THE EFFECTS OF CLIMATE CHANGE ON SPATIOTEMPORAL CHANGES OF HAZELNUT (CORYLUS AVELLANA) CULTIVATION AREAS IN THE BLACK SEA REGION, TURKEY

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Abstract. Turkey ranks the first among the hazelnut producers in the world. The purpose of this study is to question whether or not the hazelnut plant that grows under natural climate conditions will be affected by climate change. Spatial and temporal change simulations have been done in order to define the actual and the future status of hazelnut cultivation areas. The Marmara and the Black Sea regions have been chosen as study areas of hazelnut production in Turkey. The possible evolution of the current climate conditions to affect hazelnut cultivation in the upcoming 90 years and the estimated changes to occur in hazelnut areas have been asserted in the study. In order to determine the future climate conditions, the set of temperature and rainfall data of the upcoming 90 year period (2011 - 2100) obtained from the A2 scenario of RegCM3 regional climate model has been used and by taking the averages of each 10 year period, it has been simulated with the MATLAB software. While an increase of up to 6 ºC in temperature for the upcoming 90 years can be expected to have negative effects on hazelnut cultivation depending on the A2 scenario (the worst), no change has been observed in the rainfall scale that may negatively affect hazelnuts. In particular, it has been observed that this temperature change may cause vertical and horizontal changes in hazelnut areas. Accordingly, it has been anticipated that hazelnut cultivation on the coast line between 0 - 250 m may get affected in a negative way and the areas exceeding 1500 m that are not currently suitable for hazelnut cultivation may become arable lands due to vertical change.

Keywords: *climate change, spatiotemporal change, hazelnut (Corylus avellana), Black Sea Region*

Introduction

The subject of this study is to determine the possible effects of climate change on hazelnut production in Turkey. Climate is a factor closely controlling the formation of geographical environment and living conditions of humans. Agricultural activities constitute one of the most important areas for the adaptation of various human activities with climate change (IPCC, 2007). Among human activities agriculture is the most highly dependent on weather conditions and climate. Climatic conditions have the greatest significance on the cultivation of agricultural products and their productivity (Szenteleki et al., 2012; Gaál et al. 2011; Adams et al., 2001; Atalay, 1994; Mall et al., 2007; Sivakumar et al., 2000; Sivakumar, 2006; Rotter et al., 1998). The variability in temperature especially plays a determining role in the productivity of horticulture (Wheeler et al., 2000, Trnka et al., 2004). For this reason, short and long term variations in weather conditions and climate affect agricultural activities and especially

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agricultural production and cause fluctuations in production (Challinor et al., 2003; Hansen, 2002; Oram, 1989). This situation poses a serious risk for the products that have an economic value in agricultural aspects. Besides type, technical and cultural factors, hazelnut growing is also related to environmental and particularly climatic conditions (Beyhan and Odabaş, 1996). The hazelnut, having found the world's most suitable ecology for its cultivation in the Black Sea Region of Turkey, has a significant share in agricultural economy of Turkey. Turkey ranks the first in hazelnut production and exportation in the world and provides 70% of the world production and about 75 % of the exports. The importance of hazelnut agriculture in Turkey can be better perceived by taking into consideration its share in the total hazelnut production of the world. The average hazelnut exports of Turkey in 2009 and 2010 amounted to 1.5 billion dollars (FTG, 2010). Based on the aforementioned reasons, the hazelnut and the prediction of its potential future production areas arise as an area that deserves attention.

So as to prevent or minimise the effects of climate change, climate change scenarios should be developed for the future and impact analysis should be accomplished according to these scenarios. The climate change shall have effects on a spatiotemporal scale. For the better preparation of countries against the results of climate change and so that they can adapt themselves to this change, determining which sectors in which areas will be affected and to what extent is highly important.

Fruits have a distinctive role in determining the effects of climate change on agricultural production. The areas that are suitable for fruit growing under today's conditions may not have adequate characteristics for cultivation in the future. Besides, as fruits are perennial plants, they need a couple of decades for growing. (Koski, 1996). It takes time to adapt to the changing climate for this reason. Since fruit growing is an agricultural activity with relatively high levels of economic return, it is necessary to implement pilot climate - agriculture projects in the fields where cultivation is the most suitable for the future. The aim here is to model whether the crop will change its geographical location rather than making crop estimations assuming that climate changes will be experienced on a regional basis. The primary thing to do in such studies is to identify the necessary environmental conditions for the cultivation of plants and to adequately model the growing process of the plant under these conditions. It has been observed in the literature search that the studies on annual plants are prevailing. Not a wide number of studies have been conducted on perennial plants up to know. This study will contribute to the literature in both terms of content and methodology for hazelnut being a perennial crop. Being the first study conducted on perennial crops in the field of impact assessment of climate change in Turkey and the first spatiotemporal analysis in terms of past - current - future phases of hazelnuts from the perspective of climate, it will provide a basis for the future studies.

Since the hazelnut is a perennial crop, like other perennial horticultural crops it takes many years to cultivate it in any ecology, to determine its ecologic conditions, to grow and to breed. On the other hand, in the case of any annual crop, while cultivators plant a crop in a field one year, they can plant another type of product in the same field for the next year in case the crop becomes less profitable especially by being affected by climatic conditions. However this situation is not valid for perennial crops. Another critical condition for the hazelnut is that as it is cultivated on sloping fields whose topographic characteristics are not suitable for the planting of annual crops, it is not easily replaceable with some other crop. Therefore it is crucial to take measures against possible climate changes in the future for these kinds of horticultural perennial crops that have a high economic value. The effects of temperature and rainfall are among the climatic parameters having a distinctive role in the natural cultivation conditions of hazelnuts that have been identified in this study.

Study Area and Data

It has been suggested that the hazelnut was cultivated for the first time in Northern Anatolia in the 4th and 3rd centuries (B.C.) (Köksal, 2002). The Black Sea region, the study area where hazelnut agriculture is done at the highest level in terms of area and crop amounts in Turkey, is also located in this area (*Fig. 1*).

Figure 1. *Location map of the study area (Marma ra and Black Sea Region in Turkey)*

The annual average temperature and rainfall data recorded for the period 1930-2009 from 273 meteorological stations located in the Marmara and the Black Sea Regions have been used in the study as meteorology station data from Turkish State Meteorological Service. The temperature and rainfall conditions in Turkey have been investigated according to the agrometeorological requirements of hazelnuts. Accordingly, the areas where the hazelnut has been cultivated for economic purposes in Turkey have been determined statistically (production - hectare). Ordu, Giresun, Trabzon, Samsun, Düzce, and Sakarya in the Black Sea Region are the provinces that have been chosen as the sample areas. The long and common period of (1975 – 2009) annual average temperatures of these provinces have been determined as between 13-16 °C *(Fig. 2)* and the rainfall values have been determined over 700 mm *(Fig. 3)* in accordance with the optimal conditions of hazelnut cultivation. This means that these areas have optimum conditions for hazelnut cultivation statistically.

Temperature and rainfall data of the A2 scenario obtained from RegCM2 climate model have been used as model data. Temperature and rainfall data of this model are in netcdf data format and cover the years 2011 - 2100. They are in 30 km resolution and Turkey scale (Dalfes et al., 2008). NCEP / NCAR reanalysis data were used for the years 1961 - 1990 determined as the reference period (30 years) in the evaluation of the results of the model. In addition, by determining the reanalysis data from the obtained value, the difference in temperature and rainfall possibly to occur in the future is obtained. Temperature and rainfall values have been interpolated by taking into consideration the altitude values in the topography in both station data and model data. 1 km * 1 km Gtopo30 digital elevation model data have been used for this interpolation process (USGS, 2010).

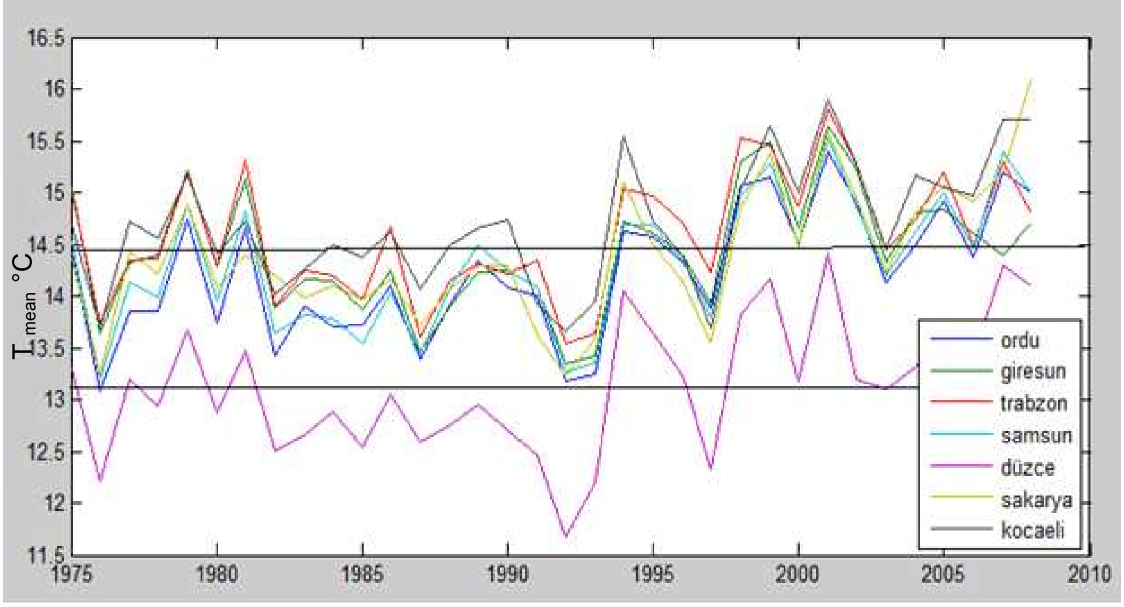

Figure 2. *Annual mean temperature (Tmean°C) of long years term in the study area (1975-2009)*

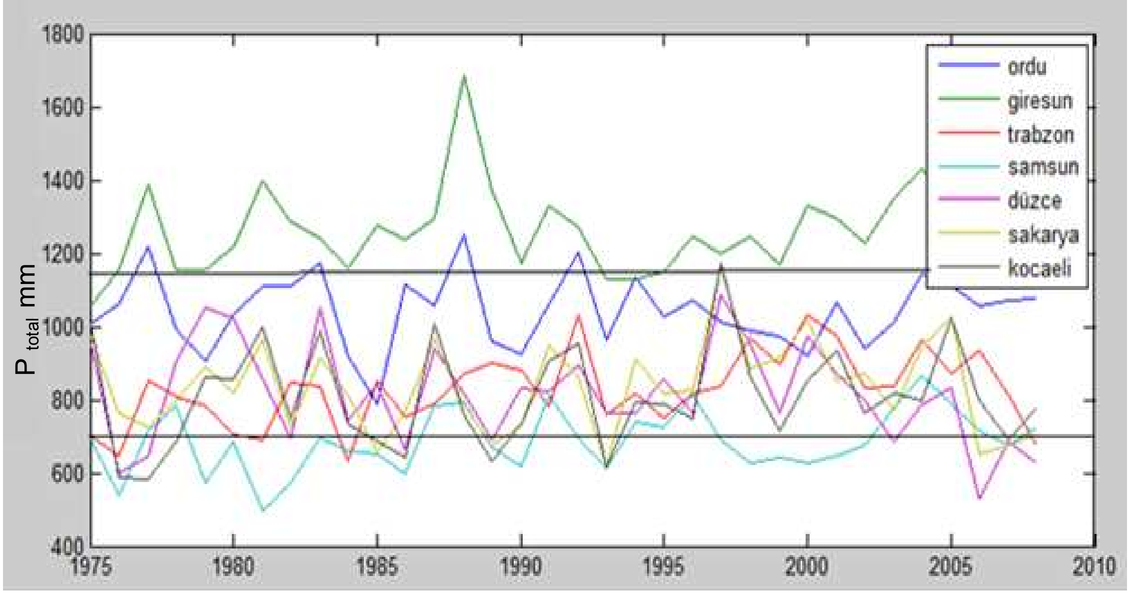

Figure 3*. Annual rainfall (Ptotal mm) of long years term in the study area (1975 - 2009)*

Methodology

The methodology used in the study is comprised of three steps. First of all, the optimal climate conditions of hazelnuts in the study area have been determined.

Secondly, daily climate data of meteorology stations at the study area have been analysed according to the agrometeorological requirements of hazelnuts. Thirdly, the climate data obtained from RegCM3 regional climate model of the A2 climate scenario to be used in the study and the NCEP_NCAR data of the reference period used as reanalysis data have been analysed according to the agrometeorological requirements of hazelnuts. With an aim to estimate the average temperature and rainfall amounts in Turkey in the period between 2011 - 2100, (a) the temperature and rainfall data sets of the determined periods shall be interpolated according to the Gtopo 30 digital elevation model data coordinates (1 * 1 km) and their resolution shall be increased. (b) The topography effect on the temperature and rainfall data of which the resolution has been increased shall be tried to be eliminated through altitude correction. (c) The difference between the temperature and rainfall data obtained from regional climate models and the rainfall data obtained from the reference period shall be accepted as the rate of change. (d) This difference change, by taking the average of each decade, shall be added to the meteorology station data (2011-2020, 2021-2030…2091-2100) and the temperature and rainfall data shall be simulated for the future using MATLAB 7.0 software.

The MATLAB 7.0 software has been used in the analysis and monitoring of the data used in this study. MATLAB is flexible software for analysing multidimensional climate data (Ustaoglu, 2012a). Gtopo30 digital elevation model data have been used to eliminate the topography effect on both station and model data.

Identification of agrometeorological characteristics of hazelnuts

First, it shall be determined statistically whether the study area is suitable for hazelnut cultivation according to specific climate requirements of the hazelnut. For this purpose, the threshold values (limit values) of temperature and rainfall data necessary for hazelnut cultivation in the Black Sea ecology have been extracted from literature and expert opinions. According to these, the hazelnut grows under the most suitable temperature conditions between 13- 16 °C. In terms of rainfall, rain amounts over 700 mm are suitable for hazelnut cultivation without requiring irrigation (Köksal, 2002). Hazelnut trees can be seen on bush layers of the forests up to an altitude of 1500 m (Yaltırık, 1988).

Analysis of station data

In order to determine the past and the current climate conditions at the study area, meteorological data for the period 1930-2007 from 273 stations have been analysed in the MATLAB software. In order to increase the resolution of the annual temperature, rainfall and altitude data of the meteorology stations dispersed over the topography, they have been interpolated with grid data commands and transformed into Gtopo30 (1*1 km) coordinate system. Altitude factor correction has been applied to the obtained temperature and rainfall values of meteorology stations of which resolution has been increased. While lapse rate (0.649) was used for temperature; Equation 1. was used for rainfall for altitude correction.

$$Y_h = Y_0 + 54h \qquad \text{(Eq. 1)}$$

Y_0 means the annual rainfall of the reference station; Y_h means the annual rainfall of the searched station; and h means the altitude difference between the two stations in hectometer (Erinç, 1996).

According to cultivation conditions of hazelnuts, the fields under 1500 m for altitude (*Fig. 4*), the fields having a temperature value between 13°C – 16°C for temperature and the fields receiving rainfall over 700 mm for rainfall have been investigated. By doing this, the long years temperature and rainfall data that have been interpolated and corrected from altitude factor, have been obtained and mapped.

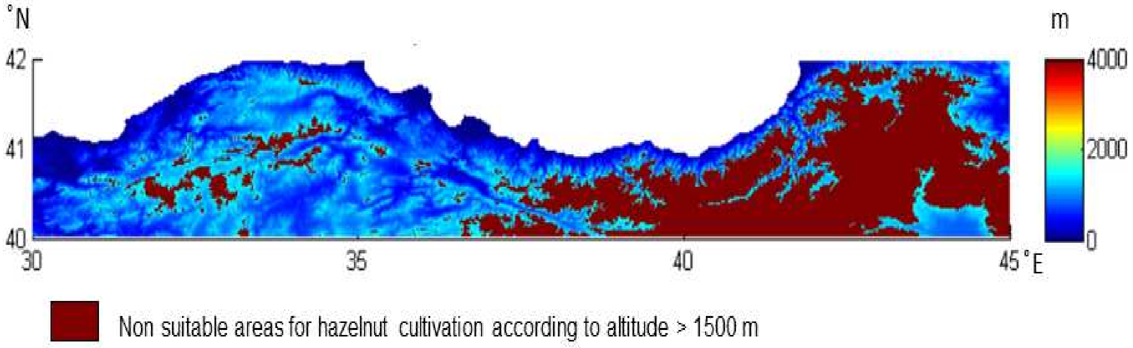

Figure 4. *The upper limit of hazelnut cultivation areas with a low level of 1500 metres altitude.*

Analysis of the model data

The global climate models used in climate simulations for the future have low resolutions (150-200 km) and they do not have any regional features. For this reason, a regional climate model that has a higher spatial resolution value (30 * 30 km) has been used in this study to gather more accurate results on the topography. Regional climate models as one of the dynamic downscaling methods are successfully used for this purpose. These models get their start and limit conditions from global model outputs and can be operated in higher resolutions (20-30 km) where the topographic features are also reflected (Demir et al., 2007). But the topography in Turkey shows a high level of diversity. For this reason, while this resolution is adequate on the shores and in areas at lower altitudes, the spatial resolution is hard to control in the highlands (Tubiello et al., 2002, Huntingford et al., 2005). To this end, the temperature and rainfall data sets have been interpolated with the linear interpolation method and their resolution has been increased in this study and altitude correction has been applied on the rainfall data set. The precision of the data has been increased in this way.

To do this, the temperature, rainfall and altitude values of long term average (1930 - 2007) of the temperature and rainfall data, gathered from 273 meteorology stations that are operated by General Directorate of State Meteorology and have different observation dates, have been interpolated with the linear interpolation method and have been mapped by correcting the altitude. As the interpolation will be made with the linear interpolation method in the analysis of the temperature and the rainfall data, numerous station data are necessary to obtain accurate results on the topography. For this reason, a common observation period has not been defined for the meteorology stations used in this study (Ustaoglu, 2012b).

The temperature and rainfall data obtained from the RegCM3 regional climate model have been systematically organised and monitored in the MATLAB software. The gridded temperature, rainfall and model altitude data of the A2 scenario have been transformed into the Gtopo30 (1*1 km) coordinate system and have been interpolated to increase the resolution. Altitude factor correction has been applied on the temperature and rainfall values of which resolution has been increased. To do this, Gtopo30 altitude has been determined from the altitude data of the model of which resolution has been increased and has been multiplied with temperature (0.649) and rainfall (-54) coefficients and added to the temperature and rainfall of the model. NCEP / NCAR reanalysis data for the period 1961–1990 that was determined as the reference period have been used in the evaluation of the results obtained from the model (Dalfes et al. 2008). In addition, by determining the reanalysis data from the value obtained from the model, the possible difference in temperature and rainfall in the future has been obtained. Consequently, the temperature and rainfall data of the A2 scenario have been monitored by taking their annual averages per decade (2011 – 2020), (2021 – 2030)…. (2091 – 2100). The obtained values have been added to the station data and the future temperature and rainfall conditions of the hazelnut cultivation areas have been investigated.

Results

According to the simulation results of pessimistic scenario A2, the increase in temperature values for the upcoming 90 year period divided into decades has been determined as approximately 6 °C in Turkey *(Figs. 5a-5b).* This situation means more heating and exceeding the growing limit (13 - 16 °C) of the hazelnut cultivation areas according to the optimal temperature conditions of today. Thus, it has been predicted that a vertical zone shift will occur depending on the decrease in temperature with altitudes in hazelnut cultivation areas.

The results have shown that the changes to occur in the rainfall amounts of 2011-2100 at the study area tend to increase when compared to the rainfall amounts of today *(Figs. 6a-6b).* This condition shall have a positive effect on hazelnut cultivation as it exceeds 700 mm which is the minimum cultivation limit for hazelnuts on the whole of the study area. This increase is more significant especially in the Eastern Black Sea Region located in the east of the study area where hazelnut cultivation is intensive *(Figs. 6a-6b).* As a result, it has been detected that the changes in the temperature values between 2011–2100 are more significant compared to the rainfall values. This situation is more obvious in the maps drawn separately by adding the differences from the reference period to the A2 scenario according to the temperature and rainfall requirements of hazelnuts and also altitude conditions *(Figs.7a-7b).* Particularly after 2050, it has been seen that horizontal changes (shift from north to south) occur in hazelnut production areas according to climate change *(Figs. 5a-5b, Figs. 7a.-7b.).*

Conclusions

In this study, spatiotemporal change simulations have been made in order to define the actual and the future position of hazelnut production fields. The effects of climate change shall show differences in temporal and spatial scales. Based on the suggestion that climate changes will be experienced on a regional basis, the aim here is to model whether or not the product will change its geographical location rather than making crop estimations.

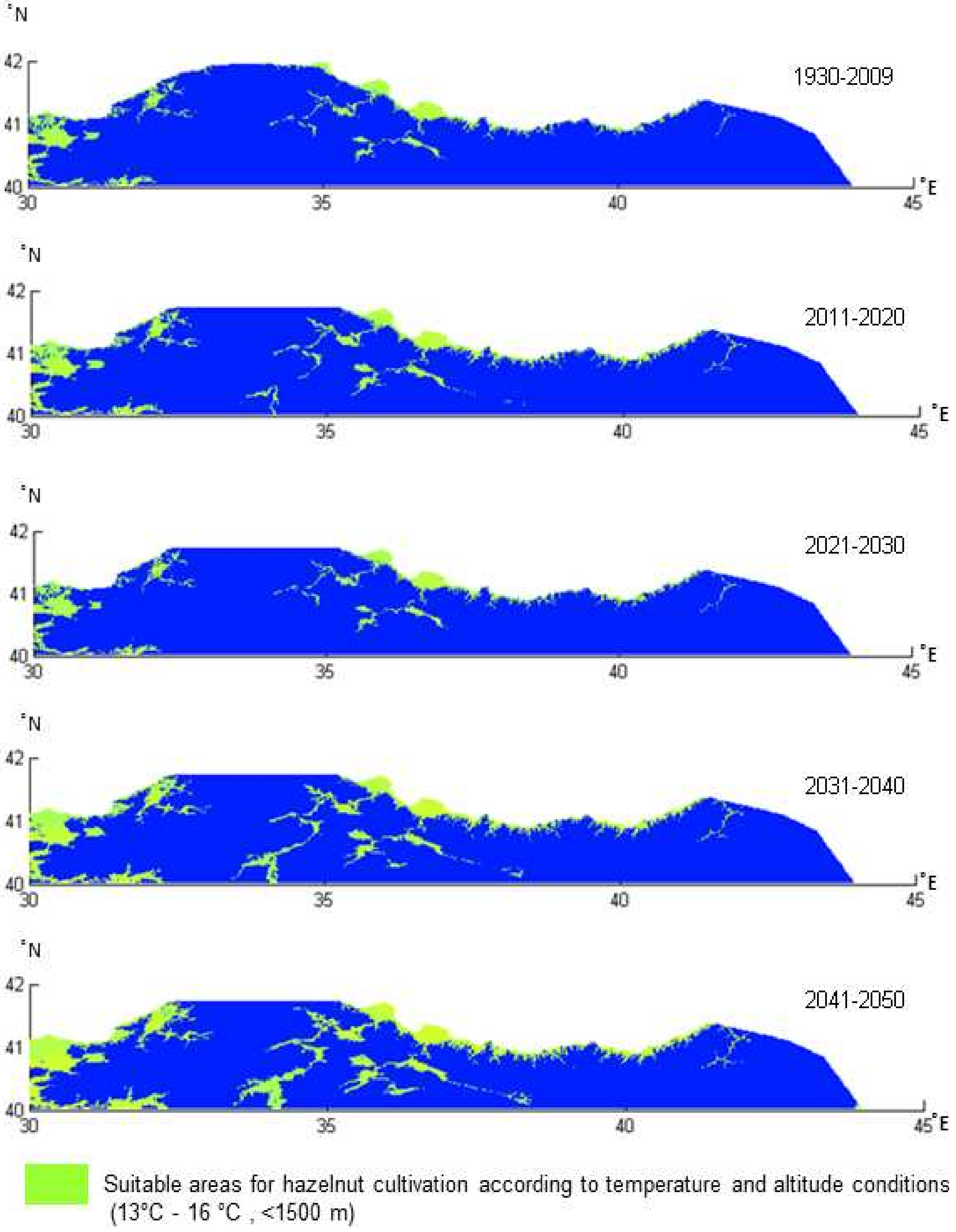

***Figure 5a**. Average temperatures (°C) and altitude conditions of potential hazelnut production areas (13 – 16 °C and < 1500 m.) in Turkey according to the long term years average meteorological stations temperature data (1930 - 2009); average temperatures (°C) and altitude conditions of possible hazelnut production areas (13 – 16 °C and < 1500 m.) in Turkey according to A2 scenario between 2011 - 2020, 2021 - 2030, 2031 - 2040, 2041 -2050.*

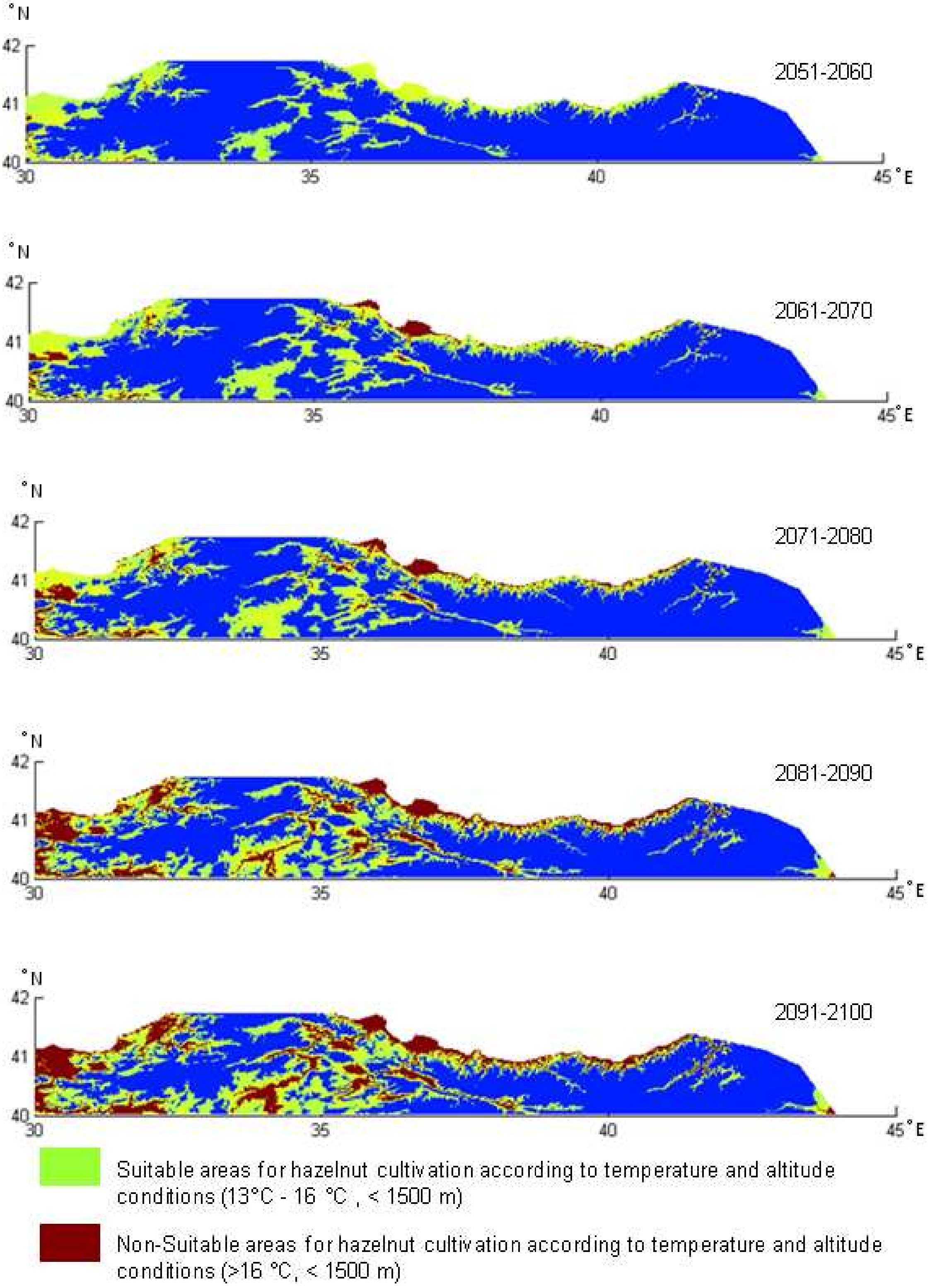

Figure 5b. *Average temperatures (°C) and altitude conditions of possible hazelnut production areas (> 16 °C and < 1500 m.) in Turkey according to A2 scenario between 2051 - 2060, 2061 - 2070, 2071 - 2080, 2081 - 2090, 2091 - 2100.*

