Leaf Growth and Photosynthetic Performance of Two Co-existing Oak Species in Contrasting Growing Seasons

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Abstract – Ecophysiological investigations of *Quercus petraea* and *Quercus cerris* were performed at the Sikfőkút research site in the dry and humid growing seasons of 2003 and 2004. The results suggested that leaf growth and the photosynthetic apparatus of *Q. petraea* exhibited higher sensitivity to drought in 2003 than that of *Q. cerris*. In leaves of *Q. petraea*, chlorophyll content showed larger inter-annual and within-canopy variability than in those of *Q. cerris*. Fully developed leaves of *Q petraea* showed lower SLM which indicated higher leaf cell wall elasticity allowing them to maintain a water spending strategy, while high specific leaf mass (SLM) values reflected a water saving strategy for *Q. cerris*. Water use efficiency of *Q. cerris* was higher than in the case of *Q. petraea*, which may provide an advantage for this species in dry periods. In the contrasting years the final leaf area and leaf mass of both species were determined by the amount of rainfall and temperature conditions during the period of early exponential phase of leaf growth. As indicated by the low values of the Fv/Fm chlorophyll fluorescence parameter the photosynthetic apparatus of both species exhibited high susceptibility to abiotic stress factors in early spring. A large VAZ cycle pool indicated that zeaxanthin dependent heat dissipation was the main contributor to photoprotection of photosynthetic apparatus in young leaves but in fully developed leaves the relatively high light saturated ETR and low P_{max} as well as the maintenance of high Fv/Fm even in severe dry periods reflected the potential involvement of photorespiratory electron transport in photoprotection of both species in summer. Drought in 2003 may have resulted in serious depletion of dry matter reserves influencing the vitality of trees in following year. *Q. petraea* showed lower photochemical activity in the successive vegetation period after the dry year than *Q. cerris* which suggested lower tolerance to drought in the long term.

oak / drought / leaf growth / photosynthesis / photochemical efficiency of PSII

Kivonat – Cseres-tölgyes fafajainak levélnövekedése és fotoszintetikus teljesítménye kontrasztos időjárású években. A síkfőkúti cseres-tölgyes erdőállományban végzett vizsgálatok eredményei alapján megállapítható, hogy a kocsánytalan tölgy levélnövekedése és fotoszintetikus apparátusa nagyobb klimatikus érzékenységet mutat, mint a csertölgyé. A kocsánytalan tölgy esetében a klorofill-tartalom nagyobb évek közötti eltérést, és klimatikus változékonyságot mutat, mint a csertölgynél. A kocsánytalan tölgy kisebb SLM értékekkel jellemezhető, mint a csertölgy, ami az előző fajnál nagyobb, az utóbbinál pedig kisebb sejtfal elasztikussággal társul. Az SLM és a WUE alapján

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megállapítható, hogy a *Quercus petraea* vízpazarló stratégiával, a *Quercus cerris* inkább vízmegőrző stratégiával rendelkezik. A két tölgyfaj fáinak adott vegetációs periódusban kifejlődő végleges asszimiláló lombfelületét és tömegét a levélnövekedés exponenciális fázisában uralkodó hőmérséklet és csapadékviszonyok nagymértékben befolyásolják. A lombfakadáskor és a levélnövekedés idején fellépő aszálynak nemcsak a levélnövekedés üteme, hanem a fák egész évi produkciója szempontjából súlyos következménye lehet. Nem csak a szerves anyag produkciójuk és a következő évi fiziológiájukat is meghatározó szerves anyag raktár csökken, hanem a fák legyengült állapotba kerülnek és a károsítókkal szemben is fogékonyabbá válnak. Mindkét tölgyfajra jellemző, hogy a fotoszintetikus apparátus a tavaszi időszakban nagy sérülékenységét és abiotikus stressz-tényezőkkel szembeni érzékenységét mutat. A nagy VAZ ciklus pigment készlet azt jelzi, hogy a fiatal levelek fényvédelmében a zeaxantin akkumulációval kapcsolódó hő disszipáció a meghatározó folyamat. A kifejlett levelekben a magas ETR ellenére alacsony P_{max}, és a száraz periódusban is magas Fv/Fm arra utalnak, hogy nyáron a xantofill ciklus mellett mindkét fajnál fontos szerepet kap a fotorespiráció a fényvédelemben. Az aszályos évet követő vegetációs időszakban a kocsánytalan tölgynél jelentkező alacsonyabb fotokémiai aktivitás a csertölgyhöz képest a vitalitás nagyobb mértékű gyengülését jelzi.

tölgy / aszály / levélnövekedés / fotoszintézis / PSII fotokémiai hatékonysága

1   INTRODUCTION

Numerous current scenarios on future climate change in Central Europe predict elevated temperatures and simultaneous reduction of rainfall in growing seasons which will increase the frequency and duration of summer drought (IPCC 2001). The reduced soil water availability as the main limiting factor for trees may have an adverse influence on the abundance and biomass production of European broad-leaved forests. There are several signs that climate change has already resulted in a shift of distribution and/or vigour of natural vegetation and further consequences are also forecast (Geßler et al. 2007). Climatic change and prolonged summer drought stress have been suggested as major contributing factors to the decline of central European forests in recent decades (Jakucs et al. 1986, Mészáros et al. 1993).

Severe summer drought such as that which occurred in 2003 may have long-term consequences for the forest condition by making the trees susceptible to other abiotic and biotic stresses appearing simultaneously or in subsequent growing seasons.

The climate projections for Hungary predict a reduction in the total area of natural climate-zonal forests and a gradual shift of transition between forest-steppe and forest zones (Mátyás – Czimber 2004). The analyses showing the close relationships between the decline of health condition of zonal forest trees and the summer water shortage of their habitats have strengthened such predictions (Berki – Rasztovits 2004). Longer drought periods are expected to affect very seriously the tree species and forests occurring in transitional habitats in the North Hungarian Central Range, especially the mixed stands of Turkey oak (*Quercus cerris*) and sessile oak (*Quercus petraea*). A massive decline of oak (mostly sessile oak) has also been reported for forests of transitional habitats (Jakucs et al. 1986).

Although the climatic requirements of *Q. petraea* and *Q. cerris* have been well described on the basis of distribution pattern, the information on physiological traits and mechanisms determining the organic matter production and tolerance to fluctuations of weather and soil water availability are still lacking. For that reason the aim of this study was to characterise the physiological traits of *Q. petraea* and *Q. cerris* naturally co-occurring in a mixed forest stand by monitoring the fluctuation of leaf growth parameters and the functioning of photosynthetic apparatus within the canopy. Special focus has been on physiological responses of the two oak species to one of the most extraordinary droughts recorded for Hungary, which was experienced during the summer of 2003. Ecophysiological measurements performed during growing season of the humid year 2004 served as the reference of those in the dry year 2003.

Seasonal investigation of leaf physiological traits in an extreme growing season may provide an explanation for the differences in tolerance to environmental constraints and competitive abilities of co-existing tree species. This information may also be useful for predicting the effects of climate change on climate-zonal species and for modelling responses of forests to environmental stresses.

2 MATERIALS AND METHODS

2.1 Site conditions

The investigations were performed in the Sikfőkút long-term ecological research site established in 1972 in the Bükk Mountains, North Hungarian Central Range (Jakucs 1985). The site is situated at 320-340 m above sea level and is covered by a 85-90 year-old stand of sessile oak- Turkey oak forest community. From the start of the Síkfőkút project the forest stand has been untouched. Based on an average of 50 years the mean annual temperature is 9.9°C and the annual precipitation is 6.1 mm. The bedrock is miocenic grebble and the soil is deep brown forest soil.

The investigations were carried out in a 50 m x 50 m quadrat of the central 1 ha area of the site where a 25 m tower was built at the start of the long-term project for meteorological records and vegetation sampling. At this location the present composition of the tree layer consists of 84% *Q. petraea* and 16% *Q. cerris*. A substantial decline of sessile oak has occurred at the site since the 1980s which has resulted in drastic thinning of the tree layer, appearance of large gaps and gradual alteration of the vertical and horizontal dominance pattern of the forest stand (Mészáros et al. 1999). Reports on temperature, light conditions and soil moisture content have revealed drastic changes in microclimate within the interior of declining forest stand (Antal et al. 1997).

Compared to records from the early 1970s the present number of *Q. petraea* trees in the site is 60% lower. *Q. cerris* has also suffered a reduction in the number of individuals but only by 20%. (Koncz et al. 2005). Repeated field surveys have indicated an increase in the basal area of individual trees in both species (Mészáros et al. 2007) as compared to the period before decline (Jakucs 1985), but it was higher in *Q. cerris* (*Table 1*). However, when the present basal area of trees is calculated for 1 ha, *Q. petraea* oak shows a 57% decrease in total basal area, while *Q. cerris* exhibited a moderate increase (Koncz et al. 2005).

Table 1. Basal area of two tree species in the Sikfőkút forest in 1974 (Jakucs 1985) and in 2003

Species	Mean basal area of tree canopy (m^2)		Degree of change (%)
	1974	2003	
Qurrcus petraea	11.1	12.6	**+13.6**
Quercus cerris	13.8	18.2	**+32.6**

In the present state of the forest stand the shrub layer in the canopy gaps show a similar structure (Mészáros et al 1999) to that reported for the edge of the forest (Mészáros et al. 1981). *Acer campestre* and *Acer tataricum* exhibited very intense growth and have formed a second, lower canopy layer of the stand. In spite of the opened canopy layer, regeneration of both oak species is rather poor and the cover of the herb layer is low. The latter observations, together with the large extent of oak decline, suggest that the habitat can be considered as a transitional one for sessile oak - Turkey oak forest (*Quercetum petraeae-cerris*).

2.2 Measurements of weather conditions

The investigations were performed during the 2003 and 2004growing seasons. The weather conditions (temperature, relative humidity, rainfall, and photosynthetically active radiation, PAR) were monitored by means of automatic sensors with dataloggers (Onset Co., USA) located at the top of the meteorological tower. The processing of records was performed by BoxCar 4.3 Pro software. The soil moisture content was measured using the gravimetric method on sampling days. Soil samples were taken from the top 300 mm layer at three points of the study quadrats near the sample trees. To prevent water loss soil samples were placed in plastic bags prior the measurements.

2.3 Measurements of ecophysiological traits

Leaf samples were collected regularly during the growing seasons. In spring and early summer the interval between samplings was shorter (1-2 weeks) than later (3-4 weeks). Four trees of each species growing close to the meteorological tower and less than 10 m apart from each other were selected at random for measurements. Small twigs were cut from the sun and shade layers of sample trees with telescopic shears from the tower or from the ground.

Leaf area was measured by an AreaScope leaf area meter (developed at the Department of Botany, University of Debrecen), leaf dry mass was measured after drying at 85°C Leaf discs taken for biochemical analysis were frozen in liquid nitrogen and kept at -70°C until processing.

Chlorophyll fluorescence parameters (Fv/Fm, $\Delta F/Fm'$) were measured with a PAM 2000 fluorometer (WALZ, Germany) (Schreiber et al. 1994). Fv/Fm was measured after 1 h dark acclimation. $\Delta F/Fm'$ of light acclimated samples was used for calculation of electron transport rate, ETR = $\Delta F/Fm'$ x PPFD x 0.84 x 0.5 as suggested by Genty et al. (1989).

Photosynthetic pigment composition of leaves was measured in 80% acetone extract. Chlorophylls were determined by the spectrophotometric method (Shimadzu UV/VIS spectrophotometer) using the equations of Wellburn (1994). Carotenoid composition was measured by reversed phase HPLC method (UV/VIS HPLC, Jasco, Japan), with application of zeaxanthin as standard.

Leaf gas exchange parameters were assessed using a LA2 infrared gas analyser (ADC, UK) under ambient air and saturating light conditions supplied by a portable lamp. Ratio of light-saturated photosynthesis (Pmax) to transpiration rate (E) was used for estimation of water use efficiency (WUE).

3 RESULTS

3.1 Weather conditions

Concerning the weather conditions the two study years were completely different, especially in the seasonal distribution and the total amount of rainfall and temperature fluctuations (*Figure 1*). In 2003, after a dry winter period the precipitation was 30% less during the vegetation period than in 2004. The mean daily air temperature was significantly higher in the growing season of 2003 than in the respective period of 2004.

In 2003 low values of Gaussen-Bagnouls' xerotherm index (*Table 2*) indicated persisting drought for spring and early summer, the main period of canopy development.

The soil moisture content was low in the spring of 2003 and fell to 15% (f.m.) in June and remained around this value till the end of growing season (*Figure 2*). Although there was a large amount of rainfall in July it could not moderate the soil water deficit. After the drought

of 2003 the soil water budget did not fully recover during the winter months and low soil moisture occurred again in the topsoil during summer of 2004.
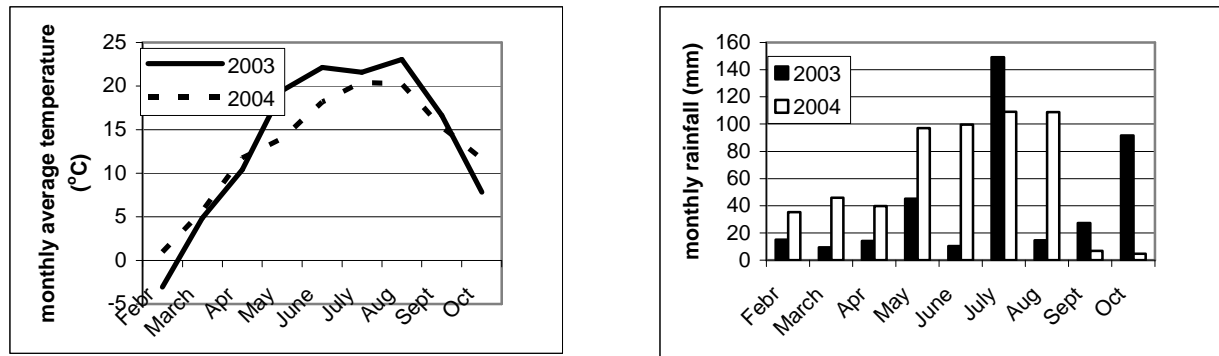

Figure 1. Monthly averages of daily mean temperature and monthly sums of rainfall in growing seasons of 2003 and 2004 at Síkfőkút Research Site

Table 2. Values of Gaussen-Bagnouls' xerotherm index in growing seasons of 2003 and 2004. Bold values indicate the ecologically dry months

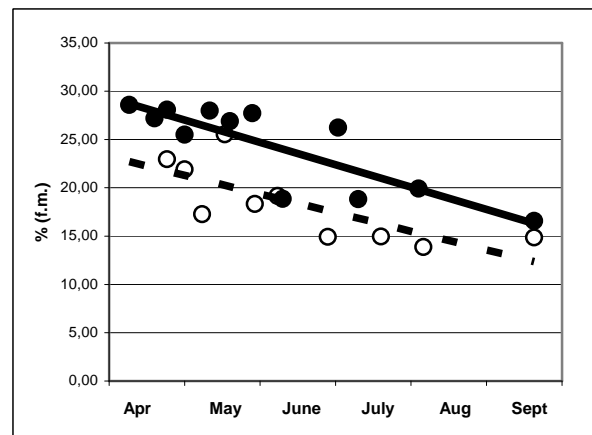|	2003	2004
March	**0.599**	2.684
April	**0.333**	1.119
May	**0.774**	2.328
June	**0.156**	1.629
July	2.301	1.998
August	**0.209**	1.794
September	**0.548**	**0.353**

Figure 2. Soil moisture content (0-30 cm) in growing seasons of 2003 and 2004 at Síkfőkút Research Site

3.2 Leaf growth

Q. petraea showed larger inter-annual and within-canopy variations in area and mass of fully developed leaves than *Q. cerris* (*Figure 3*). In the upper canopy of both species leaf area was similar in different growing seasons but in shade layer it was significantly larger in the humid 2004 than in 2003.

The persisting drought in 2003 resulted in a large reduction of leaf mass in both canopy layers of *Q. petraea. Q. cerris* showed slight inter-annual changes in leaf mass; only the mass of fully developed shade leaves was smaller in 2003 as compared to 2004. The differences in leaf growth between the canopy layers between species and years appeared clearly in the exponential phase of leaf development (*Figure 4*). The drought in the spring and early summer of 2003 resulted in smaller slopes of growth curves of leaf mass in both canopy layers of both species than in 2004. The specific leaf mass (SLM) of expanded sun and shade leaves of *Q. petraea* was 15-20% lower in 2003 (*Figure 3*). This reflected decreases of density and/or thickness of leaf. In case of *Q. cerris* the inter-annual variation of SLM was less (3-10%).
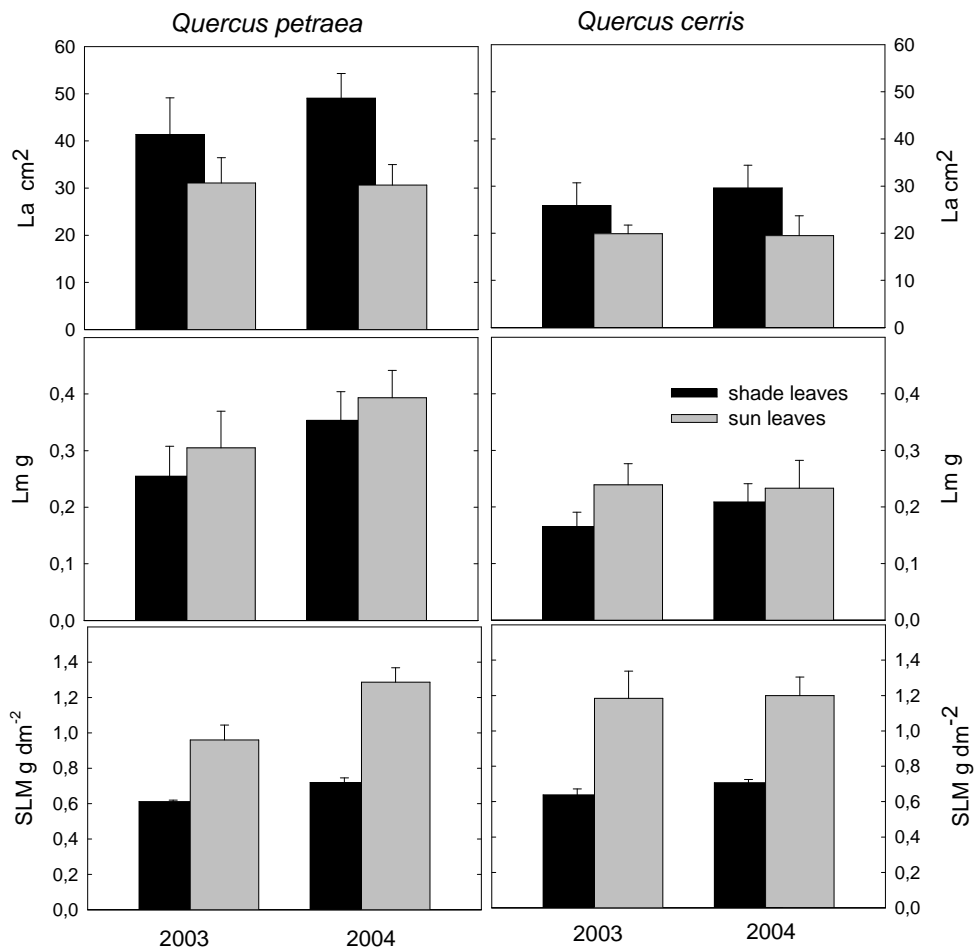
Figure 3. Leaf area, leaf mass and specific leaf mass (SLM) of fully developed sun and shade leaves of Quercus petraea and Quercus cerris in 2003 and 2004.
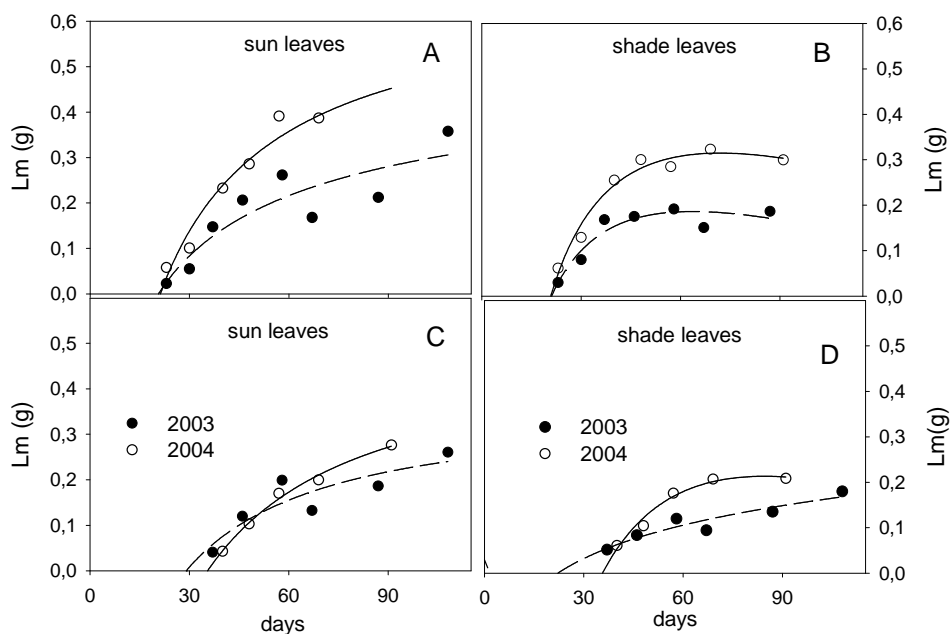

Figure 4. Exponential phase of leaf mass increment in sun and shade canopy layers of Quercus petraea (A and B) and Quercus cerris (C and D). 0 day indicates 1 April.

3.3 Photosynthetic pigments

Leaf chlorophyll content per unit dry matter increased from spring until summer in sun and shade leaves of both species (*Figure 5*). Carotenoid content per unit dry matter was higher in spring than in summer. Fully developed leaves in both canopy layers of sessile oak contained lower concentrations of all pigment groups in 2003 than in 2004. The chlorophyll content of leaves of Turkey oak was similar in different years but total carotenoid content was lower in 2003.
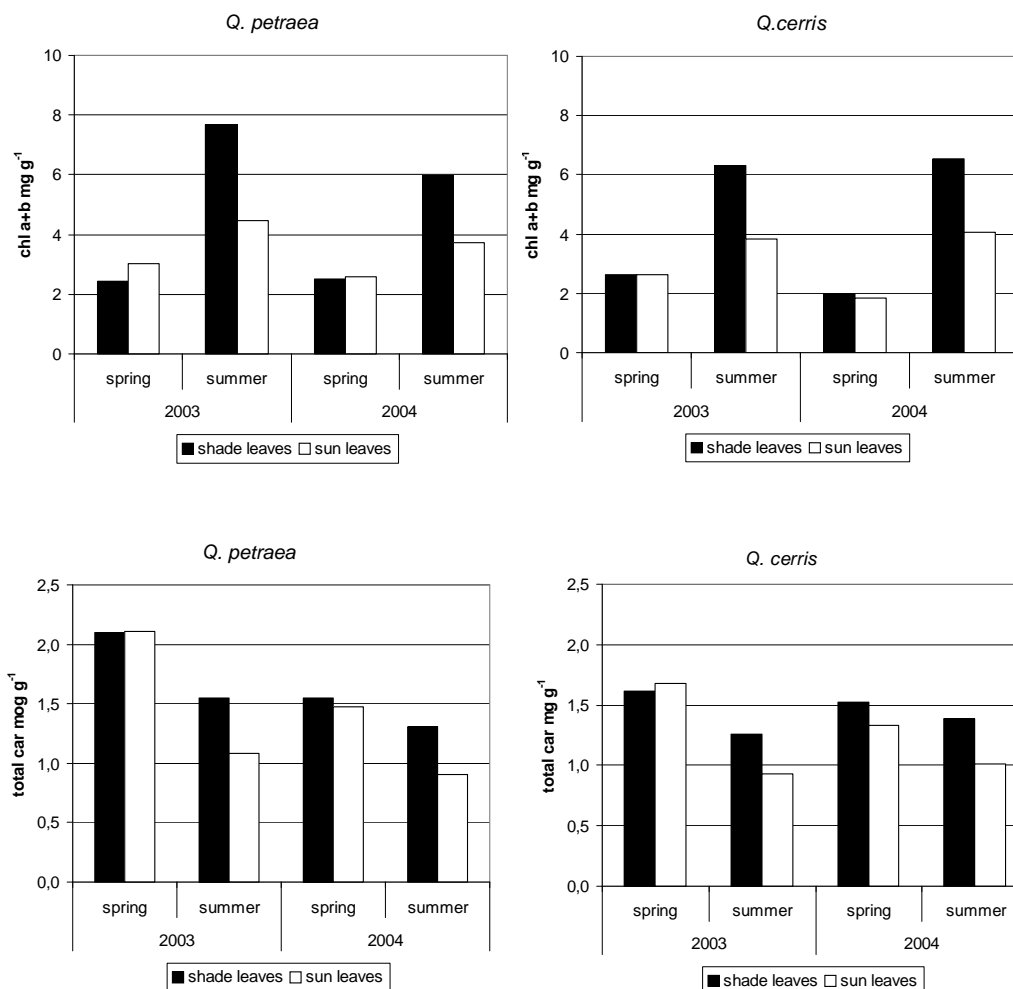

Figure 5. Chlorophyll and total carotenoid content (mg g^{-1} dry matter) in sun and shade leaves of Quercus petraea and Quercus cerris in growing seasons of 2003 and 2004.

Similarly to the carotenoid content per unit of dry matter, a significant reduction in the total carotenoid pool expressed on a chlorophyll basis (mmol mol^{-1} chlorophyll a+b) was also observed in summer (*Figure 6*). Although sun leaves contained less carotenoids per unit dry matter than did shade leaves (*Figure 5*) similarly to chlorophylls the total carotenoid pool per unit of chlorophyll was higher in sun leaves (*Figure 6*).

The differences in this biochemical trait between the canopy layers were larger for *Q. petraea*. The variation of carotenoid pool in the early and late growing seasons appeared to be closely correlated with the changes in the total content of pigments taking place in the photoprotective VAZ cycle pool (**V**iolaxanthin, **A**ntheraxanthin, **Z**eaxanthin) (*Figure 6*).

3.4 Light saturated photosynthesis rate and electron transport rate within the canopy of trees

Leaf gas exchange parameters and the electron transport rate of fully developed leaves were investigated at the study site in the first week of July, 2004 when experimental conditions did not indicate severe drought. Therefore these data can only be used as an indication of interspecific variation in photosynthetic parameters and description of photosynthetic efficiency of two oak species. Both species exhibited relatively low light saturated photosynthesis rate (*Table 3*) which changed with the light adaptation character of the leaves. *Q. petraea* exhibited two or three times higher P_{max} in sun leaves than in shade leaves. The decline of P_{max} within the canopy of *Q. cerris* was smaller. The transpiration rate of both species was also the highest in the upper part of the canopy but it showed slighter reduction towards the shade layer of trees (*Table 3*). Water use efficiency was higher for *Q. petraea* in each layer of the canopy. In contrast to low photosynthesis rate both species maintained relatively high light saturated ETR values. ETR was higher at saturation light intensity for both canopy layers of *Q. cerris* than for *Q. petraea* (*Table 3*).
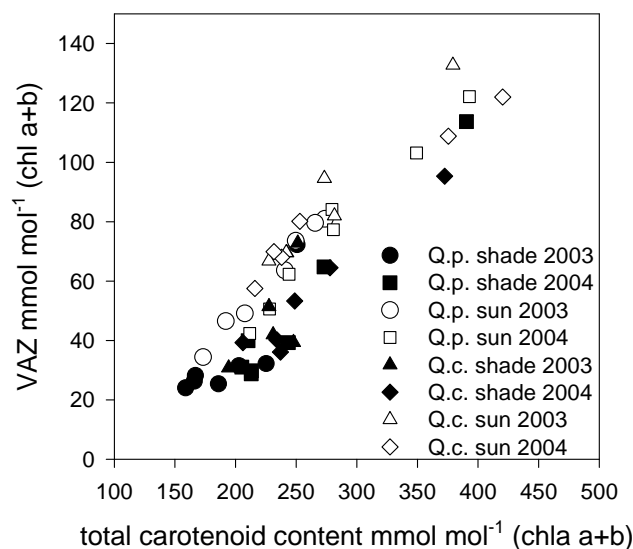

Figure 6. Changes in total carotenoid content and VAZ cycle pool in sun and shade leaves of Q. petraea and Q. cerris in spring and summer of 2003 and 2004.

Table 3. Stomatal conductance (gs), light saturated CO2 assimilation rate (Pmax), transpiration rate (E), Water use efficiency (WUE) and electron transport rate (ETR) of sun and shade leaves of Quercus petraea and Quercus cerris. The measurements were performed on 5-7 July 2004. Mean values and ± 1 SE are presented (n = 18).

		g_s (mmol m^{-2} s^{-1})	P_{max} (μmol m^{-2} s^{-1})	E (mmol m^{-2} s^{-1})	WUE (μmol CO_2 mmol^{-1} H_2O)	ETR (μmol m^{-2} s^{-1})
Q. petraea	sun leaves	362.7±26.7	8.33±0.44	3.78±0.13	1.82±0.06	109.1±18.4
	shade leaves	168.6±11.9	3.34±0.38	2.79±0.09	1.08±0.10	60.91±11.5
Q. Cerris	sun leaves	486.9±44.4	8.06±0.54	3.73±0.24	1.96±0.11	126.7±10.9
	shade leaves	349.6±41.8	6.26±0.56	3.29±0.23	1.67±0.09	109.4±26.3

3.5 Seasonal changes of maximum photochemical efficiency of leaves

The seasonal course of maximal photochemical efficiency of PSII (Fv/Fm) measured at noon in the dark-adapted state (*Figure 7*) resembled that of chlorophylls (*Figure 5*) and leaf growth (*Figure 4*). In the early growing season leaves exhibited lower Fv/Fm values in each year. Fv/Fm was always lower in sun leaves of both oak species in each year but the variability of Fv/Fm within the tree canopy was higher in *Q. petraea*. In 2003 Fv/Fm ratios were slightly lower (by 1-3%) for fully expanded sun and shade leaves in both species.
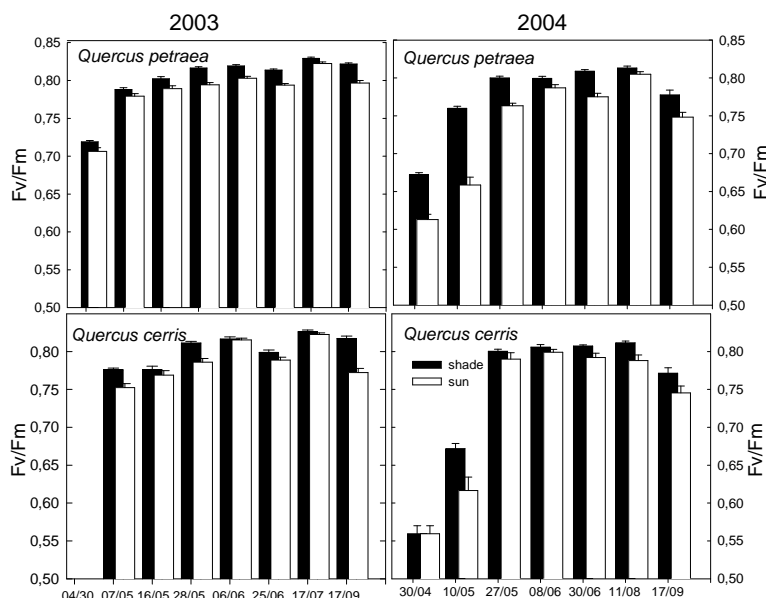

Figure 7. Seasonal changes in maximal photochemical efficiency measured at noon in sun and shade leaves of two oak species in 2003 and 2004.

4   DISCUSSION

The years in which the investigations were performed differed significantly in weather conditions. 2003 was an extreme year for the forest stand and trees experienced drought stress from the start of crown development. Growing season of 2004 was colder and rainfall during the main period of canopy expansion was significantly higher and showed more even distribution from April to September. In 2003 the soil moisture content decreased to around 15% in June and July. In May and June of 2003, during the main period of leaf development, the temperature was higher than in 2004.

Leaf growth of *Q. petraea* was less tolerant to drought than that of *Q. cerris*. Drought slightly affected the leaf area expansion of *Q. petraea* but reduced significantly the leaf mass increment. It suggests that sessile oak invested less assimilates into producing structural carbohydrates in the dry year (2003) than did *Q. cerris*, but instead it maintained a similar leaf area as in 2004. As a result, SLM was lower in 2003 than in 2004. In contrast to *Q. petraea*, *Q. cerris* showed small plasticity of leaf growth traits in corresponding canopy layers in response to the alteration of soil water availability in different years and maintained smaller leaf area and leaf mass but higher SLM, particularly in sun leaves.

