surfaces are brittle, but the S2 cell wall layer is also often extracted. Bordered pits do not shear; the shear line avoids the pits.

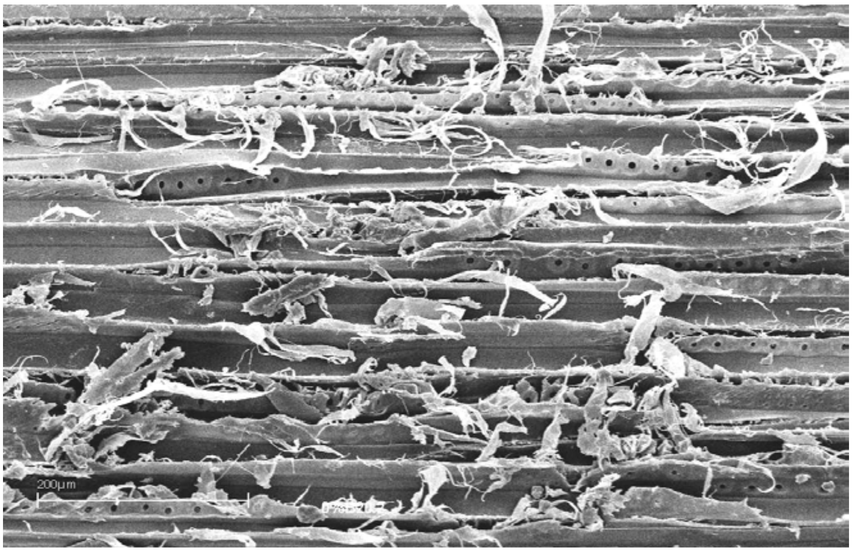

Figure 10. Shear fracture surface of spruce at 0% MC after tensile test

At 12% MC, the fracture surfaces were very similar to those at 0% (*Figure 11*). Most tracheids showed brittle transwall failure. At some locations, bundles of tracheids were pulled out and brittle shear fracture can bee seen on their sides. The MC increase did not change the character of tensile type fracture surfaces.

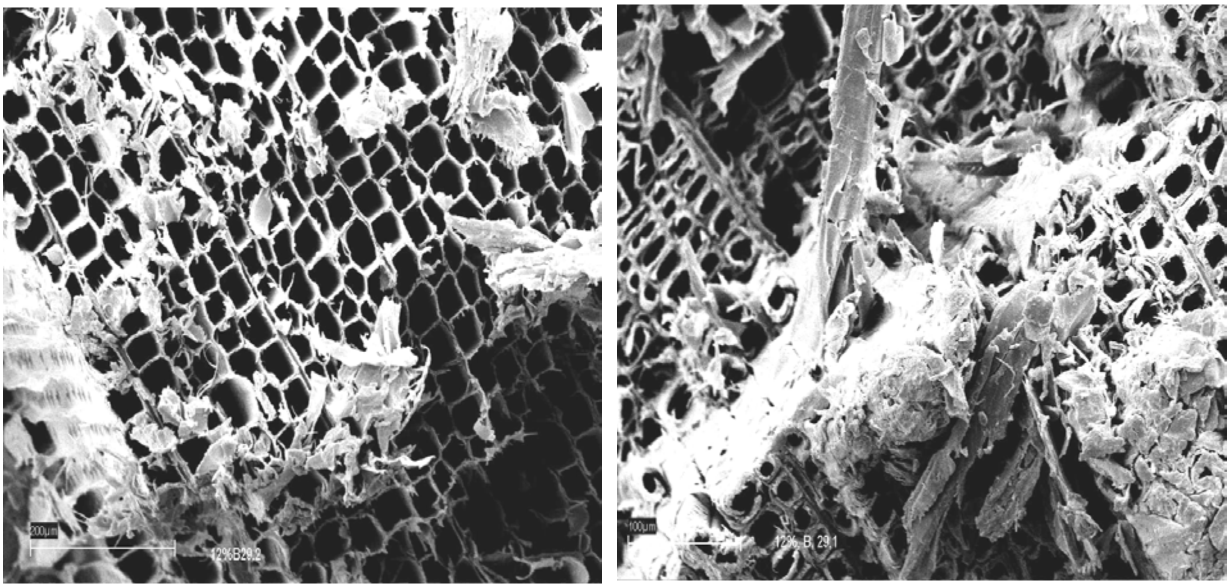

Figure 11. Tensile fracture surface of spruce at 12% MC after tensile test

The shear fracture at 12% MC originated through the brittle transwall shear failure of tracheids (*Figure 12*). Ray parenchyma cells fail in shear too (right picture arrow). The pull out of S2 cell wall layers is also visible, but the number of pull-outs did not change considerably with increasing MC.

Figure 12. Shear fracture surface of spruce at 12% MC after tensile test

Near the saturation point of spruce the character of the tensile fracture surfaces does not differ from the other two MC classes (*Figure 13*). The left-hand picture shows well the typical step-wise break of wood cells. On the horizontal planes tracheids broke with a brittle transwall failure (right-hand picture); on the vertical planes cells failed in shear. The number of tracheid bundle pull-outs does not change at 26% MC compared to 12% MC. Pull-outs are results of combined tensile and shear fracture.