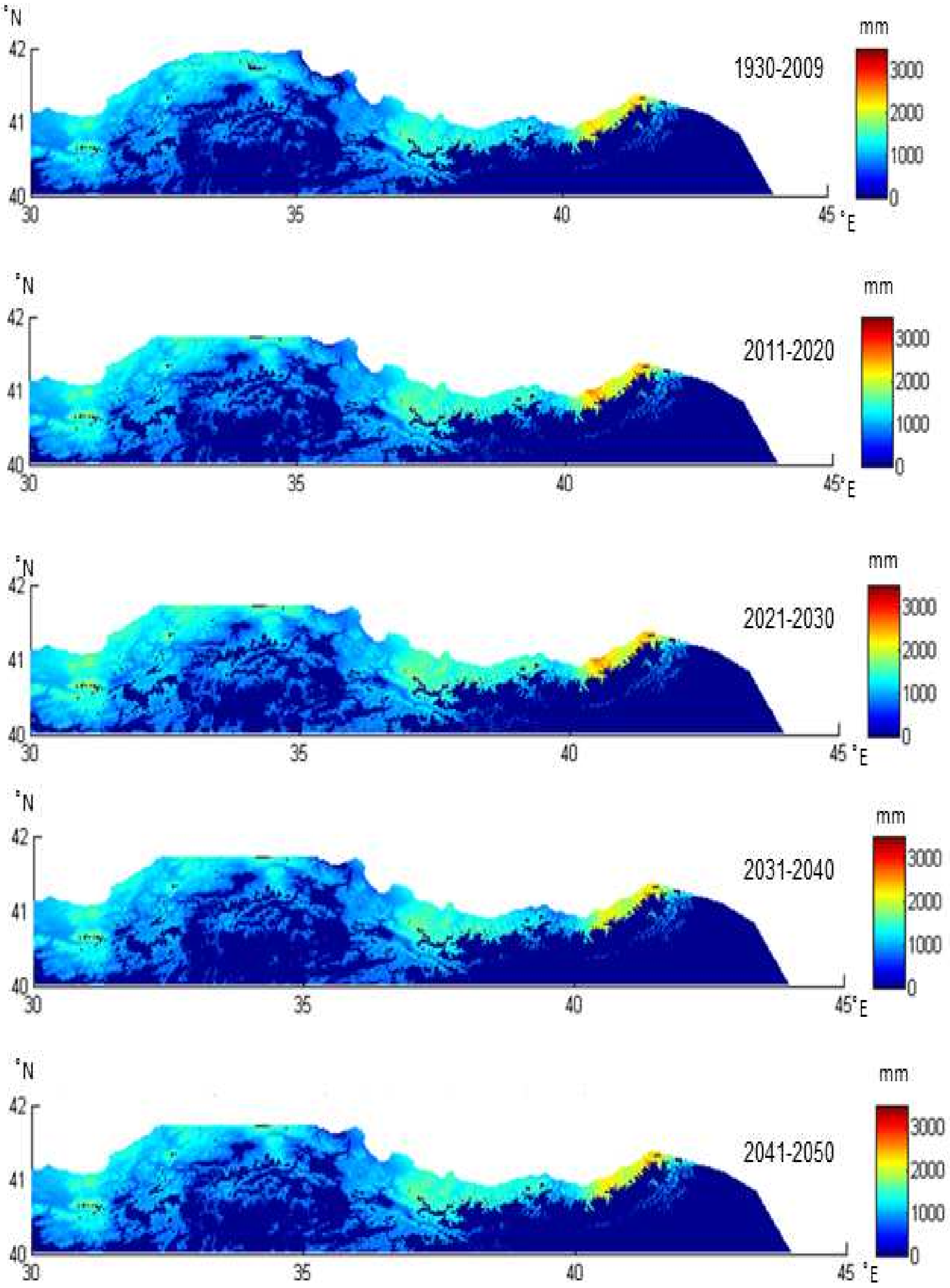

Figure 6a. *Annual rainfall (mm) and altitude conditions of potential hazelnut production areas (> 700 mm and < 1500 m.) in Turkey according to the long term years average meteorological stations temperature data (1930 - 2009); Annual rainfall (mm) and altitude conditions of possible hazelnut production areas (> 700 mm and < 1500 m) in Turkey according to A2 scenario between 2011 - 2020, 2021 - 2030, 2031 - 2040, 2041 -2050.*

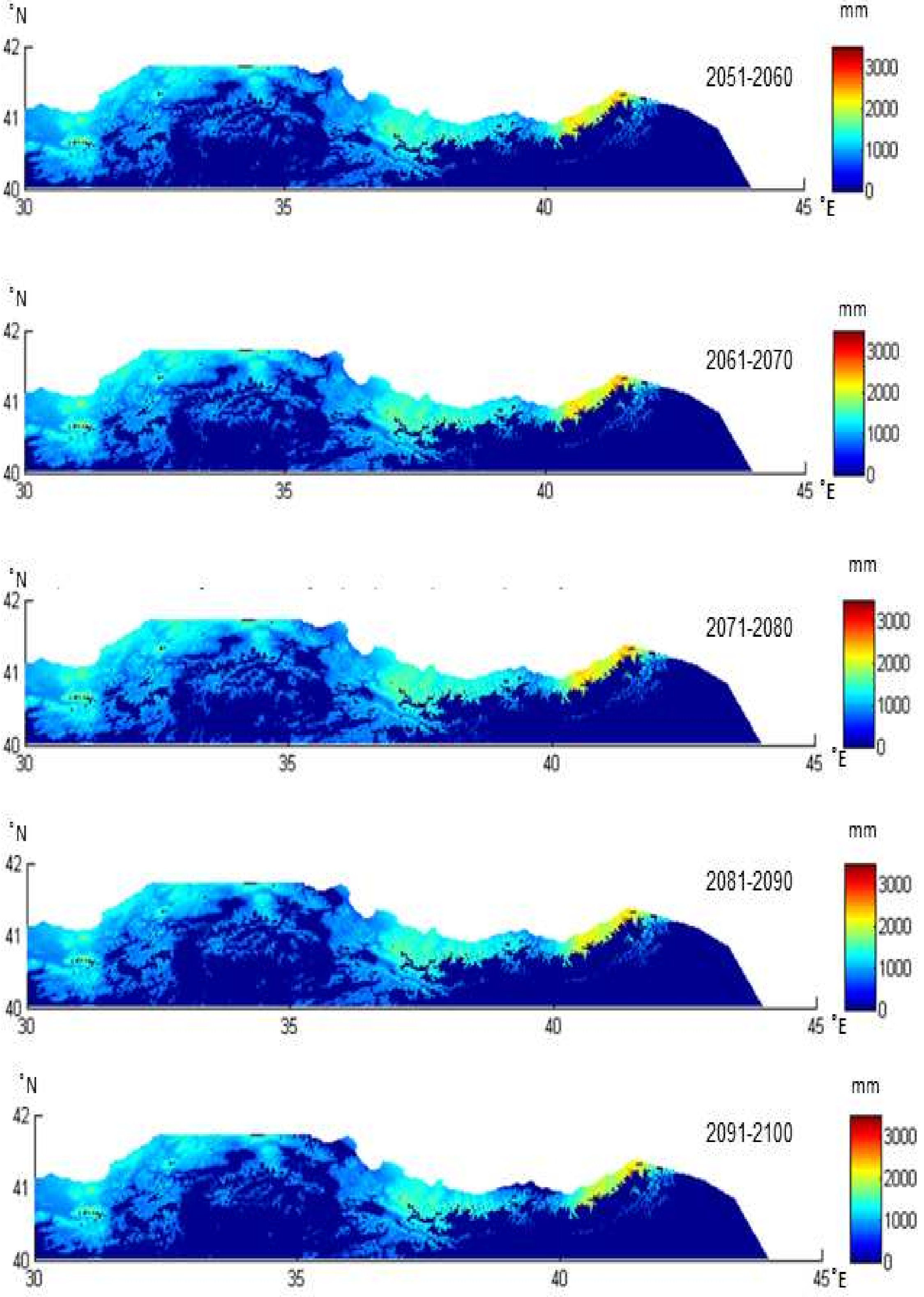

Figure 6b*. Annual rainfall (mm) and altitude conditions of possible hazelnut production areas (> 700 mm and < 1500 m.) in Turkey according to A2 scenario between 2051 - 2060, 2061 - 2070, 2071 - 2080, 2081 - 2090, 2091 - 2100.*

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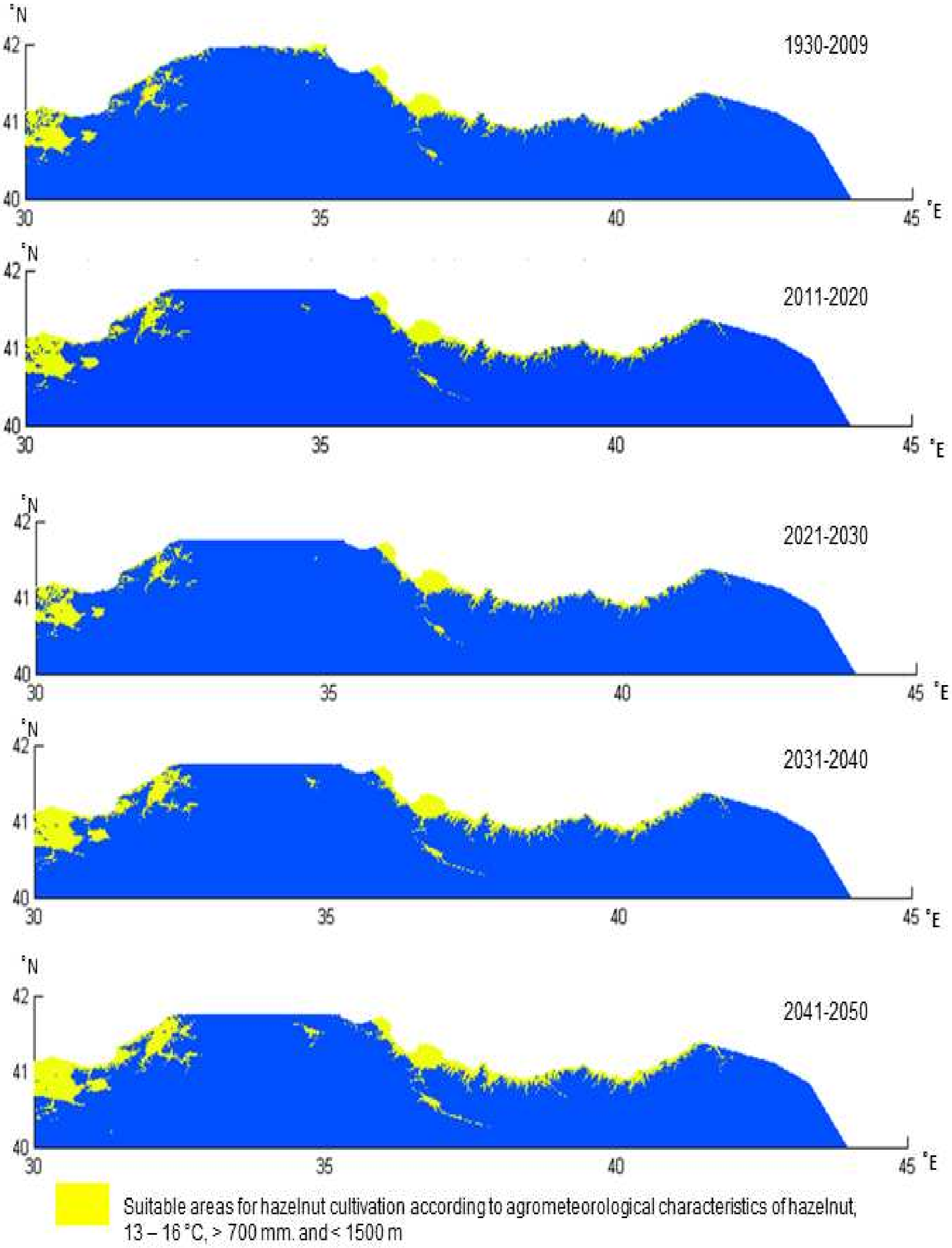

Figure 7a. *Average temperatures (°C) annual (mm) and altitude conditions of potential hazelnut production areas (13 – 16 °C, > 700 mm. and < 1500 m.) in Turkey according to the long term years average meteorological stations temperature data (1930 - 2009); average temperatures (°C) annual rainfall (mm) and altitude conditions of possible hazelnut production areas (13 – 16 °C, > 700 mm. and < 1500 m.) in Turkey according to A2 scenario between 2011 - 2020, 2021 - 2030, 2031 - 2040, 2041 -2050.*

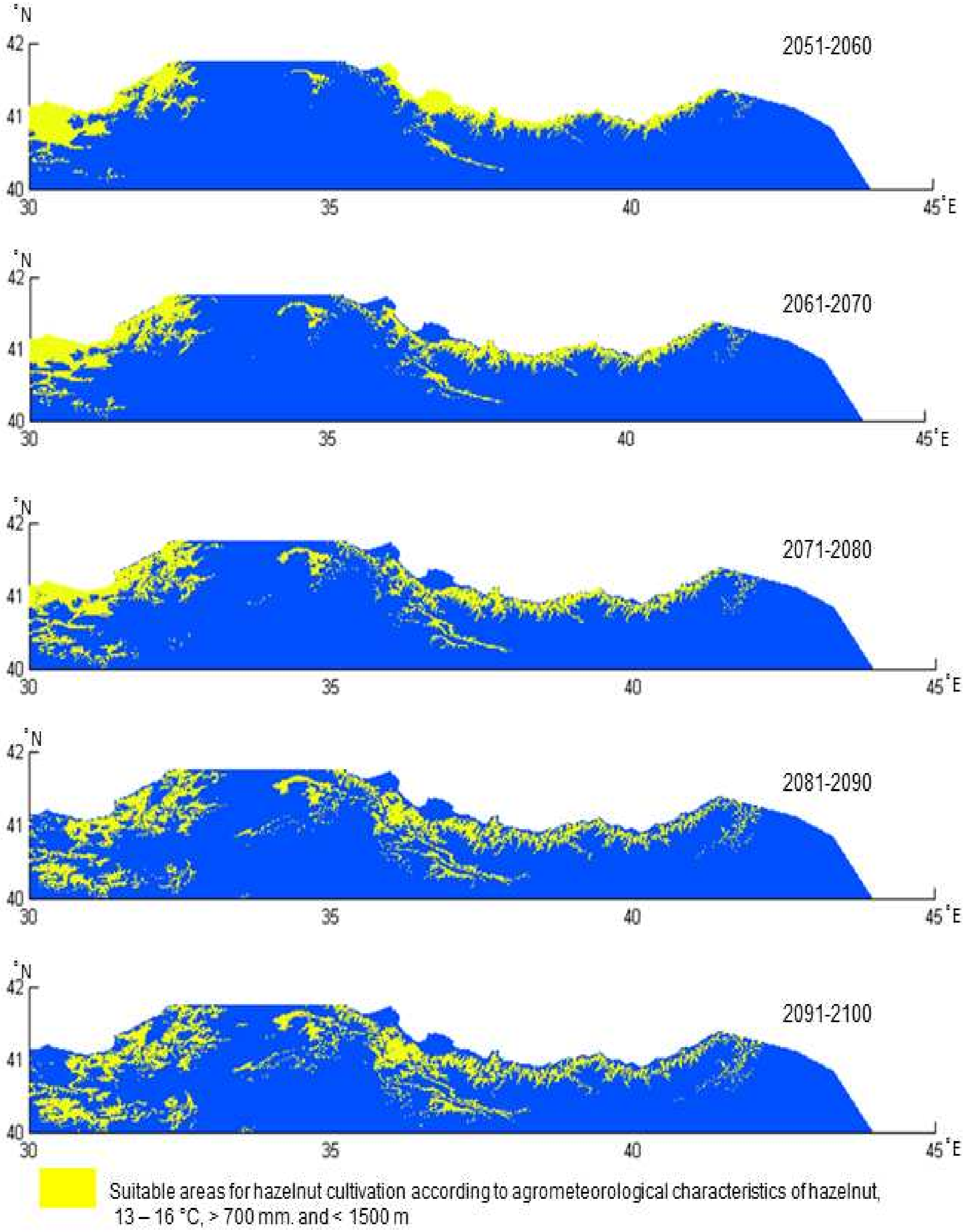

***Figure 7b**. Average temperatures (°C) annual rainfall (mm) and altitude conditions of possible hazelnut production areas (13 – 16 °C, > 700 mm. and < 1500 m.) in Turkey according to A2 scenario between in Turkey between 2051 - 2060, 2061 - 2070, 2071 - 2080, 2081 - 2090, 2091 - 2100.*

Taking A2 as the basis among the global climate change scenarios, the future hazelnut cultivation areas in Turkey have been investigated in 10 year periods with simulations to estimate the spatiotemporal change. According to the results of the simulation, it has been detected that the change in temperature values between 2011 - 2100 will be more significant when compared to the rainfall. Accordingly, an up to 6 ºC increase in the average temperature has been detected for the upcoming 90 years in the region. It has been estimated that the change in temperature conditions may cause a vertical and horizontal change in hazelnut cultivation areas. Especially the increasing temperature values may have a negative effect on hazelnut cultivation activities on the coast line between 0 - 250 m. A horizontal change has been seen particularly from coast to inland. On the other hand, the areas exceeding 1500 m that are not currently suitable for hazelnut cultivation may become arable lands due to vertical change. The possible need of cultivators for new hazelnut cultivation areas due to the climate change may result in deforestation of forested lands. Due to increasing temperature values on the coastal zone of the region, it is necessary to start developing alternative crops suitable for warmer conditions and introducing them to farmers. This should be considered especially on the coast line which has a dense population. If such operations are delayed until later, the effects of climate change on hazelnut cultivation which is the most significant crop and the most important income source of the region will bring along new socioeconomic problems.

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DEAD TREES IN BEECH STANDS OF THE BIESZCZADY NATIONAL PARK: QUANTITATIVE AND QUALITATIVE STRUCTURE OF ASSOCIATED MACROFUNGI

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Abstract. The quantitative and qualitative structure of dead standing trees and coarse woody debris as well as the occurrence of associated macrofungi were analysed in beech stands of the Bieszczady National Park. On average, 55.55 m^3/ha of dead wood, of which 64% was coarse woody debris, was found in three study plots. Elevation above sea level and distance from the upper treeline had a significant impact on the quantitative and qualitative structure of dead trees in the stand. When approaching the upper treeline, the thickness of the coarse woody debris decreased, and the share of the dead standing trees increased. Similarly, the type of dead tree distribution in the study area changed from random in the lowermost stand, to regular in the middle range of elevation above sea level, and to clustered in the uppermost plot. The majority of coarse woody debris was in the II and IV degrees of decomposition, whereas dead standing trees were usually in the 4th stage of decomposition. A total of 30 species of macromycete fungi were recorded, including 4 from the list of endangered species. Tinder fungus (*Fomes fomentarius* (L.) Fr.) was the most frequently observed species. It was shown that the species diversity of fungi is closely associated with the quality of dead trees. Most fungal taxa were recorded on coarse woody debris in the IV degree of decomposition and on dead standing trees in the 3rd stage of decomposition.

Keywords: *dead standing trees, coarse woody debris, beech forests, forest stand structure, spatial trees' distribution, Macromycetes*

Introduction

Leaving dead trees in the forest is crucial for biodiversity conservation in forest biocenoses. Numerous authors (Piotrowski and Wołk 1975, Stevens 1997, Solon and Wolski 2002, Gutowski et al. 2004, Christensen et al. 2005, Pasierbek et al. 2007) clearly demonstrate the beneficial effects of the presence of dead wood in forest ecosystems on plant species diversity. Dead trees are the habitat for many rare and protected fungal species (Piltaver et al. 2002, Heilmann-Clausen and Christensen 2003, Nordén et al. 2004, Ódor et al. 2006, Holeksa and Maciejewski 2009, Pouska et al. 2010). Additionally, vertebrates usually use dead trees for shelter, as places for reproduction and the acquisition of food, and as a construction material (Solon and Wolski 2002, Gutowski et al. 2004, Gutowski 2006). Despite the key role of dead trees in biodiversity preservation in forests and the awareness that it is necessary to leave them in the stand, this issue is still disputed. In protected areas of mostly non-production function such as national parks, natural succession and the accumulation of large amounts of dead matter are generally acceptable phenomena (Przybylska et al. 1996, Pasierbek et al. 2007). In contrast, the presence of dead trees in managed stands is

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reasonable only in the absence of threats from cambio- and xylophagous insects, forest fire hazard or obstacles in conducting breeding work.

The issue of the role of dead trees in protected Polish forest ecosystems has been rather well elucidated in Białowieża National Park (BNP) (Kirby et al. 1991; Solon and Wolski 2002, Gutowski et al. 2004). In other countries, this issue has been studied mainly by Kirby et al. (1998) in Great Britain, Krankina et al. (2002) in Russia, Nilsson et al. (2003) and Ekbom et al. (2006) in Scandinavia, Jankovský et al. (2004b) in the Czech Republic, Winter et al. (2005) in Germany, and Kraigher et al. (2002) in Slovenia. The majority of references cited mainly refer to the quantity, not the quality, of dead biomass remaining in forests. However, the form and degree of decomposition of the woody material are key elements in terms of biodiversity. In view of the above, effort was made to analyse the quantitative and qualitative shares of the spatial distribution of and the macrofungal diversity associated with coarse woody debris and dead standing trees in selected beech stands of Bieszczady National Park (BdNP), which has the largest share of forest and strictly protected area of all the national parks in Poland (Winnicki and Zemanek 2003).

Study area

The research was conducted in beech stands of the BdNP, in three rectangular 0.10-hectare (transect 20 m x 50 m) plots on the mountainside of Rozsypaniec (49°3' N; 22°45' E) (*fig. 1*). The locations of the transects were chosen to constitute a gradient in elevation. The centre of the first plot was located at 1035 m above sea level, the second at 1091 m, and the third at 1146 m. The study plots have a westerly aspect and were characterised by ground slope from 18 to 30°. The plots represent fresh montane forest habitat, with fertile mountain beech forest prevailing (Dentario glandulosae-Fagetum community). The inventoried beech stands were in the optimal stage and were multi-storeyed. The conservation status of the study areas has preserved the original character of the examined stands.

Material and methods

Dead trees were inventoried in each of the study plots in August 2011. Their size, form, quantity, degree of decomposition and spatial distribution in the stand were recorded. Additionally, their associated fungi were determined to species level. When possible, fungi were identified in the field based on their fruiting bodies. Macromycetes that were not successfully identified in the field were subject to identification in the laboratory with the use of a STUDAR M microscope and fungal identification manuals (Breitenbach and Kränzlin 1986, Beran 2004). The systematics of macrofungi are given after Cooper and Kirk (2012).

Dead trees were classified into the following groups: (1) dead lying trees (both lying trees, logs and fragments thereof at least 1 m long and with a diameter greater than or equal to 10.00 cm on the thinner end), (2) dead standing trees, i.e., standing declining trees and snags of broken trees with a height over 1.30 m and diameter at halfheight greater than or equal to 5.00 cm and (3) stumps not higher than 1.30 m and with a base diameter greater than or equal to 10.00 cm. The degree or stage of decomposition was determined for each item of dead wood, using the classification of Maser et al. (1979) as modified by Bobiec et al. (2005). The degrees of decomposition in woody debris were described by Roman numerals and Arabic numerals referred to stages of decomposition in standing trees. Four stages of decomposition were distinguished in still-standing trees, and the coarse woody debris was evaluated using five degrees of decomposition (*tab. 1*). During the inventory of stumps, their height and diameter at the base was measured. For coarse woody debris, *i.e.,* declining and broken trees, the height and thickness of the logs was measured at their halfheight. Halfheight-diameter measurements of lying trees were conducted only for the first three degrees of decomposition (1 - 3), whereas the length of coarse woody debris was measured for all distinguished degrees of decomposition. Diameter measurements were not performed on dead lying trees classified with degrees 4 and 5 of decomposition due to the flattening of their cross-section and fragmentation. There were 9 such trees in plot 1, and in plots 2 and 3, there were 7 and 6 cases, respectively. At the same time, living trees with diameter at breast height greater than or equal to 5 cm were measured at each study plot. Diameter at breast height and height were measured for the trees that met the above criteria. The diameter of trees was measured with a circumeter with an accuracy of 0.1 cm, and the height was determined with a Sunto altimeter, rounding the values to 0.1 m. The share of trees at the study plots in various degrees of decomposition was calculated on the basis of length, with reference to the sum of the lengths of all pieces of coarse woody debris in each stage of decomposition. Coarse woody debris in which a great diversity of decomposition stages in different parts was observed was assigned the predominant degree of decomposition. However, when verifying the share of particular

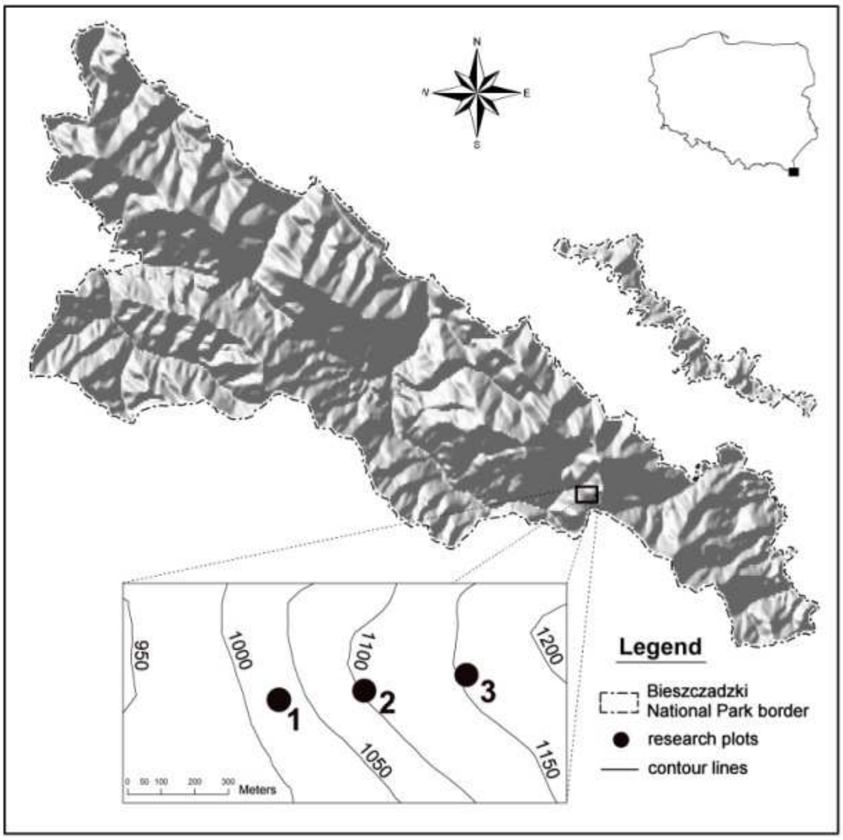

Figure 1. *The location of the study area in the topography at the Bieszczady National Park*

degrees of decomposition of standing trees, their thickness was taken into consideration. The thickness of dead trees was evaluated for all standing trees, and in coarse woody debris, only for trees representing the first three degrees of decomposition. Huber's equation was used to calculate the thickness of coarse woody debris (Bruchwald 1999). Only in one case, because of the preserved branches and relatively large dimensions of the dead standing tree, was thickness estimated based on Czuraj's tables of standing tree thickness (Czuraj et al. 1960). To determine the thickness of broken trees, snags and declining trees with very small dimensions, Huber's equation was also used. The thickness of living trees growing in the study plots was calculated using Denzin's equation (Czerepko 2008).

The Cartesian coordinates of all trees in the study plots were also identified during the study, adopting the centre of the plot as the origin. The coordinates of trees were used for graphical representation of their location in the field, which was prepared in a scale of 1:200 in AutoCad LT (test version 2010). On this basis, the type of spatial distribution in the study plots was determined for dead trees. The coordinates of butts were used as the reference points for the distribution of coarse woody debris.

The statistical and mathematical analysis used Ripley's K(t) function to determine the type of distribution of dead trees in the analysed stands (Szwagrzyk and Ptak 1991). Using Ripley's K(t) function, the distribution of distances between trees was compared with the ideally random model of distribution to assess whether the pattern was regular, random or clustered (Moeur 1997). In the performed analyses of spatial distribution of the objects on the plane, a modification of the K(t) function was applied in the transformed form of this function's estimator L(t). A Monte Carlo procedure and the method of determining the confidence intervals suggested by Mariott (Moeur 1997) were applied to determine the confidence levels. For this purpose, for the number of objects and the plots' area adopted in this study, a sufficient number of random arrangements (100 simulations) was generated, reaching a 95% level of confidence. The above analyses of dead tree distribution in the plots were carried out using the Patar software package (Szwagrzyk and Ptak 1991).

The differences between the thicknesses of the dead trees in different study plots, due to the failure to meet the assumptions of parametric tests (the lack of normality distribution of the variable), were determined using the nonparametric equivalent of one-way ANOVA, *i.e.,* using the Kruskal-Wallis test. The significance of differences was given for the α=0.05 level of significance. The statistical analyses were carried out using the Statistica PL software package, version 9.01.

Results

A total of 50 dead trees were inventoried in the study plots. The greatest number (n=22) was found in plot 3 and the least (n=10) in plot 2 (*tabs. 2 and 3*). Coarse woody debris had the largest share, both quantitative and qualitative, among the distinguished forms of dead trees. In total, 34 dead lying trees (68.0% of thickness of all dead trees) were found in the analysed area, which with the exception of one piece of wood, were all logs (*tab. 2*). Declining trees and whole dead standing trees prevailed quantitatively among dead standing trees. In terms of thickness, the highest values were related to snags of broken trees, whose share compared to the growing living trees reached 9.0% (*tab. 2*).