In comparative studies with a wide range of trees species it was revealed that SLM is positive correlated with modulus of leaves' cell wall elasticity which inversely relates to cell wall elasticity (Salleo – Lo Gullo 1990). This relationship is a well accepted indicator of interspecific differences in drought tolerance. In general, tree species showing lower SLM and

lower modulus of elasticity (more elastic cell wall in leaf tissues) occur preferably in more mesic sites. However, species with higher SLM and less elastic leaf area are better adapted to drier sites (Corcuera et al. 2002). It can also be stated that the functional correlation between the two leaf traits is not so well revealed. It is assumed that SLM depends more on the amount of mechanical tissue (mainly cells with lignified cell wall) and thereby reflecting the leaf density and thickness, while modulus of elasticity is more sensitive to thickness and cellulose content of cell wall, indicating primarily the maximal amount of water accumulated in cells at full turgor of leaves.

The lower SLM and more elastic cell walls of leaves observed in *Q. petraea* in 2003 allow this species to store adequate amounts of water at low leaf (and soil) water potential such that it can afford to transpire more than was transported from the roots. In this way *Q. petraea* acclimated to the severe drought conditions through exhibiting a water-spending strategy. In comparison, the higher SLM of *Q. cerris* supposed less elastic cell walls and more rigid anatomy in the leaf that allowed the adoption of a water-saving strategy. The two different strategies for controlling the leaf water relations may be advantageous for the two species co-existing at the same site. The water-spending strategy of *Q. petraea* can permit it to absorb water from the soil at the expense of a larger loss of water through transpiration; therefore this species must adopt a specific drought tolerance mechanism for maintaining the leaf turgor for leaf physiology as optimal as possible when leaf water potential is reduced. However, such a strategy cannot be sufficient when drought persists. At the same period *Q. cerris* showed a water-saving strategy that allows it to avoid the larger water loss and moderate the water absorption. Therefore this species may be more successful in prolonged drought periods.

These different strategies might explain the differences in water use efficeincy of leaves between the two species. *Q. cerris* was characterised by a higher water use efficeincy during the same measurement conditions than *Q. petraea*.

The rate of leaf mass increase was very similar in the initial phase of leaf development in both study years but it was substantially reduced earlier in 2003 and continued more slowly until the date of full expansion of leaves than in 2004. Nevertheless, not only zero growth but reduction of average leaf mass was also observed due to the prolonged drought in June particularly for *Q. petraea*. As a result, we observed a transient phase of negative leaf growth rate reflecting the impairment of leaf carbon balance (Mészáros et al. 2007) which could only recover after the short heavy rain in July.

Alteration of growth traits during drought has been reported for other tree species. Sessile oak seedlings adapted to drought by reducing the leaf:root ratio (Thomas 2000) and decreasing the ratio of leaf to fine root biomass (Thomas – Gausling 2000). Large reductions in annual biomass and tree circumference for adult pine and beech trees were also reported as a result of drought in 2003 as compared to humid years (Granier et al. 2007).

The chlorophyll contents of shade and sun leaves were higher in 2003 than in 2004, particularly in *Q. petraea*. The higher leaf chlorophyll content per unit of dry matter in drier year can be considered as a compensating mechanism for the reduced leaf area and mass.

Studies on a wide range of species showed that maintenance of photosysthesis rate at the level which provides a positive carbon balance of leaves during stress requires efficient photoprotection of photosynthetic apparatus including carotenoids (Long et al. 1994) In contrast to *Q. petraea*, *Q. cerris* invested less in synthesis of carotenoids in the dry year than in the humid year which suggests that other leaf traits and processes may also be effective in avoiding the effects of excess light under limiting water availability.

Chlorophylls and carotenoids exhibited clear seasonal trends for both species. In spring carotenoids were synthesised earlier than chlorophylls and showed high concentrations in young leaves in the whole crown of the trees. It reflected the fact that these compounds

played important role in photoprotection of expanding tree crown before the photochemical efficiency and the carbon assimilation capacity of trees were low and chloroplast development was incomplete. Carotenoids/chlorophyll ratios correlated negatively with the Fv/Fm values during the growing seasons.

Depression of Fv/Fm in young leaves took place with a simultaneous adjustment of the pigment composition in both species. The high carotenoid content in developing leaves seems to be an important stabilising biochemical trait of the two species for the balance between light absorption and its utilisation in the photochemical reactions particularly when heat stress and water stress may result in more serious down-regulation of photosynthetic CO_2 assimilation such as appeared in the hot spring and early summer of 2003. The depressed Fv/Fm and down-regulated CO_2 assimilation in spring obviously increase the demands on photoprotective processes such as non-assimilatory electron transport and non-radiative dissipation of absorbed light energy (Demmig-Adams – Adams 1992). The non-radiative (heat) dissipation of excess light energy is mediated in leaves of oak species by the operation of xantophyll cycles, a largest part of VAZ cycle and a small part of lutein-epoxid cycle (Mészáros et al. 2005). Young leaves of both species accumulated VAZ cycle pigments (violaxanthin, antheraxanthin, zeaxanthin) by 1,5-2,5 times higher than fully developed leaves. It suggests a greater demand on photoprotection against the high light intensity in developing leaves of the tree crown which may be accelerated significantly when other environmental stresses appear. The low midday values of Fv/Fm in spring indicated the susceptibility of photosynthetic apparatus of both species to photoinhibition.

Our measurements showed that both species exhibited relatively low P_{max} of fully developed sun leaves at saturated light which was also reported for other late-successional tree species (Bassow – Bazzaz 1998). However, in contrast to the low CO_2 assimilation rate, both oak species showed high ETRs at saturation light intensity. Due to a loose canopy structure *Q. cerris* maintains a relatively higher ETR not only in sun leaves but also in the shade leaves. These results suggest that sun exposed leaves of both species must develop substantial non-assimilatory (photorespiratory) electron utilisation for avoiding PSII photoinhibition (Kozaki – Takeba 1996) in the summer period when high light levels are accompanied by high temperatures. Increased photorespiration has also been reported to be involved in the maintenance of high ETR for a savanna tree species (Franco – Lüttge 2002) and for Norway spruce (Spunda et al. 2005).

Increased photorespiratory electron utilisation can also explain that in spite of relatively low P_{max} both species have the capacity to maintain high maximal photochemical efficiency of PSII (Fv/Fm) in summer. It also suggested that functioning of photosynthetic apparatus was generally less impacted even during summer drought than leaf growth, and could maintain a reduced but positive carbon balance of leaves, with the exception of a negative growth rate for *Q. petraea* in June 2003. The mean midday levels of Fv/Fm of fully developed leaves remained around 0.80 in both summer periods: *Q.cerris*: sun leaves 0.803 (2003), 0.792 (2004), shade leaves 0.813 (2003), 0.806 (2004); *Q. petraea*: sun leaves 0.801 (2003), 0.782 (2004), shade leaves 0.816 (2003), 0.805 (*2004*). This reflects a high degree of resistance of the photosynthetic apparatus to chronic photoinhibition in summer which was also reported for other tree species (Spunda et al. 2005, Mészáros et al. 1998). However, the midday levels of Fv/Fm were lower than the maximal value (0.832 ±0.004) potentially reached by dark-adapted leaves of plants with optimal physiological condition (Björkmann – Demmig-Adams, 1987) in the absence of stress.

Beside the potential involvement of photorespiratory electron transport in photoprotection the low CO_2 assimilation rate also increases the demand on non-radiative dissipation of absorbed light energy in the upper part of crown in the summer period. However, in contrast

to fully expanded leaves the higher VAZ pool in spring indicated that the latter process might have a more significant role in photoprotection in young leaves of both species.

Our results show that sun leaves of both species were always characterised by more depressed Fv/Fm and larger VAZ cycle pool than shade leaves during the whole growing season of both years. The midday depression of Fv/Fm correlated with the de-epoxidation of violaxanthin into antheraxanthin and zeaxanthin, and the zeaxanthin dependent heat dissipation in sun leaves (Mészáros et al. 2006). Both species showed larger impairment of maximal photochemical efficiency and lower Fv/Fm in the wetter year (2004) than in 2003. This indicated lasting drought effects on the photochemical activity of leaves of both species, but *Q. petrae*a was more affected than *Q. cerris*. Such a time lag of drought occurring during the previous growing season on the physiological traits was also reported for other species (Bréda et al. 2006, Granier et al 2007). This may be a consequence of reduced amount of carbohydrates, lipid and protein reserves formed in the end of 2003 and also the damage to roots and irreversible xylem embolism. These together might weaken the trees for long period and accelerate their susceptibility to stresses including the large scale gradation of phytophagous insects particularly at sites with low fertility and transitional position. However, the questions of how drought extremes may influence the competition between the two existing oak species, and whether they may result in serious tree dieback in the investigated forest, require further studies.

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Effects of Artificial Regeneration Methods on Mortality, Growth and Shape of Oak Seedlings in a Central European Oak-Hornbeam Stand

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Abstract – This paper analyses the results of an artificial regeneration experiment carried out in an oak-hornbeam stand. The effects of initial seedling density (10200, 14300, 35700 stems per hectare), spacing geometry (140 cm x 70 cm, 240 cm x 40 cm), chemical (with Erunit and Nabu) and mechanical weeding of pedunculate (*Quercus robur*) and sessile oak (*Quercus petraea*) were examined at the age of eight years. The mortality of *Q. robur* seedlings was independent of the initial density but that of *Q. petraea* increased with it. Height and diameter growth of both species significantly decreased with the density, and the values of the diameter-to-height ratios (DHR) became smaller as the density increased. At approximately the same seedling density the mortality was lower but the seedlings were shorter, thinner and the values of DHR were smaller if the distance between stems was much lower than that between rows. Mechanical or chemical weeding did not affect considerably seedling mortality, growth or shape in any of the spacing types.

weeding / *Quercus petraea* / *Quercus robur* / seedling development / seedling survival / spacing

Kivonat – Mesterséges felújítási eljárások hatása az újulat öngyérülésére, növekedésére és alakjára egy közép-európai gyertyános-tölgyesben. A tanulmány egy gyertyános-tölgyesben végrehajtott mesterséges felújítási kísérlet eredményeit mutatja be. Kocsányos (*Quercus robur*) valamint kocsánytalan tölgy (*Quercus petraea*) esetében a felújítás nyolcadik évében vizsgáltam a kiindulási csemeteszámnak (10200, 14300, 35700 db/ha), a hálózat geometriájának (140 cm x 70 cm, 240 cm x 40 cm) valamint vegyszeres (Erunit és Nabu vegyszerekkel) és mechanikus ápolásoknak a hatását. A kocsányos tölgy öngyérülése nem függött a kiindulási csemeteszámtól, ugyanakkor a kocsánytalan tölgyé a csemeteszámmal emelkedett. A csemeteszám emelkedésével a magassági növekedés ill. a vastagodás mindkét fafaj esetében csökkent, és a csemeték nyurgábbá váltak. Megközelítőleg azonos kiindulási csemeteszám mellett a tőtávolság csökkentésével (és így a sortávolság növelésével) az újulat öngyérülése csökkent, ugyanakkor a csemeték magassága és vastagsága is csökkent, valamint felnyurgultak. A mechanikus ill. a vegyszeres ápolás egyik hálózati típus esetében sem befolyásolta jelentősen a csemeték növekedését ill. alakját.

ápolás / *Quercus petraea* / *Quercus robur* / újulat fejlődése / újulat mortalitása / ültetési hálózat

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1 INTRODUCTION

One of the most important periods in the life of managed forests is the regeneration. It determines the subsequent development of the growing stand (Ovington – MacRae 1960). Thus, the regeneration technique must be chosen with special care from ecological and economical points of view.

The costs of regeneration strongly correlate with the biological aspects of the applied technique. Methods less suitable for seedling survival and development are more expensive while planting must be repeated and the regeneration period is longer. Costs of seeds or seedlings are possibly high if regenerating artificially. Thus, determining the optimal seed or seedling number is of great importance. To do this, four questions must be answered: How does seedling density influence 1. the mortality and 2. the growth of the developing stand as well as in long-term 3.the shape and 4. the wood structure of the individual trees?

In artificial oak regenerations, wide spacing with low number of seedlings was often applied in Central Europe (Weaver – Spiecker 1993). However, using high number of seeds or seedlings with closer distance between stems can be more advantageous from three points of view (Varga 1966, Savill and Spilsbury 1991):

1. the canopy of the growing stand closes faster so weed competition decreases sooner;
2. the shape of the seedlings may become better while forking is inhibited due to the shading of the neighbouring seedlings;
3. there is a greater supply for natural or artificial selection.

Furthermore, smaller distances between stems can facilitate height growth to some extent in the case of some species (Fekete 1938, Szodfridt 1959). It is also clear that more seedlings can utilize site productivity better as long as spacing is not too dense which leads to a greater intraspecific competition and consequently to slower seedling growth (Szodfridt 1959, Harmath 1961, Solymos 1983, Harkai 1987, Kolb – Steiner 1990). Other disadvantages of denser spacing are its obviously higher costs and technical difficulties with silvicultural treatments (weeding, cleaning; Varga 1966). The effects of spacing on oak seedling survival and growth are still poorly known.

Costs of weeding can be high at both artificial and natural regeneration. At the beginning of regeneration herbs can influence survival and growth of seedlings in two main ways (Magyar 1933): by shading (competition for light) and by root competition (competition for water; Harmer et al. 2005, Harmer – Morgan 2007). Thus, chemical or mechanical weeding can facilitate seedling survival and growth of oak as well as those of other tree species (Ovington – MacRae 1960, Jarvis 1964, Csesznák 1980, Kolb et al. 1990, Kolb – Steiner 1990, Collet – Frochot 1996, Collet et al. 1996, Chaar et al. 1997, Collet et al. 1997, Collet et al. 1998, Kelly 2002, Coll et al. 2003). There is an important difference between the chemical and mechanical protection. While in the former case usually the whole plant dies with its root system, in the latter in most cases only the above-ground part is killed. In this way shading effect decreases but root competition does not. So seedling growth may remain inhibited (Davies 1985, Löf 2000). On the other hand, weed competition does not hinder seedling development by all means (Madsen 1995). Furthermore, in some cases even the total protection from root competition of herbs did not lead to higher seedling growth intensity (Szappanos 1969).

Weeding experiments of oak were usually quite short-term analyzing data of 1-4 years (Szappanos 1969, Collet and Frochot 1996, Collet et al. 1996, Chaar et. al 1997, Collet et al. 1997, Löf 2000). Some studies (Collet et al. 1998, Kelly 2002) were longer-term, but the combined effects of different weeding treatents and spacing types were not examined.

The aim of the present study is to determine the effects of different spacing types and weeding treatments on oak seedling survival and growth simultaneously in a sessile oak–

hornbeam and a pedunculate oak–hornbeam stand: How do spacing geometry, initial seedling density, mechanical and chemical weeding influence the mortality, growth and shape (lankiness) of the seedlings?

2   MATERIALS AND METHODS

2.1 Study area

The study stand (subcompartment Káld 46 B, approximately 11.1 ha, 47°09'N, 17°00'E) is growing on rusty brown forest soil, 200 m above sea level. The climate is characterized by a diagram (*Figure 1*). The whole study area was fenced against game in 1994.
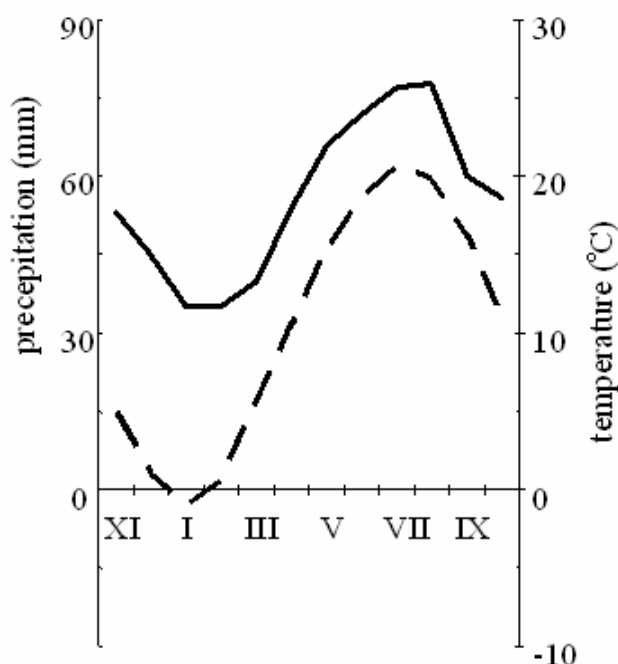

Figure 1. Climate diagram for characterizing the study stand. Monthly precipitation (solid line) and temperature (broken line) were measured at two nearby meteorological stations, Káld and Pápa, respectively from 1901 to 1950. Source: Kakas (1967).

The mixed parent stand consisted of sessile oak (*Quercus petraea,* net area rate 32% – data of the Hungarian National Forest Service), turkey oak (*Quercus cerris*, 24%), hornbeam (*Carpinus betulus*, 24%) and pedunculate oak (*Quercus robur*, 20%) before starting the regeneration. The closure of the parent stand was approximately 95%. At this time the stand was nudum (i.e. the ground vegetation was very sparse).

In the initial stage of regeneration high cover of fleabane (*Erigeron canadensis*) was characteristic. Later on thistle species (*Cirsium sp.*) and *Erigeron annuus* proliferated. From the third year on bushgrass (*Calamagrostis epigeios*) occurred in high abundance. Finally, by the fifth year the cover of blackberry (*Rubus spp.*) has reached high values in some spots endangering seedling survival and growth.

2.2 Silvicultural treatments

The whole stand was divided into 12 blocks of approximately identical size (*Figure 2*). Blocks No. 1-2, 5-8, 11-12 are included in the present study.
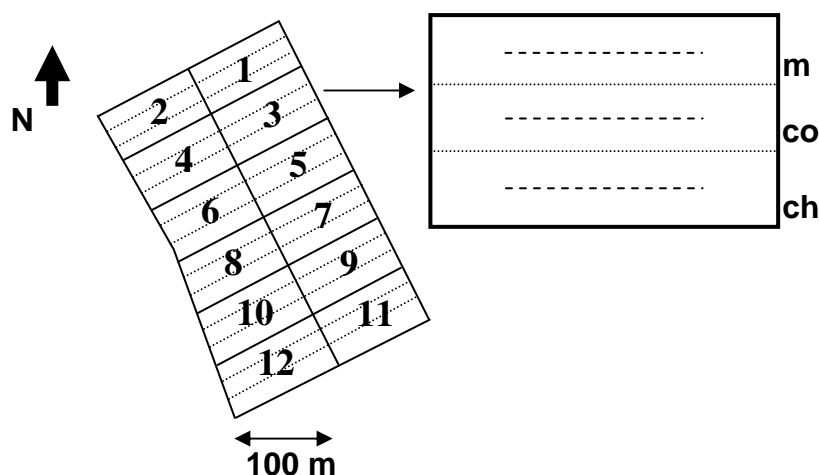
Figure 2. Experiment design. The study stand was divided into 12 blocks of approximately identical size. Each block consists of three plots in which different weeding treatments (mechanical weeding – m; control – co; chemical weeding – ch) were applied. Seedlings were sampled along 50 m long transects (broken line) in the middle of each plot.

No site preparation was applied on the study area before planting. One year-old seedlings of *Quercus robur and Q. petraea* were planted in different spacing types in the spring of 1995 (*Table 1*). One of the applied densities (14 300 stems per hectare) is that which is recommended by Danszky (1963) for oak-hornbeam stands growing in this region of Hungary.

Table 1. Spacing types of artificial regeneration

Blocks	Species	Row dist. (cm)	Stem dist. (cm)	No. stems per hectare
1.	Q. rob.	140	70	10200
2.	Q. pet.	140	70	10200
5.	Q. rob.	240	40	10400
6.	Q. pet.	240	40	10400
7.	Q. rob.	140	50	14300
8.	Q. pet.	140	50	14300
11.	Q. rob.	140	20	35700
12.	Q. pet.	140	20	35700

At the beginning of the regeneration all blocks but No. 11 and No. 12 were sprayed with Erunit. Afterwards, every block was divided into three plots in accordance with the applied weeding method (one control plot, one plot weeded chemically and one plot weeded mechanically). Seedlings of goat willow (*Salix caprea*) and aspen (*Populus tremula*) were cut in all plots in 1999. In the plots weeded mechanically the above-ground biomass of the competing vegetation was removed in July 1997 and in July 1998.

Chemical weeding was carried out with chemicals Erunit and Nabu in March 1997 and in June 1998, respectively. The second treatment was not performed in blocks No. 1 and No. 2 due to unfavourable weather conditions. Because of the high cover of bushgrass Nabu had to be sprayed in blocks No. 11 and No. 12 in May 1997. Erunit inhibits the germination of mono- and dicotyledons alike for three-four months. One liter Erunit contains 300 g acetochlor, 200 g atrazine and 30 g antidote AD-67. The applied concentration was 7 l/ha. Nabu kills monocotyledons selectively. The agent of Nabu is sethoxydim (12.5%). Nabu was sprayed in concentration of 4 l/ha. Both chemicals can

reduce root competition. In 2000 woody species were weeded out in all plots. Afterwards, further weeding treatments were not necessary.

2.3 Sampling

Sampling was carried out in 2003 and started with a pilot sampling to analyze the effect of sample size on the value of the mean of the dependent variables (seedling height and diameter). That is, much more seedlings were sampled in some chosen plots (on which the variance of seedling height and that of seedling diameter were the highest according to visual estimation) than the estimated required minimum. From the data the fluctuation of the mean value with increasing sample size was determined. The sampling size from which the fluctuation was smaller than 5% was considered as the required minimum sample size. Based on the obtained data heights and diameters at breast height of all seedlings were measured along 50 m long transects in the middle of each plot (*Figure 2*) except for plots of blocks No. 6, No. 11 and No. 12. In the latter plots transects were divided into 10 m long sections due to the high number of seedlings. Heights and diameters at breast height of all seedlings were measured along the two end and the middle sections.

2.4 Data analysis

The shape of the seedlings was characterized with the quotient of the diameter and the height (d/h). Since both diameter and height were expressed in meter the quotient has no dimension. Data were evaluated with analysis of variance using BIOMstat 3.3 program (2002). For checking normality and homogeneity of variances the Kolmogorov-Smirnov and F-max statistics (Hartley 1950) as well as log-anova tests (Martin – Games 1977) were used, respectively. Where assumptions of parametric ANOVA could not have been met Kruskal-Wallis ANOVA was applied. The effects of weeding were studied in each block (i.e. in the case of each spacing type, *Table 1*) separately.

3 RESULTS

3.1 Effects of seedling density at the same row distance

Considering all plots, the average mortality of pedunculate and sessile oak was similar, 21.3% and 26.4%, respectively. Mortality of pedunculate oak doesn't correlate strongly with the initial seedling number in any of the plots (*Table 2a, b*). In contrast, mortality of sessile oak seems to increase with it in every plot. Height and diameter growths as well as DHR of the seedlings decreases significantly as seedling number increases (*Table 2a, b*). These effects are similar in the cases of both oak species and all weeding types.

3.2 Effects of spacing geometry at the same seedling density

Seedling survival was higher in all but one plots in which the differences between the two distance types (distances between rows and distances between stems) were greater (*Table 3a, b*). On the other hand, seedlings of both species were significantly shorter, thinner and DHR values were higher in these plots.

Table 2a. Effects of initial seedling number on mortality, growth and shape of Q. robur seedlings at row distance of 140 cm. The age of the regeneration was 8 years.

Weeding	No. stems per hectare	n	Mortality (%)	h (cm)	d (mm)	(d/h) x 10^{-3}
me	10200	53	26	380** (89)	34.5** (14.3)	8.8 (3.0)
me	14300	78	22	330 (61)	27.1 (10.9)	8.0 (2.3)
me	35700	112	25	243** (73)	16.6** (9.9)	6.2** (2.8)
co	10200	62	13	342 (73)	28.9 (11.5)	8.2 (2.1)
co	14300	73	27	344 (75)	28.0 (11.2)	7.8 (2.3)
co	35700	121	19	262** (77)	16.3** (9.9)	5.6** (2.5)
ch	10200	48	33	350** (74)	31.2** (13.1)	8.6** (2.4)
ch	14300	74	26	291 (84)	21.8 (11.5)	6.9 (2.6)
ch	35700	120	20	279 (83)	16.5** (9.8)	5.4** (2.5)

Table 2b. Effects of initial seedling number on mortality, growth and shape of Q. petraea seedlings at row distance of 140 cm. The age of the regeneration was 8 years.

Weeding	No. stems per hectare	n	Mortality (%)	h (cm)	d (mm)	(d/h) x 10^{-3}
me	10200	53	26	345** (79)	31.0** (12.8)	8.6** (2.7)
me	14300	73	27	275 (81)	19.7 (11.3)	6.5 (2.9)
me	35700	102	32	250* (76)	16.1* (10.4)	5.8* (2.7)
co	10200	53	26	346** (66)	30.1* (12.1)	8.4 (2.3)
co	14300	72	28	303 (84)	24.7 (13.5)	7.5 (3.0)
co	35700	95	37	269** (68)	17.4** (9.7)	5.9** (2.4)
ch	10200	59	17	352** (59)	31.2** (10.2)	8.7** (2.0)
ch	14300	83	17	269 (77)	19.7 (10.6)	6.8 (2.6)
ch	35700	80	47	247* (76)	14.9** (8.3)	5.7** (2.4)

Quotients in the last column are the averages of quotients calculated for each seedling. Standard deviations are showed in parentheses. Plots in which 14300 seedlings were planted were compared to the two other plots in the case of each weeding treatment. If the difference was significant it is indicated only at data of the two latter plots. h – average height of the seedlings; d – average diameter at breast height of the seedlings; me – plots weeded mechanically; co – control plots; ch – plots weeded chemically; *Q. rob. – Quercus robur*; *Q. pet. – Quercus petraea*; * - *p*<0.05; ** - *p*<0.01.

Table 3a. Effects of spacing geometry on mortality, growth and shape of 8-year old Q. robur seedlings.

Weeding	Spacing (cm x cm)	n	Mortality (%)	h (cm)	d (mm)	(d/h) x 10^{-3}
me	140 x 70	53	26	380 (89)	34.5 (14.3)	8.8 (3.0)
me	240 x 40	111	11	300** (70)	24.5** (12.1)	7.7* (2.8)
co	140 x 70	62	13	342 (73)	28.9 (11.5)	8.2 (2.1)
co	240 x 40	114	9	291** (75)	24.0** (11.8)	7.8 (2.8)
ch	140 x 70	48	33	350 (74)	31.2 (13.1)	8.6 (2.4)
ch	240 x 40	94	25	324 (77)	26.3* (12.3)	7.7* (2.4)

Table 3b. Effects of spacing geometry on mortality, growth and shape of 8-year-old Q. petraea seedlings.

Weeding	Spacing (cm x cm)	n	Mortality (%)	h (cm)	d (mm)	(d/h) x 10^{-3}
me	140 x 70	53	26	345 (79)	31.0 (12.8)	8.6 (2.7)
me	240 x 40	66	12	288** (70)	23.4** (11.5)	7.6 (2.7)
co	140 x 70	53	26	346 (66)	30.1 (12.1)	8.4 (2.3)
co	240 x 40	66	12	305** (73)	23.7** (11.4)	7.3* (2.5)
ch	140 x 70	59	17	352 (59)	31.2 (10.2)	8.7 (2.0)
ch	240 x 40	48	36	299** (69)	23.9 (12.3)	7.5** (2.4)

Standard deviations are showed in parentheses. Significance level is indicated only at the data of plots of spacing 240 cm x 40 cm. For abbreviations see *Table 2*. * - *p*<0.05; ** - *p*<0.01.

3.3 Effects of weeding

Weeding did not improve seedling survival of any of the two oak species in any of the spacing types (*Table 4*). On the contrary, in some blocks survival of pedunculate oak seemed to decrease due to weeding. Seedling growth was not promoted considerably either by mechanical or chemical weeding. In some blocks (No. 7, No. 8, No. 11 and No. 12; *Table 4*) seedlings, which were weeded ("w-seedlings") were even significantly shorter and thinner than seedlings, which were not weeded. In contrast, in some other blocks (No. 1, No. 2 and No. 5) "w-seedlings" are significantly taller and thicker though most of these differences are not important from silvicultural point of view. Weeding practically didn't influence seedling shape.

Table 4. Effects of weeding on mortality, growth and shape of oak seedlings, at the age of 8 years

Blocks	Weeding	n	Mortality (%)	h (cm)	d (mm)	(d/h) x 10^{-3}
1.	me	53	26	380* (89)	34.5* (14.3)	8.8 (3.0)
1.	co	62	13	342 (72)	28.9 (11.5)	8.2 (2.1)
1.	ch	48	33	350 (74)	31.2 (13.1)	8.6 (2.4)
2.	me	53	26	345 (79)	31.0 (12.8)	8.6 (2.7)
2.	co	53	26	346 (66)	30.1 (12.1)	8.4 (2.3)
2.	ch	59	17	352* (59)	31.2* (10.2)	8.7* (2.0)
5.	me	111	11	300 (70)	24.5 (12.1)	7.7 (2.8)
5.	co	114	9	291 (75)	24.0 (11.8)	7.8 (2.8)
5.	ch	94	25	324** (77)	26.3 (12.3)	7.7 (2.4)
6.	me	66	12	288 (70)	23.4 (11.5)	7.6 (2.7)
6.	co	66	12	305 (73)	23.7 (11.4)	7.3 (2.5)
6.	ch	48	36	299 (69)	23.9 (12.3)	7.5 (2.4)
7.	me	78	22	330* (61)	27.1 (10.9)	8.0 (2.3)
7.	co	73	27	344 (75)	28.0 (11.2)	7.8 (2.3)
7.	ch	74	26	291** (84)	21.8** (11.5)	6.9* (2.6)
8.	me	73	27	275 (81)	19.7* (11.3)	6.5 (3.0)
8.	co	72	28	303 (84)	24.7 (13.5)	7.5 (3.0)
8.	ch	83	17	269** (77)	19.7* (10.6)	6.8 (2.6)
11.	me	112	25	243* (73)	16.6 (10.0)	6.2* (2.8)
11.	co	121	19	262 (77)	16.3 (9.9)	5.6 (2.5)
11.	ch	120	20	279 (83)	16.5 (9.8)	5.4 (2.5)
12.	me	102	32	250* (76)	16.1 (10.4)	5.8 (2.7)
12.	co	95	37	269 (68)	17.4 (10.0)	5.9 (2.4)
12.	ch	80	47	247** (76)	14.9 (8.3)	5.7 (2.4)
All	me	648	22.6 (7.4)	228 (128)	29.2 (8.5)	7.2 (2.9)
All	co	656	21.4 (9.7)	231 (122)	30.0 (8.0)	7.1 (2.7)
All	ch	606	27.6 (10.5)	221 (122)	29.6 (8.3)	6.9 (2.7)

Plots, which were weeded were compared to the control plots. Significance level is indicated at the data of the former plots. Standard deviations are showed in parentheses. For abbreviations see *Table 2*. * - $p<0.05$; ** - $p<0.01$.

4   DISCUSSION

Higher seedling number increased mortality of sessile oak. The survival of pedunculate oak during the first eight years of the regeneration was determined by other factors not investigated in this study. On the other hand, intraspecific competition between the seedlings

inhibited growth and decreased DHR. The results are in accordance with earlier experiments studying other tree species (e.g. Szodfridt 1959, Harmath 1961, Solymos 1983, Harkai1987). Spacing geometry is very important from silvicultural point of view (Varga 1966). If the distance between rows is large enough (e.g. 240 cm) weeding can be mechanised easily. According to the results, however, larger distance between rows didn't compensate for smaller distance between stems at the same seedling density. Because of the small stem distance competition between the seedlings became more intense. This slowed seedling development and decreased DHR. On the other hand, survival of seedlings was much higher in this case. The reason for this phenomenon is not clear. These results disprove the hypothesis of Varga (1966) who concluded that applying large row and small stem distance is just as appropriate for seedling development as the application of equal distances between rows and stems.

Weeding did not improve seedling survival of any of the two oak species. This does not mean that the herb layer could not inhibit seedling development because it is possible that immediately after the weeding occasions "w-seedlings" grew faster. However, in the long-term the effects of the applied weeding treatments are negligible from silvicultural point of view. It must be taken into consideration, however, that weather conditions of 1997 were not favourable for spraying Erunit and this could have influenced the results. Presumably, because of the low precipitation of that year only a small amount of this chemical could infiltrate into the soil leading to low effectiveness of protection. Furthermore, decrease of the cover of bushgrass due to spraying Nabu promoted indirectly the proliferation of blackberry and dicotyledons of tall growth. Thus, weed competition was not reduced effectively enough by this chemical either.