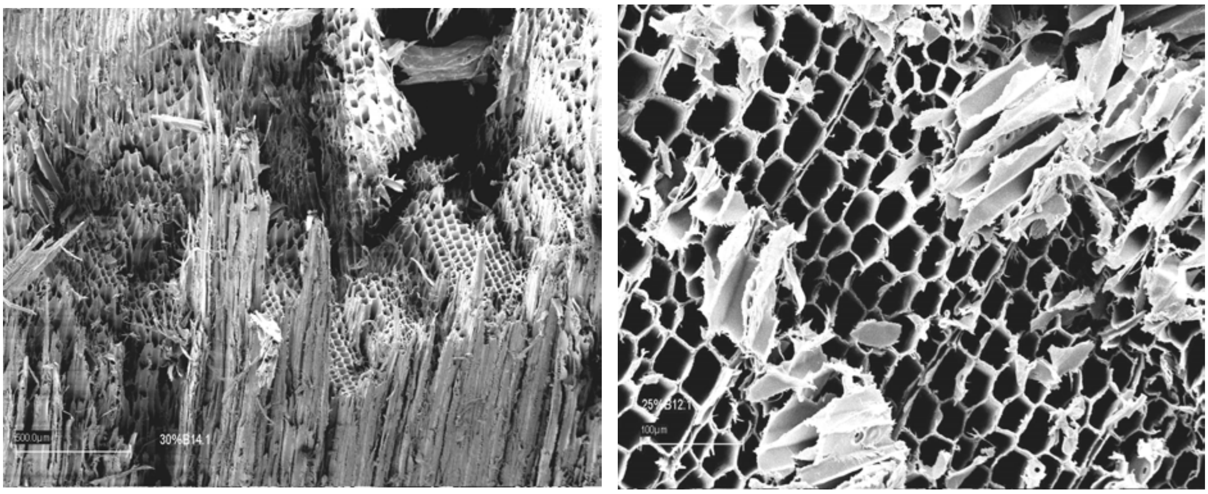

Figure 13. Tensile fracture surface of spruce at 26% MC after tensile test

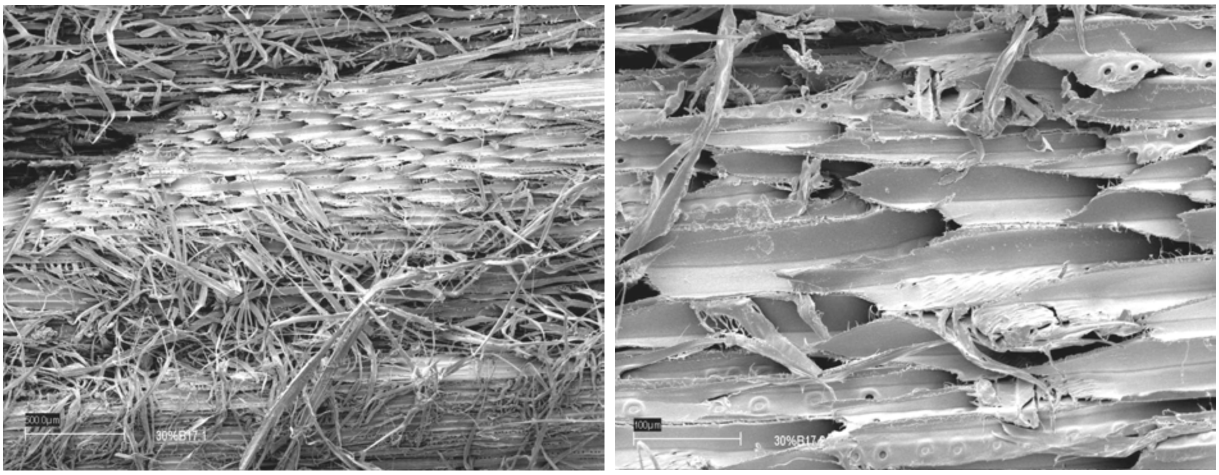

Figure 14. Shear fracture surface of spruce at 26% MC after tensile test

The shear type fracture at 26% differs from the former cases (*Figure 14*).

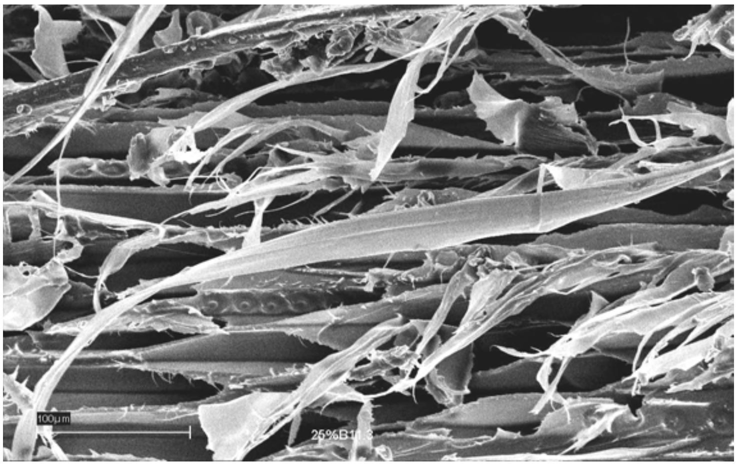

Figure 15. S2 cell wall layer pull-outs in spruce at 26% MC after a tensile test

The brittle shear character partly remains, as shown in the middle of the left-hand picture and on the right-hand picture. However, the number of S2 layers pull-outs increases considerably (*Figure 15*). The predominance of such intrawall failures indicates ductile, plastic failure at 26% MC.

Summarizing the experiences of fracture surface analysis at different MC's, we can state that the characteristic fracture mode of wood is brittle tension and shear.

The brittle character does not change considerably with increasing MC. The effect of MC near the saturation point is considerable, where the predominance of intrawall failure - namely the extraction of the S2 cell wall layer - increases. In this case the failure mode is mixed, partly brittle, and partly plastic. This changes can promote the decrease of sum of events at the saturation point because during the pull out of cell wall layers originate supposedly smaller energy events than in case of brittle fracture and a part of this events remain under the thresh- hold level of measurements.

CONCLUSIONS

Based on the AE experiments, the fracture behaviour of wood is similar to brittle materials. The micro-damage process starts near the ultimate strength. The decreasing number of events with increasing MC is a consequence of the decreasing number of friction-type events and of the increasing acoustic attenuation of wood. The maximum frequency of measured events properties does not change, indicating that the number and character of fracture-type events do not change with changing MC. The increasing MC does not significantly influence the range and properties of AE events. This means that the micro-damage process does not vary notably.

The analyses of fracture surfaces supports the results of AE experiments. The main damage mode of wood is brittle tension and shear. This brittle character does not change considerably with increasing MC. This explains why the AE experiments gave nearly the same measured and calculated parameters. These results support the assumptions of other researchers i.e. the mechanical properties of wood change with increasing MC only gradually, but not fundamentally (James, 1961). This presumption is valid at the level of micro-damage processes too.