***Table 1**. Degrees and stages of dead tree wood decomposition, including dead tree forms **

Form of dead trees			
Coarse woody debris		Dead standing trees and stumps	
Degree	Criteria for evaluation	Stage	Criteria for evaluation
I	Texture intact, circular, natural color of wood, bark intact, branches < 3 cm, log leaning on branches	1	Tree dead for less than 1 year
II	Texture intact, circular, natural color of wood, bark slightly damaged, no branches < 3 cm, log begins to sink	2	Tree dead for 1-3 years
III	Texture – larger hard fragments, circular, faded color of wood, fragmented bark, no branches < 3 cm, almost entire log on the ground	3	Flaking bark, partial decomposition of wood, lack of thinner branches
IV	Texture – small pieces, oval shape, faded color of wood, no bark, no branches < 3 cm, entire log on the ground	4	No bark, advanced decomposition of wood, no branches
V	Texture soft and loose, oval shape, faded color of wood, no bark, no branches < 3 cm, entire on the ground	5	Strongly decomposed stump
		6	Almost completely decomposed, low stump

*Classification by Maser et al. [1979] modified by Bobiec et al. [2005]

***Table 2**. Quantity and volume structure of various forms of dead trees inventoried in the study plots at the BdNP*

Dead wood type		N [pcs.]	Volume [m^3/10ar]	Share in relation to living trees [%]	
				quantity	volume
Coarse woody debris	Log	33	4.4	20.8	9.6
	Whole dead trees	1	6.3	0.6	13.8
	Total	34	10.6	21.4	23.2
Stumps and dead standing trees	Stumps	4	0.3	2.5	0.7
	Snags of broken trees	3	4.1	1.9	9.0
	Declining trees and whole dead standing trees	9	1.6	5.7	3.6
	Total	16	6.0	10.1	13.1
In total - dead standing and lying trees		50	16.6	31.4	36.3

The average volume of the dead trees per hectare of the analysed plots was 55 m^3 (*tab. 3*). In plot 1, the volume of the coarse woody debris (91.83 m^3/ha) was over 10 times higher than the volume of the dead standing trees (9.04 m^3/ha). The opposite pattern was observed in the highest-situated plot (no. 3), where the coarse woody debris volume was 13.34 m^3/ha lower than the thickness of dead standing trees (*tab. 3*). The

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differences in the volumes of coarse wood debris and of dead standing trees between the study plots were statistically significant (H (2, N=40)=12.072, p=0.0024 for plots 1 and 3; p=0.0090 for plots 2 and 3). In total, the share of different dead tree forms in the thickness of trees in the study plots ranged from 0.8% (plot 3) to 10.7% (plot 1) for the coarse woody debris. For the dead standing trees this share ranged from 1.04 % in plot 1 to 13.2% in plot 2 (*tab. 3*).

Table 3. *Volume (m^3/ha) of coarse woody debris and dead standing trees and their percentage compared to living trees occurring in the study plots at the BdNP*

Dead wood type		Study plot (no.)									Mean±SD
		1			2			3			
		N [pcs.]	m^3ha^{-1}	%	N [pcs.]	m^3ha^{-1}	%	N [pcs.]	m^3ha^{-1}	%	m^3ha^{-1}
Coarse woody debris	Logs	12	28.79	3.36	7	12.75	4.89	14	2.36	0.82	14.63±13.32
	Whole trees	1	63.04	7.31		-			-		21.01±36.40
Stumps and dead standing trees	Snags of broken trees	1	8.69	1.04	2	32.02	12.03		-		13.57±16.56
	Stumps	3	0.12	0.01	1	2.96	1.13		-		1.02±1.67
	Declining trees and whole dead trees	1	0.23	0.02		-		8	15.70	6.58	5.31±9.00
Total dead standing and lying trees		18	100.87	11.72	10	47.73	18.05	22	18.06	7.40	55.55±41.95

When analysing the size features of the examined trees in the stand in relation to the elevation above sea level, a downward trend of biometric parameters was demonstrated with increasing elevation, particularly with regard to the height of the trees (*fig. 2 and 3*). In plot 1, there were 41 trees with diameter at breast height below 40 cm (2nd class), representing 84.0% of all inventoried living trees. The share of trees with diameter at breast height over 40 cm in the total number of living trees in the plot reached 16.0% (*fig. 2*). Given the height, the predominance of trees below 25 m was observed (*fig. 3*). In the next two plots, the number of trees with DBH less than 40 cm increased and accounted for 74.0% of all inventoried living trees in plot 2 and 90.0% in plot 3. At the same time, the height of the trees in plot 3 was the lowest of all the study plots (*figs. 2 and 3*).

The share of coarse woody debris and dead standing trees in various degrees and stages of decomposition was different in each study plot. In plots 1 and 3, the diversity of decomposition degrees of the coarse woody debris was significantly higher than of the dead standing trees (*fig. 4A and B*). In both study areas, all degrees of decomposition of the coarse woody debris were recorded. The share of each degree of decomposition of the dead lying trees in plot 3 was similar and evenly distributed among the five degrees, whereas in plot 1, the majority of coarse woody debris was in the II degree of decomposition (57.0%) (*fig. 4A*). Almost all dead standing trees (96.0%) were characterised by the 3rd stage of decomposition, and this was observed in both study plots (*fig. 4B*). Relatively small differences in degrees and stages of decomposition of dead wood were observed in plot 2. The highest shares, 80.0% of the coarse woody debris and 76.0% of the dead standing trees, were characterised by the IV degree and 4th stage of decomposition (*fig. 4 A and B*).

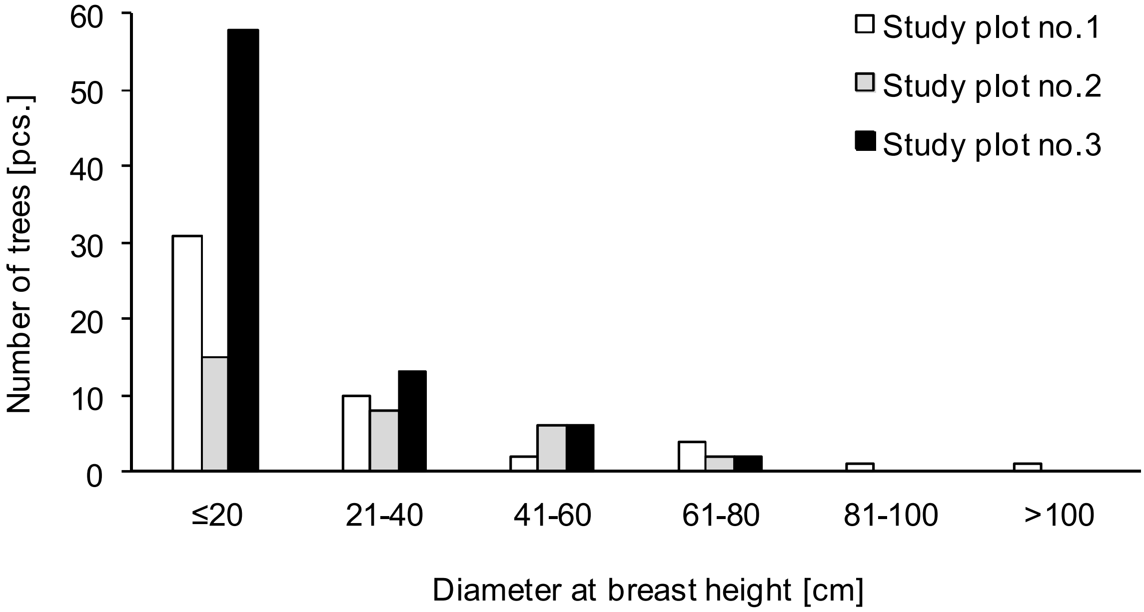

Figure 2. *The structure of diameter at breast height of living trees in the study plots at the BdNP (no. 1: n=49, no. 2: n=31, no. 3: n=79)*

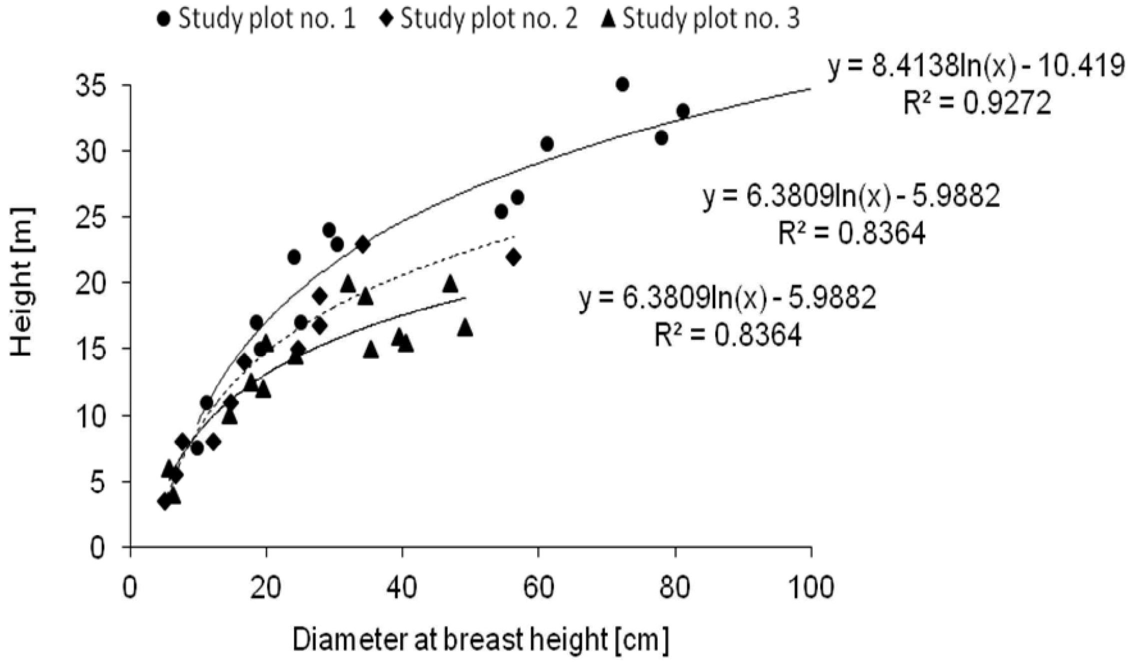

Figure 3. *The curve of height of living trees growing in the study plots at the BdNP*

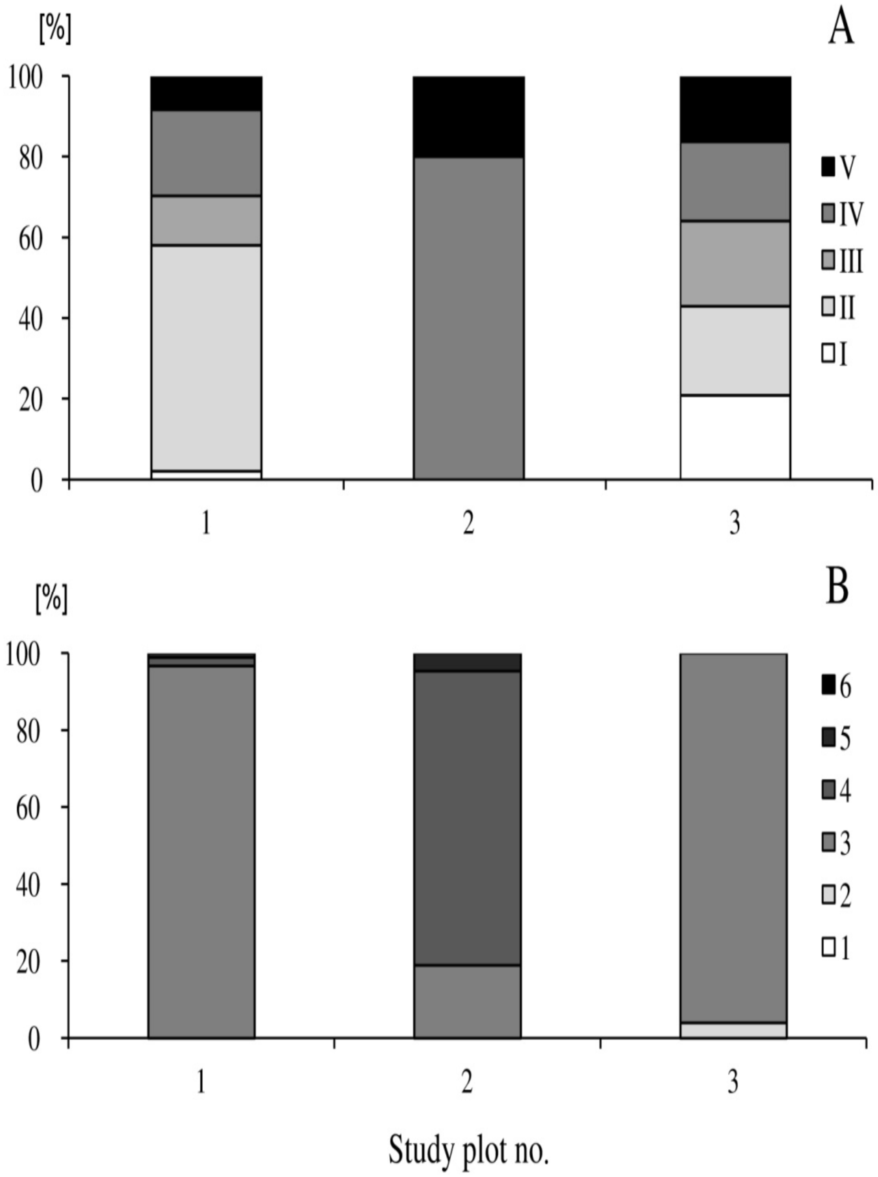

***Figure 4**. The percentage of degrees of coarse woody debris decomposition (A) and stages of dead standing trees decomposition (B) in the study plots at the BdNP*

Spatial distribution patterns of dead standing and lying trees, determined using Ripley's K(t) function, differed in the various study plots. A regular distribution was found in the lowermost plot 1 (*figs. 5A, 6A*), whereas in plot 2 (*figs. 5B, 6B*) and plot 3 (the uppermost) (*figs. 5C, 6C*), the distribution of the dead trees in the stand was statistically significantly random and clustered, respectively.

The inventory of macrofungi carried out in the study plots found a total of 30 fungal species, which were most frequently affiliated with the order Agaricales. Plot 2, where 17 taxa were recorded, of which 10 occurred only in this particular plot, harboured the greatest diversity of macrofungal species. The smallest number of fungi associated with dead trees was found in plot 3. Nevertheless, 11 fungal species were identified, including 2 that occurred only in this particular plot (*tab. 4*).

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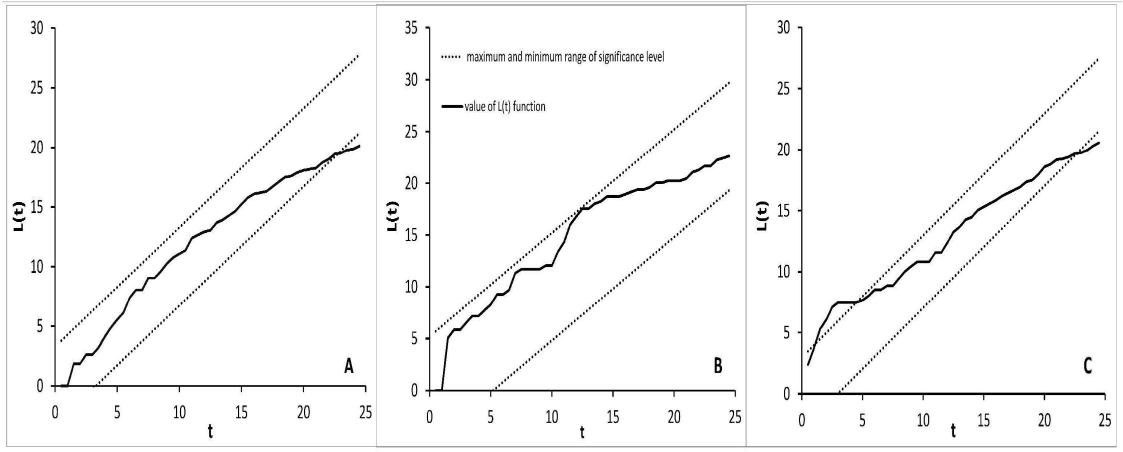


***Figure 5**. Diagrams of the L(t) function for the distribution of dead trees in beech forest localised at Rozsypaniec slope at the Bieszczady National Park (A- study plot no. 1 at 1035 m.a.s.l. - regular tree distribution, B- study plot no. 2 at 1091 m.a.s.l. - random tree distribution, C- study plot no. 3 at 1146 m.a.s.l.- clustered tree distribution)*

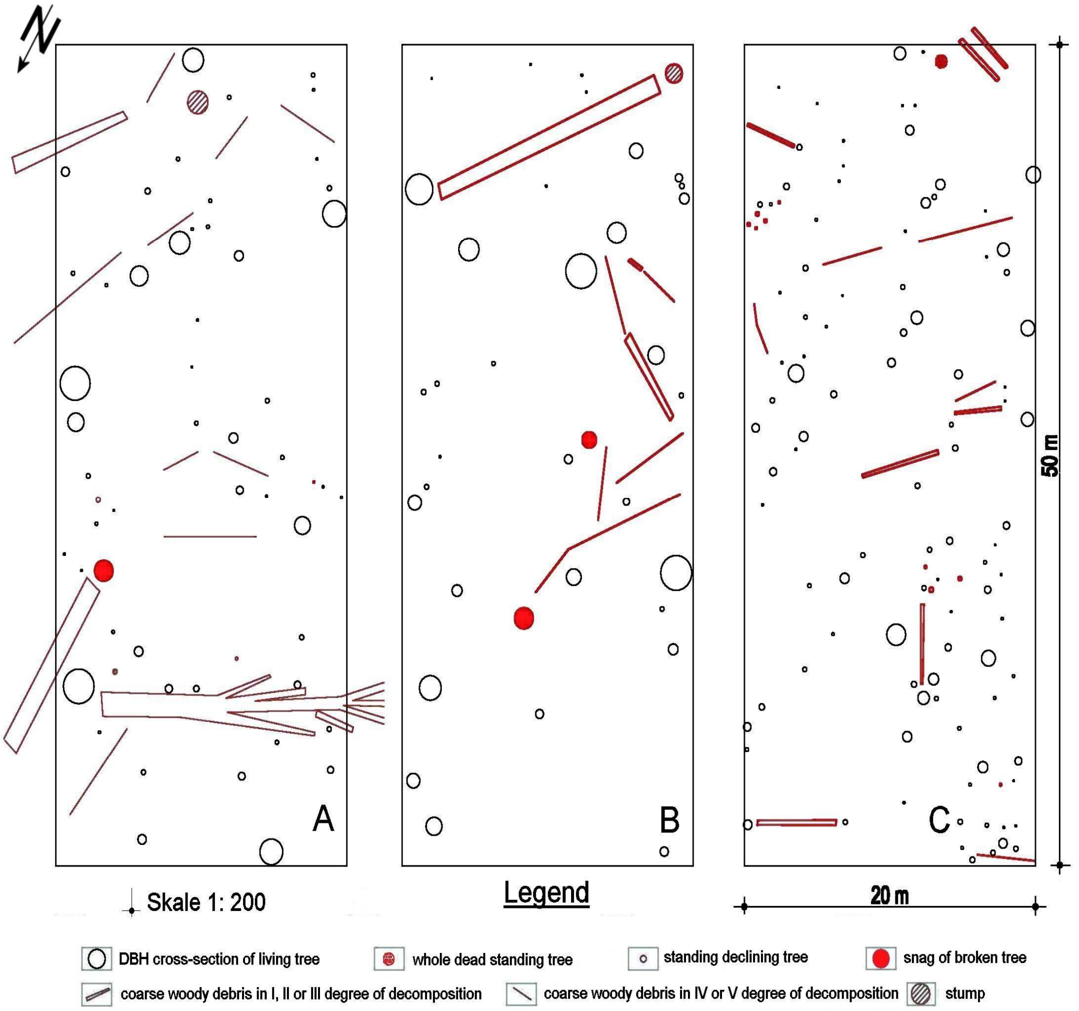


***Figure 6.** Horizontal projection of living and dead tree stumps and their arrangement in the study plots at the BdNP (A - study plot no. 1, at 1035 m.a.s.l., B - study plot no. 2, at 1091 m a.s.l., C - study plot no. 3, at 1146 m a.s.l.)*

Table 4. *List and frequency* (%) of macrofungi associated with coarse woody debris and dead standing trees in the study plots at the BdNP*

Species name (**Red List species: R, rare, E, endangered)	Study plot (no.)			Area in total
	1	2	3	
Basidiomycota, Agaricales				
Megacollybia platyphylla (Pers.) Kotl. & Pouzar	5.5	-	-	2
Pluteus aurantiorugosus (Trog) Sacc	5.5	-	-	2
*Phaeomarasmius erinaceus (*Fr.) Scherff. ex Romagn.** (R)	5.5	-	-	2
Pleurotus ostreatus (Jacq.) P. Kumm.	5.5	-	-	2
Lycoperdon pyriforme Schaeff.	5.5	10	-	4
Lycoperdon perlatum Pers.	-	20	-	4
Mycena flavescens Vel ** (R)	-	10	-	2
Psathyrella sp.(Fr.) Quél	-	10	-	2
Marasmius alliaceus (Jacq.) Fr.	-	20	14	10
Pluteus nanus (Pers.) P. Kumm.	-	10	-	2
Mycena haematopus (Pers.) P. Kumm.	5.5	10	-	4
Pseudoclitocybe cyathiformis (Bull.) Singer	-	10	-	2
Oudemansiella mucida (Schrad.) Höhn.	5.5	10	9.1	8
Crepidotus sp. (Fr.) Staude	-	-	4.5	2
Armillaria sp. *(rhizomorphs)* (Fr.) Staude	5.5	30	4.5	10
Basidiomycota, Polyporales				
Ganoderma applanatum (Pers.) Pat.	16.7	-	-	6
Fomitopsis pinicola (Sw.) P. Karst.	5.5	-	9	6
Steccherinum ochraceum (Pers.) Gray	-	10	-	2
*Mycoacia aurea (*Fr.) Erikss & Ryw.** (E)	-	10	-	2
Fomes fomentarius (L.) Fr.	22	30	32	28
Phlebia livida (Fr.) Bres.**(E)	-	10	-	2
Phanerochaete laevis (Pers.:Fr.) Erikss Ryv.	-	-	4.5	2
Basidiomycota, Russulales				
Stereum hirsutum (Willd.) Pers.	17	20	14	16
Ascomycota, Xylariales				
Eutypa spinosa (Pers.) Tul. & C. Tul.	5.5	-	-	2
Hypoxylon sp. Adans.	-	10	-	2
Hypoxylon fragiforme (Pers.) J. Kickx f.	-	10	-	2
Hypoxylon cohaerens (Pers.) Fr.	-	-	14	6
Xylaria longipes Nitschke	17	-	4.5	8
Ascomycota, Helotiales				
Bisporella citrina (Batsch) Korf & S.E. Carp.	-	20	9.1	8
Ascomycota, Pezizales				
Scutellinia sp. (Cooke) Lambotte	5.5	-	-	2

*The frequency was expressed as the percentage of dead wood with a given fungal species in the total number of analysed dead wood

The species *Fomes fomentarius* (L.) Fr. was the most frequently recorded (28.0%) and was identified 4 times (22.0%) in plot 1, 3 times (30.0%) in plot 2 and 7 times (32.0%) in plot 3. *Stereum hirsutum* (Willd.) Pers. (16.0%), *Marasmuis alliaceus* (Jacq.) Fr. (10.0%) and Honey fungi *Armillaria* sp. (Fr.) Staude (10.0%) were also frequently observed fungal species. The occurrence of other fungal species was occasional (*tab. 4*). Among the inventoried fungal species, four taxa, *viz. Phaeomarasmius erinaceus* (Fr.) Scherff. ex Romagn. (R) (*Pic. 1A*), *Phlebia livida* (Pers.) Bres (*Pic. 1B*), *Mycena flavescens* Vel. (*Pic. 1C*) and *Mycoacia aurea (*Fr.) Erikss & Ryw. (*Pic. 1D*), were identified as included in the IUCN Red List of Threatened Species. It was demonstrated that significantly more fungi occurred on dead lying trees (77.3%) than on standing trees (10.7%). In terms of degree and stage of decomposition of the analysed material, the greatest abundance of macrofungal species was observed on the coarse woody debris in the IV degree of decomposition, in the 5th stage of decomposition on stumps, and in the 3rd stage of decomposition on the remaining forms of dead standing trees (*tab. 5*).

Table 5*. Frequency (%) of macrofungi on dead standing and lying trees depending on the degree and stage of decomposition in study plots at the BdNP*

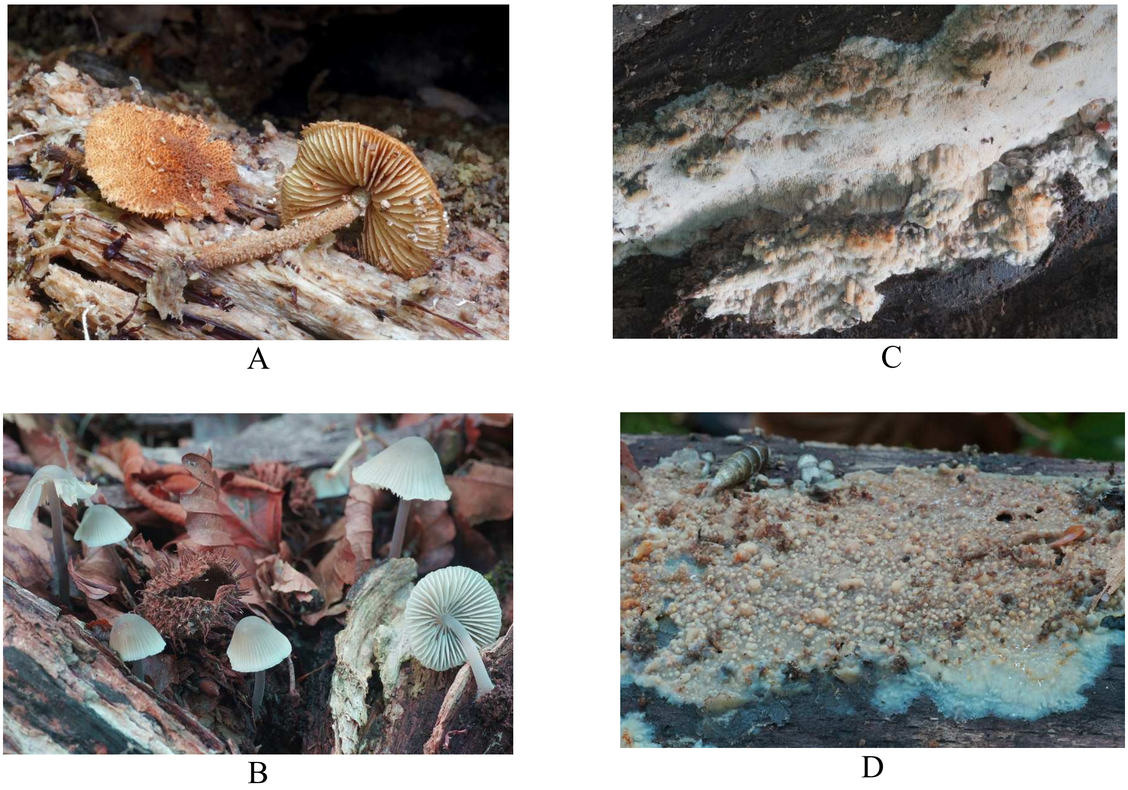
	Degree of decomposition Dead wood type	I	II	III	IV	V		In total degrees I - V
Coarse woody debris	Logs	3.4	17.2	25.9	41.4	12.1		77.3
	Whole trees	-	100.0	-	-	-		10.7
	Stage of decomposition Dead wood type	1	2	3	4	5	6	In total stages 1 - 6
Stumps and dead standing trees	Stumps	-	-	-	-	100.0	-	1.3
	Snags of broken trees	-	-	66.7	33.3	-	-	4.0
	Declining trees and whole dead trees	-	40.0	60.0	-	-	-	6.7