Negative effects of weeding treatments observed in some blocks could be partly the consequence of weeding mistakes (e.g. accidental removal of oak seedlings in plots weeded mechanically). On the other hand, the lower cover of the herb layer in the plots weeded chemically let aspen and goat willow establish and grow.

5   CONCLUSIONS

According to the results, planting approximately 10 000 seedlings per hectare seem to be enough for the successful regeneration. Planting more seedlings slows down the growth and is more expensive. However, later on, effects of the initial seedling number on wood structure must be studied as well (Igboanugo 1990). Considering the same seedling density, from biological point of view it is more advisable to reduce the difference between row and stem distances. It is unnecessary to carry out weeding treatments every year.

The conclusions are valid primarily for stands which have similar stand structure and occur under similar site conditions as the study stands of the present experiment. However, even in these cases further research must be carried out to make the results more general.

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Gap Regeneration Patterns in a Semi-natural Beech Forest Stand in Hungary

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Abstract – The authors studied the effects of canopy openness, substrate features and herbaceous species cover on regeneration in eight natural canopy gaps and the surrounding stands in a semi-natural beech forest stand. Canopy openness was estimated by spherical densitometer, with relative light intensity being calculated using hemispherical photographs along gap-canopy transects. The high variance of relative light intensity and canopy openness values reflects the heterogeneity of canopy structure. Total cover of herbaceous species in and around gaps also reflected fine-scale canopy heterogeneity. Herbaceous species composition varied with total coverage, e.g. *Urtica dioica* dominated the dense herb layer found in the gaps. Tree individuals of various species and size classes showed different spatial patterns. Substrate features, canopy openness and also understorey herb density, all affected these patterns as consequence of the different ecological preferences of tree species in establishment and development, and their different sensitivity to browsing.

fine-scale disturbance / herbaceous layer / browsing / canopy openness / substrate features

Kivonat – Lék-felújulási mintázat vizsgálata egy magyarországi természetközeli bükkösben. A cikk egy természetközeli bükkös nyolc lékjében elvégzett vizsgálatot mutat be, amely a lék felújulása és a lombkorona-záródáshány, aljzati tényezők illetve a lágyszárú borítás közti kapcsolatot kutatja. A lombkorona-záródáshiány becsléséhez szférikus denziométert használtunk, illetve három lék fénymintázatát halszemoptikás képekkel is jellemeztük. A záródáshiány és a megvilágítottság értékei tükrözték a heterogén lombkorona-szerkezet sajátságait. A lágyszárúak borítása a finomléptékű fénymintázatra reagált. A lágyszárúak összborításának függvényében más-más lágyszárú fajok kaptak domináns szerepet a gyepszintben. A különböző méretosztályba és fajhoz tartozó csemeték változó térbeli megoszlást mutattak. A vizsgált változók együttesen komplex módon befolyásolták a fafajok megtelepedési és fejlődési feltételeit.

finomléptékű dinamika / lágyszárú szint / vadrágás / záródáshiány / aljzati tényezők

1 INTRODUCTION

Disturbance is a permanent feature of forest ecosystems, determining species composition, structure and process (Attiwill 1994, McCarthy 2001). Disturbance events range from the small-scale disturbance of single tree-falls or crown-breaks to the large-scale disturbance caused by e.g. catastrophic windstorms. Depending on the intensity and area of disturbance,

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gaps of different sizes are formed in forest stands at different points of time identifying the "gap-phase" in the forest developmental cycle, and creating different mosaic patterns in forest stands (Watt 1947, Runkle 1985, Busing – White 1997, McCarthy 2001). The importance of gap dynamics in forest ecosystems was discovered in the early 20th century, and intensive investigation of gap dynamic features are dated from the late 1970s (McCarthy 2001).

Gap formation changes the amount of total incident light reaching the ground level and influences nutrient and moisture availability (Collins et al. 1985, Denslow – Spies 1990, McCarthy 2001, Ritter et al. 2005, Mihók et al. 2005, Gálhidy et al. 2006), providing potential establishment sites for regeneration. Microclimate of gaps may accelerate seed germination and increase growth rates of herbs and woody species compared to below-canopy (Collins – Pickett 1988, Denslow – Spies 1990, Goldblum 1997, Brokaw – Busing 2000, Schumann et al. 2003, Holeksa 2003). Abiotic and biotic conditions can be very different both within individual gaps and among different sites (Nakashizuka 1985, Vitousek – Denslow 1986, Collins – Pickett 1987, Runkle 1989, Platt – Strong 1989, Kwit – Platt 2003). Different concepts have been formulated describing the relationship between resource heterogeneity and tree recruitment. According to the *gap partitioning* hypothesis, resource gradients (e.g. incident light) display a continuum in flux and concentration along the gap – canopy gradient – determined by, among others, the surrounding stand or gap size (Ricklefs 1977, McCarthy 2001). Species show different habitat preferences along this continuum, and in consequence, partition the gap environment (Poulson – Platt 1989, Sipe – Bazzaz 1994, Busing – White 1997). Other studies show that the effects of *micro sites* often override the gradual resource continuum, highlighting the role of specific substrates (e.g. logs, pits and mounds) in tree regeneration processes (Beatty 1984, Schaetzl et al. 1989, Peterson – Campbell 1993, McCarthy 2001). Although gaps have become an important focus of interest in the last few decades, "generalizations about the role of gap processes in the determination of forest composition and structure are less clear and likely to vary among different forest ecosystems" (Denslow – Spies 1990). Although there are examples from European temperate deciduous forests (Schmidt et al. 1996, Schumann et al. 2003, Holeksa 2003, Mihók et al. 2005, Ritter – Vesterdal 2006, Gálhidy et al. 2006, Naaf – Wulf 2007) the vast majority of gap-studies have been conducted in the temperate (deciduous and coniferous) forests of the United States and Japan and also in tropical forests (see McCarthy (2001) and references therein) focusing mainly on tree regeneration processes. Only a few studies concentrate on herbaceous species and the effect of herbaceous species on tree regeneration (Maguire – Forman 1983, Collins et al. 1985, Hughes – Fahey 1991, Collins 2003, Schumann et al. 2003, Galhidy et al. 2006, Naaf – Wulf 2007). However, herbs can affect abiotic variables, compete with seedlings, and consequently influence the success of tree regeneration in gaps (Maguire – Forman 1983, Abe et al. 1995, Castleberry et al. 2000, Collins 2003).

Several Hungarian authors have studied different aspect of beech regeneration. Márkus (1959) studied the number of beech seeds in a 100 year old beech stand in the Bakony Mts, Hungary. He showed that at edges seed numbers per unit area were higher than within the stand. Mendlik (1989) found similar patterns, while he compared stand centre with edge. Márkus and Mátyás (1966) carried out a country-wide survey of seed production in Hungary. They collected data from 611 forest ranges from all over the country representing all forest regions where beech occurs. They found large variation within each forest region, but the average differences in the amount of beech seeds produced in different forest regions could be explained by the climatic differences of previous year. Májer (1982) published historical data on beech seed crops in the Bakony Mts., covering 242 years. A heavy crop can be expected (on average) once every 14 years, an average crop every 7 years, and a poor crop every 3-4 years. However, heavy crops can occur at short intervals (1948, 1951). Török (2000, 2006) developed a new method of beech regeneration in the Bakony Mts. He took into account the

dynamic nature of forest types and the different courses of change following canopy opening depending on slope aspect and steepness. In order to provide optimal conditions for beech regeneration, he applied uneven cutting regimes taking into account both the original forest type and the direction of shade that old trees shed.

The aim of our study was to investigate how the presence of gaps affects regeneration processes in a semi-natural European beech forest stand. More specifically, our aims are:

1) To test if there are differences in canopy openness and incident light intensity between gap plots and below-canopy plots.
2) To test if there are differences in herbaceous species cover between gap plots and below-canopy plots.
3) To test if the amount and species composition of regeneration are different in gap plots and below-canopy plots.
4) To show any correlations between regeneration and the studied potential explanatory variables (canopy openness, substrate features and herbaceous species cover).

2 METHODS

The study was conducted in the Őserdő Forest Reserve, Northern Hungary. Őserdő is a small (25 ha) stand situated on the plateau of the Bükk Mountains (48° 03'N, 20° 27'E). Elevation ranges from 830 to 900 m. Mean annual temperature is 6.1°C (January: -4.1°C, July: 15.5°C), the annual precipitation is 896 mm. The bedrock is limestone, the soil is characterized as shallow to medium brown forest soil, but on steeper slopes, rendzina soils occur. In the southern part of the reserve the terrain is rather flat with typical karstic topography. The stand is dominated by European beech *(Fagus sylvatica L.)*, with small proportion of other species, e.g. European ash (*Fraxinus excelsior* L.)*, sycamore (*Acer pseudoplatanus* L.) and wych elm (*Ulmus glabra* Huds.). The age of the dominant beech trees varies between 150-200 years. The stand was managed and cut in the past, but it has developed undisturbed during the last 60 years. The stand structure is heterogeneous with trees of different size-classes, canopy gaps, and regeneration patches. The shrub layer is nearly absent, but the forest floor is covered with a dense herb-layer. Most frequent species are *Galium odoratum* (Scop.), *Glechoma hederacea* L., *Hordelymus europaeus* (L.) Jessen, and *Sanicula europaea* L. The Reserve has been protected since 1942.

According to the analysis of an aerial photograph taken in 2000, the total gap area was 9191 m^2, which is 4.3% of the reserve area. Average gap size was 61 m^2 (standard deviation: 71.33). The smallest gap was 4 m^{2,} while the maximum gap size was 378 m^2 (see also Kenderes et al. in press).

Eight canopy gaps (two large, where the maximum diameter = 1-1.5 x tree height and 6 small, where the maximum diameter = 0.5 x tree height) were selected in winter 2001/2002. *Table 1* shows the size attributes of the chosen gaps. We defined a "gap" as a canopy opening created by the death of at least one canopy tree. The shapes of the selected gaps were close to regular circles in cases of small gaps, but the two large gaps were irregular.

Table 1. Area and perimeter of the studied gaps (S: small, L: large)

Gap ID	S3	S8	S11	S1	S2	S12	L10	L5
Area (m^2)	39	24	27	36	40	60	178	203
Perimeter (m)	28	19	20	28	24	39	55	103

The age of the gaps were determined using aerial photographs from 1975, 1980, 1993 and 2000. Five gaps were identified in the 1975 photo, and one in the 1980, 1993 and 2000. We

used the date of the aerial photographs, where the gaps first appeared, to refer to the age of the gaps (i.e. 28 years in the case of the 1975 photos).

We used a systematic sampling design, with 5-meter grid resolution and 1m x 1m quadrats (*Figure 1*). In cases of small gaps, the grid went 5-15 m below the closed canopy. In cases of large gaps, the distance was 15-25 m respectively. Altogether, 657 quadrats were recorded: 64 in and around small gaps, 136 and 137 in and around large gaps. In each quadrat, *relative cover of substrate types* (intact soil, mineral soil, coarse woody debris (CWD), stem of a living tree and stone), *relative cover of herbaceous species, number of individuals belonging to each tree species* in 4 size classes below 1.3 m (0-10 cm, 10-20 cm, 20-50 cm, 50cm<) and seedlings with cotyledons separately were recorded in July 2002.
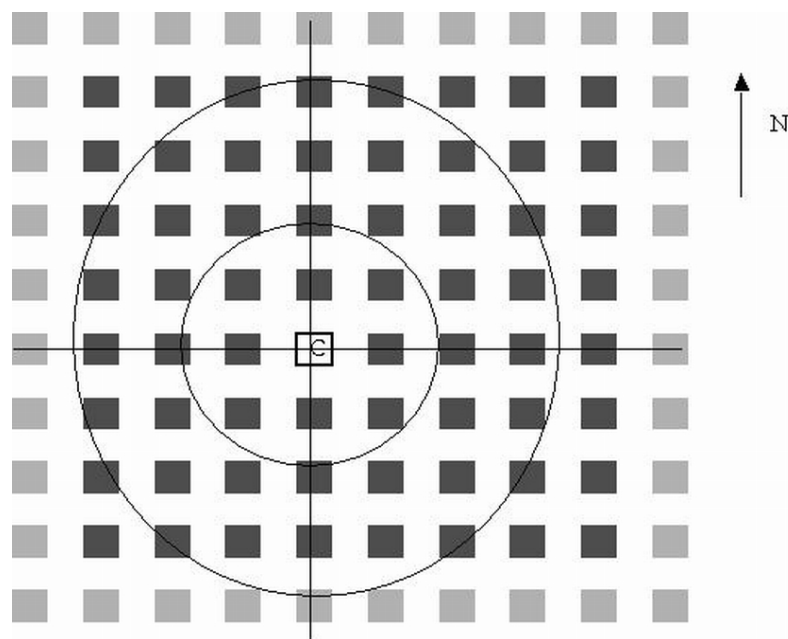

Figure 1. Sampling design in small (dark cells) and large gaps (light cells).
1 m x 1 m quadrats are signed by filled cells, gaps are signed by circles.
Straight lines show the transects along which estimation of canopy openness was made and
hemispherical photographs were taken.

C*anopy openness* was estimated by spherical densiometer (Lemmon 1956) in every gap along the N-S and E-W transects running along gaps – below-canopy gradients in 2003 (see *Fig. 1*). The spherical densiometer is a simple instrument for estimating canopy cover. It consists of a convex or concave mirror with a grid of 24 squares, within each of which the observer scores canopy cover at four equally spaced points. In order to characterize relative light intensity (in Percent of Above Canopy Light, PACL) in small and in large gaps, hemispherical photographs with Sigma-adapter fisheye lens on a Canon AE1 camera were taken at 70 cm in height, above the ground. The photographs were taken in three gaps – one large, one small with high advance regeneration (5-7 m) and one small with no advance regeneration above 0.5 m. This was along the N-S and E-W transect running along gaps – below-canopy gradients in 2003 (*see Fig. 1*). Altogether, 28 photos were taken (9 and 6 in small gaps, 13 in a large gap, 17 in below-canopy plots, 11 within in-gap plots). We used a crown mirror to group the quadrats as "in-gap" or "below-canopy" quadrats. If the canopy was not visible in the crown mirror, we considered the quadrat as a gap-quadrat. At the edge, we identified the quadrats as "below-canopy" if more than half of the mirror area reflected the canopy.

Hemispherical photographs were analysed using a Windows-based software, hemIMAGE (Brunner 2002). Relative light intensity (in Percent of Above Canopy Light, PACL) was calculated in a certain location for a given period of time: 1st March to 31st October. With hemIMAGE, the direct and the diffuse site factor can be calculated separately for a given location.

As the sample size was small and did not show normal distribution, a nonparametric Mann-Whitney U test was used to compare the recorded vegetation and environmental variables between gaps, versus below canopy and small versus large gaps. Ordination analysis was employed by Canoco for Windows 4.5 software (Ter Braak - Smilauer 2002). Since in the exploratory detrented correspondence analysis the maximum length of gradient exceeded 4SD, and the data showed a strong unimodal response, a canonical correspondence analysis was carried out. Abundance of tree species and abiotic variables (intact soil, mineral soil, coarse woody debris (CWD), stem of a living tree, stone and coverage of herbaceous plant species and canopy openness) recorded in the quadrats were included in the analysis. Interactions between abiotic factors and species' abundances were tested by calculating the Spearman Rank Order correlation.

3   RESULTS

3.1 Light conditions

Light conditions differed considerably depending on gap size, however, the relative light intensity under the canopy showed high variability and high mean and maximum values. Under the canopy, mean total relative light intensity (PACL) was between 4-5%, around the gaps. In small gaps, it reached 4-5% as a maximum with a 2-3% average, whereas in large gaps, the total PACL mean values reached 8% and maximum values reached 12%.

Canopy openness estimates obtained by the spherical densiometer were consistently higher than the relative light intensity estimates obtained by analysing hemispherical photographs. However, canopy openness values showed strong significant positive correlation with diffuse light values (Spearman Rank Order Correlation, R=0.45, p<0.01, N=28). Canopy openness values reflected gap geometry, they showed a clear gradient from below-canopy position to gap centre. Maximum values were approximately 25% in the centre of small, and 37% in that of large gaps. Below canopy variance of canopy openness was very high (mean = 12.26, variance = 20.65), and the maximum values were similar to those in the gap plots in small gaps - reflecting the structural heterogeneity of the canopy. Canopy openness was significantly (Mann Whitney U Test p<0.001, N=84) higher in large gaps than in small gaps, and also showed significant difference between in-gap and below-canopy plots, both in small and in large gaps (Mann Whitney U Test, p<0.05, N=84), which was in favour of in-gap position.

3.2 Herbaceous vegetation

Altogether, 57 herbaceous species were found. Most frequent species were (in descending order): *Viola reichenbachiana, Mercurialis perennis, Galium odoratum, Sanicula europaea, Hordelymus europaeus, Glechoma hederacea, Aegopodium podagraria, Oxalis acetosella,* and *Mycelis muralis.* Species with the highest total coverage were (in descending order): *Galium odoratum, Mercurialis perennis, Sanicula europaea, Glechoma hederacea, Urtica dioica, Euphorbia amygdaloides, Viola reichenbachiana,* and *Hordelymus europaeus.*

Table 2. Mean of total cover (as the result of the addition of individual species cover) of herbaceous species from grids in the gaps
(S: small, L: large, number indicates the gap no.)

Gap ID	Valid N	Mean	Minimum	Maximum	Standard Error
S1	64	27.53	0.00	99.02	3.04
S2	64	14.44	0.00	67.20	2.18
S3	64	17.74	0.00	100.00	2.49
S8	64	42.51	8.20	104.10	2.62
S11	64	45.48	3.00	104.00	2.45
S12	64	43.98	3.02	88.00	2.43
L5	137	16.52	0.00	89.10	1.98
Ll0	136	34.66	0.00	131.10	2.52

Total cover of herbaceous species varied greatly both within and between gaps, and around them (*Table 2*). Total cover was significantly (Mann Whitney U test, $p<0.01$) higher in the in-gap plots of large gaps than below canopy. There was no significant difference in small gaps between in-gap and below-canopy quadrats in terms of herbaceous cover if all plots were pooled. However, if individual gaps were treated separately, significant differences were found in the case of three small gaps between in-gap and below canopy plots. In one gap, herbaceous vegetation was more abundant in plots under the canopy, because tall regeneration was present in the gap. Canopy openness showed a strong significant positive correlation (Spearman Rank Order Correlation, $R=0.53$, $p<0.01$, $N=84$) with total cover of herbaceous species.

The relative cover of individual herbaceous species varied greatly among plots with different total coverage (data not shown). Existence of some species, *e.g. Urtica dioica* and *Geranium robertianum* is characteristic in plots with high (>60%) total cover, whereas others (e.g. *Oxalis acetosella, Galium odoratum*) showed preference for plots with lower cover or did not show any preference.

3.3 Regeneration

The percentage of the saplings/seedlings with visible browsing damage can be seen in *Table 3*. Tree regeneration is under high browsing pressure, according to the observations, and nearly 50% of the higher saplings of each species were affected by browsing. The high game pressure can also be concluded from the fact that saplings with a height between 50 cm and 2 m are extremely rare.

Table 4 shows the mean number of individuals per quadrat for each tree species in *a* – the whole grid; *b* – in the in-gap quadrats; *c* – in below-canopy quadrats. When plots of all gaps were pooled, total number of tree seedlings and saplings did not differ significantly between in-gap and below-canopy quadrats. Beech and ash saplings, taller than 50 cm, were more abundant in gaps than under canopy (Mann Whitney U Test, $p<0.1$). Although, this result was greatly affected by the patterns found in one small and one large gap. Spatial pattern of tree regeneration was rather gap-specific, when in-gap and below-canopy plots were compared.

Table 3. The percentage of tree individuals in different height classes with visible browsing damage

Tree regeneration	Height classes (cm)	Percentage of individuals with visible browsing damage
Acer campestre *		3.7
Acer campestre	0-10	0.0
Acer campestre	10-20	50.0
Acer platanoides	0-10	22.2
Acer platanoides	10-20	35.5
Acer platanoides	20-50	33.3
Acer pseudoplatanus *		0.0
Acer pseudoplatanus	0-10	27.1
Acer pseudoplatanus	10-20	50.9
*Fagus sylvatica**		0.0
Fagus sylvatica	0-10	23.9
Fagus sylvatica	10-20	31.4
Fagus sylvatica	20-50	40.0
Fagus sylvatica	>50	0.0
*Fraxinus excelsior**		0.7
Fraxinus excelsior	0-10	30.8
Fraxinus excelsior	10-20	46.7
Fraxinus excelsior	20-50	60.4
Ulmus glabra	0-10	25.0
Ulmus glabra	10-20	42.8
Ulmus glabra	20-50	55.5

*: seedlings with cotyledons

Table 4.a Mean number of saplings per quadrat in the whole grid in each gap.

GAP ID	*Acer platanoides*	*Acer pseudoplatanus*	*Fagus sylvatica*	*Fraxinus excelsior*	*Ulmus glabra*	*All saplings*
S1	1.36	0.22	0.53	2.19	0.09	4.48
S2	0.20	0.06	1.23	0.92	0.03	2.45
S3	0.13	0.02	0.58	0.64	0.00	1.36
S8	0.89	0.53	0.47	0.63	0.00	2.53
S11	0.86	0.38	0.42	5.17	0.06	6.91
S12	2.09	0.16	0.89	3.22	0.08	6.45
L5	0.18	0.04	1.92	0.67	0.00	2.85
L10	0.37	0.51	0.58	3.07	0.04	4.60

Table 4.b Mean number of saplings in the in-gap quadrats in each gap

GAP ID	*Acer platanoides*	*Acer pseudoplatanus*	*Fagus sylvatica*	*Fraxinus excelsior*	*Ulmus glabra*	*All saplings*
S1	1.00	0.44	0.67	2.78	0.11	5.33
S2	0.22	0.00	1.11	0.56	0.00	1.89
S3	0.00	0.00	0.75	0.25	0.00	1.00
S8	1.00	0.00	0.33	0.67	0.00	2.00
S11	1.33	0.00	0.00	3.67	0.00	5.00
S12	1.50	0.00	1.83	3.50	0.00	6.83
L5	0.18	0.12	3.94	0.71	0.00	5.06
L10	0.15	0.38	0.77	1.92	0.00	3.23

Table 4.c Mean number of saplings in the below-canopy quadrats in each gap

GAP ID	Acer platanoides	Acer pseudoplatanus	Fagus sylvatica	Fraxinus excelsior	Ulmus glabra	All saplings
S1	1.42	0.18	0.51	2.09	0.09	4.35
S2	0.20	0.07	1.25	0.98	0.04	2.55
S3	0.13	0.02	0.57	0.67	0.00	1.38
S8	0.89	0.56	0.48	0.62	0.00	2.56
S11	0.84	0.39	0.44	5.25	0.07	7.00
S12	2.11	0.16	0.75	3.21	0.08	6.34
L5	0.18	0.03	1.63	0.67	0.00	2.54
L10	0.39	0.53	0.56	3.20	0.05	4.75

According to the results of canonical correspondence analysis (CCA) the first two canonical axes explained a 12.3% variance of species data and a 77.6% of species-environment relation (*Figure 2*).
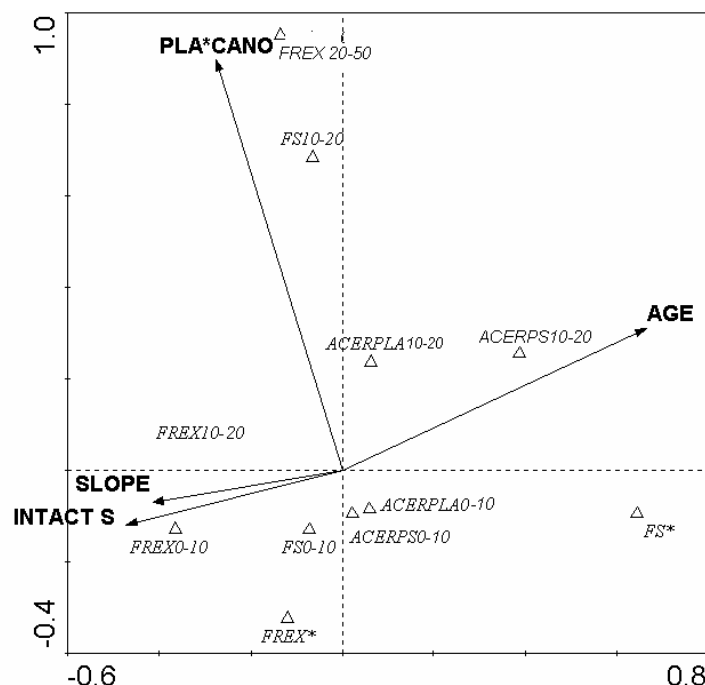
Figure 2. Species and environmental variables biplot of the canonical correspondance analysis.

PLA*CANO: variable combined from the interaction of total herbaceous coverage and canopy openness, AGE: age of the gaps, INTACT S: intact soil, SLOPE: slope; FS*:
F. sylvatica seedling, FS10: *F. sylvatica* 0-10 cm, FS20: *F. sylvatica* 10-20 cm, FS50: *F. sylvatica* 20-50 cm, FREX: *Fraxinus excelsior,* ACPLA: *Acer platanoides,* ACERPS: *Acer pseudoplatanus*

The most important variables were: *a,* variable combined from the interaction of total herbaceous coverage and canopy openness (PLA*CANO) (p-value 0.0040, F-ratio=3.51; number of permutations=499). *b*, age of the gaps (AGE) (p-value 0.0060, F-ratio=2.91; number of permutations=499). *c,* intact soil (INTACT S) (p-value 0.0080, F-ratio=2.64; number of permutations=499), and *d*, slope (SLOPE) (p-value 0.050, F-ratio=1.82; number of permutations=499). The first axis (x) had the highest correlations with age (0.66), whereas the second axis (y) had the highest correlation with the interaction of total herbaceous coverage and canopy openness (0.9).

According to the CCA, increasing canopy openness and herb cover seemed to enhance the occurrence of larger saplings, whereas smaller seedlings (<10 cm) were situated at the lower values of axis 2. Beech seedlings – unlike other species, most remarkably ash – seemed to prefer plots with relatively low proportion of intact soil as a substrate. Furthermore, the occurrence of beech seedlings was positively correlated with higher age; however, this result can be based upon the high number of seedlings in one older gap.

Results of correlation analyses (Spearman Rank Order Correlation) corresponded well with the results obtained by ordination. Young regeneration (10-20 cm) of all tree species showed significant positive correlation (Spearman Rank Order Correlation, N=657, p<0.01) with proportion of intact soil. The number of first year seedlings of ash also showed significant positive correlation with proportion of intact soil, whereas that of beech was positively correlated (Spearman Rank Order Correlation, N=657, p<0.01) with proportion of mineral soil. Saplings of all species showed significant positive correlation (Spearman Rank Order Correlation, N=657, p<0.01) with total cover of herbaceous species, except for first year beech and ash seedlings. Canopy openness seemed to be in positive relation with the number of higher beech saplings (>10cm, Spearman Rank Order Correlation, N=84, p<0.1 and p<0.05), whereas ash seedlings showed just the opposite (Spearman Rank Order Correlation, N=84, p<0.1).

The relationships between sapling density and herbaceous vegetation cover need more investigation, as the relationship between these variables is not linear, and they can be confounded by the effects of canopy openness on both of these variables. In order to analyse the effects of canopy openness and herb species cover on seedling density, more or less separately, plots were grouped by canopy openness values: <18% and >18%, and by total cover of herb species: <50% and >50% (Table 5).

Table 5. The four groups of quadrats (11, 12, 21, 22) according to the values of the canopy openness and coverage of herb species

	11	12	21	22
Canopy openness (%)	<18	>18	<18	>18
Cover of herb species (%)	<50	<50	>50	>50
Number of quadrats	46	12	15	11

Figure 3 shows how unevenly beech seedlings of different height classes were distributed among the four groups. Other species showed partly similar patterns. The highest beech seedling density was characteristic in quadrats, where herb layer was dense and canopy openness was low; whereas the lowest density was observed in quadrats where herb layer was dense and canopy was opened (*Figure 3*).

Plots with high herbaceous vegetation cover had different species composition, depending on canopy openness. As the results of the Mann-Whitney Test show, the mean cover of *Aegopodium podagraria, Mycelis muralis, Sanicula europaea,* and *Urtica dioica* was significantly (p<0.05) different in quadrats belonging to the two compared groups: where total cover of herb species > 50% and canopy openness < 18% or canopy openness > 18%. Cover of *Urtica* was much higher in quadrats under open canopy, whereas cover of the other three species was higher in quadrats with lower canopy openness. The Spearman Rank Order Correlation furthermore showed a very strong negative correlation (R=-0.61, p<0.01, N=657) between the total number of regeneration and cover of *Urtica dioica.*
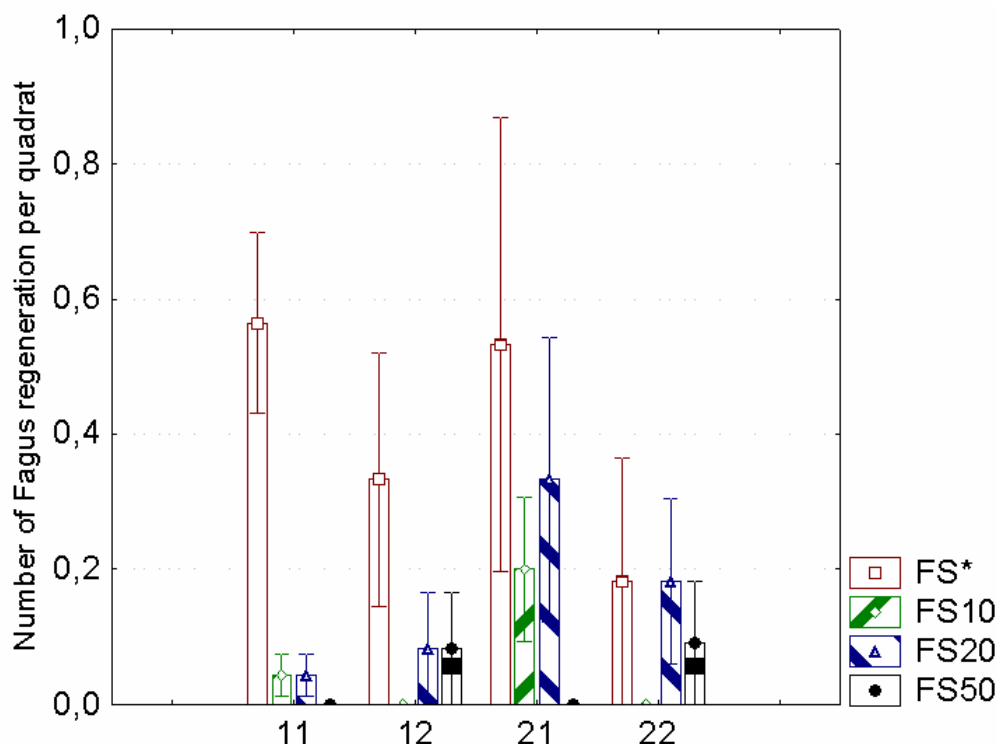
Figure 3. Mean number of Fagus sylvatica seedlings and saplings
in the four groups of quadrats.
Canopy openness < 18% and total cover of herb species: < 50% (11),
canopy openness > 18% and total cover of herb species: < 50% (12),
canopy openness < 18% and total cover of herb species: > 50% (21), and
canopy openness > 18% and total cover of herb species: > 50% (22).
FS*: *F. sylvatica* seedling, FS10: *F. sylvatica* 0-10 cm, FS20: *F. sylvatica* 10-20 cm, FS50: *F. sylvatica* 20-50 cm.
Columns represent mean, whiskers represent standard error.

4   DISCUSSION

The high variance of relative light intensity and canopy openness values found both in gaps
and below-canopy, reflects the heterogeneity of canopy in this semi-natural beech stand.
It was only in larger gaps, where we found more diffuse light reaching the ground than under
canopy near the gaps during the vegetation period, however, no significant increase of direct
light could be recognized. Results of other gap-studies in temperate forests show increases of
incident light depending on gap-size as well (Collins – Pickett 1987, Collins – Pickett 1988,
Canham et al. 1990, McCarthy 2001 and references therein). The observed spatial variation in
light conditions, however, should focus our attention to the applicability of the gap-
partitioning hypothesis. Gap/non-gap situations therefore should not be treated as binary
variable, but rather a continuum, which can be characterized by gradients of variables such as
canopy openness or relative light intensity. Natural dynamics does create structural
heterogeneity, which makes gap-studies – based on sharp dichotomy of gap versus non-gap
environment – difficult (Lieberman et al. 1989).