In conclusion we can state that the properties of micro-damage processes do not change significantly with increasing MC, and that main failure mode of wood is thus brittle tension and shear.

Acknowledgments: Financial support of the OTKA Fund (Hungarian Scientific Research Fund project number: T 34107) is gratefully acknowledge.

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Annex. Measuring equipment

AE measuring apparatus:
- manufacturer: KFKI Hungary
- type: DEFECTOPHONE 4 channel AE equipment

Logarithmic Amplifier:
- manufacturer: KFKI Hungary
- type: Nez-220-BP32
- frequency range: 20-600 kHz
- dynamic range: 80 dB

AE detectors:
- manufacturer: DECI CO.
- type: SE-1000-H
- frequency range: 20-250 kHz

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Colour homogenisation of hardwood species by steaming

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Abstract – For colour homogenisation three hardwood species, black locust (*Robinia pseudoacacia* L.), beech (*Fagus silvatica* L.) and Turkey oak (*Quercus cerris* L.) were investigated. Steaming was applied to change the colour. Steaming parameters (steaming time and temperature) were varied to find the optimum of treatment. The results are given in the CIE L*, a*, b* colour co-ordinate system. Black locust wood was most sensitive to the steaming temperature. With rising temperature, the colour change was faster and less time was needed for homogenisation. The behaviour of the other two wood species was different from black locust but similar to each other. Below 95°C homogenisation was insensible to temperature and within one day the colour change stopped. Above 95°C the colour change was continuous but without further colour homogenisation. The optimum homogenisation time was found about 12 hours at 80-95°C temperature range and 6 hours at 110°C for Turkey oak, and 18 hours at any temperature for beech.

steaming / colour homogenisation / black locust / beech / Turkey oak

Kivonat – Lombos faanyagok színhomogenizálása gőzöléssel. Három fafaj, akác (*Robinia pseudoacacia* L.), bükk (*Fagus silvatica* L.) és csertölgy (*Quercus cerris* L.) színhomogenizálását vizsgáltuk. A színváltoztatáshoz gőzölést alkalmaztunk. Változtattuk a gőzölési paramétereket (gőzölési idő és hőmérséklet), hogy meghatározzuk az optimális értékeket. Az eredményeket a CIE L*, a*, b* színkoordináta rendszerben adtuk meg. Az akác faanyag nagyon érzékeny volt a gőzölési hőmérsékletre. Emelkedő hőmérséklettel a színváltozás felgyorsult, és egyre kevesebb időre volt szükség a színhomogenizáláshoz. A másik két faanyag gőzölési tulajdonságai eltértek az akácétól, de egymástól alig különböztek. A homogenizálás 95°C alatt független volt a hőmérséklettől, és egy nap után a színváltozás megállt. A 95°C fölötti hőmérsékleteken a színváltozás folyamatos volt egy nap után is, de további színhomogenizálás nem történt. Cser esetében az optimális homogenizálási idő 80 és 95°C között 12 órának, 110°C-nál pedig 6 órának, míg bükk esetében 18 órának adódott a hőmérséklettől függetlenül.

gőzölés / színhomogenizálás / akác / bükk / csertölgy

1 INTRODUCTION

Black locust heartwood has by nature a yellowish to greenish brown colour caused by a number of chemical substances such as robinetin deposited in cell lumina and cell walls. The less appealing and extremely inhomogeneous colour causes serious marketing problems of products made from black locust. In order to be competitive on the market, the colour

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appearance of black locust, particularly of products with large surfaces, such as flooring or furniture fronts, needs to be technically modified and homogenised before secondary processing (Molnar 1998, Tolvaj – Faix 1996, Tolvaj et al. 2000, Horváth 2000, Horváth – Varga 2000).

Beech wood often has red heartwood and Turkey oak has dark heartwood together with light sapwood. These great colour differences with definite irregular colour margins reduce the value of wood considerably.

These days, a new method of homogenising wood's colour is emerging. Mitsui and his co-workers discovered that UV treatment before steaming amplifies the darkening effect of steaming (Mitsui et al. 2001, Mitsui 2004, Mitsui et al. 2004)

The colour change is related to the change of the conjugated double bound chemical systems. These bounds can be found in lignin and in the extractives. Thus, the colour changes in the examined temperature range originate mostly from the alterations of the extractives. Flavonoids play a significant role in the discoloration of wood (Németh 1997). Melcerová et al. (1993) found that the tannins in black locust participate in the condensation reaction caused by hydrothermal treatment at 80 and 120°C.

This research was performed with the aim to change and homogenize the colour of wood by steaming. For observation of the colour change, the CIE L*a*b* colour co-ordinate system was used which is a useful routine for an objective determination of colour changes of wood (Tolvaj – Faix 1995, Mitsui et al. 2001).

2 MATERIAL AND METHODS

For laboratory steaming black locust (*Robinia pseudoacacia* L.), beech (*Fagus silvatica* L.) and Turkey oak (*Quercus cerris* L.) wood specimens were investigated. Specimens were prepared with the size of 200x60x20 (mm) and only those without any wood defects were used for the tests. Dark and light heartwood surfaces were also prepared. The treatment was carried out in a steam chest at 100% relative humidity in the temperature range of 80-130^{o}C (black locust), 80-95^{o}C (beech) and 80-110°C (Turkey oak), respectively. Wood specimens were placed in a large desiccator with distilled water for conditioning the air to maintain maximum relative humidity. The desiccators were heated in a drying chamber to the indicated temperatures. The steaming process started with a six hours heating process. The temperature was regulated automatically around the set values with a tolerance of ± 0.5^{o}C. Specimens were removed after 1, 2, 3, 4, 5 and 6 days. The temperatures above 100°C were generated in an autoclave. Specimens were removed from here after 6, 12, 24 and 48 hours.

Before making colour measurements, the steamed wood specimens were subsequently conditioned for one month at room temperature. The specimens were then cut with a sharp circular saw through the centre parallel to the longer side and the newly prepared surfaces were used for colour measurements. For the colour measurements a MINOLTA 2002 colorimeter was used. The reflection spectrum was measured in the 400-700 nm regions. From these data, the L*, a*, b* colour co-ordinates were calculated based on the D65 light source. On each specimen, colour measurements were taken at 10 randomly chosen spots and the results were used for further analyses.