Discussion

The occurrence of dead trees in forest ecosystems is one of the most important indicators of environmental biodiversity conservation (Stevens 1997, Czerepko 2008, Müller and Bütler 2010). Competition and disturbances caused by biotic and abiotic factors are fundamental processes in forest biocenoses responsible for the presence of dead trees in the stand. The intensity of self-thinning processes is also largely a derivative of the habitat's fertility and the species composition of the stand (Solon and Wolski 2002, Gutowski et al. 2004, Holeksa and Maciejewski 2006). Leaving dying trees in coniferous stands, particularly spruce stands, favours the massive occurrence of cambio- and xylophagous insects, whereas in deciduous forests, increasing the amount of coarse woody debris and dead standing trees does not significantly affect the emergence and development of secondary pests (Stevens 1997, Köster et al. 2004, Starzyk et al. 2008). The count and volume share of dead trees in the stands is also affected by forest management and functions of stands (Wolski 2002). A relatively small abundance of dead trees in managed forests is usual when compared with forests under protective status (Dudley and Vallauri 2005, Czerepko 2008). In forests with non-production functions related to the conservation of natural environment, the presence of dead standing and lying trees is positively correlated with the term of their protection. The highest abundance of dead trees (on average 220 m^3/ha) is observed in montane forests, in solid and mixed beech stands under strict protection for more than 50 years, whereas lower values (117 m^3/ha) are observed in stands under protection for shorter time (Christensen et al. 2005). Yet even as a deficiency of dead standing and dying trees is unfavourable for the maintenance and improvement of environmental biodiversity (Müller and Bütler 2010), their excessive accumulation in the forest, *i.e.,* over 60.0% of living tree volume, is also undesirable. The excessive share of dead matter may lead to environmental biocenotic imbalances and the consequent decay of tree stands (Jankovský et al. 2004b, Pasierbek et al. 2007). The presence of dead trees in the forest is modulated by the spatiotemporal variability of factors structuring their occurrence. Thus, there are significant differences in the amount of dead trees in various regions and forest complexes. The thickness of dead trees in reserves ranges from 27.6 m^3/ha (Karula reserve) and 48.53 m^3/ha (Lahemaa reserve) in Estonia, through 107.3 m^3/ha (Lang-Leitn reserve) in Austria, to 132 m^3/ha (Knéhyné-Certův mlyn reserve) in the Czech Republic (Jankovský et al. 2004b, Köster et al. 2004, Rahman et al. 2008). On the other hand, the thickness of coarse woody debris and dead standing trees in the area of the Białowieża Forest ranges from 87 to 392 m^3/ha, and in the area of Seiteseminen National Park in Finland, the dead matter resources range from 100 to 232 m^3/ha (Nilsson et al. 2003, Dudley and Vallauri 2005). The differences in the number of dead trees remaining in tree stands are also determined by the species composition of the stands. It is estimated that in Europe, the average thickness of dead lying and standing trees in reserves with predominance of beech reaches 130 m^3/ha and 20 to 70 m^3/ha in central Europe (Müller and Bütler 2010). In Poland, however, the average thickness of dead matter in beech stands is 9.6 m^3/ha, ranging from 0 to 298 m^3/ha (Czerepko 2008). Among the common forest types in the country, the highest average abundance of dead trees (over 42 m^3/ha) is observed in mountain beech stands. Similarly, in Central Europe the majority of studies on the amount of dead trees in forest biocenoses concern beech stands (Kraigher et al. 2002, Christensen et al. 2005, Ekbom et al. 2006, Oheimb et al. 2006, Müller and Bütler 2010). The studies carried out in the stands of the Bieszczady National Park indicate that the average thickness of dead standing and lying trees in the stands of the Rozsypaniec massif is 55.5m^3/ha. This places the discussed stands significantly above the average thickness of dead trees, both in the country and in the Carpathian land itself (Czerepko 2008). Nevertheless, the thickness of dead trees was significantly different between the study plots, as a decrease in thickness of dead matter was observed with increasing elevation above sea level. In the lowermost plot the thickness of the coarse woody debris and the dead standing trees was six times greater than the thickness of the dead trees inventoried in the uppermost plot. The decrease in the thickness of dead lying and standing trees together with the increasing elevation above sea level is most likely related to the biometric parameters of living trees in the study plots. According to Stevens (1997), Szymański (2000) and Holeksa and Maciejewski (2006), the biometric parameters of trees in the stand have a significant effect on the amount of dead trees. There is a close relationship between the increase in size of standing trees and the thickness of coarse woody debris. Therefore, in the stand located the nearest to the top treeline, characterised by inhibited growth in height and thickness, the thickness of various forms of dead tree-wood was relatively small. The abundance of dead trees is not the only important information about the biological diversity of the environment. The form, arrangement and decomposition rate of the dead matter are also important from the point of view of preferences of various organisms that use dead trees (Piotrowski and Wołk 1975, Stevens 1997, Gutowski et al. 2004). The presence of dead wood of a certain shape and size is crucial for the survival of numerous endangered species (Piotrowski and Wołki 1975, Solon and Wolski 2002, Gutowski et al. 2004, Gutowski 2006). Woodpeckers (*Picinae*) are one of the examples, for whom the presence of dead standing trees in the forest is often essential for finding food, shelter and nesting (Ciach 2011). On the other hand, coarse woody debris, due to its ability to retain moisture, is the site for the growth of mosses, liverworts and fungi (Piotrowski and Wołk 1975, Stevens 1997, Solon and Wolski 2002, Gutowski et al. 2004). According to Christensen et al. (2005), coarse woody debris contributes greatly to the thickness of dead trees in European beech stands. The average thickness of coarse woody debris is almost three times greater than the thickness of dead standing trees. In montane forests, characterised by greater abundance of dead standing trees compared to lowland and foothills forests, there is almost twice as much coarse woody debris. Tree stumps, followed by coarse woody debris, are the most common types of dead trees in Polish forests, whereas whole lying trees, standing declining trees and whole standing trees are least common (Czerepko 2008). It is estimated that the average thickness of lying trees is 4.2 m^3/ha (logs: 4 m^3/ha, whole dead lying trees: 0.2 m^3/ha), whereas the average thickness of dead standing trees reaches 5.4 m^3/ha (stumps: 2.6 m^3/ha, standing declining trees: 0.8 m^3/ha, whole dead standing trees: 2.1 m^3/ha). When analysing the share of various forms of dead trees in the total volume of dead matter of the Carpathian land, it was found that logs account for the most volume (18.76 m^3/ha). The other forms of dead standing and lying trees, such as stumps, standing declining trees, whole dead standing trees or whole dead lying trees reach significantly smaller thickness: 5.85 m^3/ha, 5.1 m^3/ha respectively, which constitutes 54.6% of the thickness of all dead trees (Czerepko 2008).

The study carried out in 2011 in beech stands, located on the hillsides of the Rozsypaniec mount, proves that the amount of the coarse woody debris outweighs the amount of the dead standing trees, but in this case the differences between the volumes of the discussed forms of dead wood were significantly greater (16.10%). Moreover, the volume share of the distinguished forms of dead trees differed between the study plots. The coarse woody debris clearly dominated in the lowermost plot 1 (91% share of the volume compared to the remaining forms of dead trees). In the next two stands (plots 2 and 3), this proportion was reversed, in favour of dead standing trees, representing 73% and 87% of the thickness of inventoried dead trees in plot no. 2 and uppermost plot, respectively. According to Christensen et al. (2005), the double prevalence of dead standing trees in the total dead matter accumulated in mountain beech stands over the lowland and foothills beech forests results from the presence of spruce and fir in the former stands. Coniferous trees are more susceptible than deciduous trees to damages and dieback caused by insect feeding, which is the primary causal agent of standing deadwood. *Picea abies* (L.) Karst is highly susceptible to damage caused by cambio- and xylophagous insects, especially by the European spruce bark beetle (*Ips typographus* L.) (Coleoptera, Scolytinae) (Kuś and Kuś 2004; Starzyk et al. 2008). Moreover, standing declining trees of coniferous species remain longer in the stand, and their decomposition is also slower than that of deciduous trees (Christensen et al. 2005, Ekbom et al. 2006, Holeksa and Maciejewski 2009).

Taking into consideration the distribution of dead trees in the study plots, it was observed that elevation was a crucial factor for the spatial distribution of dead trees. The lowermost stands were characterised by regular or random distribution of dead matter, and in the uppermost beech stands, clustered distribution of dead trees was observed. Trees growing in harsh mountain conditions, located close to the top treeline, produce the so-called biogroups through contact with each other and by their root systems growing together (Rigg and Harrar 1931, Graham and Bormann 1966, Loehle and Jones 1990, Karaś 1995). The clustered distribution of dead trees in the uppermost study plot indicates the collective nature of tree life, which results in their self-thinning during the dieback. This phenomenon seems to be crucial to ensure adequate living conditions for various groups of organisms with specialised ecological requirements and for the evolution of microhabitats.



A C

B D

***Picture 1**. The occurrence of macromycete fungi on European beech dead wood in the Rozsypaniec massif at the Bieszczady National Park (A - Phaeomarasmius erinaceus (Fr.) Scherff. Ex Romagn; B - Phlebia livida (Pers.) Bres; C - Mycena flavescens Vel.; D - Mycoacia aurea (Fr.) Erikss & Ryw.), (photos by Bolesław Kuźnik, August, 2011)*

The biodiversity of the environment is also determined by the degree of decomposition of dead trees. On one hand, due to the release of organic matter content, the decomposing wood of dead trees is important for nutrient cycling. On the other hand, decomposing wood affects vital functions of trees. The rate of decomposition of dead trees depends on the species and parameters of trees and on prevailing climatic conditions (Holeksa and Maciejewski 2009, Müller-Using and Bartsch 2009). A faster rate of decomposition of dead coarse woody debris and smaller standing trees is recorded in warm and humid climates and during frost (Stevens 1997). Tree decomposition may take from several to even a few hundred years (Gutowski et al. 2004). In lower subalpine deciduous stands growing in the Carpathians from 600 to 1200 m above sea level, dead tree decomposition lasts from several years to several decades (Holeksa and Maciejweski 2009). With the progressive decomposition of dead trees, their structure, wood colour and bark cover, and thereby the occurrence of accompanying organisms, are all changed (Solon and Wolski 2002, Gutowski et al. 2004, Pasierbek et al. 2007, Czerepko 2008). In Polish stands, the majority of coarse woody debris is in the III stage of decomposition (29.5%) (Holeksa and Maciejweski 2009). All dead lying and standing trees in the reserves are mainly in the I and II degrees of decomposition, whereas the stumps are in degrees IV and V (Pasierbek et al. 2007). On the other hand, the majority of dead standing trees and coarse woody debris in the beech stands of the BdNP were in the IV stage and 4th degree of decomposition, *i.e.,* the structure of the trees was heavily compromised. The accumulation of trees in the IV degree and 4th stage of decomposition may indicate a relatively slow process of organic matter decomposition on the mountainsides of the Rozsypaniec massif. The slow process of dead trees' decomposition leads to the long-term dynamic succession of microhabitat conditions, followed by the succession of organisms. It is estimated that a single tree, from the moment of death to complete decomposition, is inhabited by several to hundreds of species of mosses, liverworts, fungi, plants and insects. Currently, due to the insufficient number and small diversity of dead trees in forests, the previously mentioned groups of organisms are among the most endangered species. Forest fragmentation, preventing the even distribution of dead trees, is a major barrier to spreading of many saproxylobiontic species (Stevens 1997, Gutowski 2006).

Among numerous organisms occurring on dead trees, fungi play the most important role in the decomposition of dead matter. Wood infested by fungi may in fact contain approximately 1.5 times more nitrogen and water than those devoid of fungi. Fungi also secrete substances (carbohydrates, proteins and acids) that are used by other organisms for vital functions (Gutowski et al. 2004, Jankovský et al. 2004a, Holeksa and Maciejewski 2006). The species from families of bracket fungi (*Poliporaceae*) and corticoid fungi (*Corticiaceae*) are the most common groups occurring on dead trees and causing their decomposition (Olsson 2008). Detailed studies on the species diversity of fungi associated with dead trees in beech stands were carried out in Denmark, Belgium, Slovenia, the Netherlands and Hungary, inventorying a total of 457 fungal taxa. The greatest species diversity was observed in Belgium and Denmark, and the largest share of protected species was detected in Hungary and Slovenia (Ódor et al. 2006). In the Czech Republic, Jankovský et al. (2004a), by examining the mycoflora of dead standing and lying trees in the Vélky Polom and Želazné Hory reserves, observed the presence of 220 fungal species, including saprotrophs living on the decomposed wood of dead trees. Eighty-four species of fungi occurring on small wood pieces of barkless trees, 142 species on the bark of coarse woody debris, 282 species on stumps and 10 species on declining trees were found in the hornbeam forests of Białowieża National Park (Gutowski et al. 2004). So far, 1054 fungal species have been reported in Bieszczady National Park, of which 146 occur in rare sites in Poland and 85 occur only in the Park. The occurrence of 30 macrofungi species was observed in the inventoried study plots in the BdNP. According to the valuation of fungi, based on the number of positions, degree of risk of extinction and their origin (Kujawa 2011), the majority of the recorded species belonged to the IV category, which is the average value. The observed diversity includes such species as yellow fairy cups (*Bisporella citrina* (Batsch) Korf. & Et. S. E. Carp.)*, Hypoxylon fragiforme* (Perst.) J. Kickx f.*,* tinder fungus (*Fomes fomentarius* (L.) Fr.)*,* red banded polypore (*Fomitopsis pinicola* (Sw.) P. Karst.), and *Oudemansiella mucida* (Schrad.) Höhn. The only species with high value (category III) found in the study plots was *Hypoxylon cohaerens* (Pers.) Fr. Interestingly, the presence of species characterised by a very high value was recorded (category II) - *Phaeomarasmius erinaceus* (Fr.) Scherff. ex Romagn. (R), *Phlebia livida* (Pers.) Bres and *Mycena flavescens* Vel. These fungal species are on the red list of threatened species (Wojewoda and Ławrynowicz 2006).

Conclusions

The research indicates that there is a relationship between elevation and the amount and form of dead wood in the beech stands of Bieszczady National Park. The share of dead standing trees compared to coarse woody debris increased when approaching the top treeline, while the thickness of both living and dead trees decreased. The high average amount of dead matter in the beech stands of the Rozsypaniec massif of 55.5 m^3/ha reflects the very good condition of the discussed forests, promoting biodiversity and the occurrence of saproxylic organisms. The coarse woody debris had the largest quantity (68%) and thickness share (64%) of the dead trees at the study plots. Analysis of the degree of dead tree decomposition revealed that the II degree was the most frequently represented phase of tree decomposition and that the diversity of decomposition progress was greater in coarse woody debris than in standing trees. The diversity of the coarse woody debris decomposition stages was also directly and proportionally related to the elevation of the plot above sea level. The evaluation of distribution structure of dead trees in stands demonstrated the clustered distribution of dead matter in the uppermost plot. On one hand, this spatial structure indicates the aggregate character of tree distribution in the stand, but on the other hand, it reflects the collective character of the self-thinning process.

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INFLUENCE OF ELEVATED CO2 ASSOCIATED WITH CHICKPEA ON GROWTH PERFORMANCE OF GRAM CATERPILLAR, *HELICOVERPA ARMIGERA* (HÜB.)

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Abstract. Influence of increased CO_2 concentrations (550 and 700 ppm) on host (Chickpea, *Cicer arietinum* L.) and its insect herbivore (Gram caterpillar, *Helicoverpa armigera* (Hüb.)) was studied in relation to ambient CO_2 (380 ppm) concentration under laboratory conditions. The foliar chemistry of chickpea under elevated CO_2 revealed low nitrogen and high carbon content with increased C: N ratio but no change in phenol content. This alteration in food quality significantly affected the growth parameters of *H. armigera* in the form of increased food consumption, gain in larval weight and more fecal matter production. Larval duration was also extended by one day under elevated CO_2 over ambient. Further, reduction in the fecundity (535 eggs/ female) was observed in the individuals raised under elevated conditions compared to ambient situation (580 eggs/ female). Diluted quality of food had a significant effect on growth performance indices of insect. Increase in approximate digestibility and relative consumption rate by the larva was observed under elevated CO_2 situation. The reduced efficiency of conversion of ingested food (35.88 %) and digested food (37.88 %) was observed under similar situation. As a result, the relative growth rate was down by 5.22 % and 6.20 % under both elevated CO_2 conditions. In a nutshell, it can be concluded that increased CO_2 concentrations has the negative effect on the growth and development of *H. armigera*.

Key words: *CO_2 concentration, climate change, Helicoverpa armigera, chickpea, developmental biology*

Introduction

Gram caterpillar, *Helicoverpa armigera* (Hub.) is a highly polyphagous pest known to cause serious economic damage to many field crops of arid and semiarid tropics across the globe. In India, it is a major pest of pigeon pea, chickpea, sunflower, sorghum and tomato crops. In Southern states of India, it breeds throughout the year completing over eight generations. The first generation usually starts in early June, coinciding with the onset of pre-monsoon showers either from the adults possibly emerging from diapausing pupae or from larvae that have been surviving on off season crops and weeds during summer. Initially, the species survives in low numbers on weeds, early-sown corn, sorghum, mung bean and groundnut but later builds up the population before shifting to pigeon pea in October-November and then to chickpea in November-March. Chickpea, the last notable crop of the season grown extensively across India, acts as a main breeding ground for *H. armigera* harbouring at least two generations. Thus, chickpea plays a crucial role in the mass breeding and sustenance of the pest for the next season (Bhatnagar, 1980). Success of carryover of the pest to the

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next season mainly depends on fitness of the host on which it completes the last generation and the environmental condition during the transitional period.

The present change in climate is closely linked with the rise in atmospheric carbon dioxide (CO_2) levels from 280 to 387 ppm since the start of the Industrial Revolution. And current levels of CO_2 are expected to double by 2100 (IPCC 2007). Such rise in CO_2 levels affects the biological system of living organisms, including insects (Guerenstein and Hildebrand, 2008). Since fitness of any herbivorous insects depends on nutritional status of their host, any change in the quality of host plants can affect their growth, development, population dynamics and survival. The extent of growth, yield and biochemical responses of plants to elevated CO_2 depends on the photosynthetic pathway. Crops with C_3 photosynthesis respond markedly to increasing CO_2 concentrations by inhibiting photorespiration, making photosynthesis more efficient, however, leaf nitrogen and protein concentrations ultimately decrease by more than 12 % (Ainsworth and Long 2005). Such a loss of nitrogen and protein significantly diminishes the nutritional value of plant affecting growth and development of insect herbivores either directly or indirectly. In contrast, plants with C_4 photosynthesis will respond little to rising atmospheric CO_2 due to saturation of photosynthesis (Leon Hartwell and Vara Prasad, 2004).

Chickpea (*Cicer arietinum* L.) being a C_3 crop makes an interesting candidate to study the nutritional changes occurring due to altered CO_2 concentrations in its growth environment and its effect on the developmental and reproductive biology of one of its important pests, *H. armigera* to assess its pest status in next generations.

Materials and methods

Open top chambers (OTCs)

Three Open top chambers (OTCs) of 4 x 4 x 4 m dimensions, are established at Central Research Institute for Dryland Agriculture (CRIDA), Hyderabad (17° 38' N; 78° 47' E). Elevated CO_2 concentrations of 550 ± 25 ppm (Condition I) and 700 ± 25 ppm (condition II) were maintained in two chambers and ambient CO_2 (380 ± 25 ppm) in the third chamber. Carbon dioxide gas supplied to these chambers was maintained at set levels using manifold gas regulators, pressure pipelines, solenoid valves, rotameters, sampler pump, CO_2 analyzer, PC linked Program Logic Control (PLC) and Supervisory Control and Data Acquisition (SCADA). The fully automated OTCs are first of their kind in India, which not only maintains the desired level of CO_2 but also the temperature and relative humidity (Vanaja et al., 2006).

Seeds of Chickpea Var. MNK-1 (Kabuli type) were sown in plastic pots (19 cm height, 17 cm diameter) and were kept in all the three OTCs during October 2011. Plant density and health were maintained by the adoption of proper agronomic practices.

Biochemical analysis of chickpea

Leaves of chickpea from respective OTCs were analyzed to estimate carbon, nitrogen, C: N ratio and phenol content through standard procedures. To estimate carbon, nitrogen and phenol content, leaf samples taken from 60 days old plants were dried at 80°C and subsequently ground to powder. Organic carbon was determined by Walkley Black method (1934) and nitrogen by Kjeldhahl using block digestion and steam distillation method (McKenzie, 1994). C: N ratio was analyzed by using CHN analyser (Elementar Analysen system GmbH, Germany) and total phenol was estimated by Folin-Denis method (Anderson and Ingram, 1993).

Feeding trials

Culture of *H. armigera* procured from CRIDA laboratory was maintained on artificial diet, which was prepared using chickpea leaves in a controlled chamber at 27° C with a 14-h day/ 10-h night cycle. Light intensity inside the chamber during the 14 h day period was maintained at 550µ mol m^{-2} s^{-1} with relative humidity of 60 % (day) and 70 % (night).

Eggs from the stock culture showing germ band development were surface sterilized with 10 per cent formalin for 10 minutes and washed under running tap water. Upon hatching, a day-old neonates was grouped into three batches; each batch containing 48 larvae. One batch was reared in the growth chamber maintained at ambient (380 ppm) CO_2 concentration on chickpea leaf composed artificial diet. Whereas, other two batches were reared separately in two different growth chambers maintained at 550 ppm and 700 ppm CO_2 concentrations. From fourth day onwards, larvae were bred individually by transferring them into multi cavity rearing trays (each tray having six well) on pre-weighed artificial diet prepared out of chickpea leaves harvested from OTCs maintained with respective CO_2 concentrations. Overall, 144 larvae were reared in all the three CO_2 condition with each individual larva representing a replication. On every alternative day, until the completion of the larval stage, weight of unfed artificial diet was recorded and removed. At the same time, fresh pre-weighed artificial diet was provided to individual larva. The larval and fecal matter weight (mg) was also recorded at the time of providing fresh food. After cessation of feeding which indicates the completion of larval stage, the larval duration was noted, and pupae were weighed and sexed. A pair of male and female pupae was kept separately in a plastic jar (22 cm diameter, 30 cm height) to study the reproductive biology.

In each condition, eight pairs of *H. armigera* moths were used to study the reproductive biology. Moths were provided with 10 per cent honey solution as adult food. The mouth of the container was closed with black cotton cloth to facilitate oviposition. Eggs laid on the cloth were collected everyday with the help of fine camel-hair brush and counted.

The insect performance indices were determined using the data generated from larval weight, quantity of food ingested and weight of fecal matter excreted (Waldbauer, 1968 and Srinivasa Rao *et al.*, 2009). Relative growth rate (RGR, in mg mg^{-1} d^{-1}), relative consumption rate (RCR, mg mg^{-1} d^{-1}), efficiency of conversion of ingested food (ECI, %), efficiency of conversion of digested food (ECD, %) and approximate digestibility (AD, %) were computed.

Data analysis

All the treatments were replicated forty eight times (n = 48), and results were presented as the mean value of each treatment ± standard deviation. The effects of CO_2 concentrations on larval parameters were analyzed using one-way ANOVA. Treatment means were compared and separated using the least significant difference (LSD) at $p<0.01$. The data on weight of food ingested, larval weight, fecal matter weight, larval duration, pupal weight and fecundity were analyzed using ANOVA with the help of STAR (Statistical tool for agriculture research), version 1.00.

Results

Biochemical analysis of chickpea leaves

In the present study, the nutritional quality of chickpea leaves differed significantly across all the three CO_2 concentrations. Leaf nitrogen content was distinctly lower (2.92 and 3.21 %) in elevated I (550 ± 25 ppm) and II (700 ± 25 ppm) CO_2 conditions compared to ambient (3.88%) ($F_{2,\ 4} = 749.39$; $P < 0.01$) (*Fig.1a*) However, the carbon content of leaf tissue increased significantly ($F_{2,\ 4} = 290.07$; $P < 0.01$) to 43.13 % (700 ppm) and 40.46 % (550 ppm) under increased CO_2 over ambient CO_2 (33.99 %) (*Fig. 1b*) and resulted in a significant increase of C: N ratio (*Fig. 1c*). In contrast, the phenol content did not vary significantly across CO_2 conditions ($F_{2,\ 4} = 3.00$; $P > 0.05$) (*Fig. 1d*).

Larval growth performance

Total consumption of the food (diet) by *H. armigera* larvae differed significantly across CO_2 concentrations ($F_{47,\ 94} = 5332.83$; $P < 0.01$). The mean food consumption was substantially higher in larvae fed on the diet prepared from chickpea grown at 550 (1887.5 mg) and 700 ppm (1997.5 mg) over 380 ppm (1099.5 mg) of CO_2 concentrations. Similar trend was reflected in average weight gain by the larva ($F_{47,\ 94} = 49.84$; $P < 0.01$) under elevated I (381.25 mg), and elevated II (384.16 mg) condition compared to ambient (367.91 mg) condition. Fecal matter released by larvae was considerably more under elevated I (602.50 mg) and elevated II (597.70 mg) over ambient (372.29 mg) condition ($F_{47,\ 94} = 4567.27$; $P < 0.01$). The total larval development (time taken from hatching to pupation) was extended (15.16 and 15.27 days) significantly ($F_{47,\ 94} = 184.60$; $P < 0.01$) under elevated conditions over ambient (14.06 days). The pupal weight did not vary across CO_2 concentrations (*Table 1*).

Table 1. *Effect of elevated CO_2 on growth and development of H. armigera on chickpea leaf mediated artificial diet*

CO_2 concentration (ppm)	**Total diet consumed (mg)**	**Larval weight (mg)**	**FM produced (mg)**	**Larval duration (days)**	**Pupal weight (g)**
380 (Ambient)	1099.50 ± 52.24	367.91 ± 9.66	372.29 ± 9.94	14.06 ± 0.24	0.257 ± 0.004
550 (Elevated-I)	1887.50 ± 24.45	381.25 ± 7.61	602.50 ± 18.73	15.16 ± 0.37	0.258 ± 0.005
700 (Elevated-II)	1997.50 ± 50.71	384.16 ± 4.98	597.70 ± 12.92	15.27 ± 0.44	0.259 ± 0.006
$F_{47,\ 94}$	5332.83	49.84	4567.27	184.60	NS
P	P<0.01	P<0.01	P<0.01	P<0.01	-
CV (%)	2.80	2.25	2.57	2.30	-

FM- Fecal matter

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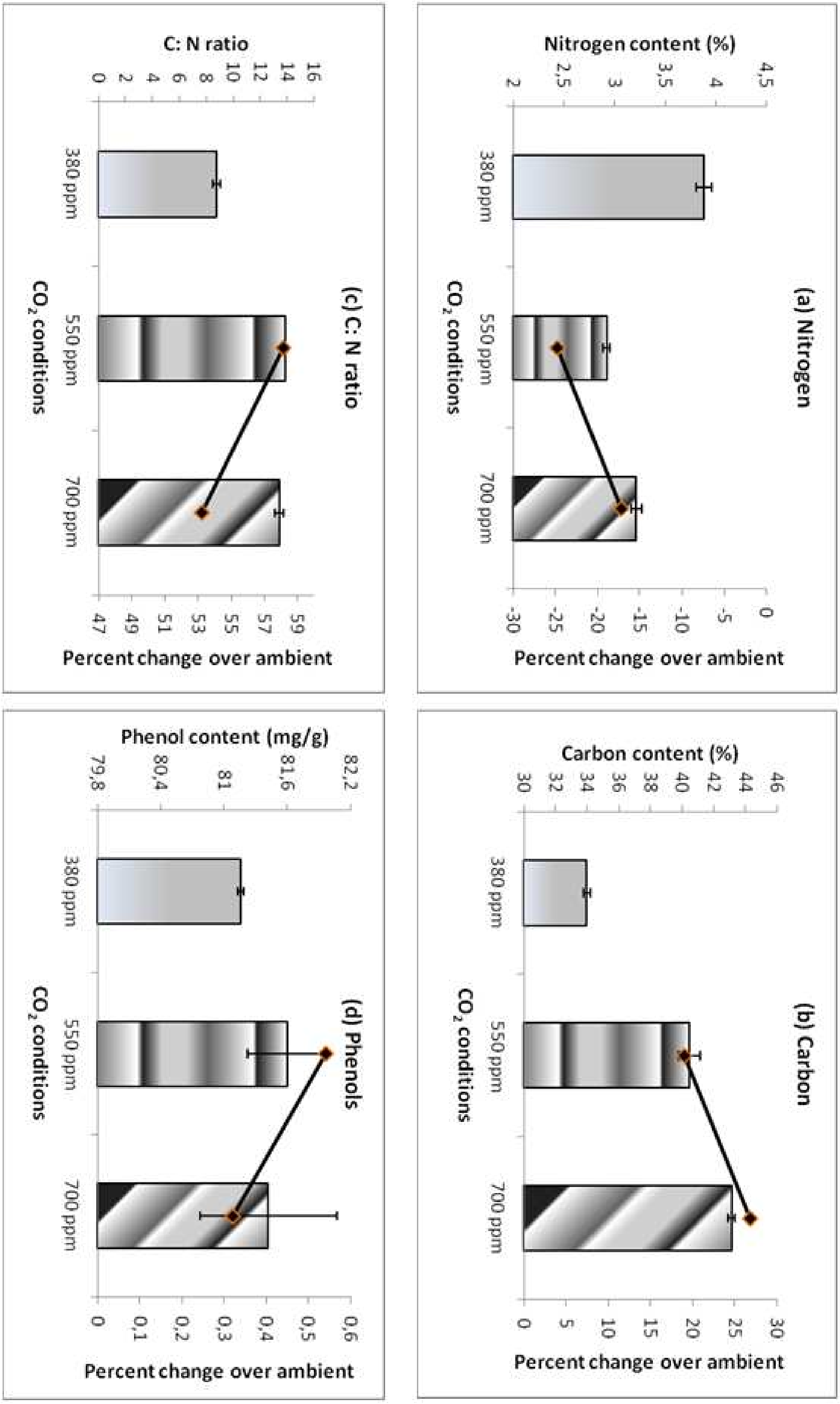

Figure 1. *Biochemical changes in chickpea foliage under different CO$_2$ conditions (a) Nitrogen (b) Carbon (c) C: N ratio and (d) Phenol content*

The approximate digestibility (AD) of the foliage by larvae was increased by about 2 % over ambient (67.81%) condition ($F_{47,\ 94} = 96.36$; $P < 0.01$). The efficiency of conversion of ingested food (ECI) was significantly lower (42.47 and 41.08 %) under elevated I and II conditions, compared to ambient (64.07 %). This was reflected in significant ($F_{47,\ 94} = 2824.30$; $P < 0.01$) lowering of efficiency of conversion of digested food (ECD) by the larvae under elevated conditions (61.54 and 58.71 %) compared to ambient (94.51 %). The relative consumption rate (RCR) was higher ($F_{47,\ 94} = 3174.26$; $P < 0.01$) under both elevated concentrations with an average of 52 - 53 mg/mg/day over ambient (36 mg/mg/day). The significant lower ($F_{47,\ 94} = 44.85$; $P < 0.01$) relative growth rates (RGR) of larvae were observed under elevated I and II concentrations (22.13 and 21.90 mg/mg/day) compared to ambient (23.35 mg/mg/day) (*Table 2, Fig. 2*). The females emerged from both elevated CO_2 conditions produced the lower number of eggs 535 and 538 eggs/female compared to 580 eggs/female under ambient CO_2 concentration ($F_{7,\ 14} = 17.56$; $P < 0.01$) (*Fig. 3*).