Systematic differences between canopy openness and diffuse light estimations (with
higher values of canopy openness) reflect the different view angle of the hemispherical lens
and the spherical densiometer. According to the measurements of Englund et al. (2000) the
view angle of the spherical densiometer is about 57°, whereas fisheye lenses have a much

broader view angle of 167º. As a result, measurements taken by the densiometer overestimate canopy openness.

Variability of total cover of herbaceous species in and around gaps also reflects fine-scale canopy heterogeneity. In general, herbaceous cover correlates positively with canopy openness, with considerable higher values of herbaceous cover in central areas of large gaps. Holeksa (2003) found differences in the abundance of understorey species between gap and under canopy position, if gaps were larger than 50 m^2; other studies are congruent with these findings (Hughes – Fahey 1991, Goldblum 1997). However, in other situations no effect of gap creation could be shown on the total cover of the herb layer (Collins – Pickett 1987, Collins – Pickett 1988), and several groups of species proved to be insensitive to gap (Collins – Pickett 1987, Collins – Pickett 1988, Hughes – Fahey 1991, Schumann et al. 2003).

According to our results, the total numbers of tree regeneration did not differ between in-gap and below-canopy plots. Regeneration – as described by e.g. Peterken (1996) – consisted of almost exclusively "tolerant species" found in the canopy layer: beech, ash, maple and elm. Poplar, willow, and birch as pioneer, "intolerant species" usually did not occur in and around gaps. Lack of pioneer, light demanding species can be interpreted as a consequence of fine-scale patterns and low intensity of disturbances, resulting in relatively small gaps which are characteristic of this semi-natural stand and the distant propagule-resources (Poulson – Platt 1989, Peterken 1996, Peterson – Carson 1996). In addition, species composition of regeneration may be also affected by preferential game browsing. According to studies in Germany and Poland for red deer, (*Cervus elaphus*) *Salix* spp. and *Populus tremuloides* are among the most palatable plants, while roe deer (*Capreolus capreolus*) also prefers willow in the summer vegetation period (Gill 1992).

The detected browsing damage affected 25-50% of the individual trees. Higher percentages of damaged saplings were found among the higher size classes. According to our results, individual trees belonging to different size classes show distinct patterns in relation to substrate features, canopy openness and herb cover. Mineral soil seems to be the preferred germination site for beech, whereas larger beech saplings and other species seem to be less abundant in this substrate. According to the observation by Fanta (1995), success of establishment depends more on soil moisture than on light conditions, and thick litter may inhibit seeds to reach the ground surface exposing them to drought. Moreover, larger beech saplings show positive correlation with canopy openness. Some studies (Peltier et al. 1997) indicate that light is a very important factor for the development of beech saplings, enhancing root development. Seedlings are more susceptible to drought in poor light conditions (Topoliantz – Ponge 2000).

We showed that taller saplings are more abundant in plots where cover of herbaceous species is higher. Since game browsing is very intensive in this region and it affects almost all tree species, the sheltering of herbs can be very important in sapling survival. Other studies support this assumption, showing that higher saplings occur in higher and denser understorey vegetation, and they explain this pattern with the same reasoning (Rao et al. 2003). If tree saplings grow on bare ground, smaller individual saplings are more susceptible to browsing, but they are protected from damage in dense herb layers until they grow above the vegetation (Gill 1992).

Moreover, according to some studies, palatable plants can be partially protected from herbivores if they are associated with patches of unpalatable plants (Pietrzykowski et al. 2003 and references therein). These findings emphasize the potential effect of herb species composition on game damage in beech forests. We also found a strong negative correlation between sapling density and the cover of *Urtica dioica*, which shows that a certain height or density of the herb layer can also have negative effects on the regeneration. However, we did

not find studies distinctively focusing on the effect of specific plant species e.g. *Urtica dioica* on the distribution of saplings.

In contrast to the above, however, few specific studies in North America focusing on the effects of herbivory and gap size found no effect of herbivory on tree seedling abundance (Castleberry et al. 2000, Collins 2003, Holladay et al. 2006), though short-term results suggested that recruits of some species in smaller gaps are more susceptible to herbivory than those in larger gaps, possibly due to deer preferentially browsing in less open areas (Castleberry et al. 2000). These studies based on exclosure experiments concluded that gap size and herb layer competition are more important factors in tree regeneration patterns than herbivory in the studied areas.

These findings leave several open questions for future research regarding the relationships between tree regeneration, herbaceous vegetation and herbivory, and the direct effect of herbaceous species on saplings survival. Future researches investigating gap regeneration processes in European broadleaved forests should include exclosure-experiments in order to investigate the effect of herbivores and gap size. Since, in Europe, deer numbers in many areas have been increasing during the last 100-200 years (Fuller – Gill 2001), the investigation of natural forest dynamics can be biased because of intense herbivory. Gap size may influence the browsing habits of larger herbivores, and have a profound effect on the herbaceous layer; however, dense herbaceous vegetation can also affect herbivory patterns. The pattern of tree regeneration therefore can be in a complex interaction with gap size, vegetation density, and browsing effect.

5   CONCLUSIONS

Our study focuses on gap regeneration patterns in a semi-natural beech forest stand. Although we only showed a snapshot of a dynamic process, we tried to interpret the findings as an outcome of several important dynamic processes: gap existence, tree regeneration, reaction of herbaceous species, and herbivory. Our findings emphasize the importance of the spatial scale of disturbances, and of the gradual change in abiotic factors (e.g. light) from below canopy to gap centre in gap-studies. Gap regeneration patterns depend not only on the ecological traits of tree species (e.g. light demanding, shade-tolerant etc.), but among others, on the composition and cover of herbaceous vegetation and on game browsing. Therefore, gap studies should focus on these factors as well, in order to get a better understanding of regeneration mechanisms of forest stands.

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History and Impact of Gypsy Moth in North America and Comparison to Recent Outbreaks in Europe

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Abstract -– The article summarizes information about the introduction, spread, population dynamics, and impacts of the gypsy moth in North America and elucidates comparisons with the importance of this forest pest in Europe. Additionally, the natural enemies (parasites, predators, and pathogens) that help regulate gypsy moth populations, are discussed at length. Gypsy moth outbreaks on both continents are associated with the presence, abundance and characteristics of oak forests. While oak forests in Europe are rather fragmented and their area has declined, oak forests in North America are both extensive and contiguous. Consequently there is an obvious disparity in the magnitude, impact, and synchrony of gypsy moth outbreaks in Europe and in North America. Even if the frequency and severity of outbreaks in Europe will increase in the future, the spread of outbreaks will be limited by the availability of suitable hosts and climatic factors. Conversely, gypsy moth will continue to spread to West and South in the United States and the area infested will increase significantly until it eventually occupies the natural distribution of oak species. Because of this prognosis, an emphasis has been placed on slowing the spread of the gypsy moth rather than treating defoliating populations.

Lymantria dispar **L / outbreak frequency / spread / North America / Europe**

Kivonat – A gyapjaslepke története és jelentősége Észak-Amerikában - összehasonlítás az utóbbi időszakok európai tömegszaporodásaival. A tanulmány összefoglalja a gyapjaslepke Észak-Amerikába történő behurcolásának, megtelepedésének, terjeszkedésének történetét. Elemzi a faj jelentőségét, összehasonlítva az európai helyzettel. A fentieken túl ismerteti a gyapjaslepke természetes ellenségeit (ragadozók, parazitoidok, kórokozók). A gyapjaslepke tömegszaporodásai mindkét kontinensen a tölgyek jelenlétével, tömegességével, illetve a tölgyesek jellegzetességeivel vannak összefüggésben. Amíg Európában a tölgyesek területe jelentős mértékben fragmentálódott és csökken az utóbbi évszázadokban, Észak-Amerikában a tölgyesek még napjainkban is nagy kiterjedésűek és összefüggőek. Következésképpen a tömegszaporodások szinkronizáltsága, nagyságrendje és hatása eltérő Európában és Észak-Amerikában. Még ha az előrejelzéseknek megfelelően a klimatikus változások miatt a gyapjaslepke tömegszaporodásai gyakoribbá és nagyobb kiterjedésűvé válnak is a jövőben, az alkalmas tápnövények elterjedése, illetve más környezeti tényezők korlátozni fogják azokat. Ezzel ellentétben a gyapjaslepke Észak Amerikában folytatni fogja déli és nyugati irányú terjeszkedését, egészen addig, amíg a tölgyek természetes elterjedési területét le nem fedi. Ebből az előrejelzésből kiindulva a hangsúly a STS (Slow the spread = a terjeszkedés lassítása) programra helyeződött át, a tömegszaporodási stádiumban lévő populációk elleni védekezés helyett.

gyapjaslepke / tömegszaporodások gyakorisága / terjeszkedés / Észak-Amerika / Európa

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1   INTRODUCTION

The exploits of the gypsy moth (*Lymantria dispar* L.) in the United States are well known and have been well documented in the scientific literature and by the media over the past 100 years. Although substantial efforts and resources have been committed to eradicate, contain, or control this pest, it is now well established in the eastern U.S. and is gradually extending its range to the south and west. Although *L. dispar* populations have declined significantly since 1990 when about 3 million ha were defoliated, this defoliator remains the most important insect pest in the deciduous forests of the eastern United States. Unlike many forest pests that threaten commercial timber values, the gypsy moth devastates not only forests but also urban forest communities and affects people. During the outbreak phase when populations can increase 100-fold in successive years, larvae can pose a hazard to human health and disrupt the public's enjoyment of outdoor activities. The defoliation caused by outbreak populations reduces the vigour and general health of forest and shade trees and renders them susceptible to attack by secondary mortality-causing agents. The intensity of tree mortality, which usually peaks 2 to 5 years after an episode of defoliation, is highly variable and site specific. In urban residential areas, expenditures by the public for spraying pesticides to prevent defoliation by the gypsy moth can be astronomical.

In this article, we synthesize and summarize in general terms the history, dynamics, and current status of the gypsy moth and its management in the U.S. and discuss differences that exist between the behaviour of populations in the U.S. and Europe and their associated impacts.

2   HOSTS AND OUTBREAKS

In Europe, distribution of the gypsy moth corresponds approximately with two vegetation zones: temperate deciduous forests and Mediterranean scrub. The northern limit proceeds through southern Sweden and Finland and descends from about 60° to 50° lines of latitude through Europe and Russia. The southern limit begins in the west in northern Morocco, Algeria, and Tunisia and proceeds east to include all of the Mediterranean islands, on a line through Israel into Asia (CIE, 1981).

The hosts for the gypsy moth in Europe vary somewhat depending on how its distribution corresponds with the predominant vegetation in various geographical regions. Close to the northern limits of its range, i.e., Lithuania, species of birch (*Betula*) and alder (*Alnus)* are the primary hosts, whereas in Spain, Portugal, and Sardinia, cork oak *(Quercus suber*) is the dominant host and stands of this species have incurred frequent episodes of defoliation. In the rest of Europe, the distribution of the gypsy moth is associated with the presence of up to seven species of *Quercus*, especially *Q. petraea*, *Q. cerris*, and *Q. robur*; however *Q. petraea* is less preferred among the Central European oaks. In Central Europe, hornbeam (*Carpinus betulus*) is often intermixed in stands of oaks and is considered to be an equally preferred host along with species of *Populus, Alnus*, and *Salix* (Hirka 2005, Csóka 2007).

Black locust (*Robinia pseudoacacia*) stands in Hungary and Slovakia are occasionally defoliated by *L. dispar* larvae however this species is not considered to be an acceptable host in the U.S. Even conifers (mainly *Picea*) can be occasionally totally defoliated during outbreaks (Csóka 2007).

Although the gypsy moth was introduced into North America in 1869, it is still considered to be an "invasive species" because it continues to spread and extend its range to the south and west and has yet to occupy fully the extensive oak forests that are native to the eastern and central regions of the United States. Conversely, *L. dispar* is native to Eurasia – outbreaks were recorded in the 1600's in Spain, 1750's in Germany, 1840's in Hungary, and

in 1880 in France. In southern regions of France and in the Balkans, *Q. suber*, *Q. pubescens*, and *Q. ilex* serve as the primary hosts for *L. dispar*. An exception to the close association between oak species and *L. dispar* populations occurs in the Danube Delta of Romania which contains 27,000 ha of *Populus* and *Salix* stands, species which serve as excellent hosts for gypsy moth larvae.

Extensive studies conducted on hosts of the gypsy moth in the U.S. provide insight as to why this pest has been and continues to be one of the major forest health problems. According to Liebhold et al (1997), among the top 20 preferred tree species ranked by their total basal area are 13 species of *Quercus, Populus* spp. (*tremuloides, grandidentata*) paper birch (*Betula papyrifera*), and American basswood (*Tilia americana*). Fifty species of oak are represented in two-thirds of the forest cover types in Eastern North America and are the dominant species in over 77 million ha of hardwood forest (Stein et al. 2003). Most or all of these species are probably equally preferred by larvae but have not been evaluated as hosts. There are oak cover types unique to regions on the west coast of the U.S. that are equally susceptible to gypsy moth populations. During outbreaks, gypsy moth larvae will also readily feed on many species of conifers [*Pinus, Picea, Abies, Tsuga, and Larix*] especially when defoliation of preferred species is severe.

According to Bogenschutz et al (1989), outbreaks of the gypsy moth are not uncommon in Central Europe yet it is not considered to be a forest pest in Germany. In general, the damage caused by *L. dispar* in Europe is greater from west to east and from north to south (McNamara, 1995). Outbreaks have been most numerous and severe in the Balkan peninsula due to the abundance of oak species and climate–high temperatures and moisture deficits – that appears to be optimal for *L. dispar* development and survival. In Serbia, 16 outbreaks have been recorded between 1862-1998, the largest occurring in 1997 when 500,000 ha were infested (Marovíc et al. 1998). In Romania, treatments were applied on 600,000 ha of forest land in 1988 to control gypsy moth populations. Twenty-two outbreaks have been recorded in Hungary between 1843 and 2007 (*Figure 1*), with a maximum of 212 thousand hectares damaged in 2005 (Csóka – Hirka 2007).
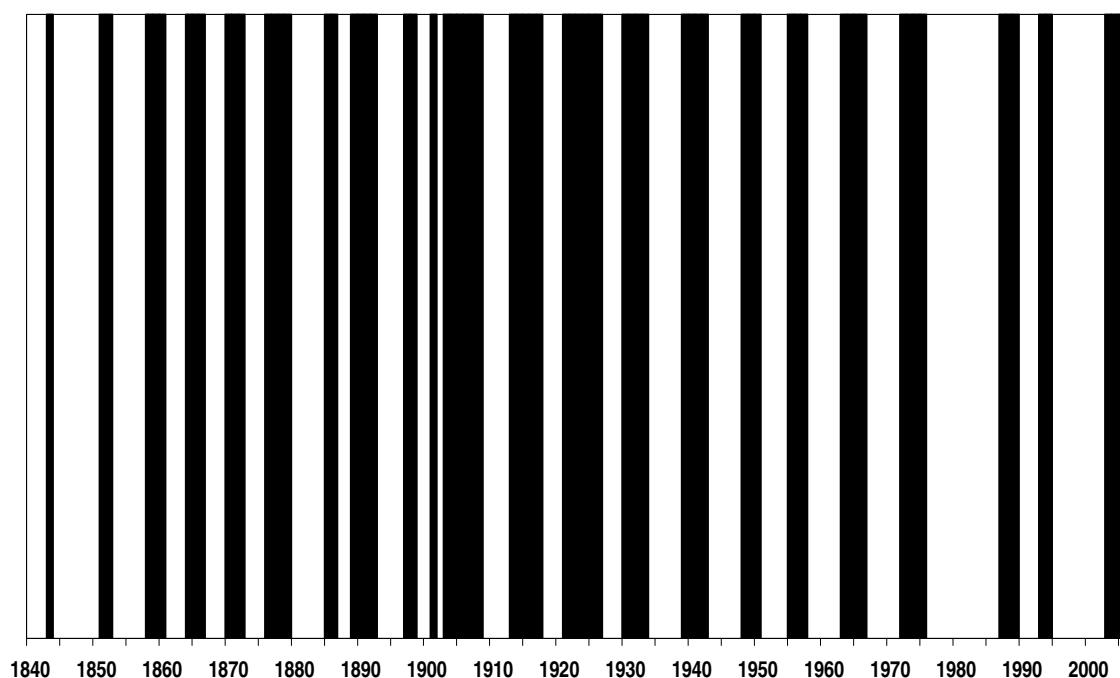

Figure1. Outbreaks of gypsy moth in Hungary from 1840 to present (Csóka – Hirka 2007)

In North America, the history of outbreaks is associated with the spread of *L. dispar* into new areas dominated by preferred species followed by the rapid expansion of populations in the absence of the gypsy moth's complex of natural enemies. The extent of outbreaks, measured by the total forested area defoliated, has worsened dramatically as the area infested has increased. Annual defoliation exceeding 500,000 ha occurred in 20 years between 1970-1995, a period when the distribution of *L. dispar* populations expanded significantly to the south and west (*Figure 2*). Over 5.2 million ha were defoliated in 1981, 3 million ha in 1990. Outbreaks are most severe in oak-pine associations which occur on dry, sandy sites and on ridgetop stands characterized by poor, shallow soils, rock outcroppings, and preferred species such as chestnut oak (*Q. prinus*).
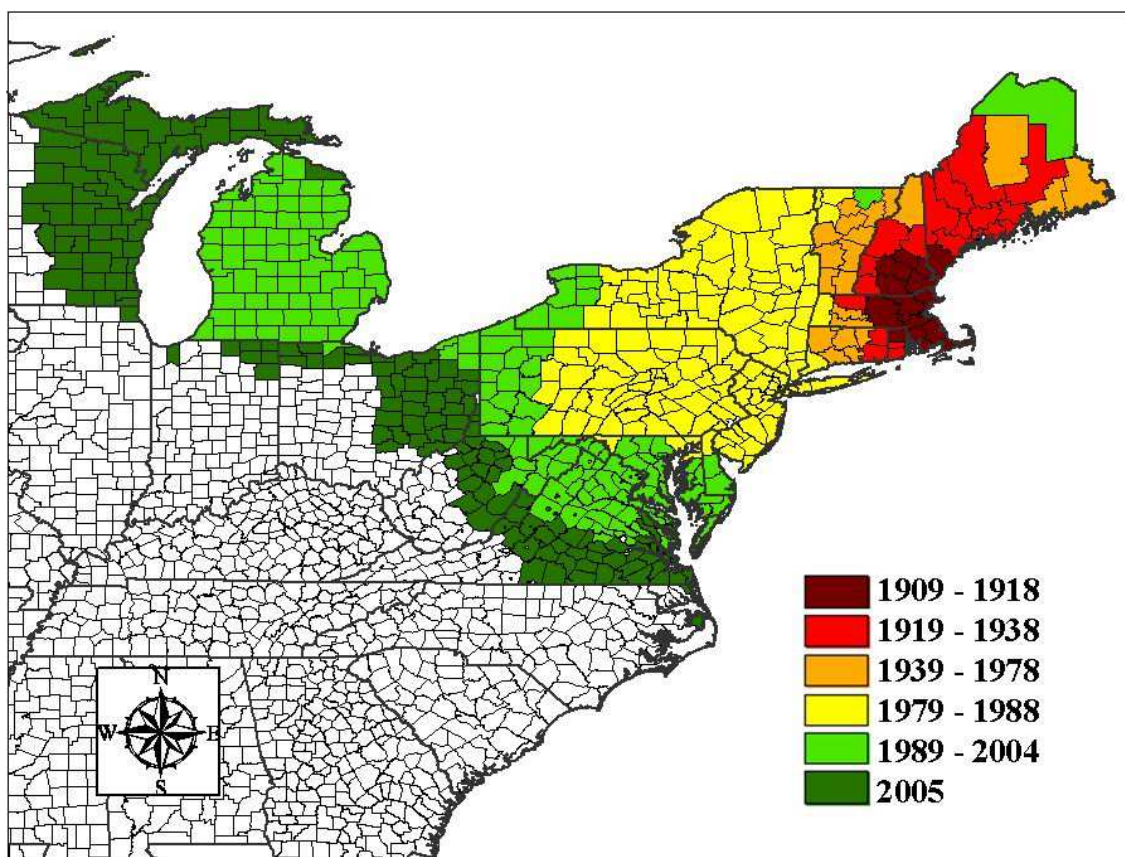

■	1909 - 1918
■	1919 - 1938
■	1939 - 1978
■	1979 - 1988
■	1989 - 2004
■	2005

Figure 2. The spread of the gypsy moth in the U.S since it was introduced in 1869

3   ESTABLISHMENT AND SPREAD

In 1869, egg clusters of the gypsy moth were transported from France to Medford, Massachusetts by a French mathematician and astronomer, Etienne Leopold Trouvelot, who was conducting laboratory experiments to cross the gypsy moth with a native silkworm, *Antheraea polyphemus* (Cramer). Somehow, larvae of the gypsy moth escaped and established on vegetation in the immediate area. It was not until the summer of 1889, 20 years after its introduction, that the insect became so abundant and destructive on fruit and shade trees that it attracted public attention. The extensive defoliation and nuisance created by enormous numbers of larvae are vividly described in Forbush and Fernald (1896). Trouvelot's poor judgement provided North America with one of its worst pest problems (Liebhold et al. 1989).

In 1890, the State of Massachusetts appropriated funds to exterminate the pest which at that time infested an area of 2539 km^2 and encompassed 30 cities and towns. Control efforts were so successful that by 1899, little defoliation was detected and only a few moths were found. Therefore, further control was terminated; this was a poor decision because by 1905, gypsy moth populations had expanded rapidly, thousands of hectares of forests were defoliated, and the pest had spread to surrounding states. In 1906, the Federal Government appropriated money to prevent the spread of the insect because it was recognized that egg masses and other life stages were being carried on commodities along major roadways. This eventually led to the enactment of a Domestic Federal Quarantine against the insect in 1912 which is still in effect today.

Despite efforts by the federal and state governments, *L. dispar* continued to spread to the north and west at an estimated rate of 9.6 km/year. Several isolated infestations were found far removed from the infested regions; additionally, a new infestation covering over 1000 km^2 was found to the south in New Jersey. This introduction was traced to a shipment of blue spruce (*Picea*) trees that had been imported from the Netherlands.

Two extensive efforts were made between 1923 and 1958 to stop or at least slow the rate of spread of the gypsy moth to the west. Between 1923 and 1941, a Barrier Zone was established that encompassed 27,300 km^2 in a north-south line from Canada to New York City (Felt, 1942). All infestation that were detected within this Barrier Zone were eliminated using chemical and mechanical methods. This program was terminated in 1941 due to a shortage of federal funds and complicated further by the nation's involvement in World War II. The Barrier Zone is credited with effectively slowing the rate of spread of the gypsy moth prior to 1941. Gypsy moth populations expanded greatly during the early 1950's, at which time state and Federal officials conducted an in depth appraisal of the problem and considered re-establishing the Barrier Zone to prevent additional spread and reduce damage (Perry 1955). In 1956 the U.S. Congress made funds available to initiate an eradication program; 223,000 ha in three states were sprayed with DDT which had been used experimentally between 1944-48 in Pennsylvania, and another 1.2 million ha were sprayed in 1957. By 1958, less than 51 ha of defoliation were recorded anywhere within the generally infested area; however, the use of DDT was curtailed because of questions that surfaced about residues on food and feed crops and concern over its detrimental effects on beneficial organisms, fish and wildlife. At this time, any hopes for eradicating the gypsy moth or even stopping its spread were abandoned.

The areas of infestation and defoliation in the eastern U.S. increased substantially between 1959-1969 and reached a peak in 1971 when over 800,000 ha were defoliated. The U.S. Congress provided a special appropriation of several million dollars over a four-year period (1975-1978) to accelerate research and development on gypsy moth with emphasis placed on developing an integrated pest management (IPM) approach (McManus, 1978). After a massive outbreak occurred in 1979-1982 – four million ha of forest land was defoliated in 1981 – it became apparent that there was a need to develop and evaluate a more aggressive approach to manage gypsy moth populations before they reach high densities that cause defoliation. Two 5-year projects were initiated to evaluate the feasibility of managing gypsy moth populations at low densities employing a monitoring system that consisted of a 1-km fixed point grid of pheromone traps. The first program was deployed on 60,000 ha in the state of Maryland (1983-1987); because of the success of this effort, the second program was initiated on five million ha in the states of Virginia and West Virginia (Reardon, 1991).

The most recent outbreak in North America occurred from 1989 to 1993 and affected forested areas in 12 different states. Over 2.8 million ha were defoliated in 1990 and the worst defoliation occurred in several of the most recently infested states to the south and west of the New England region. In contrast, there has been insignificant defoliation by *L. dispar* since

that time, a fact which has been attributed to the occurrence and spread of the fungal pathogen, *Entomophaga maimaiga* sp. nov. This will be discussed in a forthcoming section.

Liebhold et al. (1992) analyzed the rate of spread of *L. dispar* in North America using historical records and concluded that there was a high rate of spread (9.45 km/year) between 1900-1915, a low rate of spread (2.82 km/year) between 1916-1965, and a very high rate of spread (20.78 km/year) from 1966-1990 (*Figure 2*). The extended period of time when spread was minimal can be attributed to the Federal Domestic Quarantine, which restricted the movement of life stages by regulated commerce, the enforcement of the Barrier Zone and broad use of mechanical and chemical controls. The dramatic increase in spread that occurred in the latter part of the last century was probably facilitated by the following: (1) the use of DDT was abandoned and the dependency on chemical pesticides in general was diminished; (2) newly infested states to the south and west contained contiguous, mature forests where 50-60% of the total basal area of forests was dominated by oak species.; (3) the outbreaks that occurred in the 1970's and from 1979-1982 enhanced the natural and artificial spread of the gypsy moth. It's been well documented that the inadvertent transport of egg masses and other life stages from infested to uninfested areas increases dramatically during outbreak periods (McFadden and McManus, 1991). This has been the primary mechanism for spread of the gypsy moth in North America.

4   DYNAMICS OF POPULATIONS

In North America, the gypsy moth is considered to be an eruptive species because the timing of outbreaks has been irregular and difficult to predict. An enormous amount of effort has been expended to understand better why gypsy moth populations fluctuate over several orders of magnitude in consecutive years. Much of this research has been summarized in several excellent reviews (Leonard 1974; Montgomery and Wallner 1988; Elkinton and Liebhold 1990; Liebhold et al. 2000). *L. dispar* populations can persist for several years at densities so low (latency) that it's difficult to detect life stages except for male moths. When populations are released (progradation), they expand rapidly into the outbreak phase (culmination) which may persist for 1-3 years. Campbell and Sloan (1978) suggested that gypsy moth populations in North America demonstrate bimodal stability in that density dependent processes maintain densities at both innocuous and outbreak levels for long periods of time, however more recent studies suggest that there is little evidence for strong regulation of low-density populations (Liebhold et al. 2000).

The defoliation record in North America indicates that episodes of defoliation were synchronous in the New England states in the early 1900's, and there are many examples in the 20th century – apart from the severe outbreak in 1979-81 – in which defoliation appeared to be synchronous regionally. This suggests some climatic release phenomenon, though analyses of historical climate data have not established a correlation between weather and gypsy moth outbreaks (Miller et al. 1989). Williams and Liebhold (1995) reported that North American gypsy moth populations exhibit little or no periodicity, however, it has since been suggested that disjunct populations can become synchronous due to regional stochasticity, most likely related to weather variability (Liebhold and Kamata 2000). Montgomery and Wallner (1988) reported that several studies in Europe indicate that some gypsy moth populations are cyclic, with high densities developing every 8-11 years, however there had been no quantitative evaluations of cyclic patterns at that time. However Johnson et al. (2005) analyzed gypsy moth defoliation records >30 years among 11 regions across three continents (North America, Europe, Asia) and concluded that most *L. dispar* populations around the world tend to oscillate at periodicities between 8-12 yrs. Oscillations were synchronized at

distances up to ca. 1,200 km within continents, however there was no evidence for synchrony of gypsy moth populations between continents. The authors concluded that while the precise identity of the mechanisms causing these oscillations is not certain, it's possible that they are a product of one or more trophic interactions that are similar between the U.S. and Europe.

5 NATURAL ENEMY COMPLEX

5.1 Parasitoids

A program to introduce parasitoids from Eurasia into *L. dispar* populations in the Eastern U.S. began in 1905 and continued intermittently for 70 years (Hoy 1976). Although over 40 species of parasitoids were introduced, only 10 species became established and only eight species are recovered consistently and are considered to be important in U.S. gypsy moth populations – two that attack eggs, five that attack larvae, and one that attacks pupae (Fuester – Ramaseshia 1989). With few exceptions, i.e. *Compsilura concinnata*, those species that were introduced early in the last century and became established are also the most important and abundant species that are reported in European studies. This program is considered to be one of the few massive projects in biological control history.

Hoy (1976) suggested that relatively few parasitoid species were established over the duration of the release program because often times the numbers of individuals released were small, there was an insufficient host population present at the time of release, or there was a lack of alternate or overwintering hosts necessary to sustain species such as *Glyptapanteles liparidis* and *G. porthetriae*. Unfortunately, one of the common established species, *C. concinnata*, is a generalist parasitoid that attacks more than 200 species of Lepidoptera. Conservation biologists claim that *C. concinnata* is responsible for the decline in populations of silk moths (Saturniidae) and many other species that are listed as sensitive or endangered (Boettner et al. 2000).

When the egg parasitoids *Ooencyrtus kuvanae* and *Anastatus disparis* were introduced into the U.S., the latter was thought to be the more important of the two, however just the opposite occurred. *O. kuvanae* has been the dominant parasitoid found throughout the distribution of *L. dispar* in North America (Brown 1984) and commonly parasitizes between 25 to 50% of eggs in most egg masses depending on egg mass size and dimension.

A tachinid species, *Aphantoraphopsis* (=*Ceranthia*) *samorensis* (Villo) was released in the U.S. and repeatedly in Ontario, Canada between 1992 and 1996 however establishment was never confirmed (Nealis – Quednau 1996). This parasitoid is considered to be an important cause of mortality among *L. dispar* populations in France during periods of latency. Another tachinid, *Blepharipa schineri* was investigated thoroughly as a candidate for release however it was not pursued because of concern about its potential competitiveness with *Parasetigena silvestris* and *B. pratenis*.

According to Grijpma (1989), 165 species of parasitoids (109 Hymenoptera, 56 Diptera) have been recorded from gypsy moth populations throughout Europe, however only approximately 20 species are recovered consistently (Lipa 1996; Zubrik – Novotny 1992). There are many similarities among the parasitoid complexes in Europe and North America however there are a few notable differences. Whereas *O. kuvanae* is an important component of the parasitoid complex in the U.S., it is insignificant in *L. dispar* populations in Europe. Egg parasitism varies from 0 to 5% even though this species was introduced repeatedly into many European countries (Brown 1984). Two larval parasitoids, *G. liparidis* and *G. porthetriae* are among the most important species in Central Europe whereas neither species is established in North America. *Blepharipa pratensis* and *P. silvestris* are recognized as the most important species that attack *L. dispar* populations on both continents whereas

C. concinnata, which is common in the U.S., is insignificant in Europe. Hoch et al. (1999) stated that the guild of more specialized, oligophagous species are more important parasitoids of gypsy moth populations in central Europe, whereas typical generalists such as the polyphagous tachinids *C. concinnata* and *Exorista larvarum* are recorded only in low numbers. Despite the greater abundance of parasitoid species in Europe, the overall role of parasitism in the dynamics of gypsy moth populations probably is equivalent to that which has been recorded within the generally infested area of North America. Rates of parasitism and the occurrence of species within the parasite complex vary widely among sites and on the phase of the gradation under study. Liebhold et al. (2000) concluded that there is no definitive evidence of density-dependent regulation of gypsy moth populations by parasitoids.