3 RESULTS

Steaming of black locust

The effect of chemical changes induced by steaming can be observed with naked eye already after a few hours of treatment. The specimens become visibly darker and the colour changes from the unattractive greenish yellow to relatively more pleasant reddish hues. Besides the steaming parameters, colour change also depends on the original colour of the specimen. Rather large variation of natural colour of black locust heartwood is shown in *Figure 1*, where the location of numerous colour spots of randomly chosen untreated (non-steamed) specimens are plotted in the a* b* co-ordinate system. The measured colour spots are spread over a large area within the a* and b* colour co-ordinates. Considerable differences can be observed and measured not only between specimens but also within one specimen.

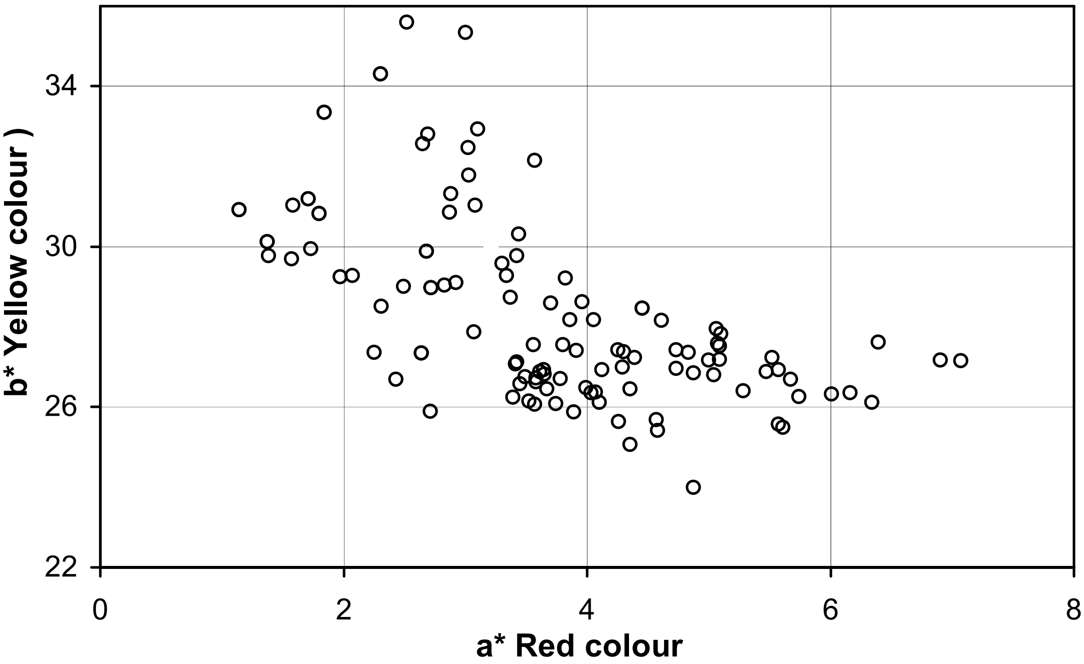

Figure 1. Natural variation of 110 randomly chosen black locust heartwood colour in the spectrum of a (red) and b* (yellow) colour co-ordinates.*

This very obvious inhomogeneity in colour can be reduced by steaming. The results are shown in *Figure 2* where corresponding colour measurements performed after steaming at 98°C temperature are plotted in the a* b* co-ordinate system as a function of steaming time. During the first day, the colour shifted towards red (increasing a* value). This change is followed by a rapid loss of yellow (decreasing b*). After four days, further colour changes become almost unnoticeable. Steaming considerably decreases the inhomogeneity of colour. The areas occupied by the colour spots are decreasing during steaming showing the colour homogenisation. Colour variation already decreases noticeably after a one-day steam treatment and continues until the fourth day. After the fourth day, this trend levels off, and at the same time, the colour change becomes very slow. At higher temperatures, the homogenisation effect was faster and the created dark surface became more and more uniform.