Table 2. *Effect of elevated CO_2 on growth performance or indices of H. armigera*

CO_2 conc. (ppm)	**Life history parameters/ indices**				
	AD (%)	**ECI (%)**	**ECD (%)**	**RGR (mg/mg/day)**	**RCR (mg/mg/day)**
380 (Ambient)	67.81 ± 1.08	64.07 ± 2.48	94.51 ± 4.27	23.35 ± 0.96	36.46 ± 0.87
550 (Elevated-I)	69.02 ± 0.62	42.47 ± 1.34	61.54 ± 1.97	22.13 ± 0.88	52.16 ± 1.13
700 (Elevated-II)	69.98 ± 0.60	41.08 ± 1.16	58.71 ± 1.69	21.90 ± 0.97	53.30 ± 1.73
$F_{47,\ 94}$	96.36	2979.59	2524.30	44.85	3174.26
P Value	P<0.01	P<0.01	P<0.01	P<0.01	P<0.01
CV (%)	1.11	3.32	3.83	3.60	2.45

AD = Approximate Digestibility; ECI = Efficiency of Conversion of Ingested food; ECD = Efficiency of Conversion of Digested food; RGR = Relative Growth Rate; RCR = Relative Consumption Rate.

Discussion

Alteration in phytochemistry of plants under the elevated CO_2 concentrations is well documented (Hunter 2001). Irrespective of the biochemical pathway (C_3 and C_4), crop exhibit reduced 'N', increased 'C' and C: N ratio due to rapid photosynthesis and growth (Norby *et al.*, 1999) of the plant. Similar change was observed in the present study also wherein, biochemical analysis of chickpea foliage, a C_3 plant revealed a significant reduction in leaf nitrogen (over 24.74 %) when grown under elevated CO_2 concentrations compared to ambient.

A significant increase in 'C' (over 26.9 %) and C: N ratio (over 58.17 %) was observed in chickpea foliage under elevated CO_2 conditions than ambient condition, which might be due to increased carbon intake by the plants when grown under elevated CO_2 conditions. Similar observation was reported by Hughes and Bazzaz (1997) in a common milkweed *Asclepia syriaca*. The phenolic content in chickpea foliage did not differ significantly across CO_2 concentrations (*Fig. 1*). Present study indicated the poor nutritional quality of the food for larvae under elevated CO_2 condition over ambient and is in agreement with Srivastava et al. (2002); Goverde and Erhardt (2003).

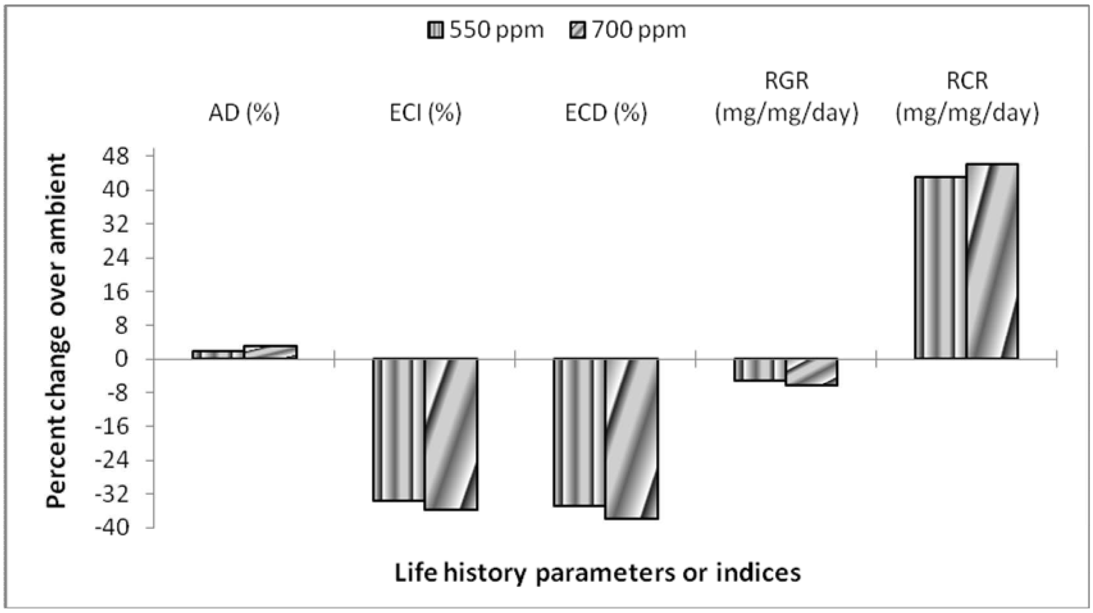

Figure 2. *Impact of elevated CO_2 on life history parameters or indices of H. armigera*

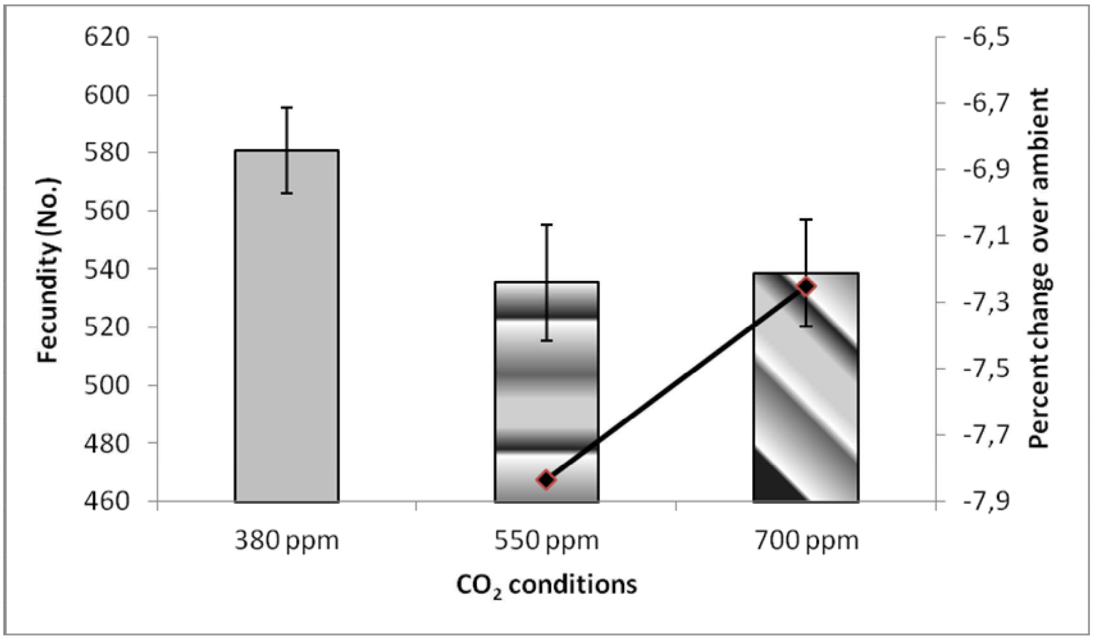

Figure 3. *Impact of elevated CO_2 on fecundity of H. armigera*

Since nitrogen is the chief constituent of proteins and is evident that chickpea plants grown under elevated CO_2 concentrations have lower protein content in their tissues, which might result in poor nutritional quality of food. Gram caterpillar, a herbivore needs higher protein content for better growth and development. If the nutritional quality of the food is low, it would try to compensate through higher consumption and intake.

In the present study, increased food consumption of 81.67 % by the larvae under elevated CO_2 conditions was noticed over ambient. This resulted in increased RCR by 46.18 % in larvae reared under elevated CO_2 concentrations. Similar observation was also made by Wu et al (2006). Increase in larval RCR under elevated CO_2 concentrations was attributed to production of fewer allelochemicals reducing the nutritional quality of food thus, promoting phago-stimulatory responses (Scriber and Slanky, 1981). Further, in spite of increased food consumption, RCR and AD (by 3.2 %), the gain in the larval weight was mere 4.41 % over ambient. This could be attributed to lower protein content and higher 'C' content and 'C: N' ratio in the plant tissues resulting reduced efficiency in the conversion of ingested food (33 %) and digested food (38 %) by the larvae grown under elevated CO_2 concentrations over ambient.

Due to poor efficiency of both ingested and digested food, much of the food consumed was resulted in higher quantity release of fecal matter (about 60 %) compared to ambient CO_2. Similar observations were made by Chen et al, 2007 who recorded 46.3 and 37.8 per cent increased food consumption and feces production, respectively by *H. armigera* when fed on spring wheat (C_3 plant) under elevated CO_2. Further, in spite of higher consumption by larvae under elevated CO_2 condition, larvae took approximately one day more to complete their period over ambient. As a result, the relative growth rate (RGR) was reduced by 5 - 6 % in elevated conditions.

There is a general prediction that the fecundity is the most common parameter for determining the effect of larval food quality on performance of the insect. A significant reduction of fecundity (6.6 %) was recorded under elevated CO_2 over ambient and similar fewer fecund females were reported by Wu et al (2006).

Succinctly, if we put together the above results, it is understood that the dilution of bio-chemical constituents of chickpea foliage caused the poor growth, development and fecundity of *H. armigera* under elevated CO_2 conditions. Based on the present study, it can be speculated that, the growth performance of gram caterpillar under elevated CO_2 conditions, affects badly resulting in poor perpetuation of the population which might reduce its fitness in subsequent generations.

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IMPACTS OF CLIMATE CHANGE ON VEGETATION DISTRIBUTION NO. 2 - CLIMATE CHANGE INDUCED VEGETATION SHIFTS IN THE NEW WORLD

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Abstract. After giving an overview of climate change induced vegetation shifts in the Palearctic region in our previous paper, in this article we review literature available in Web of Science on North and South America. We study different geographical regions such as Canada, Alaska, California, Southwestern, Eastern and Southeastern USA, the Great Lakes region, the Great Plains, intermontane basins and plateaus, Rocky Mountains and the Cascades as well as Central and South America. We summarize main results of relevant field studies, experiments and model simulations. Predicted environmental changes include temperature increases, altering precipitation patterns, droughts, permafrost thaw and ground subsidence in arctic regions, enhanced El Niño Southern Oscillation, sea level rise, increasing salinity of the vadose zone, snowpack declines and various disturbances. All vegetation types are affected by these changes, to the most important phenomena belong e.g. reduction of arctic and alpine communities, decreasing area of taiga, shrub encroachment in tundra areas, northward expansion of the tree line, reduction in wetland areas, invasion, altering forest regeneration patterns, decrease in dominance of conifer species, increased cover of salt-tolerant plant species in tidal marshes, expansion of grassland, compositional and structural changes of grasslands and forests, drying up of bogs, landward migration of mangroves, savannification of forests, expansion of chaparral as well as upward migration of species in the mountains.

Keywords: *global warming, vegetation distribution, biome, vegetation zone, plant community*

Introduction

Terrestrial ecosystems are greatly affected by climate, particularly temperature and precipitation (Holdridge, 1947; Woodward, 1987). Increases in atmospheric trace gas concentrations could warm the global average temperature significantly by the end of the 21st century (Overpeck et al., 1991). Increased temperatures would reduce the supply of soil moisture by reducing the volume of snow and increasing winter runoff, and increase the potential evapotranspiration. These processes would likely produce widespread drought-induced dieback (Neilson et al., 1992). Besides, climate change models forecast not only global warming but alteration of precipitation regimes affecting timing, frequency and intensity of precipitation events as well (Easterling et al., 2000; NAST, 2000; IPCC, 2001). Drought frequency and severity are predicted to increase across numerous continental interiors (Müller et al., 2005). Alteration of precipitation patterns has the potential to cause major changes in vegetation, soils,

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biodiversity and ecological processes in terrestrial ecosystems (Neilson et al., 1989; Brown et al., 1997; Ehleringer et al., 2001).

As climatic zones change due to climate change, so too will the productivity, composition, diversity and spatial extent of ecosystems as well as plant dominance patterns and community evenness (Suffling & Scott, 2002; Bates et al., 2006; Flantua et al., 2007; Kardol et al., 2010). As current ecosystems are temporary associations, they may re-sort into different assemblages as a response to climate change (Anderson et al., 1998). Species distributions are already affected by climate change (Hauer et al., 1997; Morin & Chuine, 2005; Morin et al., 2008; Rehfeldt et al., 2002; Hamann & Wang, 2006; Gómez-Mendoza & Arriaga, 2007; Pucko et al., 2011), and large-scale (altitudinal or latitudinal) biogeographical shifts in vegetation are predicted in response to the altered precipitation and temperature regimes (Scheller & Mladenoff, 2005; Parmesan, 2006; Adams et al., 2009; Feeley et al., 2011; Fridley & Wright, 2012; Alo & Wang, 2008; Valle-Díaz et al., 2009; Kupfer & Cairns, 1996). Projections of the response of the biosphere to global climatic change indicate 50% to 90% spatial displacement of extratropical biomes. The mechanism of spatial shift could be dominated by either competitive displacement of northern biomes by southern biomes, or drought-induced dieback of areas susceptible to change (Neilson et al., 1992). These shifts have profound ecological impacts and are an important climate-ecosystem feedback through their alteration of carbon, water, and energy exchanges of the land surface (Adams et al., 2009).

Secondary interactions (such as indirect effects of climate change on fire intensity and ozone pollution, altered disturbance regimes) also play an important role in vegetation change (Malanson & Westman, 1991; Beckage et al., 2006). Environmental responses to global change are likely to be nonlinear and thus complex (Malanson, 2001). This results in the fact that surprises are more likely than precise prediction. Besides, species interactions also strongly influence responses to changing climate and may overturn direct climatic effects and reverse community trajectories (Suttle et al., 2007).

Climate predictions suggest that changes in species' distributions will accelerate in the future (Morin et al., 2008; Allen & Breshears, 1998). Theoretically, long-range migration can play a significant role in species distribution (He et al., 2003). If climate changes at a moderate rate, species will be able to migrate and track suitable conditions that match their niche (Hewitt, 1996, 2000; Ackerly, 2003). However, the rate of human-induced climate change may exceed the physiological capabilities of some species to migrate to areas with tolerable climate limits (Anderson et al., 1998). Species which are unable to keep pace with changing range limits may experience a reduction in population size and exist in climatic disequilibrium (Dyer, 1994; Dyer, 1994b). Besides, even if a population disperses to a new region with a favourable climate, interactions with other species may prevent its establishment and further spread (Ibanez et al., 2009). Increasing temperatures and severe droughts may cause high mortality in the trailing range edge of the distribution of mountain or high-latitude plant communities, driving the species to rapid range shifts and range boundary disturbances, species replacement, and community alterations (Lenoir et al., 2008; Jump et al., 2009; Mátyás, 2010). Furthermore, human dominated landscapes will function as barriers to migration for many species (Suffling & Scott, 2002). As a consequence, many species have already suffered reductions in habitable area due to recent climate change (Parmesan, 2006). Northern ecosystems may be particularly vulnerable to climate change due to greater-than-average predicted temperature increases at higher latitudes (Körner & Larcher, 1988; Kattenberg et al., 1996).

Species respond individually to climate change (Gleason, 1926; Chuine, 2001), as all of them have different climatic tolerances (Eeley et al., 1999). Thus, predicted distribution shifts are species-specific just as they were during past climate changes (Davis, 1989; Graham, 1992; Webb, 1992). As their dispersal rate also differs, different species will not face the same risks due to climate change (Morin et al., 2008; He et al., 2003). Changes in plant community composition will result from shifting competitive abilities and seed dispersal mechanisms of individual species (Malanson & Westman, 1991; Davis, 1986; Webb, 1986; Malanson, 1993). Several authors suggest that forest communities do not respond as units (Davis, 1981; Webb, 1987; Huntley, 1991), thus, formation of novel communities can be expected as well (Pucko et al., 2011). However, permanent vegetation change will occur only if not only tree mortality patterns but tree recruitment patterns are also affected (Suarez & Kitzberger, 2008). Pucko et al. (2011) add that future species responses may become increasingly divergent as the magnitude of climate change increases since species-specific environmental thresholds will be reached and the synergistic effects of multiple anthropogenic perturbations will rise.

After discussing climate change induced vegetation shifts in the Palearctic region in our former article (Garamvölgyi & Hufnagel, 2013), in this paper we summarize observed and simulated changes of community composition and range shifts in America, based on literature available in Web of Science. Results are presented according to geographical regions, focusing on main trends and phenomena.

Projections for North America in general

Simulations for North American tree species for the 21st century by Morin et al. (2008) show that local extinctions may occur in the south of species ranges, and colonisation of new habitats is expected in the north, although these are limited by dispersal ability for most species. The loss of habitats southward will be mostly due to increased drought mortality and decreased reproductive success, while northward colonisation will be primarily promoted by increased probability of fruit ripening and flower frost survival. Morin et al. (2008) also concluded that local extinction may proceed at a slower rate than forecasted so far because of the local adaptation of the species.

Shafer et al. (2001) also conducted simulations for tree and shrub species in North America for 2090-2099 and found large changes in the potential distribution of species (*Table 1*). They also showed that shifts are mainly driven by increases in temperature and changes in the moisture index, and that the pattern of vegetation response to climate change is strongly mediated by topography. According to their results, ranges will shift not only northward and upward in elevation but in all directions. Simulated potential range expansions in eastern North America, where topographic relief is relatively low, occur in a northward direction with increases in the mean temperature of the coldest month. Simulated west-to-east potential range changes along the prairie-forest border are primarily related to changes in the moisture index. In contrast, in western North America, the simulated patterns of change in potential ranges are more disjunct, often with large distances occurring between a species' current distribution and simulated areas of future potential habitat (e.g. in the case of *Pseudotsuga menziesii*, Douglas fir).

Potential distributions of *Betula papyrifera* (paper birch) and *Picea glauca* (white spruce) are simulated to expand northward. However, while the southern range limit of *Picea glauca* contracts northward, the southern range limit of *Betula papyrifera* expands southward in the Rocky Mountains. As for the boreal tree species, relatively large areas of their current range remain suitable under future climate scenarios. In the mid-continent, potential ranges of both species are simulated to contract due to decreases in the moisture index.

In the intermountain region of the US, potential range of *Artemisia tridentata* (big sagebrush) is expected to shift northward in response to increases in the mean temperature of the coldest month, leading to a significant contraction of its current range. Increases in fire frequency under future climate scenarios could also facilitate the simulated potential range contractions because *Artemisia tridentata* does not resprout following fire events (Smith et al., 1997).

The simulated potential range of *Yucca brevifolia* (Joshua tree) is fragmented and displaced northward and eastward. Two desert species, *Carnegiea gigantea* (saguaro) and *Larrea tridentata* (creosote bush) also show significant potential range shifts. Potential range of *Larrea tridentata* is predicted to expand throughout the intermountain regions of the West into areas currently dominated by *Artemisia tridentata*. The potential range of *Carnegiea gigantea* is simulated to expand as well, with new habitats occurring both west and east of its current range. In the mountains of western Mexico, increased temperatures coupled with a lower moisture index may lead to potential range contractions of *Pseudotsuga menziesii* and *Pinus ponderosa* (ponderosa pine).

In the Pacific Northwest, potential ranges of high-elevation species, such as *Abies amabilis* (Pacific silver fir), are simulated to contract due to increases in temperature. Many Pacific Northwest species are simulated to shift from west of the Cascades and northern Sierras to the east of these mountain ranges. Affected are both conifer species, such as *Pseudotsuga menziesii* and *Taxus brevifolia* (Pacific yew), as well as broadleaf species, such as *Alnus rubra* (red alder) and *Quercus garryana* (Oregon white oak). Species which can tolerate relatively warm and dry conditions, such as *Pinus ponderosa* and *Quercus lobata* (California white oak) are simulated to expand into the area west of the Cascades and northern Sierras. Shafer et al. (2001) also concluded that many new areas of suitable bioclimatic habitat will be small and relatively isolated under the future climate scenarios, thus habitat fragmentation resulting from human land-use activities will have a significant impact on the abilities of species to disperse in response to changing climate conditions.

Table 1. *Simulated changes in distribution of certain species for 2090–2099 (Shafer et al., 2001)*

Species	Direction of range shift	Change of range size
Betula papyrifera	northward, southward	expansion
Picea glauca	northward	contraction, expansion
Artemisia tridentata	northward	contraction
Yucca brevifolia	northward, eastward	
Carnegiea gigantea	westward, eastward	expansion
Pseudotsuga menziesii		contraction (in Mexico)
Pinus ponderosa		contraction (in Mexico)
Abies amabilis		contraction
Pseudotsuga menziesii	eastward (in the Pacific NW)	

Taxus brevifolia	eastward	
Alnus rubra	eastward	
Quercus garryana	eastward	
Pinus ponderosa	westward (in the Pacific NW)	
Quercus lobata	westward	

Canada

Projected changes in climate

Temperature change in continental areas of Canada may be twice the global average at 50° N and 3.5 times at 80° N (Etkin et al., 1998). On a countrywide scale models predict increased temperatures, but these are quite variable on a regional scale (Bouchard, 2001). Suffling and Scott (2002) observed a universal warming trend in all national parks of Canada, with greater temperature increases in winter, and most dramatically in the arctic region. As for precipitation, there is generally a large increase in winter in the Prairie parks, and especially large winter increases are seen in the arctic region. However, two mainland arctic parks are predicted to experience decreased winter precipitation. Furthermore, decreased summer precipitation is projected for all regions from Ontario westward. According to Bouchard (2001), increased aridity could be critical in some Prairie areas. Extreme events could be more frequent, with serious negative effects. In northern areas, warming trends will provoke permafrost degradation, development of thermokarsts and soil instability. A sea-level rise is anticipated as well, which will make the coasts of Prince Edward Island, New Brunswick and Nova Scotia vulnerable to submersion risks.

Projected changes in vegetation

In Canada, climate change represents an unprecedented challenge to national parks (Scott et al., 2002). Biomes are expected to shift northward (Bouchard, 2001) and according to modelling results, 37-48% of Canada's protected areas could experience a substantial change in terrestrial biome type under doubled atmospheric CO_2 conditions (Lemieux & Scott, 2005). In simulations by Scott et al. (2002), a novel biome type appeared in more than half of the national parks and greater than 50% of all vegetation grid boxes changed biome type. The proportional representation of tundra and taiga/tundra declined, while more southerly biomes (temperate forests and savanna/woodland) increased. Results for boreal forest varied among the climate change scenarios. In contrast, Schneider et al. (2009) suggest that 12-21% of Alberta's boreal region will be converted to parkland and grasslands will shift northward into much of the existing parkland.

Suffling and Scott (2002) studied expected changes in Bruce Peninsula National Park and found that the anticipated drop in water level will dry the marshes and fens bordering the shoreline in many areas and dryland plants may colonise the upper fringes of the marsh complex. Decreased summer and autumn precipitation will result in a lower water table and increased drought conditions. As a consequence, marsh complexes will dry out more often and may be colonised by white cedar (*Thuja occidentalis*), resulting in a loss of plant diversity. Many plant communities may shift to more xeric species, while other species with high drought tolerance may thrive in the new conditions (e.g. *Hymenoxis acaulis*, angelita daisy). According to simulations by

Lenihan and Neilson (1995), temperate summergreen vegetation community will remain dominant or possibly shift to mixed grass prairie vegetation and invasion by southern exotic species is expected as well.

For Atlantic Parks, Suffling and Scott (2002) predict the expansion of mixed and deciduous forest and the reduction of boreal forests, as well as reduction, isolation and extirpation of arctic-alpine species and communities. In Great Lakes – St. Lawrence Basin Parks, reduction of wetland areas, expanding mixed and deciduous forest, less boreal forest and expansion of southern exotics are expected. Hogenbirk and Wine (1991) also suggest that in mid-boreal wetlands, Eurasian species might dominate early successional communities due to the shift of seasonally flooded vegetation zones from flood-driven dynamics with cool and moist environmental conditions towards drought- and fire-driven dynamics with warmer and drier conditions. In Western Cordillera Parks, some alpine assemblages may disappear from mountain peaks, beside the latitudinal and altitudinal migration of ecozones. Loss of higher elevation alpine species is predicted for Pacific Parks as well, while in Arctic Parks the northward expansion of tree line is expected. Overall, the emergence of transitory ecological communities is predicted for the latter half of the 21st century, however, ecosystem-level response to climate change will never be entirely predictable (Myers, 1995; Malcolm & Markham, 1996).

Role of fire and soils

Distribution of boreal biome subzones in central Canada is largely governed by fire occurrence (Suffling, 1995). Forecasted rise in surface air temperatures and lower summer precipitation will likely lead to increased fire season length and area burned in forested regions (Stocks et al., 1998; Flannigan et al., 1998, 2000, 2005; Bélanger & Pinno, 2008). The twofold increase in annual area burned in western North America in the last 40 years is probably linked to climate warming (Kasischke & Stocks, 2000). Areas with dry macro- or microclimate or coarse-textured soils may be particularly susceptible to more frequent fire (Larsen, 1997). Due to this, Hogg and Hurdle (1995) assume that the Boreal Plain ecozone will shrink and give way to the Prairie ecozone. Bélanger and Pinno (2008) concluded that forests supported by sandy glacio-fluvial parent materials will be the first to be impacted. In contrast, stands supported by imperfectly or poorly drained glacio-lacustrine parent materials will be less susceptible to change because of more available water and nutrients, and will thus likely take a longer time for the transition from aspen to herbaceous vegetation. Forests supported by glacial till soils may be better buffered against warming and will likely resist invasion of herbaceous vegetation for longer compared to glacio-fluvial sites. The eventual shift from forest to herbaceous vegetation due to warming will also be favoured by increased fire disturbance (Axelrod, 1985; Romme et al., 1995). Lafleur et al. (2010) also assume that soil properties may constrain species migration, locally or regionally. Thus, these antagonistic forces (warming and soil characteristics) are likely to slow down potential tree migration in response to climate change. Because tree species respond individualistically to climate variables and soil properties, new tree communities are also likely to emerge.

At the forest-tundra boundary in eastern Canada, forest degradation is triggered by unusual fire events that interact with climatic stresses on conifer seed production and lead to failures of post-fire regeneration (Payette et al., 2001). Changes in fire interval may alter patterns of forest regeneration and cause shifts between deciduous- and conifer-dominated succession trajectories (Suffling, 1995; Frelich & Reich, 1999; Dale et al., 2001). The same is confirmed by Johnstone and Chapin (2006), who found that young-burned stands had a much higher probability of regenerating to deciduous dominance than mature-burned stands in conifer-dominated boreal forests of northwestern Canada, despite the dominance of both groups by spruce (*Picea mariana* and *Picea glauca*) and pine (*Pinus contorta*) before the fire.

Concerning the rate of vegetation changes, Chapin et al. (2004) suggest these may be gradual at the northern forest limit or where seed dispersal limits species distribution. However, forest composition may be quite resilient to climate change in the central portions of a species range until some threshold is surpassed. At this point, changes can be rapid and unexpected, often causing a switch to very different ecosystem types.

Changes in Arctic vegetation

Several studies suggest that changes to Arctic vegetation such as increases in shrub abundance may result from increasing temperature (Stafford et al., 2000; Kaplan et al., 2003; Hassol, 2004; Johannessen et al., 2004; Tape et al., 2006; Notaro et al., 2007). According to observations, tall shrub tundra (vegetation dominated by tall shrubs, e.g. *Alnus viridis*, tall *Salix spp.* and *Betula glandulosa*) is encroaching into areas of dwarf shrub tundra (vegetation dominated by dwarf shrubs, e.g. *Ledum decumbens*, *Vaccinium vitis-idaea*, *Arctostaphylos rubra*, *Rubus chamaemorus* and sedges, e.g. *Eriophorum vaginatum*, *Kobresia hyperborea*) across the entire circumpolar region (Silapaswan et al., 2001; Sturm et al., 2001a; Stow et al., 2004; Tape et al., 2006). In the Mackenzie Delta region, the gradual transition between shrub and dwarf shrub suggests that this ecotone may be particularly sensitive to warming (Epstein et al., 2004a). Lantz et al. (2010) also found strong correlation between summer temperatures and vegetation type, which shows that increasing temperatures in the region (Lantz & Kokelj, 2008) are likely to alter shrub abundance and shift the position of this ecotone. Plot level manipulations of temperature and nutrient availability further support predictions that warming will increase shrub dominance in the Low Arctic (Parsons et al., 1994; Chapin et al., 1995; Bret-Harte et al., 2001, 2002; Dormann & Woodin, 2002; Walker et al., 2006). On the other hand, other vegetation communities such as lichen and moss decrease in cover fraction and biomass in response to warming (Olthof & Latifovic, 2007). The expansion of tall shrub tundra is likely to have long-term impacts also on permafrost temperatures and terrain stability across the Low Arctic (Sturm et al., 2001a; Epstein et al., 2004b; Chapin et al., 2005; McGuire et al., 2006).

United States of America

Changes in climate

According to simulations by Lenihan et al. (2008a), relatively large increases in temperature and decreases in precipitation will be the general climatic trends in the eastern half of the United States. In contrast to the East, increases in precipitation accompanied by relatively small increases in temperature are the general projections for the West. Izaurralde et al. (2005) came to similar results. According to their simulations, large and contrasting regional changes can be expected in both precipitation and temperature. The extremes include significant warming in the north-eastern region of the country, almost no change in mean annual temperature in the south-eastern part, significantly drier conditions primarily in the southern half of the U.S. and the West may be much wetter than it is today. These predictions are surprising regarding the results of Grundstein (2009), who evaluated moisture trends between 1895–2006. Grundstein (2009) concluded that the eastern half of the country has been getting wetter in the 20th century, even as temperatures have continued to increase in many areas. In particular, conditions have become wetter in the South, Northeast and East North Central regions as wetter conditions have expanded westward across the Central United States. On the contrary, many studies predict a drier climate in the central United States with an increasing likelihood of severe droughts (IPCC, 2001). Warming has been found across much of the United States, including the Northeast, West and northern Midwest, while a slight cooling trend was found in the Southeast (Lu et al., 2005; Groisman et al., 2004; Lund et al., 2001). Precipitation has also shown positive trends across the United States (Groisman et al., 2004). The western half of the country has shown higher air temperatures but no consistent pattern in precipitation.