5.2 Predators

Although predation is thought to have a substantial impact on gypsy moth populations, especially when populations are in latency, it is difficult to actually determine the importance of an individual predator or predator groups because predators by definition are generalist feeders. Shortly after the gypsy moth was recognized as a serious pest in the United States, naturalists emphasized the importance of birds as primary predators of gypsy moth larval stages (Forbush and Fernald 1896). Bess et al. (1947) were the first to suggest that small mammals (mice and shrews) were important predators of gypsy moth larvae in the litter of mesic forests. Campbell and Sloan (1977) found that predation of pupae by small mammals, especially *Peromysus leucopus*, was important in maintaining low-density populations at innocuous levels. The survival of pupae at different densities and in selected microhabitats was estimated by Smith (1985), who developed a methodology for exposing gypsy moth pupae affixed to bait boards using beeswax. Several studies have been conducted in the past 10 years suggesting that year-to-year variation in the abundance of small mammal populations, specifically *P. leucopus*, is a major determinant of change in gypsy moth populations (Elkinton et al. 1996; Jones et al. 1998). These studies indicate that the level of predation is determined by small mammal abundance, which is in turn linked to the production of acorns (mast) that are a major source of food for overwintering predator populations. However Liebhold et al. (2000) concluded that because small mammals are generalist predators and gypsy moths are a less preferred food item, they do not appear to regulate populations in a density-dependent fashion. However he does suggest that failure of acorn production may precede gypsy moth outbreaks by 2-4 years and thus contribute to the release of populations from low densities.

The importance of small mammals as predators of gypsy moth populations in Europe was ignored until preliminary studies were conducted in the Ukraine in the 1980's to measure predation of lyophilized pupae placed within four microhabitats in oak forests (Smith et al. 1998). Sherman live traps were used to estimate the diversity and abundance of small mammals on the sites. The authors found that where estimated small-mammal densities were 750/ha, 98% of pupae were destroyed within 72 hours of their placement in the litter. Ten species of mammals were identified, though *Apodemus sylvaticus* and *Clethrionomys glareolus* were the most abundant. Prior to these studies, foresters in Russia perceived that small mammals were primarily pests that destroyed forest regeneration. Recent studies in Austria using the same methodologies demonstrated that between 67 to 92% of pupae placed at the base of trees and up to 100 cm high on tree boles were destroyed by *A. sylvaticus* and *A. flavicollis*. This suggests that species of *Apodemus* apparently are the ecological equivalent of *P. leucopus* in European forests (Gschwanter et al. 2000).

References to vertebrate predation in Eurasia are fairly common however all except Rothschild (1958) emphasize the importance of birds in maintaining *L. dispar* populations at low densities e.g. Turcek (1950). Furuta and Koizami (1975) suggested that avian predators

aggregate into plots with high densities of gypsy moth larvae and cause density-dependent mortality, however most studies have been directed at measuring predation by birds of gypsy moth egg masses. Reichart (1959) concluded that 25 to 90% of eggs in overwintering egg masses were destroyed by birds. Higashiura (1989) has shown that high levels of bird predation on gypsy moth egg masses occurred in Japan however he suggests that the eggs are unpalatable to birds and are fed upon only to avoid starvation during stressful periods.

The predation of gypsy moth egg masses by birds in North America has not been well documented and there are few if any examples where overwintering egg masses have been destroyed or disrupted. Forbush and Fernald (1896) listed 38 bird species observed eating larval stages of the gypsy moth, however most of these observations were made when *L. dispar* populations were at outbreak levels, a time when predation has no significant impact on host populations (Smith and Lautenschlager, 1978). It is concluded that birds are opportunistic feeders on *L. dispar* populations and that gypsy moth life stages are not a major component in the diet of the most common North American species.

The importance of invertebrate predators in the dynamics of gypsy moth populations in the U.S. has not been determined conclusively though it is recognized that *Calasoma sycophanta* and species of ants and spiders are known to prey on gypsy moths at various life stages. Smith and Lautenschlager (1978) suggested that some of the mortality attributed to vertebrates by other investigators may actually have been caused by ground beetles and ants. The same authors provide an excellent synthesis of what is known about predators of *L. dispar*. Although *C. sycophanta* is distributed throughout the range of *L. dispar* in Europe and North America, it is abundant only during periods of gypsy moth outbreaks and also feeds on many different species of Lepidoptera (Weseloh et al. 1995). Therefore it is doubtful that this predator is important as a regulator of gypsy moth populations.

5.3 Pathogens

In North America, most high density populations of *L. dispar* eventually collapse due primarily to the action of a nuclear polyhedrosis virus (NPV) which kills mainly late instar larvae especially under conditions where there is high competition among larvae for rapidly declining host foliage. The NPV has been the most important factor causing the collapse of outbreak populations since the gypsy moth was introduced into North America. Woods and Elkinton (1987) demonstrated that NPV mortality followed a bimodal pattern- an early peak of mortality in the early instars contaminates foliage which is consumed by late instar larvae resulting in high levels of mortality. The interactions among NPV, foliage chemistry, virulence and transmission are discussed in the review by Elkinton and Liebhold (1990). The significance of pathogens other than the NPV in the dynamics of gypsy moth populations in North America usually is incidental.

According to Weiser (1987), in addition to the NPV, several species of microsporidia, a granulosis virus (GV), a cytoplasmic polyhedrosis virus (CPV), and species of fungi and nematodes cause infections in Eurasian gypsy moth populations. However, normally only the NPV and microsporidia cause significant mortality. A CPV caused 42% larval mortality in Austria in 1973 and there are reports of microsporidia causing 70% mortality at various life stages in the Ukraine (Zelenskaya, 1980) and in Yugoslavia (Sidor 1979). At least four species of microsporidia have been isolated and identified from larval populations throughout the range of gypsy moth east to Siberia. These protozoans have not been recovered from populations in North America. Individual species are being considered for introduction into the United States as a classical biological control agent.

A dramatic change in the dynamics of gypsy moth populations in the Eastern U.S. occurred in 1989 when the fungus *Entomophaga maimaiga* was first detected among *L. dispar* populations in the state of Connecticut (Hajek et al. 1990). Shortly thereafter this fungal

pathogen caused a panzootic among gypsy moth populations in the eastern U.S. (Elkinton et al. 1991) and is considered to be the most significant addition to the gypsy moth natural enemy complex in North America. *E. maimaiga* has spread rapidly into the central U.S. and north through Ontario, Canada (Nealis et al. 1999) and has also been introduced intentionally within most states where the gypsy moth is established. Unlike the NPV, which is most pronounced in high-density populations, *E. maimaiga* acts as a density-independent mortality factor and resting spores can persist in forest soils for 10-11 years, thus providing a source of inoculum over time (Weselow – Andreadis, 1992). Epizootics of this fungus often decimate high density *L. dispar* populations in its native Japan but only under humid conditions (Soper et al. 1988). However weather does not appear to be a limiting factor in North America. Although *E. maimaiga* has not been recovered in European *L. dispar* populations, it was introduced at two localities in Bulgaria and has persisted at low levels for a period of five years and caused localized epizootics in 2005 (Pilarska et al. 2006).

6   IMPACTS

The impacts that occur over time after the gypsy moth invades a new area are varied and complex. Defoliation of forests and urban trees can have profound direct and indirect effects on individual trees, components of forest ecosystems, and people. No doubt, the initial severity of the gypsy moth problem and its continued status as a serious pest in the U.S. can be attributed to the fact that it was introduced into the region of the U.S. that was dominated by hardwood forests consisting of mixed oak stands where the basal area of oak species exceeded 60%. The categories of impact that have been studied include timber (mortality and growth loss), recreation, residential, water quality, species displacement, regeneration, and wildlife to mention only a few. The literature on these subjects is very extensive and consequently we have chosen to summarize the effects of *L. dispar* defoliation on trees and forest stands. More comprehensive information on socioeconomic impacts is provided by Leuschner et al. (1996).

It was recognized during the early part of the 20th century that the initial outbreaks in the New England region (Massachusetts and surrounding states) caused extensive defoliation and tree mortality. Between 1911 and 1931, extensive records of defoliation and tree condition were collected in over 122 plots. This database was analyzed in later years and published as a monograph (Campbell and Sloan 1977) which is considered to be the definitive description of forest stand responses to the gypsy moth. As the gypsy moth spread to the south and west, data were collected by individual states mainly on levels of defoliation and tree mortality. On some dry sites where the basal area of oak was high (65-80%), mortality of oaks after 2-3 years of successive heavy defoliation exceeded 90%. Davidson et al. (1999) provide the most inclusive summary of trends in defoliation and mortality in the affected states as the gypsy moth infestation spread. Their general conclusions were as follows:

- Certain tree species (oaks) are defoliated at higher rates than other species, and frequently suffer greater mortality than less susceptible species.
- As the intensity (amount of foliage removed) and duration (number of consecutive episodes) of defoliation increases, the amount of tree mortality increases.
- Tree mortality tends to increase rapidly after 2-3 years of consecutive defoliations or if additional stressors such as drought occur.

Maximum tree mortality usually occurs 3-5 years after an episode of defoliation and is usually caused by secondary agents such as *Armillaria mellea* and *Agrilus bilineatus* which readily attack the severely weakened trees.

There is little consensus in the European literature as to the impact of gypsy moth defoliation among the countries of Central and Eastern Europe. Several references state that maximum oak mortality following gypsy moth defoliation is 25 to 30%, though there is insufficient information on levels of defoliation and subsequent tree mortality. There have been several severe outbreaks in the former Yugoslavia, the most recent occurring between 1995-1999 (Mihajlovic et al 1998). It was reported that at the culmination phase, 500,000 ha of forests, orchards, and parks were attacked and it was estimated that losses in volume increment could have been 23-50%. Another example of significant oak mortality following *L. dispar* defoliation occurred in the state of Hesse after the outbreak of 1993-94 (Gossenauer-Marohn 1995). Tree mortality was exacerbated by a period of drought and by a significant lowering of the water table in forested areas in the Rhine-Main-Valley.

There is also a difference in the complex of mortality-causing agents in Europe. Species of *Armillaria* are found throughout the region, but they are not considered as important as is *A. mellea* in causing oak mortality in North America. Rather, tree mortality is frequently attributed to other pathogens in the genera *Ophiostoma, Ceratocystis, Phytophthora,* and *Diplodia* that can be transmitted by secondary insect species such as the oak bark beetle, *Scolytus intricatus* Ratz. And in Germany, three species of *Agrilus – A. biguttatus*, *A. angustulus* and *Coraebus bifasciatus* – are considered the major cause of oak mortality. Buprestids, mainly *Agrilus biguttatus* is known in Hungary to cause significant oak mortality 1-2 years after gypsy moth damage, but sometimes after severe drought – independent of the gypsy moth damage (Csóka – Kovács 1999, Hirka 2005, 2006, Csóka – Hirka 2007).

Studies in Europe have focused more on the overall decline of oak in forests in response to multiple stressors than on the effects of individual stress agents such as the gypsy moth (Fuhrer 1998, Csóka et al. 1999).

7   MANAGEMENT ACTIVITIES

Efforts to control or manage *L. dispar* populations in the U.S.began in 1896 and have continued without interruption until today. Initially the primary goal was to eradicate the pest, however at that point in time, entomologists and politicians underestimated the severity of the threat, nor did they possess the technology to detect low density populations or to control them with pesticides. When eradication failed, a Federal Domestic Quarantine was implemented (1912) and extended efforts were made to establish Barrier Zones to prevent further spread. Although these tactics succeeded in slowing the rate of spread of the gypsy moth, they failed to prevent the accidental introduction of life stages beyond the infested region and from additional introductions from abroad.

When the use of DDT was prohibited in 1958, it was finally recognized and accepted that eradicating or preventing the spread of the gypsy moth in the U.S. was no longer an attainable goal. Since that time, decisions to suppress (spray) potentially damaging populations are made by the responsible land manager on federal lands and by the responsible state official on state and private lands, based on the assessment of the density of gypsy moth populations per unit area. Participation in suppression projects is voluntary and is conducted through a Federal Cooperative Forestry Assistance Act. The Federal Government provides ca 50% of the cost of spraying on state and private lands. Most projects are conducted on high-use recreational lands, residential areas, and on environmentally sensitive habitats.

After the demise of DDT, the chemical pesticides Orthene®, Dylox®, and Carbaryl® were used against the gypsy moth with limited success. Dimilin® (diflubenzuron) was registered for use against *L. dispar* in 1976, and by 1982, Dimilin and Btk (*Bacillus thuringiensis kurstaki)* were being used almost exclusively. The use of Btk increased greatly

after the 1980's due to the discovery of more potent strains, improved formulations, and better application technology. By 1995, Btk products Foray® and Dipel ®) were used on over 70% of the area treated aerially to suppress gypsy moth populations in North America and have essentially displaced the use of chemical pesticides. In addition to these very structured and regulated control programs, there is a vast amount of spraying and physical efforts being directed against the gypsy moth by homeowners and woodlot owners especially during outbreak years.

Two USDA agencies – the Forest Service (FS) and Animal and Plant Health Inspection Service (APHIS) – have been assigned the responsibility for protecting the forests and trees of the U.S. from the adverse effects of the gypsy moth. To this end, a new national program was initiated in 1995 that embraced the following strategies: *suppression*, to reduce high density populations of gypsy moth larvae in the generally infested area and prevent or minimize heavy defoliation; *eradication*, to eliminate isolated infestations of gypsy moth that are detected and to prevent their establishment in new areas; and *Slow The Spread* (STS), to reduce the rate of spread of the gypsy moth from the generally infested area into uninfested areas.

The need for this new approach was magnified by several recent events; (1) introduction of the Asian biotype of the gypsy moth into ports on both the east and west coasts; (2) a continued increase in the number of isolated gypsy moth infestations that have been detected outside of the generally infested area due to inadvertent introductions; and (3) a desire by the public to reduce the use of broad-spectrum chemical pesticides in favor of environmentally acceptable alternatives.

Although eradication and suppression have been components of the USDA's gypsy moth program since early in the last century, the strategy to slow the spread of the insect is new. This concept had been discussed at length for many years (McFadden and McManus 1991), and a demonstration project to evaluate this strategy was implemented in 1993 in a four-state area that encompassed more than 3 million ha. Renewed interest in reducing the rate of spread of the gypsy moth to the south and west was precipitated by the dramatic increase in the area that was generally infested between 1989 and 1994 (2.1 million ha), and by documentation that the insect was spreading at a rate of about 21 km per year (Liebhold et al. 1992).

Further justification was provided by an economic analysis of the benefits that would be realized by initiating a program to slow the spread of the gypsy moth (Leuschner et al. 1996). This analysis estimates potential program benefits over 25 years ranging from $774.8 to $3,801.5 million, (present value) under different scenarios whereby the rate of spread is reduced by 4 to 20 km per year. About 83 percent of the potential benefits are associated with residential impacts and costs associated with projected management activities.

The STS program focuses on populations in the transition zone that are not targeted for traditional eradication and suppression efforts (Sharov et al. 2002). In this zone, small populations are recently established, still at very low densities, and are discontinuous from one another. Because it is almost impossible to find life stages at these low densities, grids of pheromone traps are deployed to trap male moths and thereby delimit isolated populations. Thus the basic premise of STS is to locate and apply site-specific treatments to these isolated populations to prevent them growing together (coalescing) and thus contributing to the expansion of the population front (Liebhold et al. 1992). Results to date suggest that STS has reduced the rate of spread by ca 50% even though most of the cost is dedicated to monitoring populations and relatively small areas are being treated with environmentally acceptable tactics such a pheromone disruption, Btk, and Gypchek (Mayo et al. 2003).

8 CONCLUSIONS

During the last century, when gypsy moth populations were expanding their range to the south and west of New England and massive outbreaks occurred in newly infested forest lands, several biocontrol specialists suggested that the gypsy moth problem was more severe in the U.S. than it is in Europe because the pest's natural enemy complex in Europe was more diverse and better able to regulate populations. In fact, there are many more species of parasitoids that have been recovered from gypsy moth populations in Europe based on reports in the literature. However, with possibly a few exceptions (*G. liparidis*), the species of most importance in Europe have been established in North America and are also the most important.

Likewise, there have been entomopathogens recovered from *L. dispar* populations in Europe; however, the NPV is unquestionably the major pathogen that causes collapse of high-density populations throughout the geographic range of the gypsy moth. Species of microsporidia, which do not occur in North American populations, are common in European populations and at times cause significant levels of mortality among larvae. Conversely, *E. maimaiga*, which does not occur in Europe (except for the recent introduction in Bulgaria), is a significant cause of mortality among *L. dispar* populations in Japan and North America. Predators are not considered to be important in regulating gypsy moth populations on any continent because they usually are generalist (opportunistic) feeders that are mainly active during outbreaks when host densities are high. Therefore, it is the consensus of most gypsy moth researchers that despite the occurrence of a more diverse natural enemy fauna in Europe, their impact on the dynamics of gypsy moth populations is similar to that measured in North America.

In comparing the frequency of outbreaks between continents, Johnson et al. (2005) tested for synchrony among gypsy moth populations in 11 regions across three continents (North America, Europe, and Asia) and concluded that most populations tend to oscillate at periodicities between 8 and 12 years, However, analyses also suggest that in North America, there is evidence of a 5-year periodicity on more xeric sites, specifically oak-pine forest types that have a high basal area of oak species. Marovic et al. (1998) also reported that outbreaks in certain lowland forests in Serbia also occur every 4-5 years; however, information was not provided on the composition of these forests. Similarly high frequency of outbreaks is recorded in warmer and dryer regions of southeastern part of Hungary in *Quercus robur* stands (Leskó et al. 1994, Hirka 2006, 2007, Leskó et al. 2007).

The obvious disparity between gypsy moth outbreaks in Europe and North America is in their magnitude and impact. The area defoliated (ha) during outbreaks in Europe is much less than that which occurs within the generally infested region of North America. This can be attributed more to the reduced area of oak forests in Europe and their fragmentation into smaller parcels. For example, of the estimated 15 million ha of forest land in France, approximately 11% are classified as oak forest types (*Table 1*). In Croatia, where pedunculate oak forests used to occupy >70% of some forest regions, only 24% of the forested lands consist of oak.

Conversely, oak forests in North America are both extensive and contiguous. There are more hectares of oak type forest in each of the five U.S. states listed in Table 1 than in six of seven European countries in which *L. dispar* is still considered to be a forest pest and where control activities are deployed. The prognosis for the gypsy moth and its associated impacts in the U. S. is not encouraging. Based on an analysis conducted by Liebhold et al. (1997), there are 19 states currently not infested by *L. dispar* that contain >1 million ha of forests that are classified as susceptible to gypsy moth defoliation and damage. This suggests that the costs

associated with managing this pest will continue to accelerate and that there is a strong justification for slowing the spread of this pest into currently uninfested states.

Table 1. Forest statistics for selected countries/states affected by the gypsy moth

Location	Forest land (million ha)	Distribution % broadleaf/conifer	Oak forests (million ha)	Percentage of oak (%)
EUROPE				
Germany	10.7	29/71	1.1	10
France	15.0	64/36	1.7	11
Austria	3.9	31/69	0.7	2
Slovakia	2.0	58/42	0.3	12
Hungary	1.8	86/14	0.6	33
Croatia	2.5	86/14	0.6	24
Romania	6.3	69/31	0.8	18
USA				
Pennsylvania	6.9	94/6	3.4	49
West Virginia	4.9	91/9	3.8	78
Michigan	7.7	76/24	1.5	40
Wisconsin	6.0	80/20	2.4	40
Missouri	5.7	80/20	4.2	74

The situation in Europe is more stable in that *L. dispar* has been established in many of the same forested regions for over a century, and with few exceptions, the area of oak forests and associated preferred species has declined significantly. One exception is Hungary, which experienced its highest level of defoliation (212 thousand hectares) in 2005. During the last outbreak in Hungary, even montane beech forests occurring at higher altitudes were damaged. Most of these forests have never suffered gypsy moth damage previously (Hirka 2006). Although Hungary has only 1.8 million ha of forest land, ca. 33% of the forest is classified as "oak type". It is likely that outbreaks will continue to occur every 8-10 years in most European countries and that the Balkan countries will continue to experience outbreaks of a greater magnitude.

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On the Biology of the Bark Beetle *Scolytus nitidus* Schedl (Coleoptera: Scolytidae) Attacking Apple Orchards

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Abstract -– The biological characters of *Scolytus nitidus* were investigated both in the field and in the laboratory as well. This common shot-hole borer overwinters in larval stage on apple trees in Kashmir. After emergence the adults fly to suitable trees and undergo maturation feeding for 4-6 days. The copulation takes place at the entrance hole. The maternal gallery is one armed longitudinal, in average 4.6 cm long. The female lays 52 eggs on an average. The eggs hatch in 5 to 7 days. The larvae have 5 instars and complete their development in 38 to 50 days constructing larval galleries 5-8 cm in length. The larvae pupate for 6-18 days and finally the adults emerge to attack new suitable trees. The adults live for 45-60 days and the total life-span of this species ranges from 97 to 124 days. The seasonal distribution of various life stages and the number of generations were also recorded.

Bionomics / *Scolytus nitidus* / Scolytidae / apple trees

Kivonat – Az almafán károsító *Scolytus nitidus* Schedl (Coleoptera: Scolytidae) biológiája. Egy, az almafán károsító szúfaj, a *Scolytus nitidus* biológiai jellemzőit vizsgáltuk terepi és laboratóriumi körülmények között. A faj India Kasmír tartományában igen gyakori. Lárva alakban telel át gazdanövényén. A tavaszi kibújás után a nemzők megfelelő gazdanövényt keresnek és 4-6 napon át érési rágást végeznek. Ezt követi a párosodás. Az anyamenet egykarú, hosszirányú, átlagosan 4,6 cm hosszúságú. A nőstény bogár átlagosan 52 tojást rak le. A tojásból 5-7 nap múlva bújnak ki az álcák. Az álcastádium 38-50 napig tart, mialatt az ötször vedlő álcák 5-8 cm hosszúságú álcamenetet készítenek. A bábnyugalom 6-18 napig tart, amely után a frissen kifejlődő nemzők kirajzanak és költésre alkalmas fát keresnek. A nemzők 45-60 napig élnek, míg a faj teljes élettartama 97-124 nap közötti. A különböző fejlődési alakok pontos megjelenési idejét, valamint a generációk számát is meghatároztuk.

Biológia / *Scolytus nitidus* / Scolytidae / Malus domestica

1 INTRODUCTION

The scolytids are of great economic importance to forestry and horticulture in the temperate climatic zones including the valley of Kashmir. *Scolytus nitidus* Schedl is a predominant shot-hole borer which has caused considerable losses to fruit trees in the fruit growing areas of the valley since 1961 (Malik 1966) and its population has increased enormously during the past decade due to favourable environmental conditions, mainly, drought. On an average 5-10 per cent apple trees

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get damaged annually by the attack of this bark beetle species, which can increase upto 44 per cent in the mismanaged orchards during dry and hot weather conditions. The main damage to the tree is caused by adults entering the main branches and twigs during maturation feeding. After beetle attack, the infested branches or sometimes the entire tree may be killed during the establishment of the mother and larval galleries.

Scolytus nitidus is distributed in the Himachal Pradesh, Kashmir & Uttar Pradesh of India and Xizang (Tibet) of China on host trees – *Juglans regia, Prunus armeniaca, Pyrus malus & Cotoneaster microphylla* (Wood and Bright 1992). There is no systematic information on the various aspects of *S. nitidus* on temperate fruit tree species in Indian subcontinent except few reports of its occurrence in Kashmir (Beeson 1941, Malik 1966, Ahmad and Bhat 1987). The life history and behaviour of *S. nitidus* are complex and there is no detailed account of its biology since its taxonomic description by Schedl (1957).

Therefore, the objective of the present study was to investigate the detailed biology of *S. nitidus* in Kashmir apple orchards.

2   MATERIALS AND METHODS

2.1 Field studies

The biological data were obtained mainly from the study areas at Hazratbal, district Srinagar and from Bagh in Bandipora district consisting mainly apple trees. At both places, the orchards were having 20-45 years old trees with many cultivars like Red Delicious, Royal Delicious, Golden Delicious, American Apirouge, White Dotted Red, Benoni, Coxe's Organge Pippen, Lal Farosh, Razakh War, Chamura, Saharunpuri, Red Gold, Crimsen etc. Some felling had been done in the orchards in the previous year to initiate infestation by *S. nitidus.* In the following year trap logs were also put out as per the methods of Beaver (1967). These trap logs were cut periodically from April to September each year from 2000 to 2002. Observations of the various life stages were made once or twice weekly throughout the season on the trap logs and other infested branches of standing trees. New galleries were marked with a white dot. Further information was obtained by careful removal of bark sections both in the field and in the laboratory.

At the Bandipora experimental site the entrance holes, that the newly emerged beetles started grooving, were marked on one main branch and some twigs of a declining apple tree (Red Delicious) during April-May. After the marking dates, 10 beetle entries were dissected each day and examined for eggs to determine female maturation feeding period.

2.2 Laboratory rearing

Three sizes of wooden rearing boxes of similar design were available for use in the laboratory. The boxes were 30 × 30 × 30 cm, 46 × 46 × 46 cm and 25 × 30 × 36 cm in size having two screened, cross ventilated and three glass faces to facilitate entry of light. The branches naturally infested with *S. nitidus* were cut and placed in the rearing boxes. Fresh branches of 20-30 cm long and 2-4 cm in diameter were carefully removed from standing trees and their cut ends were sealed with wax. These uninfested branches were also put in these rearing boxes 10-15 days before adult emergence in order to induce fresh attack on them. This enabled the continuous rearing and examination of beetle development.

Few infested branches were also debarked regularly to study the various stages of the beetle under the bark. Characters of the different developmental stages including egg, larva, pupa and adult were recorded. Larval instars were separated by head capsule measurements (Beaver 1967). Mating behaviour, oviposition and gallery systems were also studied. Thus, developmental processes and durations of the pest's life stages were recorded and compared with the field results.

2.3 Scanning electron microscopy

Morphological characters were determined using scanning electron microscopy. Specimens were first placed in buffered glutaraldehyde (2.5%) for 2 hours followed by buffer washing for overnight. After this the specimens were treated with osmium tetroxide (1.0%) and then dehydrated in different alcoholic concentrations. In the next step specimens were kept in α-amyl acetate for 10 minutes followed by *Critical Point Drying* for 25 minutes using CO_2. After 2 days of open drying the specimens were mounted on stubs and coated with gold using the *Vacuum Evaporator* (HITACHI, HUS-5GB). Electron micrographs were taken with a S-3000H *Scanning Electron Microscope* (HITACHI, Japan).

3   RESULTS AND DISCUSSION

3.1 Mating behaviour

After host tree selection, the female of *S. nitidus* started to bore a small shot-hole on the bark of a declining branch. As soon as few beetles attacked, more and more flying adults of both sexes were attracted soon. The male was observed to but with his head against the abdomen of the female in the gallery a few times and then quickly turned round over the entry hole and copulation followed. Mating lasted for 30 to 90 seconds with an average of 57 seconds. However, mating lasts for 10-30 seconds in case of *S. scolytus* on elm trees (Beaver 1967). A female got mated several times by the same male or different males.

3.2 Maturation feeding

Bark dissections for female maturation feeding *(Figure 1)* showed that no eggs were collected from beetle entries on 1st and 2nd day; only 3/10 from 3-day-old entries yielded eggs; 6/10 from 4-day-old and 5-day-old entries contained eggs; while 7/10 from 6-day-old entries contained eggs; but all the 10 of 7-day-old beetle entries contained eggs. This indicated that newly emerged females mostly fed and oviposited in 4 to 6 days in the field. Maturation feeding for *S. mali* on apple trees is also completed in 4 to 6 days (Rudinsky et al. 1978). The successful maturation feeding occurred mostly on weakened trees or those with some dead branches. The feeding sites were then continued into the mother galleries.
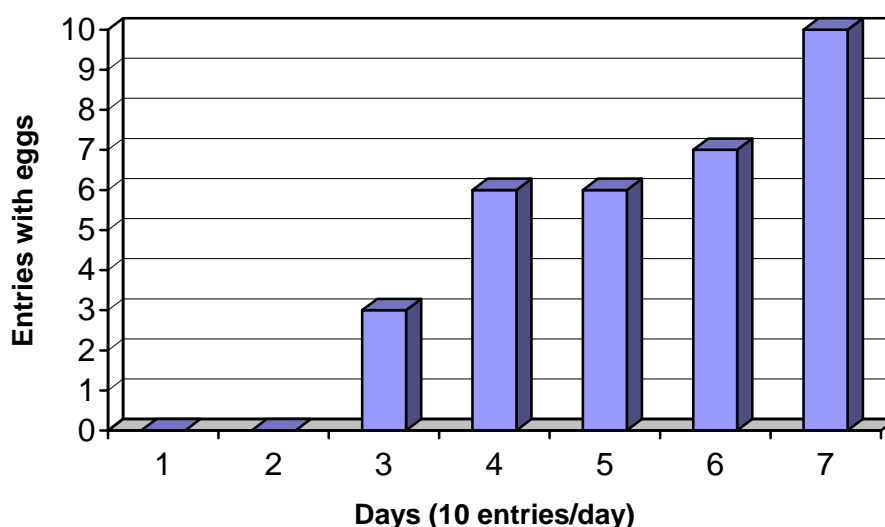

Figure 1. Female maturation period of S. nitidus

3.3 Gallery patterns

Mother gallery was made in an upward direction along the long axis of the attacked branch from which 50 to 70 larval galleries radiated, penetrating the inner bark and the sapwood surface. The vertical mother galleries ranged from 2.5 to 7.5 cm in length with a mean of 4.6 (± 1.45 SD) cm *(Table 1)*. The larval galleries were measured to be 3-8 cm in length with a mean of 6.5 (± 1.41 SD) cm *(Table 1)*. The mean difference in length between the mother gallery and larval gallery was found to be significant (P-value = 0.005). The mother galleries were made at equal distances from each other on the infested surface of the tree. The infested trunks and branches had thousands of exit-holes or shot-holes on the entire bark surface after the complete development.

Table 1. Measurement for length of gallery systems

Variable	N	Mean (mm)	SD (mm)	SEM (mm)	Minimum (mm)	Maximum (mm)
Mother gallery	12	4.625	1.448	0.418	2.500	7.500
Larval gallery	12	6.450	1.411	0.407	3.000	8.000

N= Number of observations

3.4 Life history

Bark dissections showed that eggs were deposited in small individual chambers on both sides of the mother gallery at regular distances throughout its length. On an average 52 (± 6.81 SD) eggs were laid per female, approximately 26 on each side of the mother gallery *(Table 2)*. Mother galleries were completed in 10-15 days but thereafter the female remained in the tunnel until most of the larvae had developed. She finally died in the entrance hole. The egg is slightly oval, shining, pale white and minute about 0.64 (± 0.10 SD) mm in length and 0.48 (± 0.07 SD) mm in width *(Table 3)*. The eggs in the egg niches were covered by the boring dust.