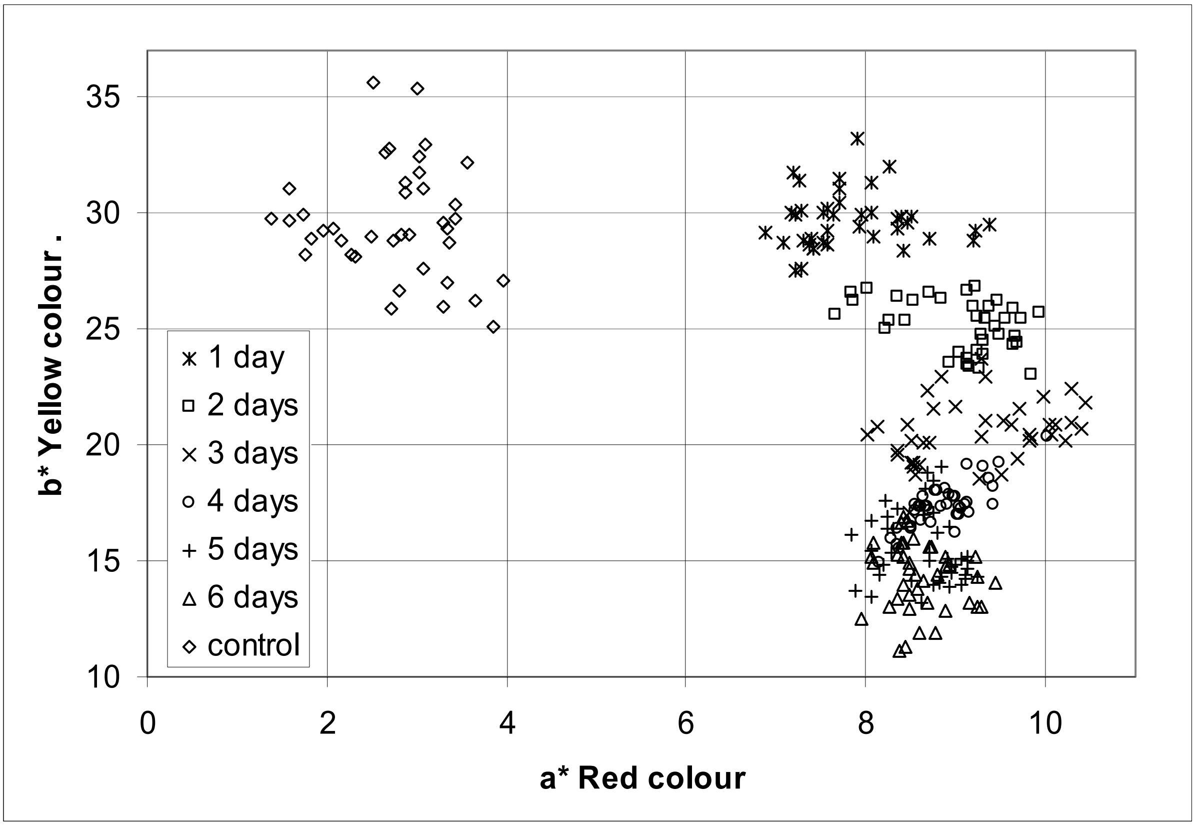

Figure 2. Colour change and homogenisation of black locust heartwood at steaming temperature of 98 °C as a function of time with respect to untreated controls (upper left)

Steaming of beech

The aim of the treatment was to reduce the colour difference between the two types of heartwood. Beech wood was steamed under atmospheric pressure. We realised that applying high pressure and high temperature the final colour was grey rather than red. So the applied temperatures were between 80-95°C. Red heartwood and white heartwood were treated parallel. *Figure 3* represents the change in lightness. It shows the great differences between red and white heartwood before steaming as well. This deviation was about 10 units in lightness. During the first 18 hours of steaming the lightness decreased rapidly. The white heartwood changed its lightness more rapidly than the red one. After this period, the lightness change was moderate or it remained constant. The 95°C treatment was an exception compared to the other temperatures. At this temperature, the decrease of the lightness was continuous in the whole examined interval. The trend lines were parallel after 18 hours of steaming (except at 95°C). It can be concluded, that the homogenisation effect has happened in the first 18 hours of steaming. This effect was not sensitive against the steaming temperature.

The yellow content of beech wood did not change considerably during steaming. In contrast, there was a marked difference in change of red content. The original colour difference in unsteamed state is well demonstrated in *Figure 4*. The red colour component of white heartwood changed a lot during the first 18 hours of steaming. After this period the change stopped. The steaming also increased the red colour of red heartwood during the first day of steaming. However, this change was moderate. After one day of steaming the red colour component of red heartwood decreased slightly. The trend lines of two types of heartwood moved towards each other. The yellow colour component of all types of examined beech wood remained intact during steaming. Comparing *Figure 3* and *Figure 4* one can conclude that the effective steaming time for homogenisation is 18 hours and is not depending on the steaming temperature. After this period the colour change is negligible. For saving energy, steaming at 80°C is recommended.

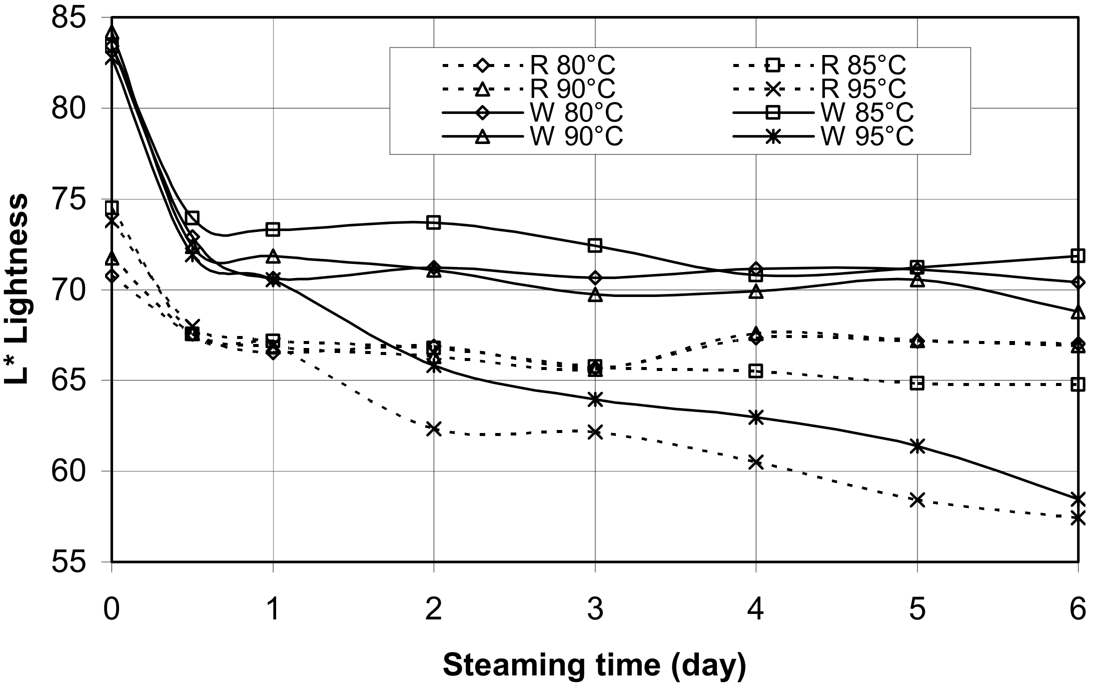

Figure 3 Lightness change of beech red heartwood (R) and white heartwood (W) during steaming