Changes in vegetation

According to their climate simulations, Izaurralde et al. (2005) suggest that climate change may increase net primary productivity slightly in the north-eastern quarter of the country and a bit southward from it, as well as in the coniferous forest of the Pacific northwest. Major losses may occur especially in the southeast. Overall, increases in net primary productivity can be expected in the west and decreases in the east.

However, the large number of future climate change scenarios used suggests that there is considerable uncertainty about possible future ecological impacts, particularly since some scenarios produce opposite sign ecological responses (Bachelet et al., 2001; Lenihan et al., 2008a). Although a number of model predictions have suggested that future climate change (including drought) will lead to extensive forest dieback and species migration (Leverenz & Lev, 1987; Solomon, 1986; Pastor & Post, 1988), such sensitivity has been questioned as well (Fischlin et al., 1995; Loehle, 1996; Loehle & LeBlanc, 1996). Loehle (1996, 1998) suggested that current models of forest response might overestimate negative responses to climate change and concluded that forests would not suffer catastrophic dieback, but would instead be replaced gradually by faster growing tree species over longer time periods. Besides, according to simulations by Neilson and Drapek (1998), transient or stepwise changes in climate have beneficial rather than negative impacts on vegetation. They also concluded that moderate warming could produce increased vegetation growth over broad areas in the United States but greater warming could also produce large areas of drought stress. Simulations by Melillo et al. (1995) also resulted in both gains and losses of total forest area depending on the scenario. Investigating impacts of drought disturbance on forests of the United States, Hanson and Weltzin (2000) found that dramatic shifts in forest productivity and/or composition in the eastern United States as a result of intensification of drought over the next few decades are unlikely to be widespread. They concluded that it is still unclear which level of drought is required to kill or severely constrain growth of mature trees. However, forests growing in shallow soils with reduced water storage capacity would respond more than forested regions with annual late-season droughts. In contrast, Williams et al. (2000) suggest that significant displacement of biome boundaries can occur even in response to rather moderate warming.

It is also still unclear, just like in Europe (Garamvölgyi & Hufnagel, 2013), whether communities will be able to keep pace with changing climate. Davis and Shaw (2001) argue that migration and adaptation would be hampered by the unprecedented rates at which climate appears to be changing in combination with ongoing changes in land use. According to Izaurralde et al. (2005), simulated land use changes are expected to be the most dramatic in the West.

Grundstein (2009) found that over the period 1895–2006, the most dramatic change has occurred across the Midwestern prairie peninsula (previously classified as tall grass prairie), where the wetter conditions have lead to a westward expansion of conditions favourable for oak-hickory-pine vegetation. Oak-hickory-pine has expanded into the South as well, where it replaces loblolly pine (*Pinus taeda*). Similarly, conditions suitable for tall grass have expanded westward into areas previously classified as short grass.

Bachelet et al. (2001) simulated vegetation distribution in the United States for the end of the 21st century and came to controversial results. Over 40% of the coniferous forests are replaced by savannas under one of the scenarios, however, under all other scenarios, coniferous forests expand slightly. Temperate deciduous forest shifts to more northern locations and is replaced by either the southeast mixed forest or savannas under most scenarios. Northeast mixed forests are replaced by either savannas or the northward-shifting temperate deciduous forest in the Great Lakes region, due to warmer and drier climatic conditions. Southeast mixed forests are replaced mostly by savannas or partially by grasslands under the two warmer scenarios. However, these savannas may recover to forests by the end of the 21st century. Tropical forests appear as a new vegetation type mostly in Louisiana, along the Gulf Coast in the Southeast, where they replace the original southeast mixed forest. The area covered by all forest types tends to decrease by the end of the 21st century under the warmest scenarios, however, moderately warm scenarios produce increases in forest area of about 20%. As for shrubland area, decreases are simulated under most scenarios, except for some, where shrubs replace grasses in areas of the Great Plains. Most shrubland losses occur in the Great Basin, where increased precipitation drives the replacement of shrubs by savannas. Savannas are simulated to increase by more than 50% under warm scenarios, however, they may also decrease according to another model. The area occupied by grasslands may remain stable, increase or decrease. Simulations for the western United States show 60% or greater reductions in the area of deserts under most scenarios due to significantly increased precipitation, a 20% increase in desert area is predicted only under the warmest scenario. Boreal forests in the Northeast shift northwards, and taiga-tundra and tundra are expected to decrease by more than 80% by the end of the 21st century, due to increases in temperature. Western coniferous forests increase in area in most simulations. Overall, Bachelet et al. (2001) observed the same trends which are typical in Europe (Garamvölgyi & Hufnagel, 2013): warming produces a northward shift of the various eastern forest types and an altitudinal shift of the taiga-tundra and tundra vegetation types. However, steep mountain slopes with unstable or poorly developed soils may limit the upslope migration of forests.

Bachelet et al. (2001) also concluded that forest areas are more sensitive than non-forest areas to potential future temperature increases. This is confirmed by the prediction according to which an average annual temperature increase of 4.5 °C could produce a reduction in vegetation density over about 50% of US forest lands, while the remaining lands would experience increased growth. An overall increase can be expected in vegetation density with moderate warming, resulting in forest expansion across the United States. However, greater warming can lead to lower vegetation density and conversions of forests to savannas and grasslands. Neilson and Drapek (1998) came to the same result, suggesting that an early green-up may be possible in response to a moderate warming, followed later by vegetation density declines due to temperature-induced droughts. According to Bachelet et al. (2001), biomes that appear most sensitive to elevated temperatures include the temperate deciduous forest and the southeast mixed forest. Conifer forests show some indication of increased sensitivity with increasing temperature, but their overall response is less clear.

Table 2. *Simulated changes in vegetation in the U.S. by the end of the 21st century (Bachelet et al., 2001)*

Vegetation type	**Model**	**Scenario**	**Character of change**
coniferous forest	MAPSS	UKMO	reduction, replaced by savannas
		all except UKMO and GISS	expansion
	MC1	CGCM1	expansion
temperate deciduous forest	MAPSS	all except HADCM2SUL	reduction, northward shift, replaced by southeast mixed forest or savannas
		HADCM2SUL	expansion
	MC1	CGCM1	reduction
		HADCM2SUL	expansion
northeast mixed forest	MAPSS	UKMO, GFDL	reduction, replaced by savannas
		all except UKMO and GFDL	reduction, replaced by temperate deciduous forest
	MC1	CGCM1	reduction
		HADCM2SUL	expansion
southeast mixed forest	MAPSS	UKMO, CGCM1, GFDL	reduction, replaced by savannas
		UKMO, CGCM1	reduction, replaced partially by grasslands
		all except HADCM2SUL	reduction, replaced by tropical forest
	MC1		stable
tropical forest	MAPSS	HADCM2SUL, CGCM1	expansion
	MC1	HADCM2SUL, CGCM1	expansion
shrubland	MAPSS	all except UKMO and HADCM2SUL	reduction, replaced by savannas

	MC1	HADCM2SUL, CGCM1	expansion
grassland	MAPSS	UKMO, HADCM2SUL	reduction, replaced by shrubland
		UKMO	expansion
		HADCM2SUL	reduction, replaced by savannas
	MC1	HADCM2SUL, CGCM1	reduction
savanna	MAPSS	UKMO, CGCM1, GFDL, HADCM2SUL	expansion
	MC1	HADCM2SUL, CGCM1	reduction
desert	MAPSS	HADCM2SUL, HADCM2GHG, CGCM1, GFDL	reduction
		UKMO	expansion
	MC1	HADCM2SUL, CGCM1	reduction
taiga-tundra and tundra	MAPSS		reduction
	MC1	HADCM2SUL, CHCM1	reduction

Table 2 shows that GCM scenarios can generate significant differences in the simulated future response of ecosystems and the same is confirmed by Lenihan et al. (2008a). In contrast to Bachelet et al. (2001), Lenihan et al. (2008a) included in their simulations fire regime as well, and came to different results assuming unsuppressed or suppressed fire (*Table 3*). Considering the role of fire may be important as Bachelet et al. (2003) predict an increase in total biomass burnt in the 21st century.

Table 3. *Simulated changes in vegetation in the U.S. for the period 2070–2099 under different fire regimes (Lenihan et al., 2008a)*

Vegetation type	Fire regime	Character of change
temperate conifer forest	unsuppressed fire	expansion
	suppressed fire	expansion
cool mixed forest	unsuppressed fire	reduction
	suppressed fire	reduction
tropical forest	unsuppressed fire	expansion
	suppressed fire	expansion
grassland	unsuppressed fire	expansion
	suppressed fire	reduction, replaced by woodland
woodland/savanna	unsuppressed fire	expansion
	suppressed fire	reduction, replaced by forest

shrubland	unsuppressed fire	reduction
	suppressed fire	reduction, replaced by woodland
subalpine forest	unsuppressed fire	reduction, replaced by temperate forests
	suppressed fire	reduction
alpine	unsuppressed fire	reduction, replaced by temperate forests
	suppressed fire	reduction

Under future climate with unsuppressed fire, the most significant change in vegetation distribution is the widespread expansion of woodland/savanna both in the Southeast, where it replaces forest, and in the interior West, where it replaces shrubland (Lenihan et al., 2008a). Besides, a near complete loss of alpine and subalpine forest vegetation can be observed in favour of temperate forest types, a northward shift of forest-type boundaries in the East, and a reduction in the extent of cool mixed forest in the Northeast. Under future climate with suppressed fire, forests in the Southeast remained stable. In the West, there is a widespread conversion of shrubland to woodland and woodland to forest. The woody encroachment also extends into the Central Plains where grassland and shrubland will be converted to woodland.

Although Bachelet et al. (2001) and Lenihan et al. (2008a) included different aspects in their simulations, comparing *Table 2* and *Table 3*, one can see that they came mainly to similar results. The direction of simulated changes is the same in both studies.

Table 4 shows results of simulations conducted by Izaurralde et al. (2005). They used a bit different vegetation types and twelve climate change scenarios, which considered increases in temperature and CO_2 concentration. In contrast to Lenihan et al. (2008a), fire disturbance was not taken into account.

In order to have a better overview, *Table 5* summarizes the main future trends simulated by the above mentioned three authors regarding several vegetation types. As Bachelet et al. (2001) considered two models and several scenarios, it was necessary to simplify, thus only the most likely changes (predicted by the most scenarios) are displayed in *Table 5*.

Table 4. *Simulated changes in vegetation in the U.S. (Izaurralde et al., 2005)*

Vegetation type	Character of change
boreal deciduous forest/woodland	expansion
boreal conifer forest/woodland	reduction
temperate/boreal mixed forest	reduction
temperate conifer forest	expansion
temperate deciduous forest	expansion
tropical deciduous forest	expansion (new vegetation type)
moist savanna	reduction
dry savanna	reduction
tall grassland	reduction
short grassland	reduction
xeric woodlands/shrub	expansion

arid shrubland/steppe	expansion or reduction
desert	expansion

Table 5. ***Comparison of simulated future changes in vegetation in the U.S. according to different authors (↑ = expansion, ↓ = reduction, – = not mentioned)***

Vegetation type	Bachelet et al. (2001)	Lenihan et al. (2008a)	Izaurralde et al. (2005)
boreal deciduous forest	–	–	↑
boreal conifer forest	↑	–	↓
temperate deciduous forest	↑ / ↓	–	↑
temperate conifer forest	↑	↑	↑
northeast mixed forest	↓	↓	↓
southeast mixed forest	↓	–	–
tropical forest	↑	↑	↑
savanna	↑ / ↓	↑ / ↓	↓
shrubland	↑ / ↓	↓	↑ / ↓
grassland	↓	↑ / ↓	↓
desert	↓	–	↑
tundra / alpine	↓	↓	–

It can be observed that predicted changes are not always clear. All three authors agree that temperate conifer forests as well as tropical forests are expected to expand, while northeast mixed forest is likely to decrease. Tundra and alpine vegetation is also predicted to lose area, however, trends regarding savanna and shrubland vary.

Alaska

Expected changes in environmental factors

According to climate change scenarios and observations, the greatest magnitude of warming will occur at high latitudes (45-65° N), with the most marked effects within the continental interiors (Hansen & Lebedeff, 1987; Lashof & Ahuja, 1990; Houghton et al., 1996; Kattenberg et al., 1996; Serreze et al., 2000; IPCC, 2001; Christensen et al., 2007). In Alaska, a warming trend of 0.75 °C per decade has been identified for the last three decades of the 20th century over land bordering the Bering Sea (Chapman & Walsh, 1993; Serreze et al., 2000). Some authors expect an increase of 3-8 °C in air temperature in the Arctic within the next 50 years (Hansen & Lebedeff, 1987; Maxwell, 1992), while others suggest a rise of 1-2 °C over 20 years and 4-5 °C over 100 years

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(BESIS, 1997). Chapin et al. (1995) suggest that regional climatic warming may already be altering species composition of Alaskan arctic tundra. Warming can affect plant community composition, biomass and productivity directly through warmer air and soil temperatures (Kane et al., 1992; Maxwell, 1992) and indirectly through alteration of soil water and nutrient availability. Increased air temperature directly stimulates plant growth and plant species shifts across a range of tundra ecosystems (Arft et al., 1999; Jonasson et al., 1999; Dormann & Woodin, 2002; van Wijk et al., 2003; Walker et al., 2006), and also stimulates soil warming and nutrient release from soil organic matter (Schuur et al., 2007). However, increased nutrient availability, in particular nitrogen, also increases plant growth and shifts species composition in many well-drained tundra ecosystems (Jonasson et al., 1999; Shaver et al., 2001; Dormann & Woodin, 2002; van Wijk et al., 2003; Mack et al., 2004; Czóbel et al., 2013; Walker et al., 2006). In addition, warming can cause permafrost (permanently frozen soil) to thaw and thermokarst (ground subsidence) to develop, which can alter the structure of the ecosystem by altering hydrological patterns within a site (Schuur et al., 2007). Nitrogen also may increase in availability as permafrost thaws (Shaver et al., 2001; Mack et al., 2004). The altered moisture regime promotes mesophilic mosses (Camill, 1999) and vascular plants in some areas (Lloyd et al., 2003), while preventing growth of other species (Jorgenson et al., 2001). The indirect effect of changing moisture regime on soil nutrient availability is also likely to affect plant growth and species composition (Schuur et al., 2007). Overall, the net effect of warming on vegetation and ecosystem dynamics is likely to be strongly dependent on moisture status following thaw (Oechel et al., 1994; Camill, 1999). Other authors emphasize an overriding influence of nutrient limitation on tundra production in the Low Arctic and suggest that environmental factors are expected to affect net primary production of the whole ecosystem only if they alter nutrient availability (Jonasson, 1992; Shaver et al., 1992). On the contrary, shoot growth of plants of individual species responds sensitively to changes in light, temperature and nutrients (Chapin & Shaver, 1985; Shaver et al., 1986, Parsons et al., 1994). The response of the species may, however, cancel out at the ecosystem level due to a redistribution of resources among species in the community (Chapin et al., 1995).

Vegetation changes – compositional shift in tundra

At high latitudes, even relatively small changes in temperature could have large consequences to boreal and tundra ecosystems (Viereck et al., 1986). Alaska's North Slope is especially vulnerable to climatic change; vegetation changes result there from the interplay of climate, vegetation response and landscape processes (Kittel et al., 2011). Climate-related changes will depend not only on the magnitude and direction of temperature and precipitation shifts, but also on storm and high wind event frequency and intensity. In the High Arctic, under warmer air temperatures and longer growing seasons, areas with sparse vegetation and deep active layers may develop a thicker and more wide-spread layer of moss (Epstein et al., 2004a). Moist non-tussock tundra responds to warming with conversion to wetlands and expanding thaw lakes as the active layer deepens and ground subsides (Kittel et al., 2011).

As for the Low Arctic, upland moist acidic tundra is the most common vegetation association and it is highly sensitive to climate warming (Epstein et al., 2004a). Paleoenvironmental studies support the conclusion that climatic change has the potential to alter current boundaries between moist non-acidic tundra and moist acidic tundra, with warming favouring moist acidic tundra (Kaufman et al., 2004). However, it is still unclear how quickly such a conversion could occur. The shift from non-acidic to acidic tundra in the mid-Holocene took on the order of centuries to millennia (Oswald et al., 2003). In their research, Schuur et al. (2007) found that aboveground plant biomass ranged from being dominated by sedges (graminoids, such as *Eriophorum vaginatum*), to becoming increasingly dominated by deciduous and evergreen shrubs (including *Rubus chamaemorus*, *Vaccinium uliginosum* and *Betula nana*) and mosses across the studied sites as thermokarst became more developed. It means that plant species and functional group shifts among sites are driven by changes occurring at the microsite level, via changes in microclimate that accompanied ground subsidence. Changes in hydrology produced by ground subsidence create a wide range of microenvironments that affect plant species composition and growth as well. Shrubs and moss prefer warm and moist sites, whereas graminoids dominate cold and dry sites.

Chapin et al. (1995) did not consider topographical changes when conducting manipulation experiments in moist tussock tundra in Alaska. Although they found contrasting responses to temperature increase and to nutrient addition by different growth forms, they came to similar results as Schuur et al. (2007) regarding changes in dominance of life forms. Chapin et al. (1995) concluded that some of the manipulations altered nutrient availability, biomass, growth-form composition, net primary production and species richness in less than a decade, indicating that arctic vegetation is sensitive to climatic change. However, short-term responses were poor predictors of longer term changes in community composition. According to their results, nitrogen and phosphorus availability tended to increase in response to elevated temperature, reflecting increased mineralization (cf. Schuur et al., 2007). Nutrient addition increased biomass and production of deciduous shrubs but reduced growth of evergreen shrubs and nonvascular plants. Elevated temperature enhanced shrub production but reduced production of nonvascular plants. At the end of the long-term treatment, deciduous shrubs dominated, and graminoids, evergreen shrubs, and nonvascular plants declined. Species richness was reduced by 30-50% by temperature and nutrient treatments, due to loss of less abundant species. In summary, resources required for growth (i.e., nutrients and light) appeared to be more critical than temperature in determining plant biomass in tussock tundra.

Shrub expansion

Increased temperatures have been observed to promote shrub expansion on the North Slope and also elsewhere in Alaska over recent decades (Chapin et al., 1995; Shaver et al., 1998; Sturm et al., 2001b; Tape et al., 2006; Strack et al., 2007; Lawrence & Swenson, 2011). The fact that moist tussock tundra would give way to moist low shrub tundra (Epstein et al., 2004a; Kittel et al., 2011) is supported by field manipulation experiments as well (Chapin & Shaver, 1996; Bret-Harte et al., 2001; Hobbie & Chapin, 1998; Shaver et al., 2001; Jonsdottir et al., 2005). However, in contrast to the study by Schuur et al. (2007), increased shrub abundance in some fertilizer treatments correlated with decreased moss abundance, as canopy closure decreased growth and survival of nonvascular mosses and lichens (Chapin & Shaver, 1996; Shaver et al., 2001). Arft et al. (1999) again came to different results, concluding that increases in deciduous shrub and graminoid cover together occurred across sites, whereas nonvascular cover decreased. However, initial responses in productivity may not entirely reflect the long-

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term trajectory of species dominance (Hollister et al., 2005). Overall, a warmer and wetter climate would promote peat formation and shrub expansion, in contrast, a warmer and drier climate may foster drier upland tundra landscapes (Kittel et al., 2011). According to Epstein et al. (2004a), the transition between tussock tundra and low shrub tundra appears to be responding most rapidly to climatic warming as this transition correlates more strongly with climate than with other environmental variables, besides, dominant species exhibit gradual changes in abundance and they have demographic properties that allow rapid increases in abundance following climatic shifts. Shrubs can achieve dominance potentially within a decade, whereas spruce trees often require several decades to centuries to achieve dominance within tundra, and Sphagnum moss colonization of non-acidic sites may require centuries to millennia of soil development (Epstein et al., 2004a).

Compositional change in boreal forests

Global vegetation models predict that boreal forests are particularly sensitive to a biome shift during the 21st century (Beck et al., 2011). In the boreal forest region of Alaska, the average mean annual temperature increased 1.6 °C from 1949 to 1999 (Stafford et al., 2000). Increased growing season and warmer temperatures over the next century are predicted to generate increases in forest in northern Alaska (Euskirchen et al., 2009; Barrett & Gray, 2011). However, thermokarsts can collapse boreal forests, to be replaced over time by meadows, bogs and lakes (Osterkamp et al., 2000). Barrett & Gray (2011) suggest that the boreal region is suspected to be a significant possible source of greenhouse gases as climate warms.

Climatic warming and associated increases in nutrient availability are expected to enhance the probability of white spruce (*Picea glauca*) surviving on the North Slope (Kittel et al., 2011). Rupp et al. (2000) suggest that the most plausible change from upland tundra in response to climatic warming is to conifer forest due to invasion of white spruce forest, because this is the forest type that most commonly occurs south of the Alaskan arctic tree line (Bliss & Matveyeva, 1992; Starfield & Chapin, 1996). The same is confirmed by Brubaker et al. (1983) and by Barrett and Gray (2011) as well. However, the Brooks Range may be an effective barrier to northward migration and expansion of this species (Kaufman et al., 2004; Rupp et al., 2000). Besides, Juday and Solomon (2000) observed significant declines in white spruce growth rates after 1976 when summer air temperatures increased. Thus, drought stress could be a controller of production and survival of these trees. Calef et al. (2005) predict that black spruce (*Picea mariana*) will remain the dominant vegetation type under all scenarios, potentially expanding most under warming coupled with increasing fire interval.

According to Juday and Solomon (2000), species of deciduous poplar and aspen (*Populus spp.*) trees appear to be better adapted to warmer and drier summer conditions than white spruce. Simulations by Leemans (1991) and Prentice et al. (1993) predict a gradual elimination of conifer species and an increase in abundance of hardwood species such as oak (*Quercus sp.*) with winter warming scenarios. The same is confirmed by Potter (2004), who suggests that taiga forests of interior Alaska have changed markedly over the past 50 years of climate warming, and whose projections predict a shift from dominance by evergreen needleleaf trees (taiga) to mixed broadleaf–needleleaf tree composition in the future. This is consistent with observations by Roland (1999) as well, who found increased colonization by paper birch (*Betula papyrifera*) seedlings with climate warming in forest plots in Alaska. Besides, following fire, early successional broad-leaved deciduous shrubs and trees (Larsen, 1965; Viereck, 1973; Payette & Gagnon, 1985) replace white spruce forests. Calef et al. (2005) suggest that deciduous forests will expand their range the most in the case of decreasing fire interval, warming or increasing precipitation.

Overall, similar changes are predicted by Beck et al. (2011), who suggest that evergreen forests will expand into current tundra while being replaced by grasslands or temperate forest at the biome's southern edge throughout interior Alaska, due to drought-induced productivity declines. According to simulations by Rupp et al. (2000), tundra could be converted to forest within 200 years, however, partial barriers may slow this conversion by 300–400 years. Simulations by Bachelet et al. (2005) show that 75-90% of the area simulated as tundra in 1922 will be replaced by boreal and temperate forest by the end of the 21st century. Ultimately, tree dispersal rates, habitat availability, the rate of future climate change and how it changes disturbance regimes, are expected to determine where the boreal biome will undergo a gradual geographic range shift, and where a more rapid decline (Beck et al., 2011). Calef et al. (2005) concluded that tundra can be replaced by forest under warming but is expected to expand under precipitation increase.

The successional switch of broad-leaved deciduous forest to white spruce forest can be accelerated by both heavy moose browsing pressure and extremely cold climate (Kielland et al., 1997). 1982). Grasslands occur under dry conditions in the boreal forest zone (Edwards & Armbruster, 1989). Under cold climatic conditions dry grassland may switch to upland tundra (Starfield & Chapin, 1996; Chapin & Starfield, 1997), however, a switch from upland tundra to dry grassland may also occur under extremely dry conditions. Dry grassland will switch to a broad-leaved deciduous forest type under not too dry climate conditions if a seed source exists (Rupp et al., 2000).

Role of natural disturbances

Natural disturbances further complicate direct impacts from temperature increase (Barrett & Gray, 2011). Barrett & Gray (2011) suggest that not only direct climate–plant interactions may cause range shifts, but other disturbance events such as outbreaks of spruce beetles. Besides, spatial features (e.g., topographic barriers) and processes, including disturbance propagation and seed dispersal, largely control the pattern and rate of short-term transient changes (Rupp et al., 2000). Under future climate change scenarios, fire emissions and the area burned are expected to increase (Bachelet et al., 2005) as longer and warmer summers can increase fire frequency, which in turn affects permafrost and alters rates of dispersal and growth for boreal species (Rupp et al., 2002; Wirth et al., 2008). According to Rupp et al. (2000), topographic barriers have little influence on fire size in low-flammability vegetation types (such as upland tundra and broad-leaved deciduous forest), but reduce the average fire size and increase the number of fires in highly flammable vegetation (e.g. dry grassland). Bachelet et al. (2005) suggest that by the end of the 21st century Alaska may become a net carbon source. The role of fire is underlined by the fact that changes in fire severity can have more effect on post-fire community composition than environmental factors (moisture and pH) do (Bernhardt et al., 2011).

California

Changes in environmental conditions

California is one of the most climatically and biologically diverse areas in the world (Lenihan et al., 2003). According to predictions, California may experience substantially warmer and wetter winters, somewhat warmer summers, and an enhanced El Niño Southern Oscillation during the 21th century (Field et al., 1999; Gutowski et al., 2000). However, Urban et al. (2000) suggest that although current general circulation models all predict warmer temperatures for California under enhanced CO_2 scenarios (VEMAP, 1995), the models do not agree on the direction of change in precipitation. These projected changes are proven by trends in the recent past as well. Southern California's climate warmed at the surface, the precipitation variability increased, and the amount of snow decreased between 1977 and 2006-2007 (Kelly & Goulden, 2008).

Vegetation changes

According to simulations by Diffenbaugh et al. (2003), vegetation in the western United States is sensitive to changes in atmospheric CO_2 concentrations, with woody biome types replacing less woody types throughout the domain. It is also sensitive to climatic effects, particularly at high elevations, due to both warming throughout the domain and decreased precipitation in key mountain regions such as the Sierra Nevada of California and the Cascade and Blue Mountains of Oregon.

A change in climate is expected to shift plant distribution as species expand in newly favourable areas and decline in increasingly hostile locations (Kelly & Goulden, 2008). According to a study by Kelly and Goulden (2008) in Southern California's Santa Rosa Mountains, the average elevation of the dominant plant species rose approximately 65 m between 1977 and 2006-2007, which appears to be a consequence of changes in regional climate. On the contrary, Crimmins et al. (2011) suggest that climate changes in California have also resulted in a significant downward shift in species' optimum elevations. Although this downhill shift is counter to what would be expected given 20th-century warming, it can be explained by species' niche tracking of regional changes in climatic water balance rather than temperature. Similar downhill shifts can be expected to occur where future climate change scenarios project increases in water availability that outpace evaporative demand. However, Lutz et al. (2010) predict declining water availability and increasing climatic water deficit for Yosemite National Park, California, resulting in accelerating changes in forest structure and composition in the future.

In Californian tidal marshes, salinity has increased because of water diversion and sea level has risen as well since 1975, which lead to the increased cover of the most salt-tolerant plant species (*Sarcocornia pacifica*, Pacific swampfire), whereas *Schoenoplectus californicus* (California bulrush), the least salt-tolerant plant species, decreased in cover (Watson & Byrne, 2012). Besides, accelerated sea level rise resulted in the large-scale replacement of *Distichlis spicata* (seashore saltgrass) predominantly by *Schoenoplectus americanus* (chairmaker's bulrush) (Watson & Byrne, 2012).

Lenihan et al. (2003) simulated future vegetation distribution for the period 2070–2099 using two models, the Hadley Climate Center HADCM2 model (HAD) and the National Center for Atmospheric Research Parallel Climate Model (PCM) (*Table 6*, *7* and *8*).

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Table 6. *Simulated changes in vegetation for 2070–2099 in California (Lenihan et al., 2003)*

Vegetation classes	HAD	PCM
alpine / subalpine forest	partly replaced by evergreen conifer forest	partly replaced by shrubland
evergreen conifer forest	partly replaced by mixed evergreen forest; net increase	partly replaced by mixed evergreen woodland; partly replaced by mixed evergreen forest; net loss
mixed evergreen forest	expansion; partly replaced by evergreen conifer forest	partly replaced by mixed evergreen woodland
mixed evergreen woodland	partly replaced by mixed evergreen forest; partly replaced by evergreen conifer forest	partly replaced by grassland; net decline
grassland	expansion; partly replaced by mixed evergreen forest	
shrubland	partly replaced by mixed evergreen forest; partly replaced by evergreen conifer forest	partly replaced by grassland; net decline
desert	partly replaced by grassland	

Table 7. *Regional examples for vegetation changes according to HAD in California (Lenihan et al., 2003)*

Replaced	Replaced by
Douglas-fir–white fir forest	Douglas-fir–tan oak forest
white fir–ponderosa pine forest	ponderosa pine–black oak forest
blue oak woodlands	tan oak–madrone–canyon live oak forest
chaparral	tan oak–madrone–canyon live oak forest; coast live oak–madrone; canyon live oak–Coulter pine; redwood and closed-cone pines
perennial grassland	tan oak–madrone–canyon live oak forest
live oak woodlands	coast live oak–madrone; canyon live oak–Coulter pine
northern juniper woodland	ponderosa pine–Jeffrey pine forest
sagebrush scrub	ponderosa pine–Jeffrey pine forest
canyon live oak–madrone forest	redwood and closed-cone pines
subalpine parks and meadow	red fir and lodgepole pine

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Table 8. *Regional examples for vegetation changes according to PCM in California (Lenihan et al., 2003)*

Replaced	Replaced by
northern juniper woodland	grassland
sagebrush scrub	grassland
oak woodland communities	grassland communities
chaparral	grassland communities
Douglas-fir–tan oak forest	northern oak woodland
Douglas-fir–white fir forest	northern oak woodland
alpine meadow communities	whitebark pine krummholtz

In summary, according to Lenihan et al. (2003), the HAD scenario predicts a warmer and wetter climate resulting in the expansion of forests and in a net increase in evergreen conifer forest. However, the simulated life-form composition is expected to change from needleleaf dominance to mixed needleleaf-broadleaf in the northern half of the state. In addition to widespread advancement of forests, another prominent feature of the response of vegetation distribution under the HAD scenario is the advancement of grassland. Under the drier and cooler PCM scenario, the expansion of grassland is predicted along with a net decline in evergreen conifer forest, mixed evergreen woodland and shrubland.