Table 2. Egg deposition by S. nitidus

Variable	N	Mean	SD	SEM	Minimum	Maximum
Eggs	6	52.00	6.81	2.78	40.00	60.00

N= Number of observations

Table 3. Measurements for developmental stages of S. nitidus

Variable	N	Mean (mm)	SD (mm)	SEM (mm)	Min. (mm)	Max. (mm)
Egg length	4	0.6449	0.0962	0.0481	0.5390	0.7700
Egg width	4	0.4813	0.0667	0.0333	0.4235	0.5775
Early larval length	4	0.7508	0.1618	0.0809	0.5775	0.9625
Early larval width	4	0.4524	0.0910	0.0455	0.3850	0.5775
Late larval length	3	5.7750	0.2700	0.1560	5.4670	5.9680
Late larval width	3	1.8865	0.1019	0.0588	1.8095	2.0020
Pupal length	4	4.0521	0.1584	0.0792	3.8500	4.2350
Pupal width	4	1.5978	0.0497	0.0249	1.5400	1.6555
Adult length	3	4.0040	0.1388	0.0801	3.8500	4.1195
Adult width	3	1.6812	0.0588	0.0340	1.6170	1.7325

N= Number of observations

The eggs hatched after an incubation period of 5-7 days *(Table 4)*. The larva on hatching was a minute white dot almost motionless, measuring 0.75 (± 0.16 SD) mm in length and 0.45 (± 0.09 SD) mm in width *(Table 3)*. As soon as the feeding started the larva became curved, legless grub *(Figure 2)* and light creamy in colour. A full grown larva was 5.77 (± 0.27 SD) mm long and 1.89 (± 0.10 SD) mm wide *(Table 3)*. The head capsule measurements *(Figure 3)* revealed that the larva passed through 5 instars before changing into pupa. The larval phase extended for 38-50 days *(Table 4)*.
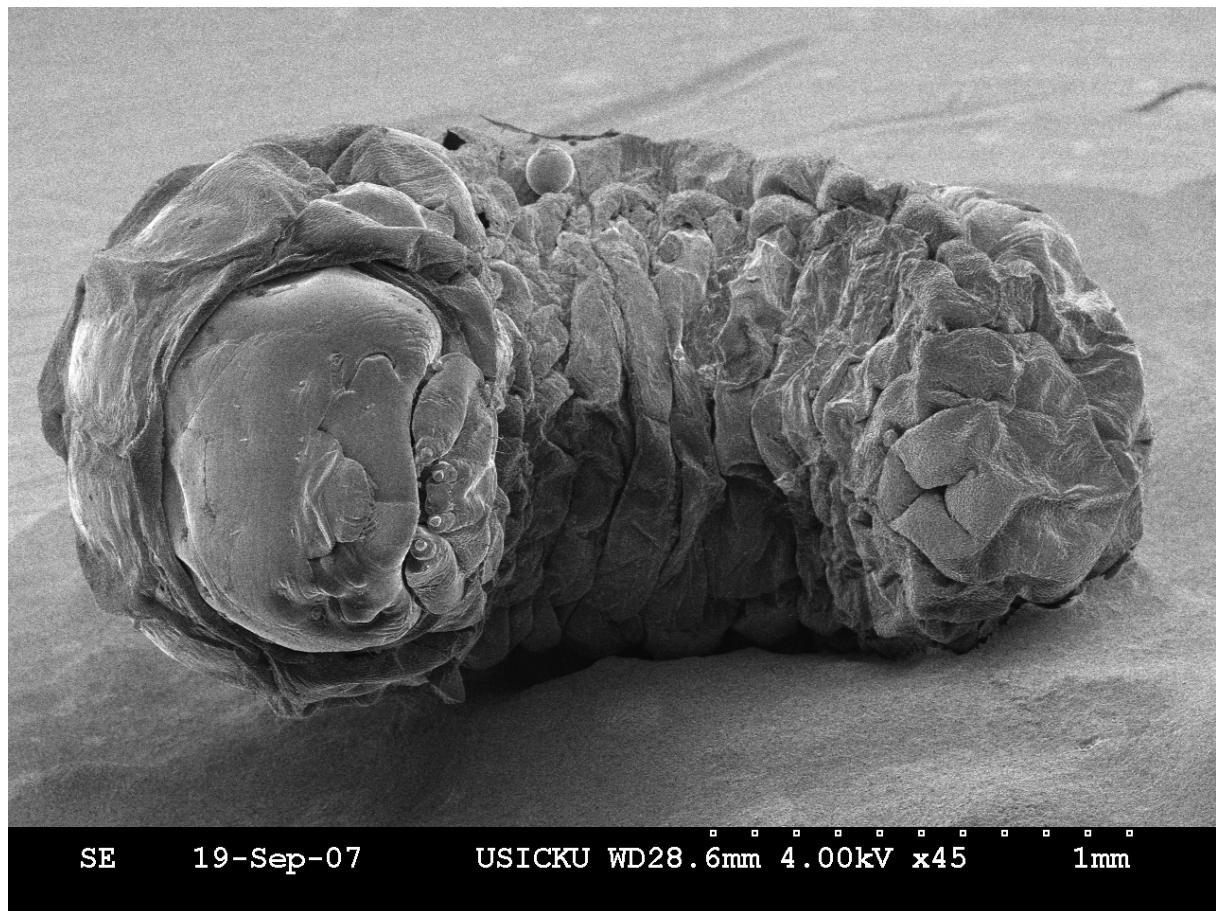
Figure 2. Larva of S. nitidus

Table 4. Developmental durations of S. nitidus on apple during 1999-2002

Developmental stage	Duration of generations (days)		
	1st	2nd	3rd (partial)
Egg	6-7	5-6	6
Larva	38-43	47-50	184-200 (overwintering)
Pupa	8-10	6-8	14-18
Adult	45-55	50-60	45-55
Total	97-115	108-124	249-279
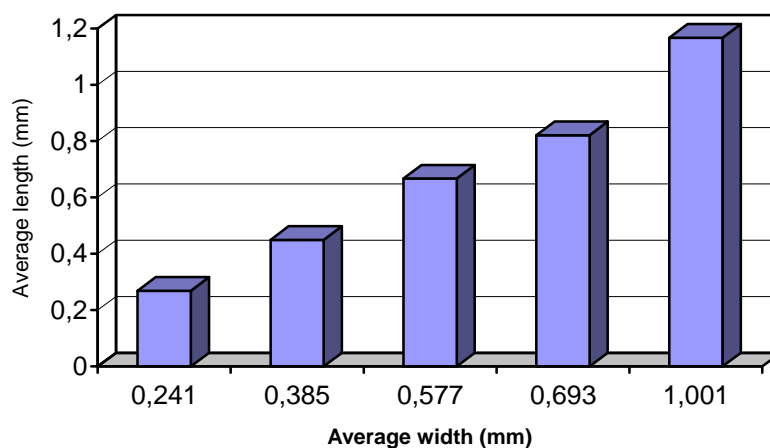
Figure 3. Head capsule measurements for different larval instars of S. nitidus

The pupation took place at the ends of the larval galleries in pupal cells. The pupa *(Figure 4)* was soft, white, averaging 4.05 (±0.16 SD) mm in length and 1.60 (± 0.05 SD) mm in width *(Table 3)*. The pupal stage lasted for 6-18 days *(Table 4)*.
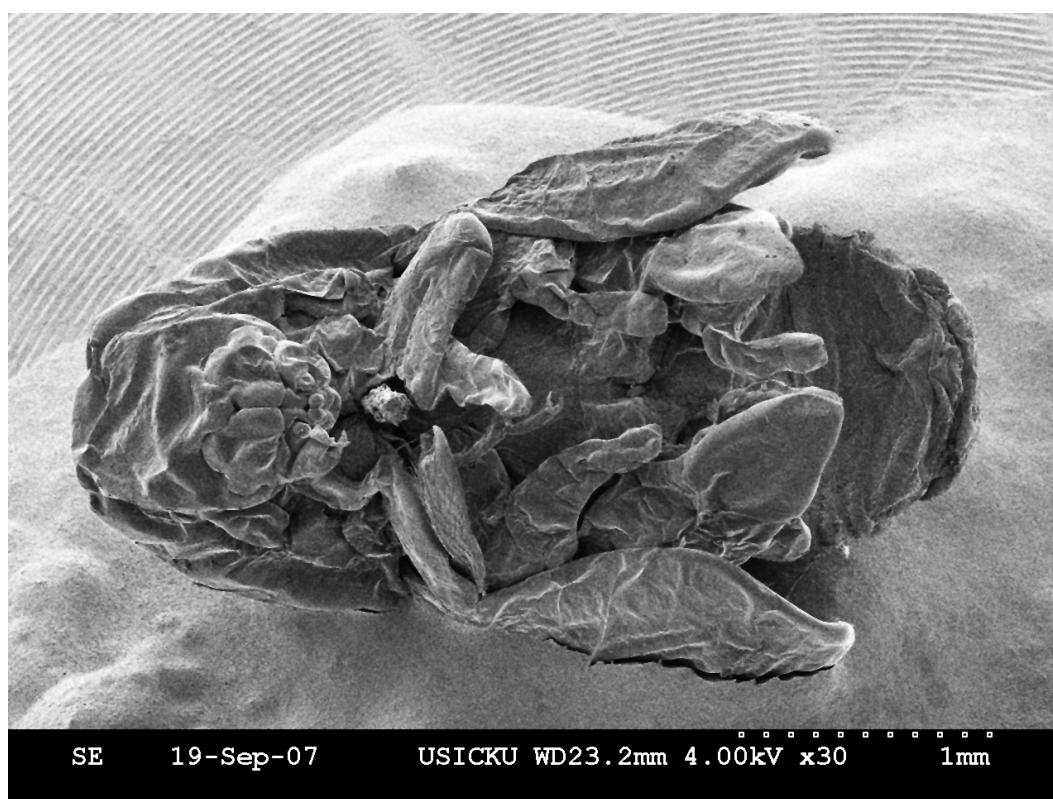
Figure 4. Pupa of S. nitidus

The adult emerged from the pupal chamber by tunnelling straight through the bark over it. After emergence, adults flew to the crown of other suitable trees to produce the next generation. The cylindrical adult *(Figure 5, 6)* averages 4.00 (± 0.14 SD) mm long and 1.68 (± 0.06 SD) mm wide *(Table 3)*. It has a shining black pronotum and dark red brown elytra with declivous abdomen *(Figure 6)*. The second abdominal sternite ascends abruptly

and perpendicularly with a minute pointed tubercle in the middle near its posterior border *(Figure 7).* The adults lived for 45-60 days *(Table 4).*
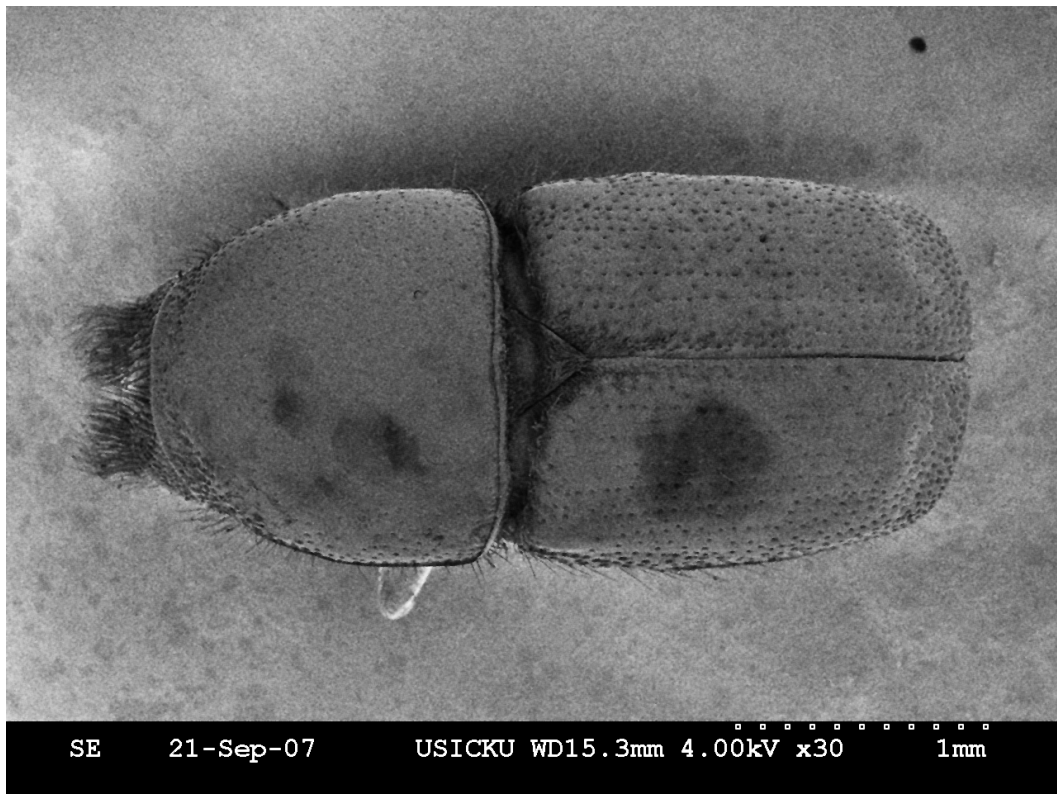
Figure 5. Adult of S. nitidus (dorsal view)
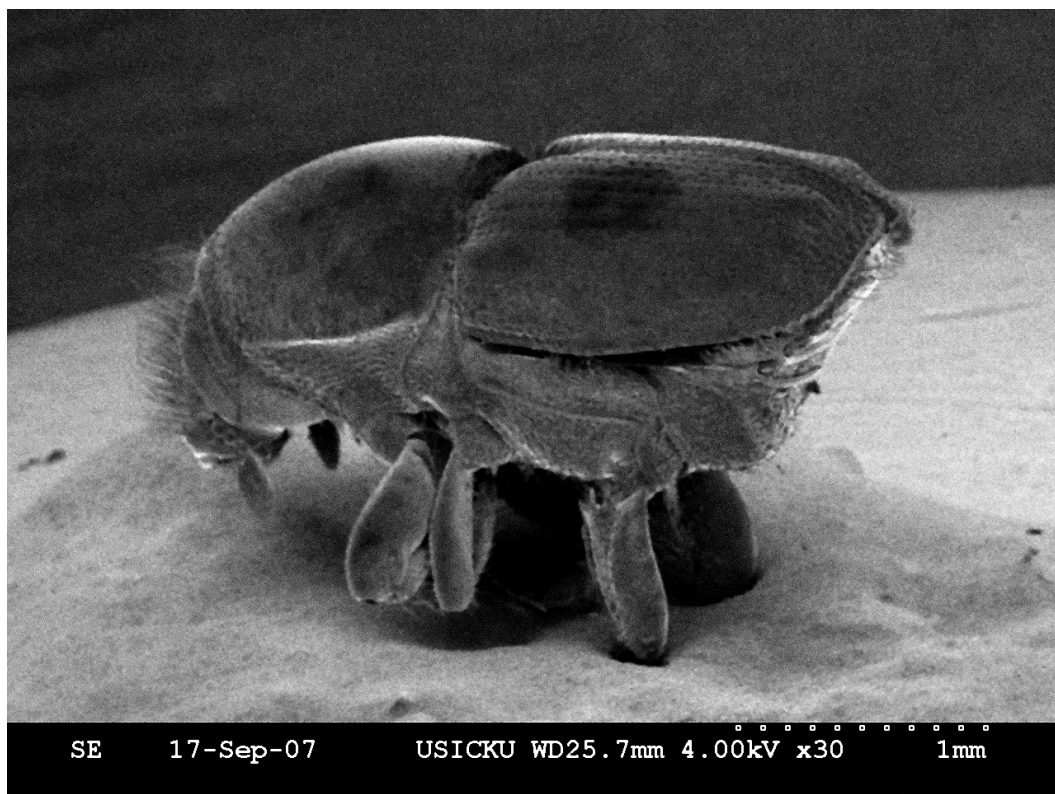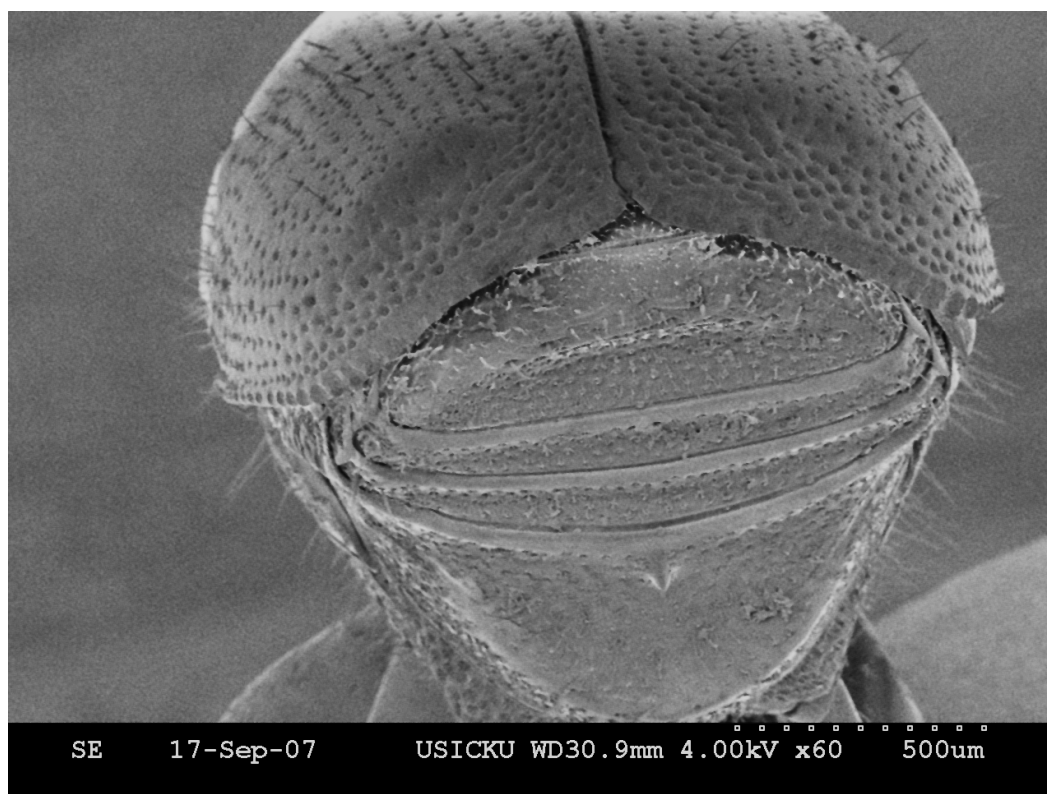

Figure 6. Adult of S. nitidus (lateral view)

Figure 7. Adult of S. nitidus (abdominal view)

3.5 Seasonal distribution

The results of the present observations *(Figure 8)* showed that *S. nitidus* overwintered in all the larval stages at the ends of their respective galleries from the end of November. The larvae remained inactive throughout the winter which resumed their activity from the first week of March of the following year. Pupation started from the first week of April and the first swarming adults appeared from the third week of April. The species produced 3 generations (the last a partial one) per year in Kashmir *(Figure 8)*. The first generation lasted from the last week of April to July having a total life span of 97-115 days *(Table 4)*. The second generation occurred from the first week of July to the middle of October with a total life span of 108-124 days while the third overwintering generation took about 249-279 days and was extended from September to May of the following year. It was also observed *(Figure 8)* that some late hatching larvae of second generation could not complete their development but overwintered as such in the last week of November and succeeded in completing 2 generations (the 2nd a partial one) only. There was a considerable overlap of 2nd and 3rd partial generations. The adults can be seen throughout the emergence period as the adults of one brood of *S. nitidus* have been reported to emerge for about 3 months (Buhroo et al. 2004). This can be due to different environmental factors, mainly, temperature to which the infested logs are exposed.

Two generations of *S. scolytus* on elm (Beaver 1967) and also of *S. mali* on apple (Rudinsky et al. 1978) were described under European conditions. Both these species overwinter in the larval stages. However, *S. amygdali* had 4 generations annually on fruit trees of Baluchistan (Janjua and Samuel 1941) and 5 generations per year on pear trees in Egypt (Kinawy et al. 1991). The developmental durations and generations of *S. nitidus* do not coincide with its related species worked out by other researchers (Beaver 1967, Janjua and Samuel 1941, Kinawy et al. 1991, Li-JiangLin et al. 1995, Mustaga 1991). The differences in the

life history of scolytid species can be explained by both species-specific variation and different environmental factors as well the variation of the biochemical composition of host trees.

	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEP	OCT	NOV	DEC
L	█	█	█	█	█							
P				█	█	█						
A	1st generation			█	█	█						
E					█	█	█					
L						█	█	█				
P							█	█				
A	2nd generation							█	█			
E								█	█			
L									█	█	█	█
P									█	█		
A	3rd generation									█	█	
E										█	█	
L											█	█

Figure 8. Seasonal distribution of S. nitidus on apple in Kashmir
(E: egg, L: larva, P: pupa and A: adult)

4   CONCLUSIONS

The common shot-hole borer *Scolytus nitidus* overwinters in larval instars at the ends of their respective galleries. After emergence in April-May the adults fly to the crown of neighbouring trees and start maturation feeding for 4-6 days. Females start boring small entrance holes through the bark of declining branches to initiate copulation with the male. Mating takes 30 to 90 seconds. After being mated several times by one or more males at the entrance hole, the female constructs mother gallery in an upward direction along the long axis of the attacked branch. The maternal gallery, in average 4.6 cm long, is made through the phloem slightly grooving the sapwood surface. The female lays 52 eggs on an average. The eggs are placed in small individual chambers regularly spaced on both sides of the mother gallery and are surrounded by fine particles of wood-dust. The eggs hatch in 5-7 days and the larval galleries radiate more or less away from the mother gallery and almost the entire phloem surface is eaten. The lengths of the larval galleries vary from 3 to 8 cm. The head capsule measurements show 5 instars during the larval phase which extends from 38 to 50 days. The larvae pupate in pupal cells at the ends of their galleries. Pupal stage lasts for 6-18 days. The pupal cells are cut in the phloem and outer bark or sometimes even in the outer layers of the sapwood. The adults live for 45-60 days. This species has two complete and a 3rd partial generations per year in Kashmir.

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The Effect of Climate Change on Soil Organic Matter Decomposition

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Abstract – In the last few decades the climate of Síkfőkút ILTER Forest (Hungary) became warmer and dryer. Due to the climate change the species composition of forest has been changing, and the total leaf litter production has been slightly decreasing. According to our long-term litter manipulation field experiment, which is part of ILTER Detritus Input and Removal Treatments (DIRT) Project, after a 4-5 year treating period, at the No Litter, No Root and No Input treatments the soil organic C and N content, the soil bacterial and fungal count, the soil pH, the soil enzyme activity, and soil respiration decreased. Increased soil temperature raises soil respiration exponentially, and thus if the average soil temperature increased by 2^oC at the dry Síkfőkút site, soil respiration would increase by 22.1%. This increase would be higher (29.9%) at a wet site, such as Harvard Forest in the USA. Increasing soil respiration can speed up global warming through a positive feedback mechanism.

oak forest, litter production, DIRT, SOM, soil respiration, soil enzymes activity

Kivonat – A klímaváltozás várható hatása az elhalt szerves anyag lebontási folyamataira. A Síkfőkúti erdő klímája az elmúlt évtizedek folyamán melegebbé és szárazabbá vált. A klímaváltozás hatására az erdő fafaj összetétele, struktúrája megváltozott, a teljes levélavar produkció csökkent. A hosszú-távú szabadföldi avarmanipulációs kísérleteink szerint, amely része az USA Detritus Input and Removal Treatment (DIRT) Projektnek, a csökkenő avarinput hatására a Nincs Avar, a Nincs Gyökér és a Nincs Input kezeléseknél, már 4-5 év múlva csökkent a talaj szerves C és N tartalma, a baktérium- és gombaszám, a pH, a talajenzimek aktivitása és a talajlégzés. Ha a globális felmelegedés következtében, a talaj évi átlaghőmérséklete 2^oC-al emelkedne, ez a szárazabb klímájú síkfőkúti cseres-tölgyesben kb. 22.1%-os talajlégzés növekedést eredményezne, míg a hűvösebb, nedvesebb klímájú Harvard Forest (USA) esetében ennél valamivel nagyobb 29.9%-os talajlégzés növekedés várható. A talajból történő többlet CO_2 kiáramlás pozitív visszacsatolásban tovább fokozhatja a globális felmelegedést.

tölgy erdő, avarprodukció, DIRT, SOM, talajlégzés, talajenzimek aktivitása

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1 INTRODUCTION

During the last few decades the long-term meteorological data of Síkfőkút Forest (Hungary) followed the global climate change, the forest climate became dryer and warmer (Antal et al. 1997).

Due to the climate change the tree species composition and the forest's structure have been changing dramatically. From 1972 till now the 68% of *Quercus petraea* and 15% of *Q. cerris* trees died and in the gaps new tree species (*Acer campestre*, *A. tataricum*) grew up from the shrub layer into the canopy level (Tóth et al. 2006).

The climate change also affects the soil organic matter (SOM). The SOM is a critical component of ecosystem, it provides cation exchange and water holding capacity, and it acts as a major control on soil pH. SOM also strongly promotes soil aggregation, and retains water for use by plants. Soil C accumulation and turnover are important global processes: soils contain about 1.5×10^{18} g C, which is 2-3 times bigger than the total amount of C in the vegetation (Schlesinger 1990). The C flux between soils and the atmosphere is huge, with soil respiration surpassing about 10 times the C flux due to fossil fuel combustion (Post et al. 1990, Watson et al. 1990). Thus, any change in rates of soil C turnover has a remarkable effect to the global C cycle. The litter input quantity and quality are taken into account under most scenarios of global climate change, but the resulting effects on SOM stability and turnover can not be predicted accurately now.

The level of SOM is influenced by litter production and added soluble organic material as input, and decomposition and leaching as output. Climate change affects on the input and output too through effects on net primary production (NPP) as well as through changes in rates of decomposition and leaching.

The litter production of Síkfőkút Forest was continuously measured from 1972 to 1976 (Tóth et al. 1985). From 2003 till now we renewed this measurement so as to get information about the effect of climate change on the litter production.

The effect of climate change on the SOM level and soil processes was studied in the framework of ILTER DIRT (International Long-Term Ecological Research, Detritus Input and Removal Treatments) project. The intercontinental ILTER network was developed by American and Hungarian scientists in 2000. The ILTER DIRT now includes five temperate forest sites including an oak forest at the Harvard Forest, MA (established 1990), a black cherry/sugar maple-dominated forest in the Bousson Experimental Forest, PA (1991), an old growth coniferous forest at the H.J. Andrews Experimental Forest, OR (1997), an oak forest at the Michigan Biological Laboratory, Pellston, MI (2004), and an oak forest in Síkfőkút Forest, Eger, Hungary (2000) (Sulzman et al. 2005). The original DIRT treatments, designed by Dr. Francis Hole at the University of Wisconsin Arboretum in 1956, consist of chronically altering plant inputs to forest soils by regularly removing surface litter from permanent plots and adding it to others (Sulzman et al. 2005). The purpose of the DIRT experiment is to assess how rates and sources of plant inputs control accumulation and dynamics of soil organic matter (SOM) and nutrients in forest soils, so this experiment is very applicable to studies of the effect of climate change on SOM and soil processes.

2 METHODS

2.1 Study site

The Síkfőkút ILTER site (47°90' N, 20°46' E, 320-340 m elevation) was established by Prof. Pál Jakucs in a mixed oak forest dominated by *Q. petraea* and *Q. cerris* in Northern part of Hungary in 1972 (Jakucs 1973, Kovács-Láng et al. 2000). Other important tree

species are *Acer tataricum* and *A. campestre.* According to Antal et al. (1997) the mean annual temperature is 10°C (1978–1994), and mean annual precipitation is 553 mm year^{-1} (1973–1996).

2.2 Measuring the litter production

Litter production was measured using the methods of Tóth et al. (1985).

2.3 The plant litter manipulation experiment

Plant litter inputs have been manipulated at the DIRT plots in the Síkfőkút Forest (SIK) since 2000. Six litter input/exclusion treatments (three replicates per treatment, *Table 1*) were located randomly at the site. Plots sizes are 7×7 m. Litter from No Litter plots were transferred to Double Litter plots several times per year. New vegetation was continually removed from the No Roots and No Inputs plots. Mosses re-grew rapidly, and were removed semi-annually.

Table 1. Treatment methods of the Detritus Input and Removal (DIRT) plots

Treatment	Method
Control (C)	Normal litter inputs are allowed.
No Litter (NL)	Aboveground inputs are excluded from plots.
Double Litter (DL)	Aboveground leaf inputs are doubled by adding litter removed from No Litter plots.
Double Wood (DW)	Aboveground wood inputs are doubled based on measured input rates of fallen woody debris.
No Roots (NR)	Roots are excluded with impenetrable barriers extending from the soil surface to the top of the C horizon.
No Inputs (NI)	Aboveground inputs are prevented as in No Litter plots, belowground inputs are prevented as in No Roots plots and plants or lichen/moss growth were discarded.

2.4. Soil sampling

The soil samples were taken from 6 places randomly in each plot, from the top 15 cm layer, using an OAKFIELD soil sampler.

2.5 Measuring methods

Soil temperature was measured hourly in each of the 18 plots by ONSET StowAway®TidbiT® temperature loggers at the centre of the plots at 10 cm soil depth. Soil moisture was measured monthly by oven drying at 105°C and a TDR instrument in the field. The bacterial and fungal count was determined quarterly by plate methods on Beef extract and on Czapek-Dox medium. Enzyme activity of soil acid phosphatase and β-glucosidase was measured quarterly according to Caldwell et al. (1999). Soil pH(H$_2$O) was measured quarterly with a Cole-Parmer pH meter. Soil C and N content was measured using a VARIO EL C-H-N-O-S instrument. Soil respiration was measured monthly using the soda lime method (Raich et al. 1990, Grogan 1998). The effects of treatments were statistically evaluated with SPSS software by analysis of variance.

3   RESULTS AND DISCUSSION

3.1 Litter production

The long-term change of the litter production (*Table 2*) reflects the change of tree species composition (Tóth et al. 2006). The leaf litter production of *Q. petraea* decreased considerably and production by *Q. cerris and Acer campestre* increased. Total leaf litter production slightly decreased. The increase in the debris fraction and the smallest leaf litter production is consequence of the huge *Lymantria dispar* gradation in 2005.

Table 2. Litter production of Síkfőkút Project kg ha⁻¹

Year	Quercus petraea	Quercus cerris	Acer campestre	Cornus mas	Other shrubs	Total leaf	Brach	Crop residue	Debris	Total litter
1972	2787	786	83	203	53	3912	458	0	178	4548
1973	2731	685	86	87	34	3623	526	326	190	4666
1974	2617	827	83	200	38	3765	689	477	209	5140
1975	3074	1063	114	277	39	4567	983	156	289	5995
1976	3019	1025	182	205	19	4450	1005	228	211	5894
Average	2846	877	110	194	37	4063	732	237	215	5249
2003	2038	660	669	208	54	3629	256	987	161	5033
2004	1054	1504	631	254	72	3515	744	2104	426	6789
2005	968	1284	274	273	36	2835	471	30	4557	7893
2006	1105	1912	900	322	123	4362	360	0	481	5203
Average	1291	1340	619	264	71	3585	458	780	1406	6230

3.2 Effect of litter manipulation treatment on the soil

3.2.1 Soil temperature

The shape of soil temperature curve is similar to a sinus curve (*Figure 1*). The litter on the soil surface acts as a heat insulation layer, therefore the litter treatments influences the soil temperature (*Figure 1-3*). This effect can be seen in the soil temperature curves as an amplitude change. The amplitude sizes of different treatments are: NI>NL>NR>C>DW>DL.
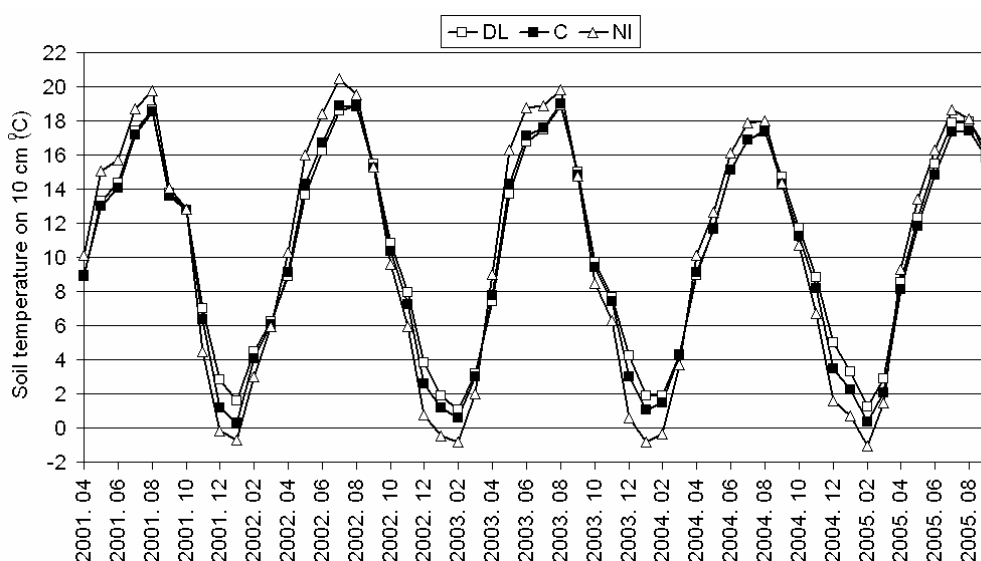

Figure 1. Effect of litter manipulation treatments (only DL, C and NI) on soil temperature in 10 cm soil depth between 2001 and 2005. (Codes explained in Table 1.)
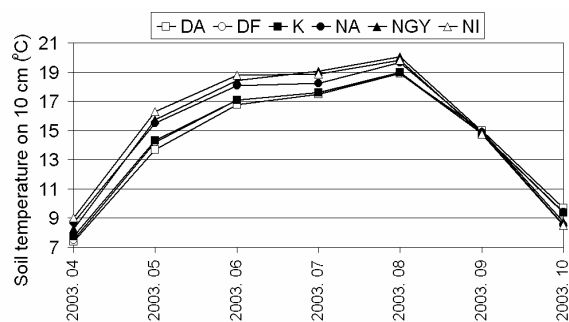
Figure 2. Effect of litter manipulation treatments on soil temperature in 10 cm soil depth over summer 2003
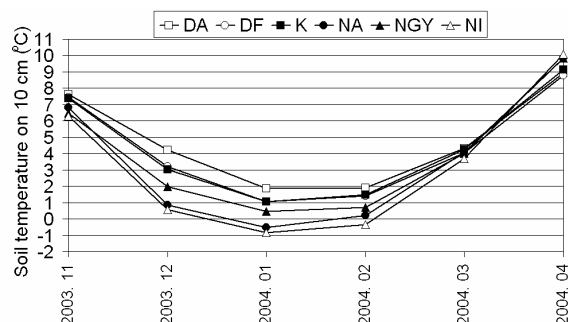

Figure 3. Effect of litter manipulation treatment on soil temperature in 10 cm soil depth over winter 2003

3.2.2 Soil moisture

The soil moisture contents both in w/w % and v/v % were similar to each other (*Figure 4, 5*). There was no significant difference between the soil moisture content at DL, NL and DW treatment compared to Control. At the same time significant differences could be seen in soil moisture contents at NR and NI treatments. In these plots high soil moisture content is a consequence of the lack of plant transpiration.
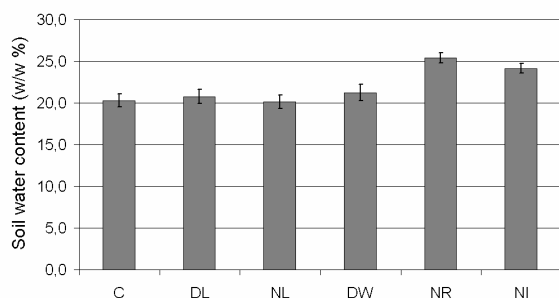
Figure 4. Soil water content % (w/w) in 0-15 cm depth (average of data between 2002 and 2005)
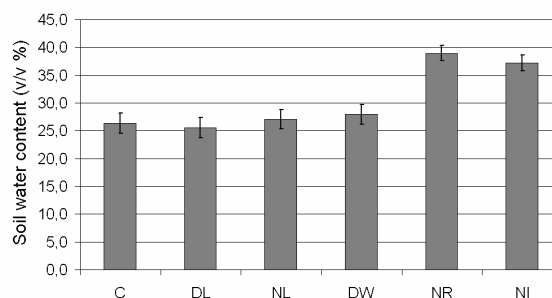
Figure 5. Soil water content % (v/v) in 0-15 cm depth. (average of the data between 2002-2005)

3.2.3 Carbon and nitrogen content of soil

In the first five years in the exclusion treatments (NL, NR, NI) C and N content of soil decreased so the long-term decrease in litter production is potentially harmful to soil fertility (*Figure 6, 7*). Surprisingly, the added litter at DL and DW treatments did not increase the C and N content of soil. An explanation of this phenomenon needs further investigation.
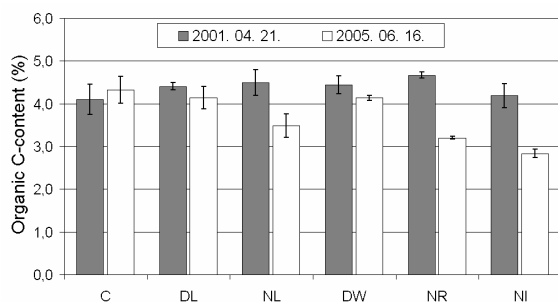

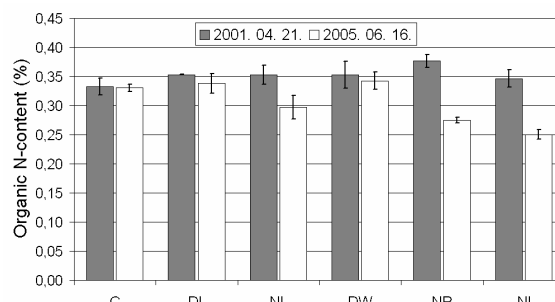*Figure 6. Soil organic carbon content in 0-15 cm soil depth.*

Figure 7. Soil organic nitrogen content in 0-15 cm soil depth.