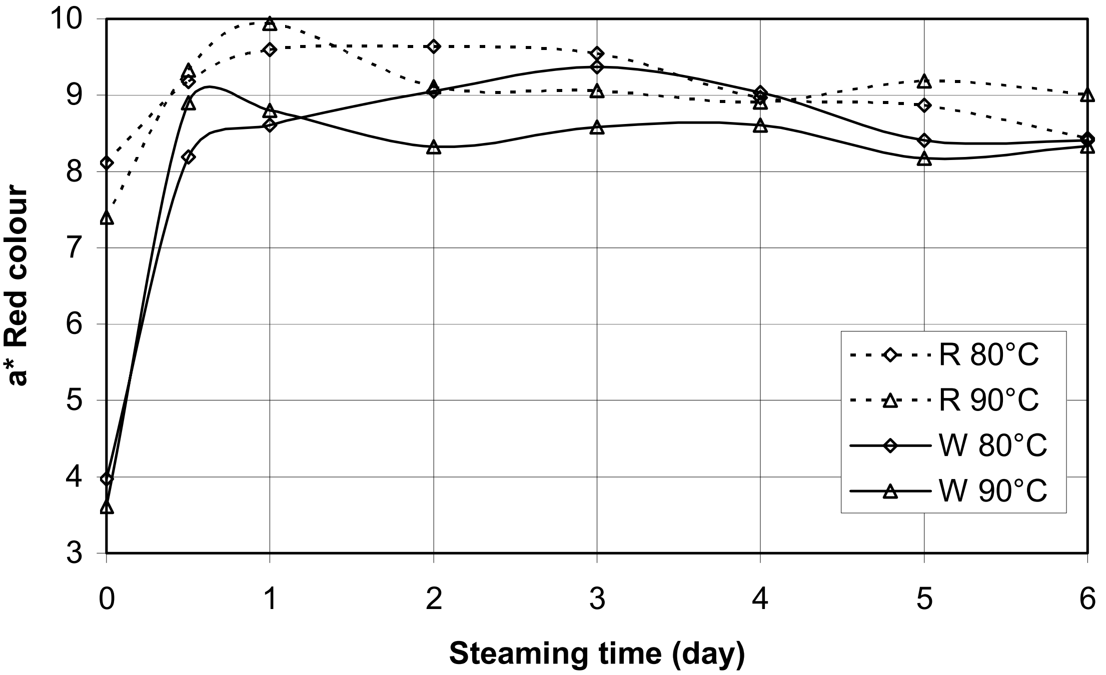

Figure 4. The change of red hue of beech red heartwood (R) and white heartwood (W) during steaming

Steaming of Turkey oak

Turkey oak has white sapwood but many trees have irregular dark grey heartwood that does not follow the year ring border. The border between the dark and white portion is usually extremely sharp. The big colour difference can be diminished by steaming. The lightness changes are plotted in *Figure 5*. Most of lightness change happened within the first 12 hours of steaming. There was a great difference above and below 100°C. At 80°C and at 95°C the decreases were similar up to 2 days. After this time the lightness change at 80°C stopped but at 95°C it decreased continuously. At 110°C the lightness change was rapid in the first 6 hours of steaming, and then the decrease became moderate. Lower temperatures (80-95°C) resulted moderate homogenisation during 2 days of steaming, but applying high temperature (110°C) the homogenisation was successful. The lightness difference was about 15 units before steaming and it decreased up to approximately 5 units during 12 hours of steaming. After this time limit the trend lines were parallel.

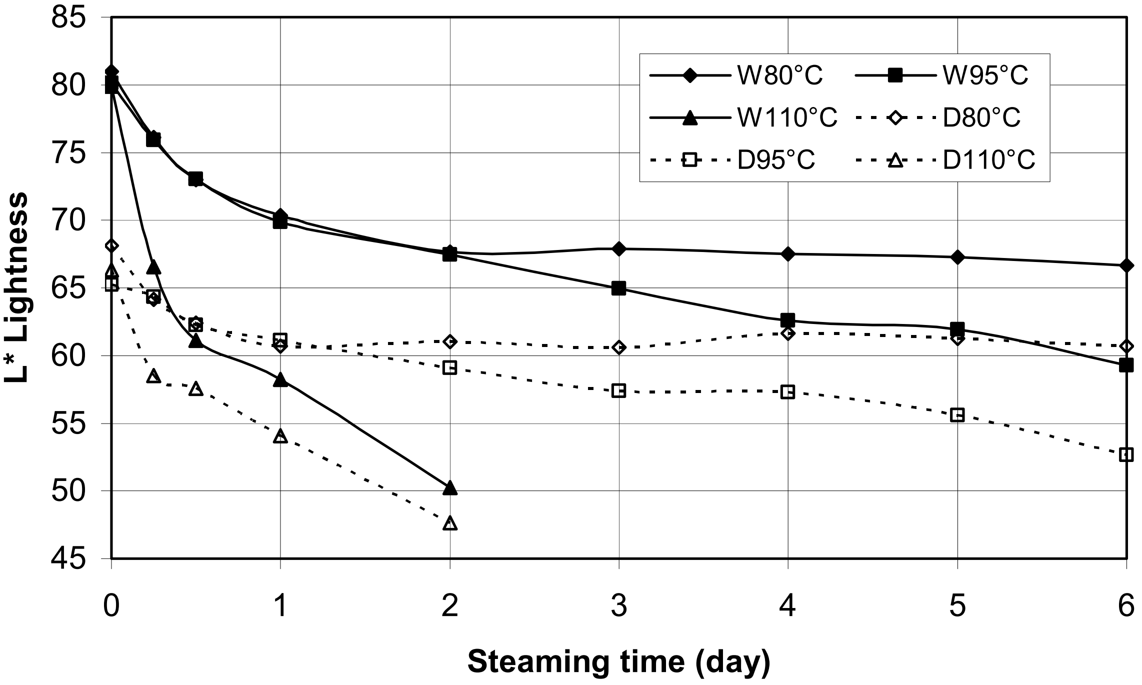

Figure 5. Lightness change of Turkey oak white sapwood (W) and dark heartwood (D) during steaming

The changes of red colour component are presented in *Figure 6*. Before steaming the dark heartwood was a little more red than the sapwood. During steaming the trend changed. The red colour component of white sapwood increased more rapidly than the same of heartwood. The trend lines crossed each other at 8 hours of steaming time (in case of 110°C treatment after 6 hours). After this time the colour inhomogeneity increased. Plotting the yellow colour components (*Figure 7*) of both type of Turkey oak samples the parallel changes were visible. These trends indicate that the steaming does not result in any homogenisation in case of yellow colour hue.