Using other climate scenarios, Lenihan et al. (2008b) came to similar results. Predicted changes include significant declines in the extent of alpine/subalpine forest due to longer and warmer growing seasons; the replacement of evergreen conifer forest by mixed evergreen forest with increases in temperature, or by woodland, shrubland or grassland with increases in fire; and an increase in the extent of mixed evergreen forest. Furthermore, a decline in mixed evergreen woodland and shrubland as well as the expansion of grassland are expected. These results are confirmed by Rehfeldt et al. (2006) as well.

In contrast to the previous studies, Urban et al. (2000) suggest that besides temperature and precipitation, supply and demand components of the water balance should be considered as well. Although temperature and precipitation can predict the location of the mixed conifer zone, several species can co-occur within this zone, as defined by the spatial scaling of microtopography and soils. Under climatic change, species might move around within this zone, more mesic species being displaced to deeper soils or more northerly exposures, while more xeric species to shallower soils or more southerly exposures.

Zavaleta et al. (2003) showed that relative dominance of functional groups may shift in grasslands due to increases in temperature, precipitation, CO_2 concentration and N deposition. They found that grassland diversity and composition were sensitive to all four of the individual global changes, supporting the fact that grasslands containing fast-growing or short-lived species are especially responsive to climate change (Grime et al., 2000). According to their experiments, the largest change in relative functional group abundance (expansion of forbs) occurs under the combination of elevated CO_2 + warming + precipitation (Zavaleta et al., 2003), which will likely affect much of California in the future (Giorgi et al., 1994). Thus, forbs – which include most of the remaining native species in Californian grasslands (Hickman, 1993) – could be the group of species in grasslands most vulnerable to environmental changes, including climate and atmospheric changes. Zavaleta et al. (2003) also suggest that individual species are more sensitive to temporal variation and extremes than to multiyear, mean changes in resource availability and environmental conditions, which is consistent with predictions by IPCC (2001).

Southwestern USA

Changes in environmental conditions

Climate models predict a warmer and drier climate throughout the southwestern U.S. in the 21st century (Seager et al., 2007; Solomon et al., 2009). Warmer temperatures and increasing frequency of droughts should cause major shifts in plant community composition and structure (Allen, 2007; Williams & Jackson, 2007) in this region via differences in mortality and drought adaptations among woody species.

Susceptibility for invasion

Plant population dynamics in arid and semiarid lands is highly dependent on water availability, thus, under future climate change these systems are expected to be drastically affected by changes in precipitation and temperature (Kerkhoff et al., 2004; Suazo et al., 2012). Changing precipitation regimes (such as changes in the amount and timing of precipitation and increases in large rainfall events) may enhance the susceptibility of habitats to invasion by non-native plant species (Weltzin et al., 2003; Bradley, 2009). Besides, this kind of susceptibility may be increased by increases in nutrient availability (Davis et al., 2000) and soil disturbance (Burke & Grime, 1996; Huston, 2004) as well since the spread and establishment of non-native plant species can be facilitated by the physical condition and resource availability of the invaded habitat (Davis et al., 2000; Burke & Grime, 1996). Invasive species compete with natives for water and soil nutrients (Brooks, 2000), and non-native species are often more efficient than natives at capturing these resources and utilize them for seed production (Monaco et al., 2003; Huxman et al., 2008; DeFalco et al., 2003). In the Mojave Desert, an experiment by Suazo et al. (2012) showed that invasion success increased with availability of unused water, at least for the grass *Schismus* spp. (Mediterranean grass). *Schismus* seemed to have the greatest invasive potential at the studied sites, as it positively responded to water availability and soil disturbance. Others have also observed similar responses by *Schismus* to increased levels of water availability (James et al., 2006; Gutierrez & Whitford, 1987; Pake & Venable 1995). Beside water availability, soil N has been suggested to be a co-limiting factor for non-native plant establishment in the Mojave Desert (Brooks, 2003; Rao & Allen, 2010; James et al., 2006). Although it is difficult to predict future patterns of invasibility, an increase in water availability and disturbance is likely to enhance invasibility in this ecosystem (Weltzin et al., 2003; Bradley et al., 2009; Bradley, 2009; Bradley, 2010).

Drought-induced mortality

Drought-induced woody plant mortality has increased globally recently and has been associated with increasing temperatures (Breshears et al., 2005; Allen et al., 2009b; van Mantgem et al., 2009; Adam et al, 2009). Accelerated plant mortality over the next century, induced by climate warming and drought (Hansen et al., 2006; IPCC, 2007; Allen et al., 2009a; Kintisch, 2009), is predicted to be especially pronounced in mountain forests of the southwestern U.S. (Rehfeldt et al., 2006; Seager et al., 2007). Adams et al. (2009) showed that experimentally induced warmer temperatures shortened the time to drought-induced mortality in *Pinus edulis* (pinyon pine), and projected increases in drought frequency due to changes in precipitation and increases in stress from biotic agents (e.g. bark beetles) could further exacerbate mortality. Shifts in vegetation distribution are expected to be most rapid and extreme at ecotones, the boundaries between ecosystems, particularly those in semiarid landscapes (Allen & Breshears, 1998). According to Allen and Breshears (1998), the most rapid landscape-scale shift of a woody ecotone ever documented occurred in northern New Mexico in the 1950s, where the ecotone between semiarid ponderosa pine (*Pinus ponderosa*) forest and pinon-juniper (*Pinus edulis*, *Juniperus monosperma*) woodland shifted extensively (2 km or more) and rapidly (in less than 5 years) through mortality of ponderosa pines in response to a severe drought. This shift has persisted for 50 years. Forest patches within the shift zone became much more fragmented, and soil erosion greatly accelerated.

The southwestern U.S., and Arizona in particular, experienced near record warm temperatures and drought during the spring and summer of 2002 (Waple & Lawrimore, 2003; Andreadis et al., 2005; Weiss et al., 2009), and plants were under severe water stress by the fall of 2002 (Simonin et al., 2006; Gaylord et al., 2007; Breshears et al., 2009). Studying an ecotone between ponderosa pine-dominated forests and pinyon–juniper-dominated woodlands in Arizona during the 2002 drought, Koepke et al. (2010) found little difference in mortality among soil parent materials for individual species or groups of trees and shrubs. They observed greater canopy dieback for shrubs than trees; mortality, however, did not differ between groups. Juniper, the dominant tree with the lowest elevational range, had the lowest mortality of all tree species. In contrast, canopy dieback during severe drought appeared to be a survival mechanism for juniper and to a lesser extent for pinyon pine, but not for ponderosa pine. As a consequence, overall tree cover will be reduced as the community shifts from a mixture of species to more monotypic stand of junipers due to high pine mortality. In addition, surviving junipers and shrubs will likely have diminished leaf area due to canopy dieback. The same is confirmed by Allen and Breshears (1998) and by Müller et al. (2005) as well, who observed higher mortality among reproductively mature trees and survival of smaller pinyons. As approximately 1000 species are associated with pinyon pine, the shift in the structure of these woodlands is expected to have large-scale community consequences.

Shifts in ecosystem types

Ecotones between oak (*Quercus* sp.) woodlands and semi-desert grasslands of the southwestern United States and northwestern Mexico have been relatively stable over the past several centuries (Weltzin & McPherson, 2000b). However, predicted changes in regional precipitation patterns and soil moisture caused by anthropogenic trace gas emissions have the potential to alter interactions between woody plants and grasses with potential ramifications for their relative abundance and distribution. According to a field experiment conducted by Weltzin and McPherson (2000b) in Arizona, *Quercus emoryi* (Emory oak) recruitment and subsequent abundance and distribution would more likely be affected by changes in summer precipitation than changes in winter precipitation. Thus, increases in summer precipitation may facilitate downslope shifts in the woodland-grassland ecotone.

As the above examples also show, temporal or spatial shifts in ecosystem types at biome transition zones are often characterized by changes in the dominant species or life form (Gosz & Sharpe, 1989). In New Mexico, large-scale shifts could be observed in dominance from grasses to shrubs over the past 50–100 years (Buffington & Herbel, 1965; Peters et al., 2012). According to a biogeographic modelling analysis, an increase in grasslands and decreases in woody vegetation are expected for parts of the southwestern US (Neilson & Drapek, 1998). Studying transitions between Chihuahuan desert and shortgrass steppe biomes, Peters (2002) also predicted shifts in dominance following directional changes in climate due to modifications in the availability of soil water. In his model, the Chihuahuan desert grass, *Bouteloua eriopoda* (black grama) dominated both sandy loam soil and loamy sand soil following a change in climate that increased summer precipitation. However, increases in winter precipitation predicted by alternative climate scenarios presumably would favour shrubs (*Larrea tridentata*, creosotebush) and grasses that respond to cool temperatures, such as *Bouteloua gracilis* (blue grama).

The importance of water availability is emphasized by Snyder & Tartowski (2006) as well, who suggest that oscillations between rainfall pulses and intervening dry periods can potentially shift the biological dominance of ecosystems. According to paleoecological records, vegetation in the Northern Chihuahuan Desert has shifted between shrublands in more arid periods, grasslands under more mesic conditions and woodlands during the wettest periods during the past 20,000 years (Van Devender, 1995; Monger, 2003). Wetter winters and drier summers likely facilitated the grass to shrub conversion during the last century (Gao & Reynolds, 2003). Increased shrub cover can be associated with both greater aridity and increased winter precipitation as shrubs have relative advantage over grasses due to their ability to access deeper soil moisture (Snyder & Tartowski, 2006). The importance of winter precipitation for woody shrubs is supported by an analysis showing greater woody plant abundance in sites with lower mean annual precipitation and a greater proportion of winter rainfall (Paruelo & Lauenroth, 1996). It is the amount and seasonality of precipitation that varies at the scale of decades that may determine which of the two functional plant types predominate. Whereas, annual or within-season variation in precipitation influences the relative productivity of the two functional types (Snyder & Tartowski, 2006). Peters et al. (2002) suggest that multiple wet years are needed to initiate a sequence of grass establishment and survival processes that can maintain upland grasslands.

Atmospheric CO_2 enrichment may alter not only the composition but even the structure of grassland vegetation (Polley et al., 2012). According to an experiment conducted by Polley et al. (2012) in tallgrass prairie assemblages in Texas, CO_2 enrichment would increase the grass contribution to community production, and favour tall-grasses over mid-grasses. The observed increase in *Sorghastrum nutans* (yellow indiangrass) was accompanied by an offsetting decline in production of the mid-grass *Bouteloua curtipendula* (sideoats grama).

Due to global climate change, stream flow regimes are also being altered (Stromberg et al., 2010). In the American Southwest, increasing aridity is predicted to cause declines in stream base flows and water tables, whereas another potential outcome of climate change is increased flood intensity. These changes may affect vegetation, e.g. increased stream intermittency would cause the floodplain plant community to shift from hydric pioneer trees and shrubs (*Populus spp.*, *Salix spp.*, *Baccharis spp.*) towards mesic species (*Tamarix spp.*) (Stromberg et al., 2010). This shift in functional type would produce changes in vegetation structure, with reduced canopy cover and shorter canopies at drier sites. Among herbaceous species, annuals would increase while perennials would decrease. If flood intensities increased, there would be shifts towards younger tree age, expansion of xeric pioneer shrubs and replacement of herbaceous perennials by annuals. Increased flood intensity would have positive feedback on disturbance processes, by shifting plant communities towards species with less ability to stabilize sediments.

Eastern USA

Changes in vegetation distribution

The change in the equilibrium distribution of natural vegetation over eastern North America over the next 200 to 500 years could be larger than the overall change during the past 7000 to 10000 years and equivalent to the change that took place over the 1000-3000-year period of the most rapid deglaciation (Overpeck et al., 1991). Some plant ranges and abundance maxima could shift as much as 500 to 1000 km during the next 200 to 500 years, and such changes would have dramatic impacts on natural ecosystems. Lassiter et al. (2000) predict a considerable northward shift of both northern and southern boundaries of the biomes in the mid-Atlantic region.

Annual temperature in New England is projected to increase by 2.2-3.3 °C by 2041-2070 and by 3.0-5.2 °C by 2071-2099 with corresponding increases in precipitation of 4.7-9.5% and 6.4-11.4%, respectively (Tang & Beckage, 2010). According to simulations conducted by Tang and Beckage (2010), regional warming will result in the loss of 71-100% of boreal conifer forest in New England by the late 21st century. The range of mixed oak-hickory forests will shift northward by 1.0-2.1 latitudinal degrees (c. 100-200 km) and will increase in area by 149-431% by the end of the 21st century. Northern deciduous hardwoods are expected to decrease in area by 26% and move upslope by 76 m on average. These shifts coincide with an approximate 556 m upslope retreat of the boreal conifer forest by 2071-2099. However, rising atmospheric CO_2 concentrations are expected to reduce the losses of boreal conifer forest from expected losses based on climatic change alone. These predictions are in line with recent trends. Beckage et al. (2008) found a 19% increase in dominance of northern hardwoods between 1964 and 2004 in the northern hardwood-boreal forest ecotone in the Green Mountains, Vermont, and observed a 91- to 119-m upslope shift in the upper limits of this ecotone. Pucko et al. (2011) found evidence that species elevational distributions and community compositions have shifted in response to a 0.49 °C per decade warming in Vermont. These species responses were complex and largely individualistic at some elevations, while at other elevations species in a given community tended to respond similarly. As for the alpine zone in New York State, Robinson et al. (2010) observed that vegetation composition changed significantly between 1984 and 2007, with an overall decrease in bryophytes/lichens and an increase in vascular plants, indicating that vascular plants were replacing bryophytes, particularly in areas not disturbed. Ibanez et al. (2007) suggest that communities found at higher elevations are in danger of regional extinction if their habitats disappear given the current climatic trends.

Due to rapid global warming, displacement of individual species is predicted as well, such as that of *Pinus taeda* (loblolly pine), which may shift over 400 km northward with only a narrow region of overlap between the current and projected future range limits (Dyer, 1994). However, potential migration rates may fall short by at least an order of magnitude of that necessary to track projected range shifts. Iverson et al. (2004) also confirmed that there can be a serious lag between the potential movement of suitable habitat and the potential for the species to migrate into the new habitat. According to their results, the proportion of new habitat that might be colonized within a century is low (< 15%) for all studied species, such as *Diospyros virginiana* (persimmon), *Liquidambar styraciflua* (sweetgum), *Oxydendrum arboreum* (sourwood), *Pinus taeda* (loblolly pine) and *Quercus falcata var. falcata* (southern red oak).

Coastal ecosystems

Although increases in precipitation are predicted for New England (Tang & Beckage, 2010), climate change may result in increased drought as well. Drought is a primary cause of mortality for island shrub and tree species (Ehrenfeld, 1990). Besides, coastal plant communities are expected to be the first to be affected by the projected increase in sea level resulting from global warming (Ehrenfeld, 1990). The current relative sea-level rise is quoted as 1.5-2 mm/year along the eastern shore of Virginia (Hayden et al., 1991) and it will affect swale vegetation more than dune vegetation (Shao et al., 1995).

On the barrier islands of the eastern Atlantic Coast of the USA, shrub (*Myrica cerifera*, wax myrtle) thickets are a major vegetation type (Shao et al., 1995). According to simulations, Shao et al. (1995) found that transpiration patterns of shrub thickets are sensitive to environmental changes including climatic change and sea-level rise. Variations in transpiration with environmental changes are physiological readjustments to the changing environments, which may result in ecological readjustment, such as distributional shifts. Results show that air temperature is less important than humidity in determining shrub thicket distributions on barrier islands, and changes in precipitation patterns are more significant than changes in quantity. Furthermore, soil water, which may rise due to sea-level rise (Ehrenfeld, 1990), is a limiting factor to the transpiration of shrub thickets and thus it plays an important role in determining the distribution of this vegetation type. As a consequence, changes in successional processes and distribution patterns of shrub thickets are sensitive indicators of climatic changes.

Effects of drought

Not only on barrier islands, but in many other ecosystems as well, drought acts as a disturbance that may initiate large-scale changes in community structure and composition (Tilman & El Haddi, 1992; Allen & Breshears, 1998; Condit, 1998; Scheffer et al., 2001; Delissio & Primack, 2003, Malatinszky et al., 2013a, 2013b). Droughts generally result in decreased productivity, diversity and establishment, increased rates of mortality and altered nutrient cycling in the community (Bollinger et al., 1990; Tilman & El Haddi, 1992; Condit et al., 1995; Sternberg et al., 1999; Penksza et al., 2009, 2011, 2013; Szentes et al., 2010, 2011a, 2011b; Delissio & Primack, 2003; O'Neill et al., 2003; Hanson & Weltzin, 2000). One mechanism by which communities change with disturbances such as drought is through changes in the rate of species turnover (Yurkonis & Meiners, 2006) since drought can open a temporal colonization window where new species enter the neighborhood (Grime et al., 1994; Davis & Pelsor, 2001; Bartha et al., 2003, 2009, 2013).

According to the results of a field study focusing on a 2-month drought event within an early successional forest system in New Jersey (Yurkonis & Meiners, 2006), drought had little long-term effect on neighbourhood structure (species richness and cover) and generated only subtle changes in neighbourhood composition. Ruderal (annual and biennial) species were more likely to change in cover and frequency due to their limited storage of nutrients and shallow root systems than the more stress tolerant perennial and woody species. Following drought, native and exotic ruderal species tended to increase in cover and frequency across the site. However, population dynamics appeared to be unpredictable and generally driven by stochastic species turnover among fields, not by large-scale shifts in species abundance. Thus, stochastic fine-scale processes can generate predictable coarse-scale dynamics within a disturbed system.

Schultheis et al. (2010) suggest that the projected increase in evapotranspiration coupled with atmospheric nitrogen deposition may lead to the drying up of bogs in the Southern Appalachian Mountains, which can lead to the system becoming a carbon source rather than a sink and to local extinction of many bog species allowing alternative ecosystems to replace the bogs.

Woody encroachment

It has been observed that abandoned crop- and pasturelands across the eastern part of North America transition from annual and perennial herbs and grasses to various states of woody dominance (Clements, 1916; Oosting, 1942; Keever, 1950; Bazzaz, 1968; Meiners et al., 2002). However, the time required for woody species to achieve dominance varies on the order of decades (Abel, 1941; Bard, 1952; Bazzaz, 1968), e.g. in the Northeast USA, fields can persist as herbaceous assemblages for more than fifty years (Mellinger & McNaughton, 1975), whereas fields in the Southeast typically transition to closed pine stands in less than a decade (Oosting, 1942; Keever, 1950). Wright and Fridley (2010) documented a clear latitudinal pattern, where the time after field abandonment required to reach certain percent of woody cover increased severalfold from the southern to the northern part of the studied area. This latitudinal pattern was associated with climatic variation, variation in soil fertility, which is generally higher in the soils of the Northeast (von Englen, 1914), and differences in the species pools of both herbaceous and woody pioneer species between regions. According to Wright and Fridley (2010), fields of the Northeast may favour herbaceous persistence due to more fertile soils, cooler temperatures and early successional species pools. Fridley and Wright (2012) concluded that early successional ecosystems may be less sensitive to broad-scale climatic trends because they are driven by interactions between species that are only indirectly related to temperature and rainfall. According to their results, seedlings of southern woody pioneer species are better able to quickly establish in fields after abandonment, regardless of climate regime. Sites of lower soil fertility also exhibited faster rates of seedling growth. This shows that climate plays a relatively minor role in community dynamics at the onset of secondary succession, and that species identity (growth rate) and site edaphic conditions are a stronger determinant of the rate at which ecosystems develop to a woody-dominated state.

Estuarine ecosystems

It is known that plant species composition shifts predictably along estuarine salinity gradients, with salt-tolerant halophytic plants dominating salt marshes and nonhalophytic wetland plants dominating tidal freshwater habitats (Simpson et al., 1983; Odum & Hoover, 1988; Mitsch & Gosselink, 2000). Studying tidal marsh plant communities in Rhode Island, Crain et al. (2004) found that freshwater marsh plants, when transplanted to salt marshes, did poorly and generally died. In contrast, saltmarsh plants, when transplanted to freshwater marshes, thrived in the absence of neighbours, but when neighbours were present, they were strongly suppressed. This means that biotic interactions also play a key role in driving plant distribution patterns along estuarine salinity gradients.

Charles and Dukes (2009) suggest that salt marsh communities may be resilient to modest warming and large changes in precipitation. If production increases under climate change, marshes will have a greater ability to keep pace with sea-level rise, although an increase in decomposition could offset this. As long as marshes are not inundated by flooding due to sea-level rise, they may be able to increase their carbon storage capability due to increases in aboveground biomass and stem heights under future climate conditions.

Southeastern USA

Changes in environmental conditions

Future climates in the southeastern United States are predicted to become warmer, with mean annual total precipitation declining up to 30% (Hengeveld, 2000). At the same time, heavy rainfall events are predicted to increase in the middle United States (Woodhouse & Overpeck, 1998; Easterling et al., 2000), which could cause sudden flooding in wetlands.

Mangrove and hardwood hammock ecosystems

In the Greater Everglades region of southern Florida, mangrove ecosystems and hardwood hammock ecosystems occupy overlapping geographical ranges (Odum et al., 1982; Odum & McIvor, 1990; Sklar & van der Valk, 2003). These two vegetation types are frequently in competition, although they are typically not interspersed but there are sharp boundaries between their uniform patches (Teh et al., 2008). Hardwood hammocks generally occupy areas of higher elevation, where salinities are low, while mangroves can tolerate higher salinity levels but also have the ability to grow in freshwater (Sternberg & Swart, 1987; Odum & Mclvor, 1990). There exists an equilibrium state at which both vegetation types are present, where the salinity of the vadose layer is at an intermediate level of lethality for freshwater hammock species (Sternberg et al., 2007).

Teh et al. (2008) suggest that because of climate change, sea level rise and storm surges are potential perturbations which may cause the vegetation to shift from hardwood hammocks to mangroves as an increase in salinities of the vadose zone induced by these events might eradicate the salinity-intolerant hardwood hammocks at higher elevations and promote landward migration of mangroves. This is confirmed by Doyle et al. (2003) as well, who observed that the occurrence of hurricanes is responsible for the composition of mangrove communities across southern Florida today. Besides, it is documented that mangroves have migrated approximately 3.3 km inland in the southern Everglades during the past half-century, largely at the expense of freshwater marshes and swamp forest (Gaiser et al., 2006). In their model, Teh et al. (2008) considered high salinity developed during the dry season to be the major determinant of vegetation distribution in Florida, and found that under stable environmental conditions, hardwood hammocks occupied the higher elevation cells, while mangroves occupied the lower ones, just like in nature. In the event of a light surge, hardwood hammocks were able to restore the salinity to low levels in a short time period by decreasing their transpiration rates. However, a medium surge event that saturated the vadose zone at 15 ppt caused the mangroves to invade the cells at higher elevation, and a heavy surge caused them to take over the entire study domain after 50 years. The rate of domination by mangroves in the high elevation cells after a storm surge was found to depend on the thickness or depth of the vadose zone. This modelling study also proves that changes in vegetation may occur not only through gradual changes in the environment, but also by a sudden disturbance event.

Simulations by Sternberg et al. (2007) show that the primary effect of changes in precipitation (caused by climate change) and ground water salinity (brought about by sea water intrusion) will be on the inland hammock frequency and not on the mangrove/hammock boundary. Decrease in precipitation relative to the average yearly precipitation of about 1,000 mm in South Florida will cause a significant decrease in hammock frequencies. The mangrove/hammock boundary, however, will only move inland to higher elevation when precipitation is drastically reduced. Likewise, increases in the salinity of the groundwater underlying the vadose zone will have a strong impact on the inland hammock frequency, but little impact on the mangrove/hammock boundary.

Changes in hydrological properties

Hydrological properties are considered to be a driving force in structuring wetland communities (Gunderson & Loftus, 1993; Mitsch & Gosselink, 2007); particularly, duration and depth of flooding are the major factors controlling plant distribution (Gunderson, 1994). Numerous studies have shown a relationship between Everglades hydropatterns and the plant communities found there (Armentano et al., 2006; Davis et al., 1994; Gunderson, 1994; Ross et al., 2003; Zweig & Kitchens, 2008; Zweig & Kitchens, 2009). Gunderson (1994) suggested that the hydrology of the Everglades is affected at three different temporal scales with the slow time scale being change in sea level, the intermediate scale being the return period of droughts and floods and the fast scale being the annual hydrologic regime which is dominated by seasonal variation in rainfall. Some authors have shown that vegetation change in response to hydrologic alteration can be relatively rapid (i.e. a few years) (Armentano et al., 2006; Zweig & Kitchens, 2008), while others argue that there can be a considerable time lag (Givnish et al., 2008; Ross et al., 2003). Nevertheless, changes in the hydrology due to climate change can potentially have profound impacts on the distribution and prevalence of vegetation communities (Jason Todd et al., 2010).

In coastal ecosystems, regeneration may be dictated by disturbances related to hurricanes, water fluctuation, and/or saltwater intrusion (Platt & Connell, 2003; Middleton, 2009a, b, c, d). These disturbances may increase in the future with climate change, particularly because of increased hurricane activity, sea-level rise (Michener et al., 1997), or declining freshwater input (Middleton, 1999). Other authors also confirm that water depth and salinity changes can greatly alter seed germination and seedling growth of species (Middleton, 1999, 2009a, d; Howard & Mendelssohn, 2000; Brock et al., 2005). Future environments may involve novel combinations of increased atmospheric CO_2 (IPCC, 2007b), temperature, sea level, salinity (Michener et al., 1997), precipitation (Easterling et al., 2000) and hurricane activity (Webster et al., 2005). In their experiment conducted in floating freshwater marshes in the Mississippi River Delta, Middleton and McKee (2012) observed that species richness was not affected by CO_2, water regime, salinity, or any of their interactions. However, density of germinating seeds and seedling biomass was influenced by the interaction of CO_2 with water regime and salinity level. Salinity, which reduced seedling biomass, was the main treatment driving seedling response patterns, flooding had less effect, and the influence of CO_2 was secondary to these. Other authors also mention that seed germination and/or seedling growth of most species decrease with increased salinity (Howard & Mendelssohn, 2000; Brock et al., 2005; Middleton, 2009a). As a consequence, higher CO_2 concentrations will not ameliorate stressful environments related to flooding or salinity levels, however, species dominance may change even if the total number of species does not (Middleton & McKee, 2012).

Middleton (1999b) also confirmed that water regime has a key role in the germination of wetland species. Flooding forms a barrier to the germination of most of them (van der Valk & Davis, 1978; Leck, 1989), and therefore, any climate change affecting the duration of flooding in swamps could affect the regeneration of species from the seed bank (Middleton, 2009d). A few studies suggest that seed bank densities shift spatially across regional watersheds in response to flood pulsing (Middleton, 1999b; Middleton, 2003) and disturbance (Middleton & Wu, 2008). In particular, shifts in water availability associated with climatic temperature or precipitation, are likely to have local and landscape effects on the regeneration dynamics of these ecosystems (Middleton, 2009d). Differences of seed germination in response to water regime are species-specific (Baskin & Baskin, 1998; Middleton, 1999), and an experiment conducted by Middleton (2009d) also confirms that seed banks from the same swamps respond differently to non-flooded versus flooded conditions. Thus, both drought and heavy rainfall have the potential to alter the regeneration dynamics of wetland ecosystems. Middleton (2009d) concludes that any climate change, which would alter hydrology, could limit the dispersal, germination, and regeneration of short-lived woody species from *Taxodium distichum* (bald cypress) swamps. *Taxodium distichum* may already be experiencing physiological stress related to the higher temperatures at the southern limits of its range (Middleton & McKee, 2004). With climate warming, *Taxodium distichum* populations may be extirpated near the southern extreme of the range (Crumpacker et al., 2001; Middleton & McKee, 2004).

Woody encroachment

Shirley and Battaglia (2006) also reported marsh loss along the northern Gulf of Mexico between the 1950s and the 1990s. In the Mississippi Delta, marsh was converted to open water along shorelines and in internal patches, but the majority of marsh loss was attributed to scrub-shrub encroachment. In the Coastal Plain, the main trend was replacement of agricultural areas by forest. Shirley and Battaglia (2006) concluded that marsh areas are especially vulnerable since they are not keeping pace with the spatial shifts in the aquatic to terrestrial transition as sea level rises.