3.2.4 Soil pH

The soil pH decreased in the exclusion (NL, NR, NI) treatments and increased in DL, DW treatments (*Figure 8*).

It is likely that the soil pH decrease in the NL, NR, NI treatments with decreasing litter input is due to decreases in litter cation inputs. The lower soil cation content decreases the soil buffering capacity which is unable neutralize the acidic substances resulting from litter decomposition.

In the DL and DW treatments with the increasing litter input, cation input increases too, which results in higher soil buffer capacity and pH.
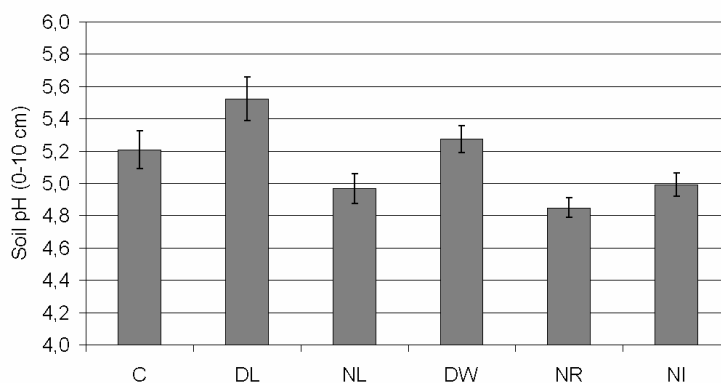

Figure 8. Soil pH (H$_2$O) in 0-15 cm soil depth
(average of the data between 2003 and 2005)

3.2.5 Soil bacterial and fungal count

The bacterial numbers at the NL, NR, NI treatments were significantly lower than in Control plots (*Figure 9*). Similar phenomenon can be observed for the fungi too, but the differences are not significant (*Figure 10*). The highest bacterial and fungal count was observed in the DL treatment but the difference is not significant compared to the Control.
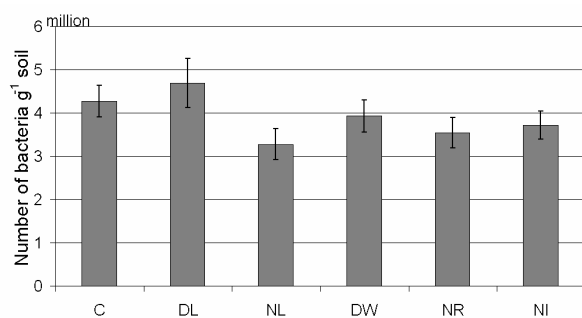

Figure 9. Bacterial count in 0-15 cm soil depth
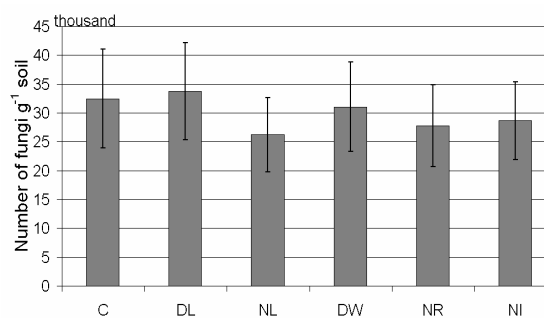*(average of the data between 2003 and 2005)*

Figure 10. Fungal count in 0-15 cm soil depth
(average of the data between 2003-2005)

3.2.6 Soil phosphatase and β-glucosidase activity

There were no significant differences in the soil phosphatase and β-glucosidase activity of different treatments in the first two years (*Figure 11, 12*). After this period, since 2003, the phosphatase and β-glucosidase activity of NL, NR and NI treatments has decreased, and at the same time at DL and DW treatments increased, although not significantly. There was a positive correlation between soil phosphatase and β-glucosidase activity.
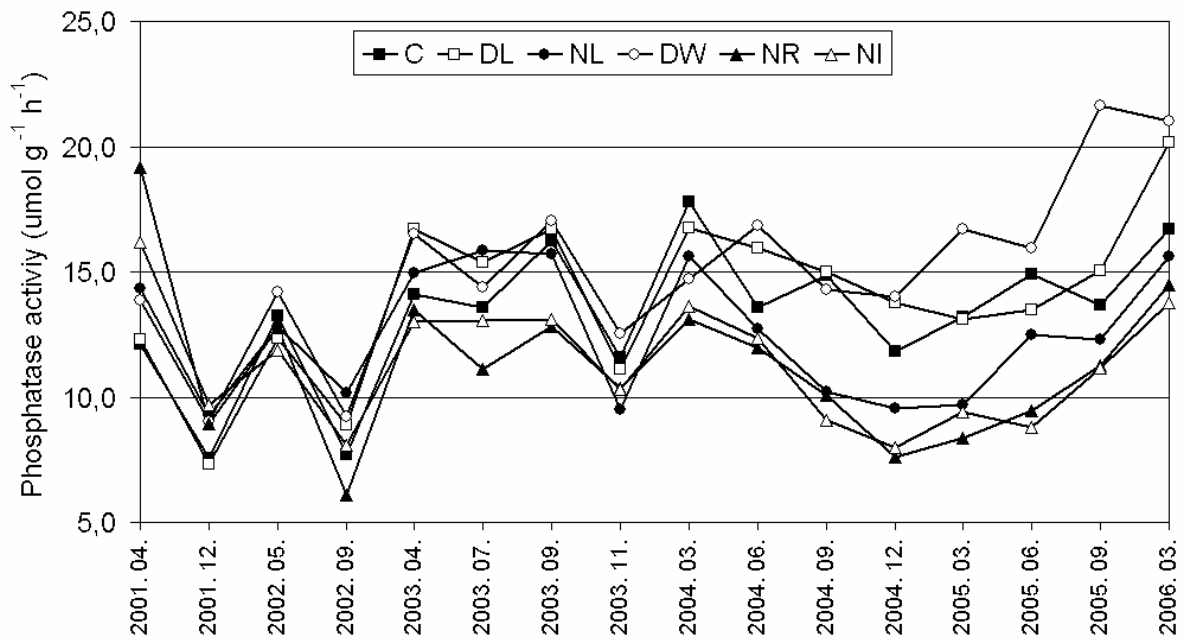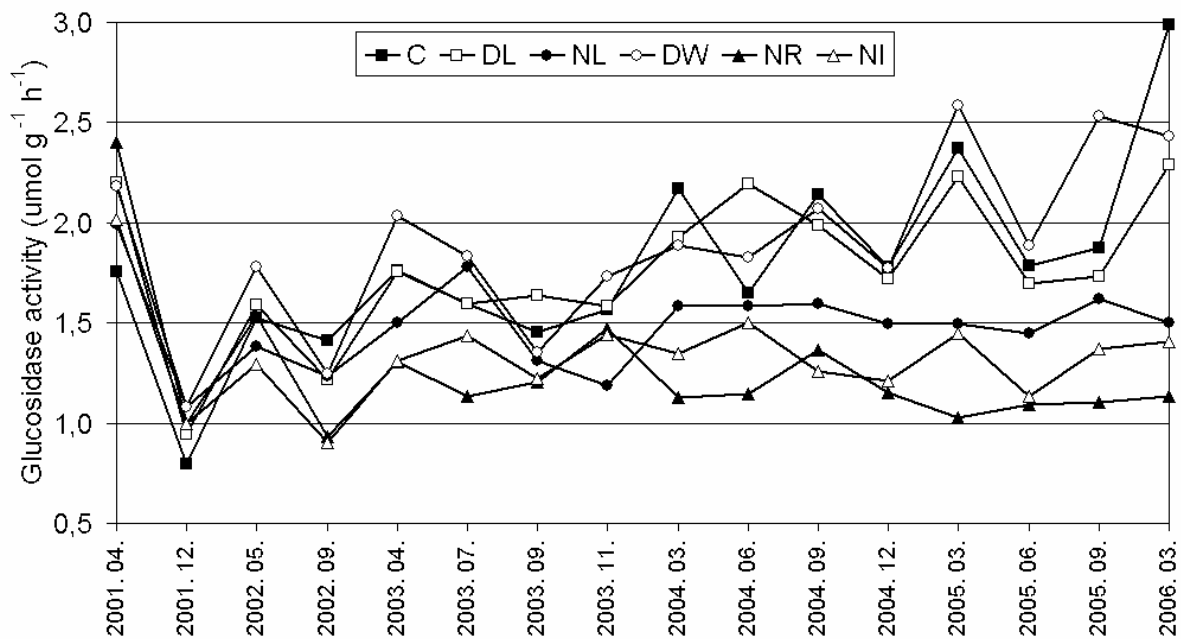
Figure 11. Changes in soil phosphatase activity

Figure 12. Changes in the soil β-glucosidase activity

3.2.7 Soil respiration

In the exclusion treatments (NL, NR, NI) soil respiration decreased significantly after 5 years, in 2005 (*Figure 13*).
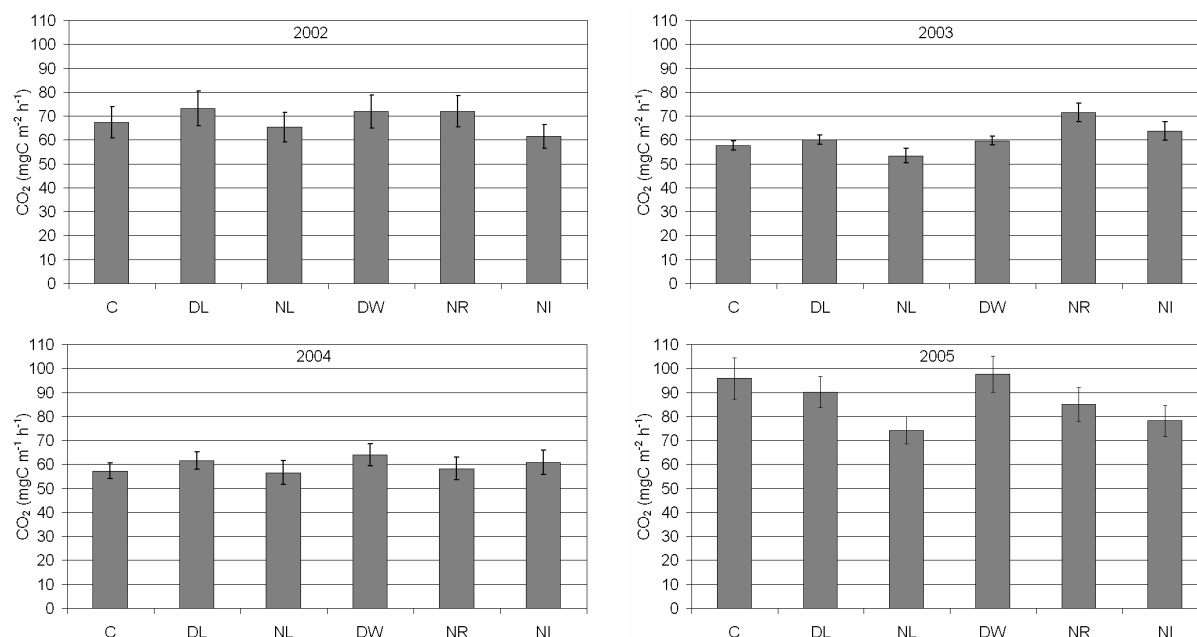
Figure 13. Effect of the litter manipulation treatment on soil respiration (yearly average)

Soil respiration was higher in every treatment in 2005. This phenomenon is possibly due to *Limantria dispar* gradation. In that year there was a large increase in *Limantria dispar* faeces deposited on the soil, which possibly increased soil respiration.

The seasonal change in soil respiration is significantly correlated with the seasonal change in soil temperature (*Figure 14*).

Figure 14. Seasonal changes in soil respiration in 2005
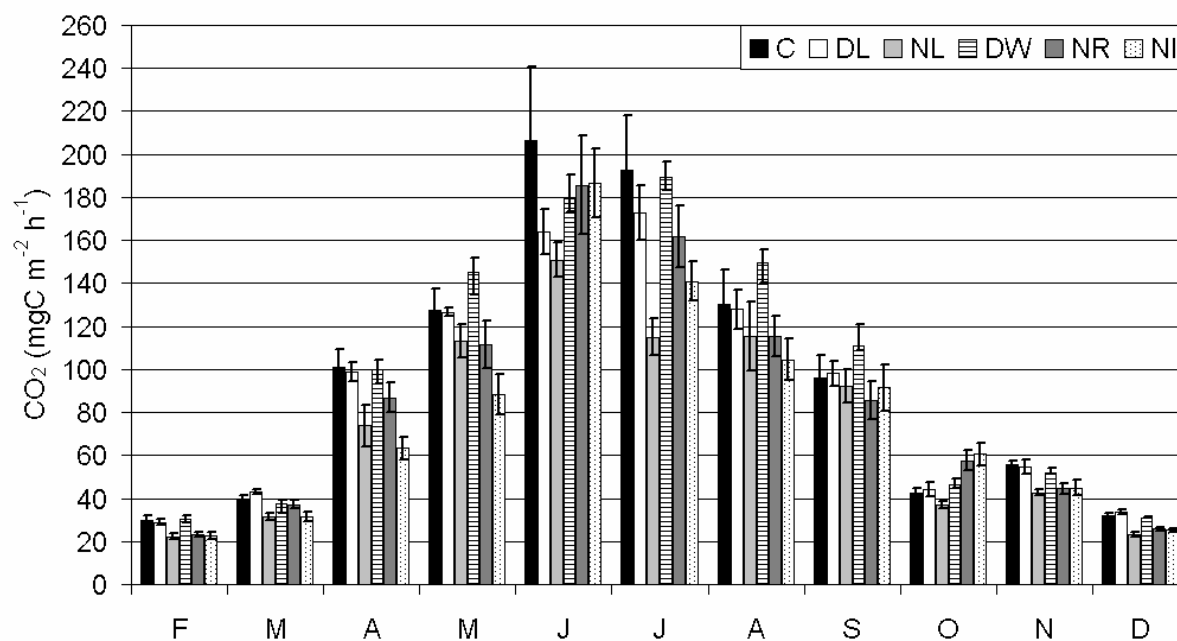
3.3 Effect of the soil temperature on the soil respiration

With increasing soil temperature, soil respiration rose exponentially (*Figure 15*). The relationship between soil temperature and soil respiration is $y = a.e^{(b.x)}$. From this equation we can calculate a Q_{10} value ($Q_{10} = e^{b.10}$). Q_{10} values calculated for the Síkfőkút Project (SIK) to

those found previously in the DIRT experiment at Harvard Forest (HFR) are compared in *Table 3*. The SIK Q_{10} values are lower in every treatment compared to those seen at the HFR.
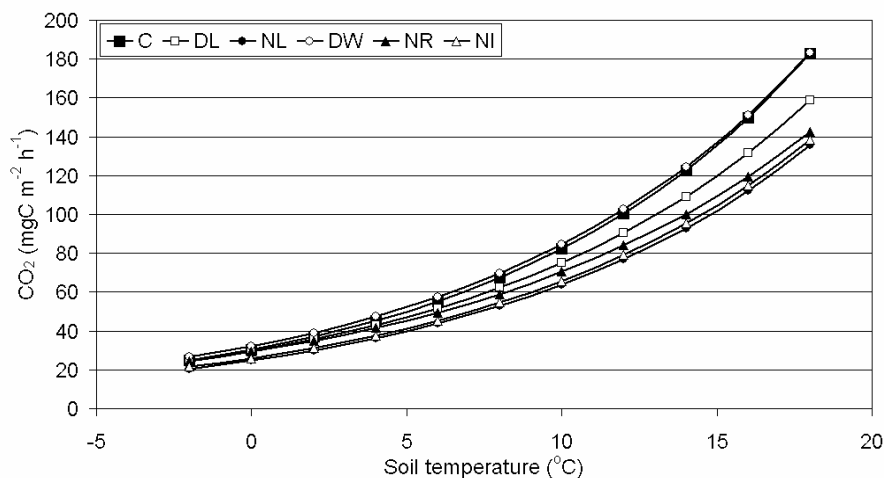

Figure 15. Effect of soil temperature on soil respiration

Table 3. The Q_{10} values of SIK and HFR for soil respiration

Treatment	Q_{10}(after 5 years treatment)	
	SIK	HFR (Micks 2002)
Control	2.7	3.7
Double Litter	2.5	3.0
No Litter	2.6	2.9
Double Wood	2.6	-
No Root	2.4	2.6
No Input	2.5	2.6

The huge 10°C soil temperature increase is not a realistic scenario, so we calculated Q_2 ($Q_2 = e^{b.2}$) instead of Q_{10}. The Q_2 shows the factor by which soil respiration will rise if the mean annual soil temperature increases 2°C. We compare Q_2 values of SIK to HFR in *Table 4*.

Table 4. The Q_2 values of SIK and HFR for soil respiration

Treatment	Q_2(after 5 years treatment)	
	SIK	HFR[*]
Control	1.221	1.299
Double Litter	1.206	1.246
No Litter	1.208	1.237
Double Wood	1.213	-
No Root	1.192	1.210
No Input	1.204	1.210

[*] Calculated date from Micks 2002

According to the *Table 4,* if the average yearly soil temperature grew by 2°C at the dry SIK site, the soil respiration would increase by 22.1% (compared to the Control). The increase would be higher (29.9%) at the wet site, at HFR (compared to the Control). Increasing soil respiration can speed up global warming through a positive feedback loop.

3.4 Effects of soil moisture on soil respiration

The effect of soil moisture on soil respiration was minor (*Figure 16*). With increases in soil moisture content, soil respiration rose slightly, but the relationship was not significant.
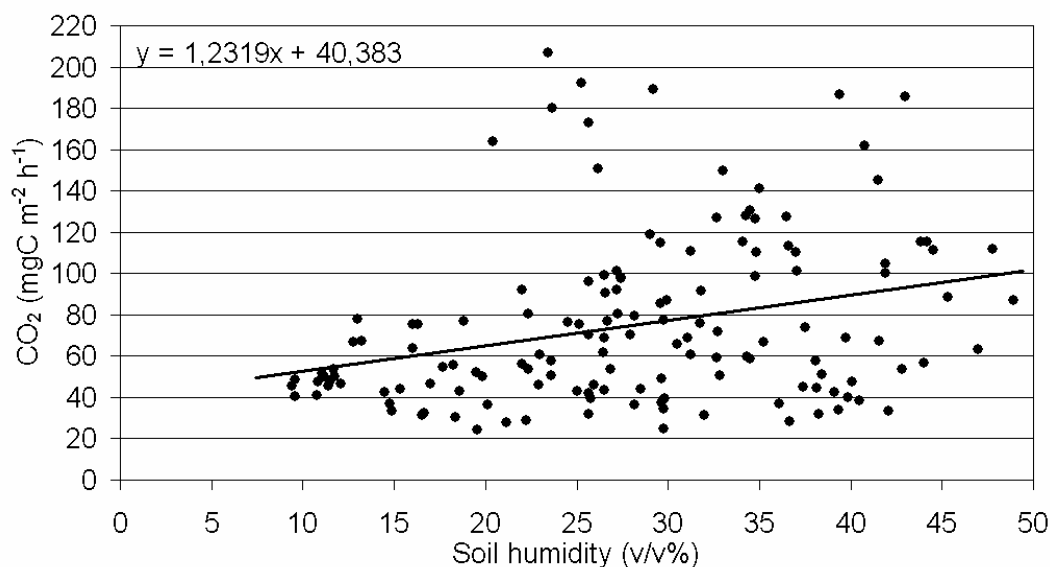

Figure 16. Effect of soil humidity on soil respiration

4 CONCLUSION

It is difficult to say, what the effect of climate change on the litter production is. During the last three decades the leaf litter production of Síkfőkút Project decreased but the total litter production increased. To substantiate the trend in litter production needs further data, so we must continue our litter production investigation in the future.

However, the decrease of leaf litter production would be harmful to the soil physical and chemical properties and the soil life. If the litter production decreased on long term, soil organic C and N content, the soil bacterial and fungal count, soil pH, soil enzyme activity, and soil respiration would decrease. At the same time the soil temperature would increase in the summer period. Increased soil temperature would raise the soil respiration exponentially which might speed up the global warming through a positive feedback mechanism.

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Changes of Temperature and Precipitation Extremes following Homogenization

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Abstract – Climate indices to detect changes have been defined in several international projects on climate change. Climate index calculations require at least daily resolution of time series without inhomogeneities, such as transfer of stations, changes in observation practice. In many cases the characteristics of the estimated linear trends, calculated from the original and from the homogenized time series are significantly different. The ECA&D (European Climate Assessment & Dataset) indices and some other special temperature and precipitation indices of own development were applied to the Climate Database of the Hungarian Meteorological Service. Long term daily maximum, minimum and daily mean temperature data series and daily precipitation sums were examined. The climate index calculation processes were tested on original observations and on homogenized daily data for temperature; in the case of precipitation a complementation process was performed to fill in the gaps of missing data. Experiences of comparing the climate index calculation results, based on original and complemented-homogenized data, are reported in this paper. We present the preliminary result of climate index calculations also on gridded (interpolated) daily data.

extreme climate indices / temperature and precipitation trends / data homogenization / climate indices on grid

Kivonat – Hőmérsékleti és csapadék szélsőségek vizsgálata homogenizált adatokon. A klímaváltozás detektálása céljából több nemzetközi, a klímaváltozással foglalkozó programban klímaindexek sorát definiáltak. Az éghajlati szélsőségek vizsgálatához, avagy az extrém indexek számításához inhomogenitásoktól (állomás áttelepítések, a mérési időpontok és a mérési módszerek változásai) mentes, jó minőségű napi adatsorok szükségesek. Sok esetben ugyanis jelentősen eltér az eredeti és a homogenizált adatok alapján számolt lineáris trend értéke nemcsak nagyságában, hanem előjelében is. Ez pedig a klímaváltozás tekintetében téves következtetések levonásához vezethet. Az OMSZ klimatológiai adatbázisban történt fejlesztés során megvalósítottuk az ECA&D (European Climate Assessment & Dataset) projektben alkalmazott extrém klímaindexek sorozatát és ezeket kiegészítettük néhány általunk kifejlesztett karakterisztikával. Az extrémumokban fellépő változások nyomon követésére lineáris trendelemzést végeztünk mind az eredeti, mind a homogenizált sorokon, ennek a vizsgálatnak a tapasztalatairól számolunk be ebben a dolgozatban. Bemutatjuk emellett a rácsponti klímaindex számítások előzetes eredményeit is.

klíma szélsőség index / hőmérséklet és csapadék trendek / homogenizálás / rácsponti klímaindex

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1 INTRODUCTION

Determining changes in the behaviour of extreme events is the main topic of several international projects. Extreme climate events can be identified in different ways. One of them is using internationally agreed, predefined indices that is day count exceeding a fixed threshold, percentile threshold, heat wave duration, etc. In the frame of the CCL (Commission for Climatology of WMO)/CLIVAR (Research programme on CLImate VARiability and predictability) (1998) program a range of climate indices were defined to detect probable changes. Such indices were calculated on temperature, precipitation and air pressure data in the ECA&D (European Climate Assessment & Dataset) project.

The ECA&D and some other special temperature and precipitation indices of our own development were applied on the Climate Database of the Hungarian Meteorological Service too. Using uniform methodology allows joining to other international programs.

Climate index calculations require at least daily resolution of time series without inhomogeneities, such as transfer of stations, changes in observation practice. The initiative projects in this field, ECA&D and APN (Asia-Pacific Network), emphasize data quality and data homogeneity.

Characteristics of the estimated linear trends are unambiguously unlike on the different time series. Frequently a decreasing trend is calculated from the original data with interruptions and gaps, while the trend fitted to homogenized data implies an increasing tendency, or reverse.

2 DATA

Extreme temperature index calculations based on daily maximum and daily minimum temperature series from the beginning of the 20th century were performed. The following stations were analysed in the period 1901-2005: Sopron, Szombathely, Mosonmagyaróvár, Keszthely, Siófok, Pécs, Baja, Kecskemét, Kalocsa, Szeged, Túrkeve, Miskolc, Debrecen, Nyíregyháza, Budapest. Implementing the index calculation, the gaps in the observation series and the inhomogeneities caused problems.

The majority of temperature series is exceptionally inhomogeneous *(Figure 1),* the original data series is biased by break points. Homogenizing of the data series is essential before using them for climate analysis.
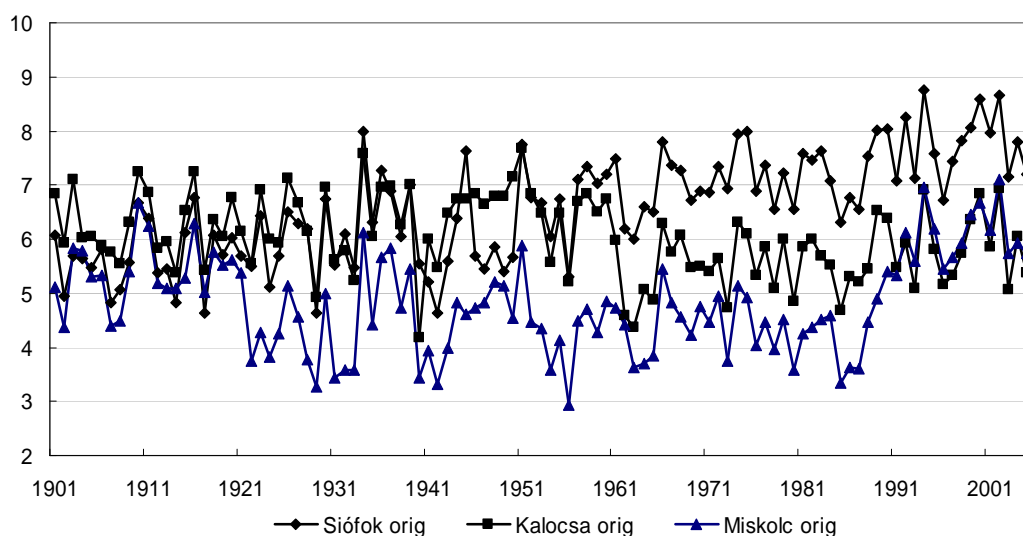

Figure 1. Annual mean of daily minimum temperatures at Siófok, Kalocsa, Miskolc stations, between 1901-2005, original data

Precipitation series are in better condition than temperatures, as turned out on analysing the amounts of daily precipitation. The precipitation indices were calculated for 37 Hungarian stations in the interval 1901-2005. The elaborated rain gauges do not cover the country evenly. The covering of Transdanubia is dense enough, the eastern part of the country is covered sparsely.

3   HOMOGENIZATION

The homogenization of data has been performed with the procedure MASH (Multiple Analysis of Series for Homogenization) (Szentimrey 1999). The original MASH procedure has been developed for homogenization of monthly series. MASH is a relative method and depending on the distribution of the examined meteorological element an additive (e.g. temperature) or a multiplicative (e.g. precipitation) model can be applied. In the software the following subjects were elaborated for monthly data series: comparison of series, break point (change point) and outlier detection, correction of series, automatic usage of metadata, verification for homogenization of daily series, quality control of daily data and complementing missing data.

Extreme climate indices are defined on daily data. The present version of MASHv3.01 (Szentimrey 2006) procedure is suitable for daily temperature elements as normal distribution is assumed and the additive model can be applied.

Daily maximum and minimum temperature series of 15 stations between 1901 and 2005 were homogenized by the MASH method. *Figure 2* shows the annual mean of daily minimum temperatures after homogenization, whereas the original data of the same stations can be seen in *Figure 1*. The obvious break points were eliminated, and the curves are running parallel, as we expected.
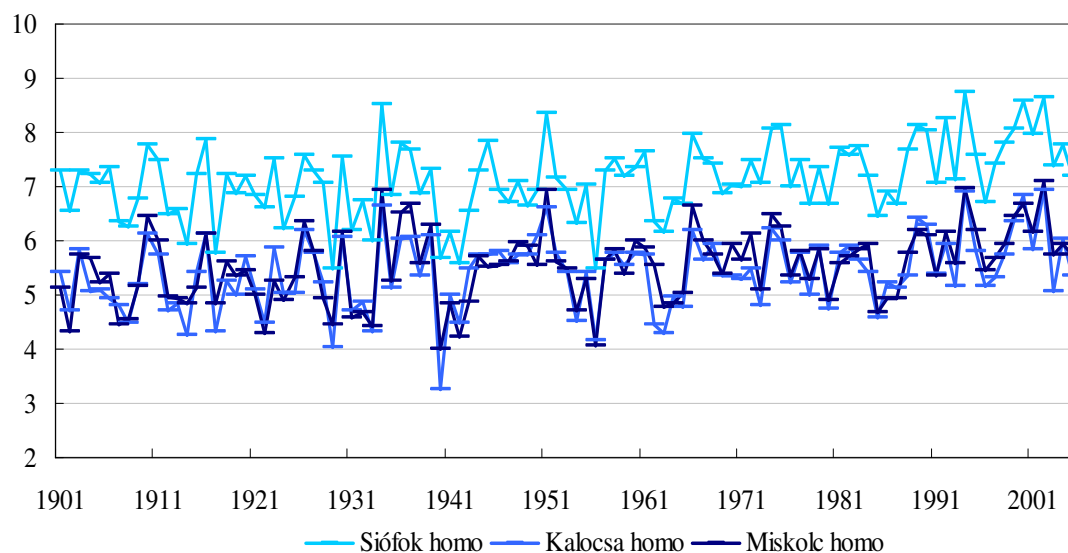

Figure 2. Homogenized annual mean of daily minimum temperatures at Siófok, Kalocsa, and Miskolc stations, between 1901 and 2005

4   CLIMATE INDEX CALCULATION IN THE CLIMATE DATABASE OF THE HUNGARIAN METEOROLOGICAL SERVICE (OMSZ)

The ECA&D indices and some other characteristics (*Table 1, 2, 3*) are built into the climate database of OMSZ. Daily maximum and minimum temperature data series were homogenized and the climate index series based on daily data have been analyzed at 15 stations between 1901 and 2005. The precipitation index calculations were executed on 37 complemented long time daily rainfall series from 1901 to 2005.