Comparing the lightness change and the change of the red colour component, the optimum steaming time at 80-95°C temperature range is about 12 hours and at 110°C 6 hours.

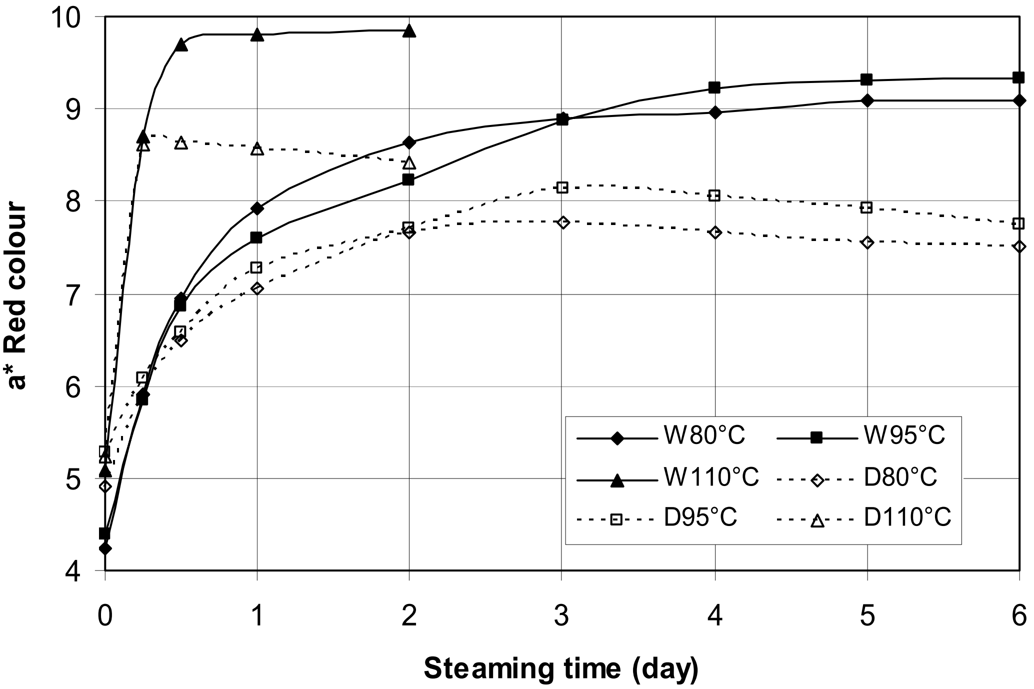

Figure 6 Change of red hue of Turkey oak white sapwood (W) and dark heartwood (D) during steaming

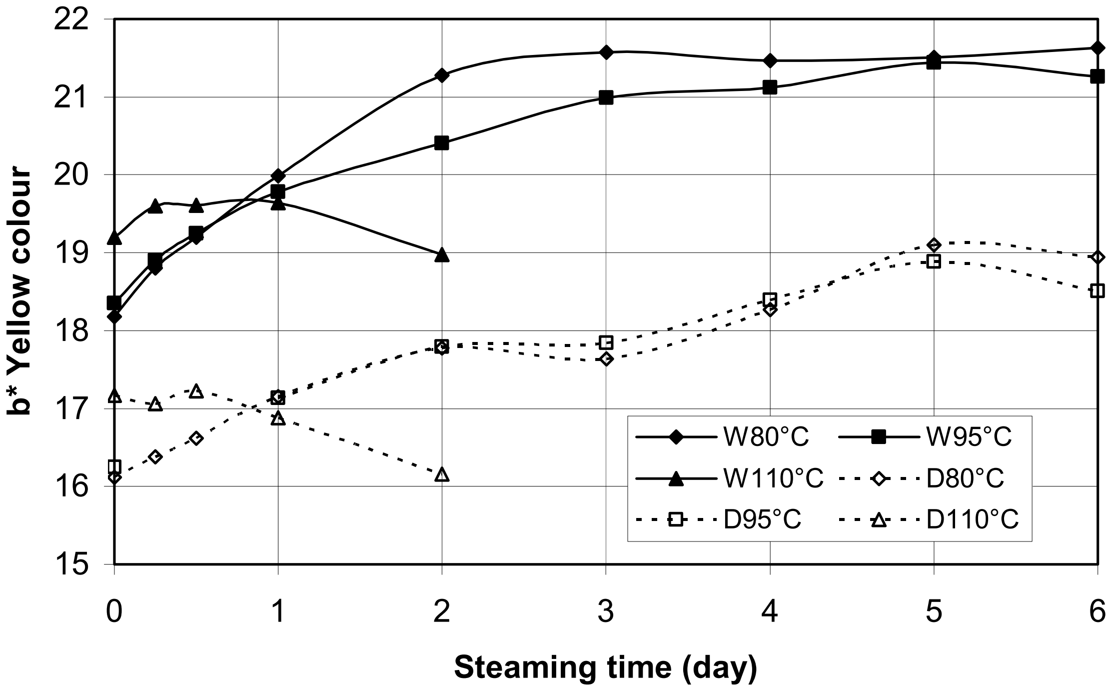

Figure 7. Change of yellow hue of Turkey oak white sapwood (W) and dark heartwood (D) during steaming

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Recycling of Impregnated Décor Paper in Particleboard

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Abstract – The effect of recycling dried impregnated décor paper in particleboard production was studied. The results of these experiments showed that by adding crushed impregnated paper the strength of the particleboards can be increased or the same board properties can be achieved with reduced amounts of applied adhesive (UF). This waste recycling technology is serving to protect the environment, forests and nature. Based on our recommendations (considering also the recent rules and regulations of waste handling) a particleboard company started to recycle their impregnated paper wastes.

recycling / particleboard / impregnated paper waste

Kivonat – Impregnált dekorpaír újrahasznosítása faforgácslapgyártásban. A szárított impregnált dekorpapír forgácslap alapanyagba történő visszaforgatásának hatását vizsgáltuk. A kísérletek eredményei azt mutatták, hogy a hozzáadott aprított, impregnált papír megnövelheti a forgácslapok szilárdságát ill. azonos lemez paraméterek kevesebb kötőanyag (karbamid-formaldehid) felhasználással is elérhetők. Ez a hulladék újrahasznosítási technika elősegíti a környezet, az erdők és természet védelmét. A javaslataink alapján (figyelembe véve a jelenlegi hulladékgazdálkodási törvényeket és rendelkezéseket) az egyik faforgácslap-gyártó cég megkezdte az impregnált papírhulladékának a forgácslapgyártásban történő újrahasznosítását.