Table 1. Extreme hot temperature indices in the climate database of OMSZ

Index/unit	Hot extremes
txx / °C	absolute Tmax
dtx25/day	summer days Tmax > 25 °C
dtx30e/day	hot days Tmax ≥ 30 °C
dtx35e/day	very hot days Tmax ≥ 35 °C
dtn20/day	tropical nights Tmin ≥ 20 °C
ditxgnr/day	heat wave duration index
ditgnr90/day	warm spell days
itxgnr90/day	maximum duration of warm spell
dtgnr90/%	Tavg > 90th percentile of normal period
dtngnr90/%	Tmin > 90th percentile of normal period
dtxgnr90/day	Tmax > 90th

Table 2. Extreme cold temperature indices in the climate database of OMSZ

Index/unit	Cold extremes
tnn/°C	absolute Tmin
dtn0/days	frost days Tmin < 0°C
itn0x/days	maximum number of frost days Tmin < 0°C
dtn0e/days	frost days Tmin ≤ 0°C
t17s/°C	heating degree days
t20s°C	heating degree days
dtx0/day	ice days Tmax < 0°C
dtx0e/day	ice days with Tmax ≤ 0°C
ditnlnr/day	cold wave duration index
ditlnr10/day	cold spell days
itnlnr10/day	maximum duration of cold spell
dtlnr10/day	Tavg < 10th percentile of normal period
dtnlnr10/day	Tmin < 10th percentile of normal period
dtxlnr10/day	Tmax < 10th percentile of normal period

Table 3. Extreme precipitation climate indices in the climate database of OMSZ

Index/unit	Precipitation Extremes
rs/mm	Precipitation sum
dr1/day	Number of wet days
r1a/mm/day	Mean wet-day precipitation
ir0xd/day	Length of longest very dry period R≤1 mm
ir1xd/day	Length of longest dry period R <1 mm
ir1xw/day	Length of longest wet period R ≥ 1 mm
dr5/day	Number of days R ≥ 5 mm
dr10 day	Number of days R≥ 10
dr20/ day	Number of days R≥ 20
rx1/mm	Maximum daily sum
rx5/mm	Maximum sum in 5 day long period
dr75gnr/day	Number of days R> 75% of normal period
pr75gnr/%	Number of days R> 75% of normal period in % of wet days
r75gnr/mm	Precipitation sum of days R> 75% of normal period
~95% 99%	

The ECA&D indices and some other characteristics (*Table 1, 2, 3*) were calculated both on the original and on the homogenized temperature data and on complemented daily precipitation measurements. Year is the base period (one index value is calculated per year) and the period of 1961-1990 is the normal of index calculations.

5   RESULTS

5.1 Temperature tendencies

All built-in climate indices in the climate DataBase can be reached and visualized on homogenized and on original data as well. The time series and the fitted trend of a certain climate index can be constructed in the DataBase. Different stations can be analysed parallel, hereby the regional differences can be shown. In *Table 4.a* and *Table 4.b* the changes of several climate indices in three overlapping periods are summarized.

These tables contain the result of the linear trend fitting. The shade of cells indicate the result of significance test at 95% level (white: no significant trend, dark grey: significant positive trend, light grey: significant negative trend). The changes in a specific time interval are presented on homogenized and on original data. We underline the importance of homogenization because the slope and direction of the fitted trend differs frequently between homogenized and original data.

The number of frost days shows a decreasing tendency the whole last century on homogenized data. From the beginning of the seventies the number of frost days per year is again slightly increasing, amplifying the extremity. The rate of increase in the number of summer days and the number of tropical nights indicates significant warming.

Table 4.a   Changes of temperature climate indices on original and homogenized data for different periods

Temperature index	Station	Period					
		1901-2005		1946-2005		1976-2005	
		homogenized	original	homogenized	original	homogenized	original
Change (days) of the number of frost days	Budapest	-7.9	-10.3	-6.1	-6.1	1.9	-1.3
	Debrecen	-5.7	-24.4	-1.7	-0.1	0.5	0.4
	Miskolc	-1.1	16.4	-0.7	-13.8	4.1	-22.6
	Mosonmagyaróvár	-10.0	1.6	-11.2	-17.1	-0.6	-5.9
	Szeged	-5.1	18.0	3.5	20.0	11.8	-9.8
	Szombathely	-10.2	7.5	-16.4	-10.5	0.5	-5.5
Change (days) of the number of summer days	Budapest	6.2	2.3	1.6	-6.0	23.4	16.2
	Debrecen	11.8	-1.0	-0.9	-7.8	30.8	22.9
	Miskolc	6.2	27.0	1.9	-15.3	32.3	18.9
	Mosonmagyaróvár	6.9	16.5	6.6	10.9	25.0	27.0
	Szeged	7.8	13.9	1.1	0.6	21.3	24.3
	Szombathely	8.2	12.2	6.5	10.1	27.8	32.7
Change (days) of the number of tropical nights	Budapest	8.5	10.3	5.7	7.4	12.2	14.6
	Debrecen	0.9	1.3	0.5	0.6	2.7	3.1
	Miskolc	1.6	2.1	1.7	3.5	3.4	5.1
	Mosonmagyaróvár	1.0	1.0	2.1	2.0	2.3	2.2
	Szeged	0.9	-3.3	0.2	-4.4	1.9	2.0
	Szombathely	0.5	0.4	0.7	0.7	1.3	1.1

Table 4.b   Changes of temperature climate indices on original and homogenized data for different periods

temperature index	Station	Period					
		1901-2005		1946-2005		1976-2005	
		homogenized	original	homogenized	original	homogenized	original
Change of the growing season length (days)	Budapest	14.6	17.2	21.0	22.3	28.7	36.1
	Debrecen	5.4	10.9	-1.5	4.0	12.3	12.2
	Miskolc	2.4	1.0	-10.1	-8.9	6.3	8.6
	Mosonmagyaróvár	13.0	17.4	12.4	19.9	12.5	18.6
	Szeged	0.5	-7.8	-0.6	-8.7	9.4	14.0
	Szombathely	16.4	16.7	20.3	18.3	16.5	30.2
Change in the number of days with daily maximum > 1961-90 normal (6 day long interval at least)	Budapest	9.4	9.9	9.5	7.7	18.4	15.8
	Debrecen	6.3	3.7	1.7	-0.4	17.2	14.0
	Miskolc	5.6	4.0	3.6	-2.3	18.2	11.9
	Mosonmagyaróvár	7.9	9.0	12.8	13.8	12.0	16.1
	Szeged	10.5	8.9	12.0	10.1	22.4	27.2
	Szombathely	10.0	15.6	9.1	17.1	15.5	28.6
Change of the number of days when daily minimum < 10% percentile of 1961-90 normal	Budapest	-19.8	-32.0	-12.0	-13.2	-6.8	-11.7
	Debrecen	-17.7	-44.6	-11.5	-13.4	-6.0	-9.4
	Miskolc	-12.9	-1.2	-15.5	-25.0	21.4	-40.0
	Mosonmagyaróvár	-11.0	-2.5	-15.2	-26.0	-4.4	-9.4
	Szeged	-1.0	20.4	-3.0	8.7	2.4	2.4
	Szombathely	-11.9	-1.3	-16.1	-15.8	-4.5	-7.3
Change of the number of days when daily minimum > 90% percentile of 1961-90 normal	Budapest	25.4	30.7	22.1	21.7	33.5	38.3
	Debrecen	8.4	31.1	8.9	12.1	30.3	36.2
	Miskolc	20.0	13.3	4.7	38.4	16.5	75.9
	Mosonmagyaróvár	17.8	10.9	19.4	31.7	22.7	31.1
	Szeged	22.4	-18.6	12.8	-18.4	32.5	32.1
	Szombathely	25.5	12.8	24.2	24.0	33.5	38.8

The growing season becomes longer, at some stations significantly. The duration of heat waves has increased significantly in the interval since 1976. The number of cold nights decreased mainly since 1901 and there are fewer cold nights in the last 30 years also, but the changes are significant only for one station.

On the whole we may conclude that the increasing trend in warm climate extremes appears more accentuated from the mid-seventies according to the global temperature tendencies.

5.2 Precipitation tendencies

Correspondingly to the temperature extremes, period changes by stations are presented in *Table 5* for three different overlapping periods. Precipitation is a variable element in time and space alike; the indices derived from daily precipitation sums are variable.

Table 5. Changes in the percentage of days with heavy precipitation for three different periods

Extreme precipitation index	Station	Period		
		1901-2005	1946-2005	1976-2005
Percentage change of days with heavy precipitation (exceeding the 95% percentile of the 1961-90 period)	Baja	-6,2	-2,3	5,3
	Bakonybél	1,4	-3,1	*17,1*
	Bakonyszentkirály	-3,2	0,1	8,9
	Balatonkeresztúr	-6,6	3,2	*11,3*
	Battonya	3,9	6,2	*13,1*
	Beled	-2,5	-3,9	*10,8*
	Budapest	-5,4	-1,5	6,7
	Debrecen	0,4	3,7	0,0
	Gölle	-1,2	-6,2	*20,9*
	Herend	-5,8	-8,6	7,3
	Iharos	-6,6	-3,2	4,1
	Karcsa	1,3	4,7	8,4
	Kemenesszentmárton	1,4	-7,7	*10,5*
	Kerta	-1,4	-6,1	8,8
	Keszthely	-8,0	-7,4	-8,2
	Kunszentmárton	1,9	1,2	6,4
	Kápolnásnyék	-7,4	-0,1	9,0
	Miskolc	0,5	1,1	12,0
	Mosonmagyaróvár	-1,3	-5,7	4,5
	Márianosztra	-3,0	-3,9	5,5
	Nagyvázsony	-1,8	-3,1	5,9
	Nyíregyháza	-2,5	-4,7	5,4
	Pincehely	-3,5	-6,6	*24,1*
	Poroszló	-8,1	-13,7	-12,7
	Pásztó	-2,2	3,7	5,0
	Pécs	2,9	7,7	*14,2*
	Pér	-5,0	2,2	*13,0*
	Ravazd	-7,1	-3,2	*10,9*
	Rinyakovácsi	-4,4	-3,6	4,3
	Siófok	-0,3	-0,3	2,5
	Sopron	-9,8	-6,3	-3,6
	Szeged	-0,3	*8,4*	*14,7*
	Szombathely	-3,8	-2,9	5,3
	Szálka	*12,1*	-0,3	8,6
	Tengelic	2,3	0,5	*14,2*
	Türje	0,6	-3,9	2,4
	Vásárosnamény	*9,0*	4,9	*10,5*

Only the percentage change of days with extremely high daily rainfall is shown in the *Table 5.* That is the percentage of days, when the daily sum exceeds the 95% percentile of the 1961-90 normal period. Considering the whole period until 2005, both increasing and decreasing trends occur. In the last most intense warming period from 1976 the percentage of days with heavy rainfall increased.

5.3 Climate index calculation in grid points

Temperature and precipitation indices calculations were extended to $0.1° \times 0.1°$ gridded (interpolated) daily data too. This resolution matches to 10 km x 10 km approximately. Gridding of homogenized daily data series was carried out by the MISH (Meteorological Interpolation based on Surface Homogenized Data Basis) interpolation procedure (Szentimrey – Bihari 2006). Note that daily observations were interpolated, not the extreme indices, hereby the gridding does not interfere with the fact that the extreme events are local phenomena, interpolation of them is not suggested.

About 1000 grid points cover Hungary; therefore the technical implementation is more complex, than analysing station series. First the index series had to be calculated in every grid point, followed by the linear trend analysis. The preliminary result of climate index calculations is illustrated on gridded (interpolated) daily data (*Figure 3 and Figure 4*).
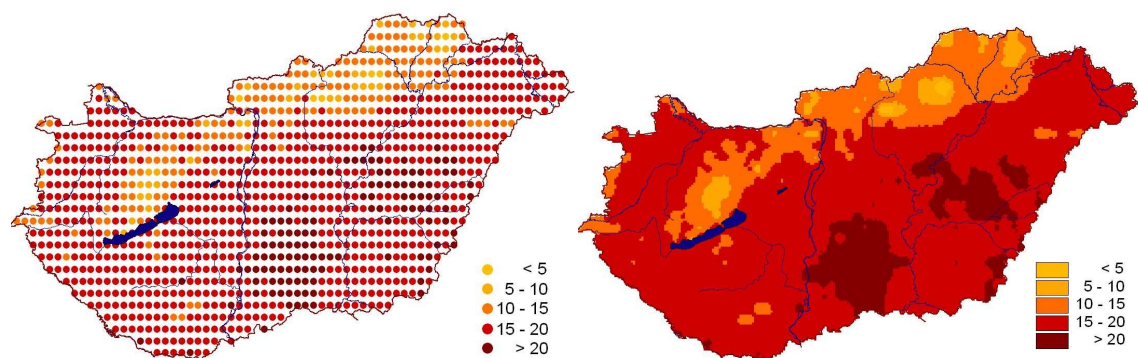

*Figure 3. Changes in the number of summer days 1976-2005,
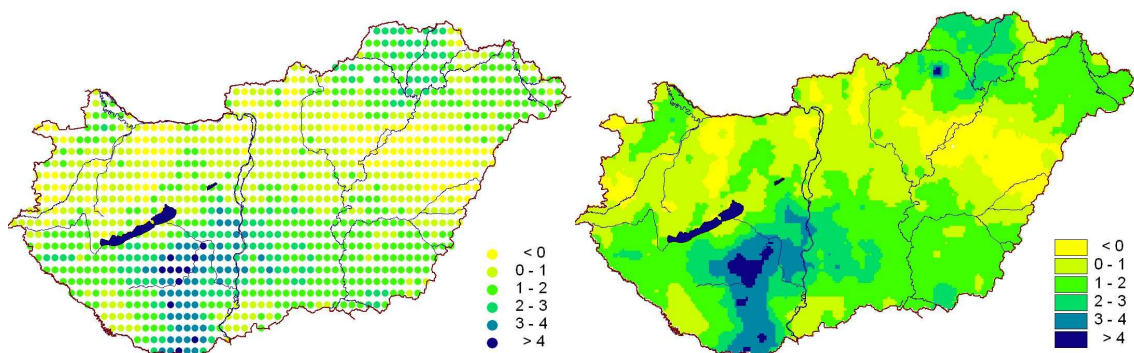in grid points and smoothed*

*Figure 4. Change in the number of days with precipitation sum >20 mm 1976-2005,
in grid points and smoothed*

The changes since 1976 in Hungary are substantial, because the warming tendencies came forward parallel to the last most intense global temperature increase In thirty years the number of summer days increased STRONGLY, except in the mountainous area. Especially high values of increase of over 20 days were calculated for the central parts of the Lowlands (Kiskúnság, Nagykúnság) the changes in rain intensity are shown in *Figure 4*. In the South Transdanubian region more days with heavy rain were registered. The other region of increasing rain intensity is the Sajó and Tisza River flood risk triangle.

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Die Natur als Ingenieur,
oder welche Grössen können Bäume haben?

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Zusammenfassung – Die Auswertung der entsprechenden Abmessungen von verschiedenen Bäumen zeigt eindeutig, dass in dem Aufbau von Bäumen die Naturgesetze in voller Wirkung entdeckt werden können. Der maximale Schlankheitsgrad (Höhe/Durchmesser) der Bäume hängt sehr streng von der Höhe ab. Der schlanke Weizenstengel hat einen großen Schlankheitsgrad von 250, die 100 m hohe Douglasie besitzt dagegen nur noch 26 und, wenn es einen 500 m hohen Baum gäbe, müsste der Durchmesser mindestens 40 m sein bei einem Schlankheitsgrad von nur 12,5! Die technische Mechanik, die auf den Naturgesetzen ruht, unterstützt voll die in der Natur vorhandenen Gesetzmäßigkeiten.

Schließlich muss man eindeutig betonen, dass eine einfache lineare Vergrößerung der Ausmasse der Bäume oder andere Objekte, wie es von Laien immer wieder hervorgebracht wird, jeder wissenschaftlichen Grundlage entbehrt.

Summary – The nature as engineer; which sizes can tree attain? The analysis of proportions of tree boles clearly shows that the overall build-up of trees satisfies the general laws of Nature. The maximum slenderness ratio (height/diameter) of trees is strongly dependent on their height. The slender wheat culm has a very high slenderness ratio of 250, at the same time, the tallest Douglas fir of 100 m height reaches only a value of 26. If a tree would achieve a height of 500 m, its diameter would measure at least 40 m and its slenderness ratio would be only 12.5.

The general relationships of engineering mechanics demonstrate that the observed regularities of selected tree sizes fully correspond to rules of Nature.

Finally, it should be stressed that a simple linear magnification of dimensions of trees of other objects, as often proposed by laymen, is lacking any scientific justification.

PROBLEMSTELLUNG

Bei näherer Beobachtung in der Pflanzenwelt zeigen sich interessante Details hinsichtlich des Körperaufbaus. Als Beispiel nehmen wir einen Weizenstengel, dessen Höhe rund 1,0 m ist, aber der Stängel kommt nur mit 4,0 mm Durchmesser aus. Das Verhältnis Höhe/Durchmesser hat einen phantastischen Wert von 250! Auf Grund dieses Beispiels ist es oft zu hören, dass der Mensch einen Turm mit ähnlichem Schlankheitsgrad kaum bauen könnte. Diese Feststellung ist natürlich in jeder Hinsicht voll begründet. Man sollte aber dabei unbedingt fragen, ob die Pflanzen diesen Schlankheitsgrad unabhängig von der Höhe erzielen können? Höchstwahrscheinlich nicht!

Um diese Frage zu beantworten, wenden wir uns erst an die Natur. Der Bambus hat einen dem Weizenstengel recht ähnlichen Aufbau, aber ist eine Grössenordnung höher. Seine typische Abmessungen sind eine Höhe von 10 m und ein Durchmesser von 12 cm (H/d = 84). Die nächste Höhenstufe sei die Welthöchste Douglasie in dem riesigen Coos County Forest, in Oregon, dessen Höhe haargenau 100 m ist, er kommt aber mit einem Durchmesser von 3,8 m aus (H/d = 26).

Die obigen Grössen können dazu angewendet werden, um einen Zusammenhang zwischen Schlankheitsgrad (Höhe/Durchmesser) und Höhe zu finden. Dieser Zusammenhang ist in *Abb. 1* dargestellt und lässt sich in der nachstehenden Form ausdrücken

$$\frac{H}{d} = \frac{Konst.}{\sqrt{H}} \tag{1}$$

wo H die Höhe der Pflanze in m, d den Stammdurchmesser bedeuten und die Konstante einen Wert von rund 250 hat.

Aus Gl. (1) kann der minimale Durchmesser für eine bestimmte Höhe berechnet werden:

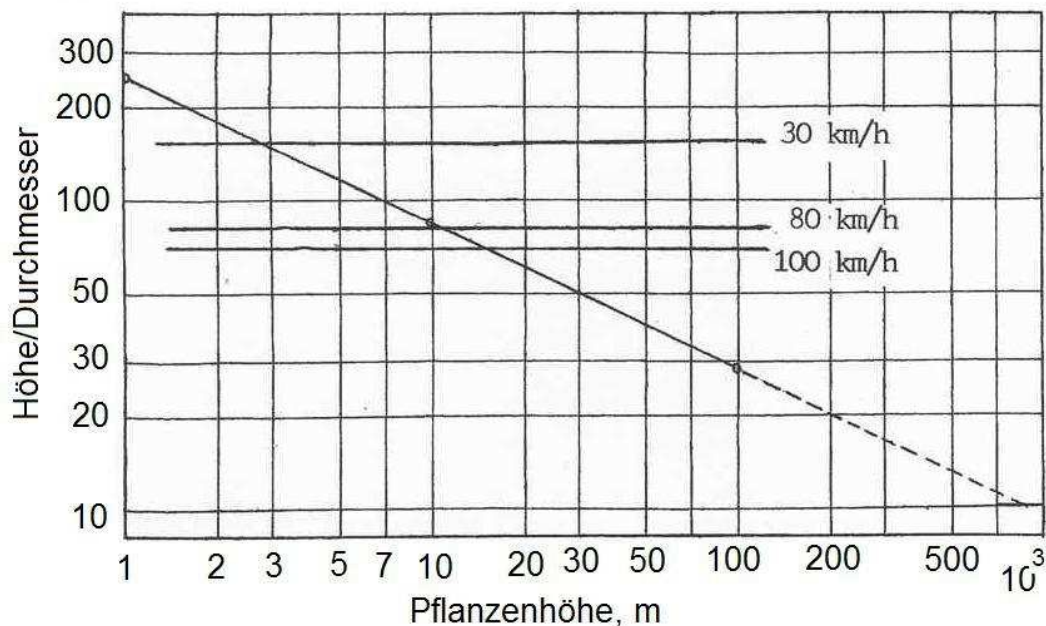$$d_{min} = \frac{H^{1,5}}{250} \tag{1a}$$

Abb.1. Naturgesetz für mögliche Schlankheitsgrade der Pflanzen, sowie
kritische Schlankheitsgrade für einzelne Windgeschwindigkeiten (s. Text)

Aus der Abbildung kann man eindeutig feststellen, dass der Schlankheitsgrad der Pflanzen sich nach der erzielten Höhe richtet.

Es soll hier noch erwähnt werden, dass die hier gezeigten Schlankheitsgrade als Maximalwerte zu betrachten sind. Viele Bäume haben geringere Höhen im Verhältnis zu ihrem Stammdurchmesser aus verschiedenen Gründen, wie z.B. genetische Eigenschaften, geringere Stammfestigkeit (z.B. bei *Adansonia digitata*), Windbruch, Lebensalter, usw.

Und was sagt die Mechanik dazu?

Wir betrachten den Stamm eines Baumes wie einen zylindrischen Körper mit einem Durchmesser *d* und mit einer Höhe *H*. Die Kraft, die den Stamm belastet, stammt aus dem Eigengewicht:

$$G = \gamma \frac{d^2 \pi}{4} H$$

und damit ergibt sich die grösste Druckspannung als

$$\sigma_{dr} = G/Q = \gamma H \tag{2}$$

wo *γ* das spezifische Gewicht des Stammes und *Q* den Stammquerschnitt bedeuten.

Es ist interessant zu bemerken, dass theoretisch ein Baum mit 1000 m Höhe gemäss Gl. (2) ohne weiteres stehen könnte.

Hohe und schlanke Objekte, wie Obelisken, haben aber immer Stabilitätsprobleme. Die kritische Bruchkraft errechnet sich wie folgt (Eulersche Gleichung):

$$P_{kr} = Konst. \frac{E\,I}{H^2} \quad\text{und}\quad I = \frac{d^4 \pi}{64}$$

und diese Kraft dividiert durch den Stammquerschnitt *F* gibt die kritische Spannung

$$\sigma_{kr} = Konst.\, E\, (d/H)^2$$

wo *E* den Elastizitätsmodul des Stammes bedeutet.

Eine Umordnung der obigen Gleichung ergibt

$$H/d = Konst. \sqrt{E/\sigma_{kr}}$$

Gemäss Gl. (2) ist die Beanspruchung (Spannung) proportional mit der Höhe H, deshalb können wir die obige Gleichung modifizieren

$$H/d = Konst. \sqrt{E/H}$$

oder, wenn wir den Elastizitätsmodul auch als Konstante betrachten, kann schliesslich die obige Gleichung wie folgt geschrieben werden:

$$\frac{H}{d} = \frac{Konst.}{\sqrt{H}} \tag{3}$$

Gl. (3) stimmt mit der von der Natur erhaltenen Gleichung genau überein.

Der theoretische Wert der Konstante in Gl. (3) ist 608 (das untere Ende eingespannt, das obere frei). In der technischen Welt benutzt man immer Sicherheitsfaktoren, um unerwarteten Beanspruchungen gerecht zu werden. In der Natur kommen solche zusätzliche Beanspruchungen wie Wind- und Schneebelastung auch oft vor, und es liegt auf der Hand, dass auch die Natur mit einem Sicherheitsfaktor rechnet. Der Sicherheitsfaktor ergibt sich

durch Dividieren der von der Natur benutzten Konstante mit der theoretischen Konstante, d.h. 608/250 = 2,43. Für einen Ingenieur ist dieser Sicherheitsfaktor vollständig annehmbar.

Auf Grund der Eulerschen Gleichung kann man eine dimensionslose Ähnlichkeitszahl für die Bäume angeben

$$\sqrt{\frac{\gamma}{E}}\frac{H^{1,5}}{d} = konstant \tag{4}$$

Der mittlere Wert für $\sqrt{\gamma/E}$ ist $6,45 \cdot 10^{-4}$ und damit hat die Konstante den Wert von 0,161 (wenn man die Einheiten Newton und Meter benutzt). Gl. (4) sagt aus, dass jene Bäume, die eine gleiche Ähnlichkeitszahl haben, die gleiche Standsicherheit besitzen.

Die häufigste Beanspruchung der Bäume stammt aus der Windbelastung. Das Biegemoment ergibt sich als das Produkt der Windkraft (Staudruck) und ihrer Angreifshöhe (H^{+}). Die angegriffene Fläche F der Laubkrone wird hier einfachheitshalber abhängig von der Baumhöhe ausgedrückt. Die Breite (B) und die Höhe (h) der Laubkrone werden relativ zur Gesamthöhe angenommen (*Abb. 2*):

$$B = b \cdot H \qquad \text{und} \qquad h = a \cdot H \qquad \text{sowie} \qquad F = a \cdot b \cdot H^{2}$$
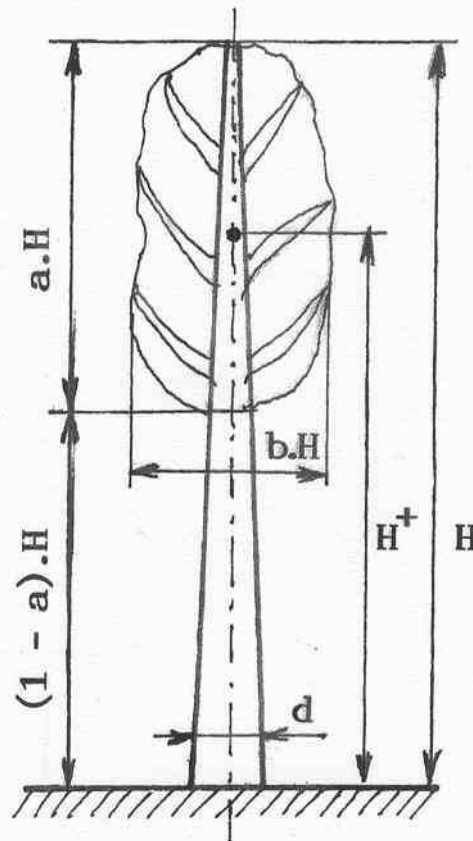

*Abb. 2. Schematische Darstellung der Abmessungen eines Baumes
bezogen auf die verglichen zur Gesamthöhe*

Die astfreie Höhe des Stammes ist damit $(1-a) \cdot H$, während der Schwerpunktsabstand der Laubkrone als $\left(1 - \frac{a}{2}\right) \cdot H$ gegeben ist. Zu den Konstanten a und b soll bemerkt werden, dass sie im Laufe des Wachstums sicher nicht unverändert bleiben. Aus Erfahrung wissen wir

aber, dass grössere und ältere Bäume im geschlossenen Baumbestand meistens eine kleinere Laubkrone haben und damit eine bessere Standsicherheit besitzen.

Die Windkraft errechnet sich aus der Formel

$$F_w = c_w F \frac{\rho}{2} w^2$$

wo c_w – den Luftwiderstandsbeiwert,
           F – die Laubfläche
           ρ – die Luftdichte,
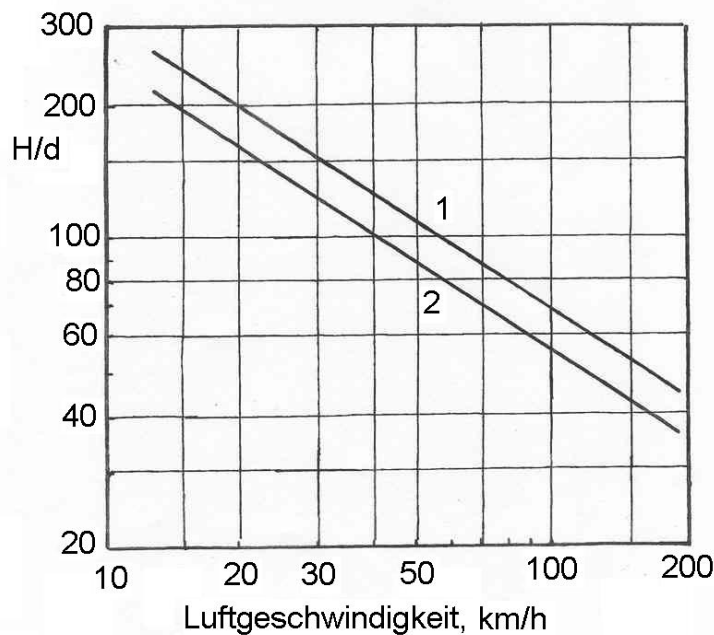   w – die Luftgeschwindigkeit bedeuten.

Abb. 3. Der höchstzulässige Schlankheitsgrad in Abhängigkeit von der Luftgeschwindigkeit für schmale und breitere Laubkrone bei $c_w = 1{,}0$; $a = 0{,}5$; Kurve 1: $b = 0{,}1$; Kurve 2: $b = 0{,}2$

Das erforderliche Widerstandsmoment des Stammes gegen Windbruch errechnet sich wie folgt

$$W = \frac{d^3 \pi}{32} = \frac{F_w H^+}{\sigma_B}$$

Nach Einsetzen der Ausdrücke für F_w und H^+ erhalten wir den folgenden Zusammenhang:

$$\frac{H}{d} = \sqrt[3]{\frac{\pi \sigma_B}{32 c_w a \cdot b \left(1 - \frac{a}{2}\right) \frac{\rho}{2} w^2}} \tag{5}$$

Gl. (5) zeigt eindeutig, dass die Standsicherheit gegen Windbelastung für ähnliche Baumstrukturen unabhängig von der Höhe ist. Mit $c_w = 1$, $a = 0{,}5$, $b = 0{,}1$ und $\sigma_B = 6000$ N/cm^2 erhält man einen kritischen Schlankheitsgrad H/d = 70 bei einer Windgeschwindigkeit von

100 km/h (*Abb. 1.*). Die obigen Zahlen zeigen, dass grössere Bäume einem Windbruch sicherer widerstehen. Unter 10 m Höhe haben die Bäume dagegen einen grösseren Schlankheitsgrad als gegen Windbruch bei 100 km/h erforderlich wäre. Glücklicherweise haben aber die jungen Bäume andere Widerstandsmöglichkeiten. Die dünnen Äste deformieren sich leicht und sie werden sich in die Windrichtung einstellen. Damit verringert sich die Windkraft erheblich. Der extra schlanke Weizenstengel ist dagegen nie standfähig bei 100 km/h Windgeschwindigkeit! Für kleinere Pflanzen ist es weiterhin vom Vorteil, dass die Windgeschwindigkeit in der bodennahen Grenzschicht kontinuierlich abnimmt. Dies bietet eine Chance der Windkraft zu widerstehen. *Abb. 3.* zeigt den höchstzulässigen Schlankheitsgrad abhängig von der Luftgeschwindigkeit für eine schmalere und breitere Laubkrone.

Schließlich muss man eindeutig betonen, dass eine einfache lineare Vergrößerung der Ausmasse der Bäume oder andere Objekte, wie es von Laien immer wieder hervorgebracht wird, jeder wissenschaftlichen Grundlage entbehrt.

Die obigen theoretischen Überlegungen zeigen, dass die Natur „voll wissenschaftlich" arbeitet und keine „überirdischen" Mittel gebraucht, die der Wissenschaft widersprechen. Dabei soll aber die Wissenschaft richtig interpretiert und definiert werden: die Wissenschaft ist die Gesamtheit jener Kenntnisse, die den Naturgesetzen folgen. Diese Definition gehört natürlich zu den strengsten.