újrahasznosítás / faforgácslap / impregnált papír hulladék

1 EXPERIMENTAL: RECYCLING OF IMPREGNATED DÉCOR PAPER

The described experimental work was initiated by one of the Hungarian particleboard companies to evaluate the possibilities of using impregnated paper in particleboard production.

There are already results on recycling of laminated particleboards as published earlier (Hatano et al. 2002), but at this time fresh wood particles were mixed with unused impregnated décor paper.

The main characteristics of raw décor paper are: high TiO_2 filling and α-cellulose content, high quality wood raw material and melamine as an additive. During impregnation the décor paper is impregnated with different chemicals (Winkler 1999).

In the dryer of the impregnation line the resin in the décor paper has not yet cross-linked, the impregnated paper contains a large amount of un-bonded adhesive. As shown in *Table 1,*

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the impregnated décor paper waste consists of only 38.75% paper, the rest 61.25% is resin compounds (Varga et al. 2004).

Table 1. Compounds of impregnated décor paper

Compounds	Distribution (%)
raw décor paper	38.75
melamine resin	20.20
urea resin	38.75
modifier	1.07
hardener of melamine	0.25
hardener of urea	0.67
cross-linking agent, anti-adherer	0.31

The Hungarian authorities consider impregnated paper waste as non-hazardous waste.

Two series of experiments were performed to evaluate the use of impregnated paper in particleboard production.

1.1 First experimental run

In the first experiment, the UF resin content was held constant (10%) and the ratio of added crushed impregnated paper waste was set to 5%, 10% and 20%. Control boards were also made without the addition of impregnated paper.

All the boards were made in laboratory. The impregnated décor paper was crushed by a hammermill and it was mixed with the particles in a blender. The UF resin was sprayed into the blender by airgun.

The mats were formed by hand in a forming frame with an internal size of 500 mm x 500 mm.

The boards were pressed in a Siempelkamp laboratory heat press with the following parameters:

- specific pressure: 4,5 Mpa
- temperature: 180 °C
- time: 3.5 min
- thickness: 12 mm

Table 2. Main properties of the particle-impregnated paper boards (1st run)

Ratio of impregnated paper (%)	Density EN 323 (kg/m^3)	MOR EN 310 (N/mm^2)	Internal-bond EN 319 (N/mm^2)	Formaldehyde content EN 120 (mg/100g)
0	704.8	16.4	0.65	2.62
5	680.2	15.9	0.86	3.35
10	709.5	18.7	0.90	3.92
20	698.2	19.8	0.87	5.23

Evaluating these results, it was found that the value of MOR increased with impregnated paper ratios up to 21%, and the value of internal-bond increased by 33% compared to the control panels. These are advantages but at the same time the formaldehyde content also increased, but the maximum value (5.23 mg/100g) was still below the standard limit value of 8 mg/100g. The results prove that:

- impregnated décor paper waste can be mixed with the raw material of particleboards in quite large amounts, with improves the physical and mechanical properties of the PB;
- it might be possible to reduce the amount of UF adhesive when adding crushed impregnated paper.

1.2 Second experimental run

Based on the above results a second experiment was performed. This time the ratio of added impregnated paper was set to a constant value of 20%, and the ratio of the UF resin was varied. The resin content was calculated in two different ways:

- calculated as a percentage of the dry matter content of both materials (impregnated paper + wood particles),
- calculated as a percentage of the wood particles only.

Control boards were also prepared with 5% and 10% UF resin. All the boards were made by the same method as in the first experimental run.

Table 3. Main properties of the particle-impregnated paper boards (2nd run)

No.	IP/UF (%)	Density EN 323 (kg/m^3)	MOR EN 310 (N/mm^2)	Internal-bond EN 319 (N/mm^2)	Formaldehyde content EN 120 (mg/100g)
1	20/0	747	15.27	0.76	3.61
2	20/5 *	718	18.08	0.80	4.82
3	20/10 *	718	18.06	0.82	5.31
4	20/5 **	757	18.39	0.79	4.50
5	20/10 **	742	18.99	0.80	5.25
6	0/5	708	12.17	0.66	1.98
7	0/10	726	18.80	0.72	2.61

* 5 % or 10 % UF resin based on the dry matter content of the wood particles + impregnated paper together
** 5 % or 10 % UF resin based on the dry matter content of the wood particles only

The addition of 20% impregnated paper has a favorable influence on the board properties. Even without adding any UF adhesive it was possible to produce particleboards with bending strength higher than the standard requirement (16 mm thick PB suitable for use in dry condition: MOR > 13 N/mm^2). When UF resin was added, the value of MOR was similar to that of the standard control board with 10% UF resin content. No significant difference could be observed between the strength values of boards with 20% impregnated paper and 10% or 5% UF content. There was also no difference between the results of boards where the resin content was based on the dry matter content of wood + impregnated paper or on the wood particles only. The values of internal-bond were higher in every case than the standard requirement (0.35 N/mm^2).

The standard deviation was calculated for physical and mechanical properties according to the relevant standards.

Although the formaldehyde content was higher when both impregnated paper and UF was added, the maximum value (5.31 mg/100g) was still below the standard limit value of 8 mg/100g.

2 CONCLUSIONS FROM THE EXPERIMENTS

Based on the strength results it can be considered possible to produce particleboard even without using adhesive, by just adding 20% of impregnated décor paper waste to the raw material. If higher strength values are required, the addition of 5% UF resin and 20% impregnated décor paper waste is more than adequate to reach the strength of a standard board with 10% of UF resin.

Of course in a PB factory there is not a high amount of décor paper waste produced, but it is a good way to eliminate this kind of waste. If the amount of the waste allows, the percentage of UF resin can be decreased.

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