In spite of investigating an old-field ecosystem instead of wetlands in the southeastern USA, Classen et al. (2010) also found that soil moisture exerted the largest influence on seedling emergence and establishment, either directly or due to other climatic change factors. Climatic change is altering communities in old-field and forested ecosystems (Chapin et al., 2000; Knapp & Smith, 2001), and multiple climate change factors, such as changes in CO_2, temperature and precipitation regimes, can interact in ways that make predicting their direct impact on ecosystems difficult (Pendall et al., 2004). It is unlikely that CO_2 concentration had any direct effect on germination and seedling emergence, however, elevated atmospheric CO_2 concentrations can lead to an increase in soil moisture (Dermody et al., 2007). Warming also affected seedling establishment primarily through its effects on soil moisture, and not directly. Besides, deleterious effects of warming were more prevalent under dry than wet conditions. However, the effect of warming was not always deleterious to establishment, for example, when elevated CO_2 was combined with warming, seedling emergence was higher. Classen et al. (2010) conclude that atmospheric and climatic change can alter the dynamics of ecosystem succession. Moreover, altered successional trajectories may result in forests with structure and function quite different from those of present forests (Mohan et al., 2007; De Deyn, 2008).

In contrast to Middleton and McKee (2012), Beckage et al. (2006) predict decreased frequency of both fires and hurricanes in the southeastern United States, and suggest that this and the CO_2 fertilization effect will shift pine savannas towards a forested state.

The Great Lakes region

Predicted changes in forest communities

General circulation models predict temperature increases of 3.11-3.67 °C and precipitation increases of 2-14% over the southern Great Lakes region (Illinois, Indiana and Ohio) (Ehman et al., 2002), whereas for northern Wisconsin, even larger temperature changes (up to 5.8 °C) are projected (Scheller & Mladenoff, 2005). Global climate change is expected to affect the growth, distribution and species composition of forests at several spatial and temporal scales (Graham et al., 1990; Randolph & Lee, 1994; Loehle & LeBlanc, 1996; Schenk, 1996; Lindner et al., 1997; Scheller & Mladenoff, 2005). Ehman et al. (2002) examined the possible responses of tree species to a twofold CO_2-changed climate scenario, and found an overall decrease in total basal area for northern conifers and northern deciduous species. The total basal area of intermediate and southern species increased only slightly under the effects of climate change (with the exception of northern red oak – *Quercus rubra*, the basal area of which decreased). *Table 9* shows how population centroids of different species groups are expected to shift under baseline as well as changed climate conditions by 2060. Ehman et al. (2002) also predicted how population centroids of regionally dominant species will shift after 80 years (*Table 10*).

Table 9. *Direction of predicted shifts for different species groups under baseline and changed climate conditions and predicted distance between the baseline and changed climate centroids by 2060 (Ehman et al., 2002)*

	Under baseline conditions	**Under changed conditions**	**Distance between centroids**
Northern conifers	east-southeast	north-westward	252.6 km
Northern deciduous species	eastward	northward and eastward	140.2 km
Intermediate species		eastward	22.4 km
Southern species		north-eastward	32.0 km

Table 10. *Direction of predicted shifts of regionally dominant species under baseline and changed climate conditions by 2060 (Ehman et al., 2002)*

	Under baseline conditions	**Under changed conditions**
White oak (*Quercus alba*)	stationary	eastward
Pignut hickory (*Carya glabra*)	stationary	eastward
Black oak (*Quercus velutina*)	eastward	eastward
Northern red oak (*Quercus rubra*)	southwest	eastward
Sugar maple (*Acer saccharum*)	eastward	north-eastward
American beech (*Fagus grandifolia*)	southward	north-eastward

According to the simulations, a significant change will be the loss of northern conifers and northern deciduous species from the study region. Under changed climate conditions, sugar maple (*Acer saccharum*) and thus the northern deciduous group may be eliminated. These results are in line with other studies suggesting that for northern conifer and northern deciduous species' populations, climate change either initiates a northward shift of the current range, a decline in dominance, or complete extirpation (Zabinski & Davis, 1989; Randolph & Lee, 1994; He et al., 1999). He et al. (1999) showed similar decreases in northern coniferous and some northern hardwood species in Wisconsin, predicting that the biomass of red pine (*Pinus resinosa*), quaking aspen (*Populus tremuloides*) and big-toothed aspen (*Populus grandidentata*) will decrease under a 5 °C temperature increase. Thus, these species might not be able to establish under warmer conditions.

For the intermediate and southern species, the effect of climate change is expected to be minor (Ehman et al., 2002). However, these results differ from those of other authors. Randolph and Lee (1994) reported community- and species-level responses of midwestern forests under a twofold CO_2 changed climate scenario. Both the southern mixed forests and the southern oak-hickory-pine forests were predicted to expand northward from their current ranges to areas formerly occupied by northern hardwood, beech-maple, elm-ash, mixed-mesophytic, Appalachian oaks, and northern and central oak-hickory forests. In turn, ranges of these more northern forest types were predicted to shift to the north. In southern Indiana, oak-hickory forest is expected to change to a southern mixed forest dominated by southern red oak (*Quercus falcata*), post oak (*Quercus stellata*), bur oak (*Quercus macrocarpa*), and loblolly pine (*Pinus taeda*) (Randolph & Lee, 1994), which is consistent with USEPA (1998) predictions. However, the expected shift towards southern oaks and hickory may be delayed because of seed dispersal limitations (Scheller & Mladenoff, 2005). Zabinski and Davis (1989) proposed that for the Great Lakes region an increase in temperature would probably result in drier conditions due to increased evapotranspiration, so beech populations might be expected to decline.

Nevertheless, Ehman et al. (2002) add that if the time frame of the simulation had been extended, the northern species groups would have been completely eliminated, and larger increases in the southern species would have been evident. Additionally, as the mentioned shift could occur in a relatively short time, some understory woody and herbaceous species associated with the northern deciduous tree community also would probably disappear from the region if they could not adapt to conditions in the oak-hickory dominated forests. Furthermore, Ehman et al. (2002) predict the loss of genetic diversity along range margins and that relict communities may also be regionally extirpated.

The above results are partly in line with those of Ravenscroft et al. (2010), who simulated shifts in forest composition under climate change in Minnesota, taking into account forest management scenarios as well. They observed a trend toward homogenization of forest conditions due to the widespread expansion of maple (*Acer spp.*). White spruce (*Picea glauca*), balsam fir (*Abies balsamea*), and paper birch (*Batula papyrifera*) were extirpated from the landscape, and additional losses of black spruce (*Picea mariana*), red pine (*Pinus resinosa*) and jack pine (*Pinus banksiana*) were projected in the high-emissions scenario. The loss of the above species is simulated by Scheller and Mladenoff (2005) as well, regardless of disturbance scenario. Ravenscroft et al. (2010) conclude that ensuring a diversity of species and conditions within forested landscapes may be the most effective means of ensuring the future resistance of ecosystems to climate-induced declines in productivity.

Predicted changes in bog and fen communities as well as in wetlands

Weltzin et al. (2000b) conducted experiments in Minnesota in order to investigate effects of climate change on bogs (dominated by *Sphagnum* mosses, ericaceous shrubs and black spruce - *Picea mariana*) and fens (dominated by graminoids, nonericaceous shrubs and trees). They concluded that the structure and function of both bog and fen plant communities will change, in different directions or at different magnitudes, in response to global or regional warming and changes in water-table elevation. Within each community, the response of plants was life-form- and species-specific (*Table 11*). According to the results, global warming may lead to an increase in the production and abundance of woody plants (in particular bog rosemary - *Andromeda glaucophylla*) in bog communities. In addition, lowered water-table elevations will also favour woody plants (Gorham, 1991). As a consequence, warm, dry bog plots may become dominated by shrubs in the future.

Table 11. *Effects of increasing water-table elevation and infrared loading on different plant functional types in bog and fen communities (Weltzin et al., 2000b)*

Bogs

	Production of bryophytes	**Production of graminoids**	**Production of shrubs**
Increasing water-table elevation	↑	unaffected	↓
Increasing infrared loading	unaffected	↓	↑

Fens

	Production of graminoids	**Production of forbs**	**Production of shrubs**
Increasing water-table elevation	↑	↑	unaffected
Increasing infrared loading	↑	↓	unaffected

Climate change is predicted to reduce water levels of the Laurentian Great Lakes, altering coastal wetland ecosystems and potentially stimulating invasive macrophytes, such as *Typha x glauca* (white cattail) (Lishawa et al., 2010). According to a field study conducted by Lishawa et al. (2010) in intact northern Great Lakes coastal wetlands, plant community composition had shifted and became more homogeneous than it was 20 years before, due to an invasion by *Typha x glauca*. Beach ridges usually protect *Typha x glauca* from wave and seiche energy, and as water levels decline, these energy-insulating microtopographic features will likely stimulate further invasion and dominance by this species, even in high quality wetlands (Lishawa et al., 2010).

The Great Plains

Altered fire regimes have the potential to cause major changes in plant community composition and structure (Bond et al., 2005; Nowacki & Abrams, 2008). In ecotones, many species are at the limits of their natural ranges, therefore vegetation may be especially sensitive to the combined effects of increased temperatures, droughts, and changes in land use and management (Gosz, 1992; Risser, 1995). Even a small change in climate can lead to major changes in vegetation in these communities, often in combination with rapid encroachment of invasive species (Allen & Breshears, 1998; DeSantis et al., 2011). An increase in the number, severity and duration of droughts due to global climate change may lead to rapid transformations becoming more common (Allen et al., 2010).

In south-central North America, drought and decreased fire frequency were responsible for changes in the composition and structure of oak (*Quercus*)-dominated forests over fifty years (Rice & Penfound, 1959; DeSantis et al., 2010). Besides, grazing may have played a minor role as well (DeSantis et al., 2011). Although these forests had exhibited changes in dominance from xeric fire-tolerant *Quercus* to mesic fire-intolerant tree species (DeSantis et al., 2010), the most significant change was the rapid

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encroachment of the native invasive eastern red cedar (*Juniperus virginiana*) due to fire suppression in this midcontinent forest-prairie ecotone (DeSantis et al., 2011). DeSantis et al. (2011) suggest that future forests subjected to fire suppression and more frequent and prolonged droughts will likely undergo continued changes in species composition.

Frelich and Reich (2010) predict a “savannification” of the forest on the prairie-forest border, owing to the loss of adult trees. This is expected to be caused by the greater frequency of droughts, fires, forest-leveling windstorms, and outbreaks of native and exotic insect pests and diseases. As a consequence, this biome boundary is predicted to shift to the northeast just like during past episodes of global warming, but in a greater magnitude and more rapidly than as if it would be solely attributable to the direct effects of temperature change.

Intermontane basins and plateaus

Water availability is the primary constraint to plant productivity in many terrestrial biomes (Rosenzweig, 1968; Webb et al.,1986; Le Houerou et al., 1988; Churkina & Running, 1998), and it is an ecosystem driver that will be strongly affected by ongoing and future climate change (Houghton et al., 2001). The within-season distribution of precipitation events has significant effects on plant and soil processes (Novoplansky & Goldberg, 2001; Knapp et al., 2002; Fay et al., 2003; Schwinning & Sala, 2004; Sher et al., 2004; Harper et al., 2005; Sponseller, 2007) and thus, on community composition and dynamics (Graetz et al., 1988; Comstock & Ehleringer, 1992; Ojima et al., 1993; Ehleringer et al., 1999). Global climate change scenarios predict a shift to larger precipitation events with longer intervening dry intervals (Groisman et al., 1999; Easterling et al., 2000; IPCC, 2007a). Community responses to altered precipitation patterns are a direct result of the timing of water availability within the soil profile (Brown et al., 1997; Schwinning et al., 2005). Ecological processes in arid and semi-arid ecosystems are particularly sensitive to within-season dynamics (Schwinning & Sala, 2004) as chronic water limitation defines this ecosystem (Parton et al., 1981) and strongly influences its physiological characteristics and species composition (Sala et al., 1992; Chesson et al., 2004).

In their experiments conducted in Colorado, Heisler-White et al. (2008) found that larger, less frequent rainfall events resulted in greater aboveground net primary productivity in the dominant grass in the shortgrass steppe, *Bouteloua gracilis* (blue grama grass). Although no significant relationship could be identified between mean event size or dry interval length and aboveground net primary productivity, similar to analyses in other grasslands (Nippert et al., 2006; Swemmer et al., 2007), the results suggest that the relative evenness of event size in combination with event number may have important effects on ecosystem function (Heisler-White et al., 2008).

Other studies have shown that reducing storm frequency and increasing rainfall quantity per storm decreases above-ground production in tall grass prairies of the central United States (Fay et al., 2002; Knapp et al., 2002). Shifting from a winter to a spring precipitation pattern reduces productivity in the sagebrush steppe of the northern Great Basin (Svejcar et al., 2003). Besides, atmospheric increases in CO_2 and climate change also have the potential to increase the competitiveness of invasive weeds in arid lands (Smith et al., 2000). Bates et al. (2006) investigated the effects of altered timing of precipitation on vegetation dynamics in an *Artemisia tridentata spp. wyomingensis* (Wyoming big sagebrush) community in the northern Great Basin and observed that shifting precipitation distribution to a spring/summer pattern has the greatest potential

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for altering productivity, composition, and structure of *Artemisia tridentata* steppe vegetation. Annual and perennial forbs native to the system were the least resistant to a timing change, declining in density, cover, and biomass. As a consequence, a long-term shift to a spring/summer dominated precipitation pattern would lead to the forb component being lost or severely reduced, and to an increase in bare ground, with the potential to reduce ecosystem biodiversity. Increased winter precipitation combined with summer drought, however, appears unlikely to cause major changes to vegetation composition or productivity (Bates et al., 2006). Nevertheless, if temperature increases as predicted by general circulation models (NAST, 2000; IPCC, 2001), the potential exists for increased annual grass establishment into areas where it is still a minor component of the *Artemisia tridentata* ecosystem. The increase in *Bromus tectorum* (cheatgrass) is of concern as its presence has altered historic fire regimes and permanently modified Great Basin plant communities (Young et al., 1987). Thus, a warmer environment coupled with a winter precipitation regime and greater CO_2 levels would likely permit invasion and dominance by *Bromus tectorum*, particularly if fire disturbances increase (Bates et al., 2006). The results of Bates et al. (2006) also demonstrate the resilience of these communities to climate perturbation as many of the vegetation shifts did not begin until the fourth year after treatments were applied.

Rocky Mountains and the Cascades

Changes in forest communities

In Washington State, conifer species dominate forest ecosystems with hardwood species abundant only in riparian areas (Littell et al., 2010). Both snowpack declines and warmer summers are projected, thus, summer water availability for plants will likely decrease in Washington forests (Elsner et al., 2010; Mote & Salathé, 2010). Littell et al. (2010) predict that the area of forest that is severely water-limited will likely increase by the 2020s and even in a greater magnitude by the 2040s and the 2080s. These changes are projected to occur on the east side of the Cascade Mountains and west side of the Rocky Mountains in the northern part of Washington State. According to Littell et al. (2010), Douglas-fir (*Pseudotsuga sp.*) is possibly one of the most climate-sensitive species regionally, thus, it may be in increasing risk at the edges of its current range in Washington. This is probably due to increases in temperature and decreases in growing season water availability in more arid environments, e.g., in the Columbia Basin. The decline in climatically suitable habitat for Douglas-fir is most widespread at lower elevations. In pine forests, climate is likely to be a significant stressor in the Columbia Basin and eastern Cascades by the 2060s (Littell et al., 2010), and projections suggest that areas with climatic conditions favourable for lodgepole pine (*Pinus contorta*) will decrease considerably. Littell et al. (2010) also conclude that in the future, the rate of forest change (change in forest type, species composition and productivity) in response to climate change will likely be driven more by disturbances (such as increases in fire area and outbreaks by mountain pine beetle) than by gradual changes in tree populations. Sudden changes to forest structure and composition caused by stand-replacing disturbances will speed up species turnover and transitions to new structural characteristics of stands and landscapes. According to Busing et al. (2007), frequent fires of low severity can alter forest composition and structure as much or more than severe fires at historic frequencies.

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An overall decrease is predicted in pine-dominated subalpine forests in the Greater Yellowstone Ecosystem as well (Schrag et al., 2008). In simulations by Schrag et al. (2008), temperature and temperature-related variables appeared to be the most influential in the distribution of whitebark pine (*Pinus albicaulis*), whereas precipitation and soil variables dominated in the case of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). As tree-line conifers are believed to be limited by temperature, they may serve as important indicators of climate change. Romme and Turner (1991) add that the upper and lower timberline appear to be particularly sensitive to climate change. The upper timberline is likely to migrate upward in elevation in response to temperature changes, whereas the lower treeline may retreat under drier conditions or move down slope under wetter conditions. According to their simulations, the extent of alpine vegetation is expected to decrease.

Besides, species with relatively narrow niches, such as plants endemic to particular soils, may be especially vulnerable to extinction under a changing climate due to the enhanced difficulty they face in migrating to suitable new sites (Damschen et al., 2010). Damschen et al. (2010) observed sharp declines in herb cover and richness in the Siskiyou Mountains of southern Oregon. Declines were the strongest in species of northern biogeographic affinity, species endemic to the region, and species endemic to serpentine soils. Overall, herb communities have shifted to more closely resemble communities found on xeric south-facing slopes.

As for the rate of forest change, Elliott (2011) suggests that considerable lag times exist between changes in climate towards more favourable growing conditions and corresponding shifts in tree establishment at the upper tree line in the Rocky Mountains.

Changes in herbaceous communities

Results from warming experiments show that two primary microclimate effects of warming are a decrease in soil moisture and an increase in nitrogen mineralization (Harte et al., 1995; Shaw & Harte, 2001). In their experiment conducted in the Rocky Mountains of Colorado, Harte and Shaw (1995) found that in the warmed plots, aboveground biomass of forbs decreased, that of shrubs increased, and that of grasses was unchanged.

Harte et al. (2006) came to similar results in their warming experiment in a montane grassland in the Colorado Rockies. They also found an increase in the aboveground biomass of sagebrush (Harte & Shaw, 1995; Perfors et al., 2003), and an approximately compensating decline in that of forbs, especially the shallow-rooted ones (Harte & Shaw, 1995; Saveedra et al., 2003; de Valpine & Harte, 2001a), whereas biomass in grasses showed no response to warming. Harte et al. (2006) concluded that the shift in primary production is associated with shifting species composition in the plant community.

De Valpine and Harte (2001b) observed in their study on 11 forb species in a montane meadow that six of those responded to warming with significant changes either in abundance, average size, flowering, or in frost damage. Some of these were favourable responses but most of them were negative. Regarding the two most abundant species, neither water nor nitrogen had a significant effect on the aboveground biomass of *Helianthella quinquenervis* (fivenerve helianthella), whereas *Erigeron speciosus* (aspen fleabane) responded to both nitrogen and water additions, but its response to water was larger than its response to nitrogen. Its final biomass increased significantly with water addition and marginally significantly with nitrogen addition, however, it declined strongly under warming.

Central and South America

Effects of climate change on tree species

In Mexico, drier conditions are predicted mainly for the northern part. By 2050 it is generally expected that several species will lose a significant portion of their area of distribution as a result of the impact of climate change (Trejo et al., 2011). For example, *Fagus grandifolia var. mexicana* (Mexican beech) is a dominant element of the cloud forest in Eastern Mexico. Under a predicted scenario characterized by +2 °C and -20% rainfall in the region, a drastic distribution contraction of this species can be expected (Tellez-Valdes et al., 2006). Zacarias-Eslava and del Castillo (2010) predict the expansion of chaparral at the expense of temperate forest and the extinction of high-altitude species in the Sierra Juarez. Comita and Engelbrecht (2009) also confirm that predicted shifts in rainfall patterns caused by global and regional climate change are expected to alter the dynamics, composition, and diversity of seasonal tropical forests. According to their studies in Panama, lower growth and higher mortality are expected at the community level in the dry season relative to the wet season and higher mortality is predicted in the drier plateau habitat relative to the wetter slope habitat.

Changes in the position along the elevational gradient for plant species are considered as a response to climate change (Alo & Wang, 2008), particularly within the area of influence of cities, as a response to the effects of urban heat islands (Gómez et al., 1998; Jenerette et al., 2007). The impact of the urban heat island on plant community distribution has been documented in several studies (Zhao et al., 2006; Jenerette et al., 2007; Luo et al., 2007), regarding mountain areas as well (Schrag et al., 2008). When the climate gets warmer in response to the urban heat island, it can be expected that plant communities will migrate up along mountain sides, to new altitudinal limits (Lenoir et al., 2008). Studying seedling survival of *Ceiba aesculifolia* (pochote), a tropical tree species, along an altitudinal gradient in a slope facing the city of Morelia in Mexico, Valle-Díaz et al. (2009) observed a general increase in plant survival with elevation. The highest survival was found 160 m higher than the altitudinal limit of the remnant adult trees in the study area, and close to the highest limit reported for the species at a regional scale. These results suggest that establishment of *Ceiba aesculifolia* has shifted upward along the altitudinal gradient in the study area. Besides, the envelope of suitable temperatures for seedling establishment is expected to shift upward more on the south face of the mountains than in the slopes facing the north. Feeley et al. (2011) came to the same conclusion by observing in Peru that most of the studied tropical Andean tree genera shifted their mean distributions upslope in the first years of the 21st century. The mean rate of migration was approximately 2.5-3.5 vertical metres upslope per year, and abundances of tree genera previously distributed at lower elevations increased in the majority of study plots. According to Feeley et al. (2011), the observed mean rate of change is less than predicted from the temperature increases for the region, possibly due to the influence of changes in moisture or non-climatic factors such as substrate, species interactions, lags in tree community response or dispersal limitations. Nevertheless, continued slower migration of tropical Andean trees would indicate a limited ability to respond to

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increased temperatures, which may lead to increased extinction risks with further climate change.

Savannization and forest encroachment

According to Bush and Hooghiemstra (2005), the impacts of climatic changes in the tropics can be severe. Future biodiversity may depend on changes in precipitation and land use patterns (Higgins, 2007). In Colombia and Venezuela, the southern boundary of the savanna vegetation, which is transitional to tropical rainforest, has migrated in the past (Behling & Hooghiemstra, 1998). Shifts of this savanna–forest transition depend heavily on annual precipitation values and the length of the dry season, while temperature change has little impact (Hutyra et al., 2005; Flantua et al., 2007). The area of the Colombian savanna has small amplitude of annual temperature change which should not influence vegetation distribution significantly (Rippstein et al., 2001).

Collevatti et al. (2011) studied effects of climate change on savanna vegetation in Brazil and concluded that distribution of savanna tree species may be highly restricted in future climate conditions because suitable places will be localized in the most disturbed area of Brazil. For *Caryocar brasiliense* (pequi), a widespread savanna tree species, the highest levels of suitability of occurrence can be found throughout the central portion of Brazil, extending to northern South and Central America and in some core areas of the Amazon (Collevatti et al., 2011). According to projections by Collevatti et al. (2011), its overall geographical limits will be widely reduced (by about 50%) by 2050. Moreover, a distributional shift will occur in the structure of climatically suitable areas within the species' range toward the southeastern region (Diniz-Filho et al., 2010), and a strong reduction in genetic diversity is expected if habitat suitability drops below 0.5 with climate change. Although other projections inferred the savannization of tropical forests, with expansion of savanna-like vegetation in South America (Hutyra et al., 2005; Salazar et al., 2007), suitability for *Caryocar brasiliense* may be restricted to the southernmost distribution of savanna vegetation (Collevatti et al., 2011). It is also possible that this species will be unable to track the current climate change due to its pace and mainly due to the fragmentation of the habitat (Jump & Peñuelas, 2005; Hoffmann & Willi, 2008). According to Collevatti et al. (2011), the more suitable places for *Caryocar brasiliense* can be found in the most disturbed regions in Brazil in the future, with the most fragmented and degraded habitats due to human occupation. This will hold back population migration and persistence, and thus, these populations may have a limited capacity to cope with ongoing climatic changes.

Studying a forest–grassland mosaic at the southernmost limit of the Brazilian (*Araucaria*) Atlantic forest, Silva and Anand (2011) found a clear shift in vegetation cover, representing a continuous process of forest expansion. Both patch formation and border dynamics occurred simultaneously, promoting a forest encroachment of 50-100 m into grasslands in all forest–grassland borders. However, the rates of forest expansion (50–100 m for forest borders and up to 30 m radius for forest patches over the past 4,000 years) were orders of magnitude slower than what has been historically observed in other forest biomes, which could be caused by edaphic constraints (Silva & Anand, 2011). On the other hand, trees have been colonizing a well-established, stable and highly diverse grass dominated ecosystem in the study site (Behling & Pillar, 2007), which is fundamentally different from what has been observed in boreal systems, where due to low or no resistance from resident vegetation, forest expansion occurs at much faster rates.

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In contrast to the above results predicting forest expansion over savanna, Salazar and Nobre (2010) assume that tropical forests might be replaced by seasonal forests or savanna over eastern Amazonia with temperature increases of 2-5 °C, when CO_2 fertilization effect is not or partially considered. A precipitation decrease greater than 30% would also trigger the shift from tropical forest to drier biomes, such as savanna and shrubland in southeastern Amazonia. However, biome changes can be considerably smaller when the optimum fertilization effect is included.

Effects of climate change on forest communities

Several studies have shown evidence of expansion of tropical forests in different parts of the world (Dümig et al., 2008; Martinelli et al., 1996; Palmer & van Rooyen, 1998; Puyravaud et al., 1994; Silva et al., 2008). The change from a colder and drier to a warmer and wetter climate after the last glacial period has promoted the expansion of water-limited forests (Dümig et al., 2008; Silva et al., 2008). In general, trees benefit more than grasses from the warmer interglacial periods that are associated with a higher atmospheric CO_2 (Ehleringer et al., 1997). Additionally, a reduction in fire frequency as consequence of a relative reduction in grass biomass, along with greater water availability, would also favour the expansion of forests (Bond et al., 2003). Silva and Anand (2011) showed that forests have been expanding over grasslands through continuous, but very slow border dynamics and patch formation. Existing paleoevidence from southern biomes also indicates that forests have been expanding over grasslands and savannas during the past few millennia (Behling et al., 2004; Behling & Pillar, 2007; Silva et al., 2008, 2011). This process coincided with past changes in climate, but biotic feedback mechanisms also appeared to be important.

Humid tropical forests depend on abundant and regular water supply and reductions in precipitation can lead to forest retraction (Behling, 2002; Pennington et al., 2004, 2006; Silva et al., 2009). Deciduous and xeromorphic forests on the other hand are adapted to strong seasonality in terms of water availability (Furley, 2007; Furley et al., 2006), and did not respond to past shifts in climate the same way as tropical humid forests. Silva et al. (2010) showed that deciduous forests covered greater areas in the past, however, despite an increase in tree cover and a decline in grasses, the extent of xeromorphic forest has remained stable. This contrasts with research that documented the expansion of riparian forests over savannas in the same region (Silva et al., 2008), and in the Amazon and Atlantic forests in northern and southern Brazil respectively (Dümig et al., 2008; Martinelli et al., 1996). Silva et al. (2010) assume that the continuous input of organic matter is the keystone for the maintenance of the xeromorphic forest structure.

Barlow and Peres (2008) predict a widespread dieback of Amazonian forest cover through reduced precipitation and emphasize the potential role of fire in the degradation of forest ecosystems as episodic wildfires can lead to drastic changes in forest structure and composition. Several future climate change scenarios project an increase in frequency and severity of droughts, which can cause long-term compositional shifts in many forest ecosystems. In Patagonia, Suarez and Kitzberger (2008) observed that drought-kill disturbance shifted species composition in favour of *Austrocedus chilensis* in a mixed *Nothofagus dombeyi* (coihue)-*Austrocedrus chilensis* (Chilean cedar) forest.

Summary list of main ideas and phenomena

North America in general

- Shifts in species distributions are mainly driven by increases in temperature and changes in the moisture index.
- Ranges will shift not only northward and upward but in all directions.
- Local extinctions in the south of species ranges, colonisation of new habitats in the north.

Canada

- Increased temperatures countrywide, increasing winter precipitation but decreasing summer precipitation.
- Tundra and taiga are expected to decline, while temperate forests and woodland are predicted to increase.
- Reduction of arctic-alpine communities.
- In the Arctic, tall shrub tundra is encroaching into areas of dwarf shrub tundra.
- The Boreal Plain ecozone might shrink and give way to the Prairie ecozone.
- Northward expansion of tree line is expected.
- Lower water table → marsh complexes will dry out more often, shift to more xeric species.
- Reduction of wetland areas.
- Possible invasion by southern exotic species.
- Increased fire season length and area burned in forested regions.
- Changes in fire interval may alter forest regeneration and cause shifts between deciduous- and conifer-dominated succession trajectories.

The United States in general

- Relatively large increases in temperature and decreases in precipitation in the eastern half of the country; increases in precipitation and relatively small increases in temperature in the West; significantly drier conditions in the South and in the central United States.
- Considerable uncertainty about possible future ecological impacts.
- Moderate warming could produce increased vegetation growth but greater warming could also produce large areas of drought stress.
- Projected changes in vegetation for the 21st century: shift of current vegetation types, emergence of tropical forest as a new vegetation type, forecast changes vary according to models and scenarios.
- Potential expansion of temperate conifer forests.
- Possibly decreasing area of northeast mixed forest, tundra and alpine vegetation.

Alaska

- A warming trend has been observed, further warming is anticipated.
- Warmer air and soil temperatures → alteration of soil water and nutrient availability, permafrost thaw and ground subsidence → altering hydrological patterns.

- Changes in environmental conditions may result in changes in plant community composition, biomass and productivity as well as in plant species shifts.
- In the High Arctic, areas with sparse vegetation and deep active layers may develop a thicker and more wide-spread layer of moss.
- In the Low Arctic, deciduous shrubs may dominate.
- Increased temperatures have been observed to promote shrub expansion, moist tussock tundra would give way to moist low shrub tundra.
- Possible increases in boreal forest due to increased growing season and warmer temperatures, however, thermokarsts can collapse boreal forests.
- Gradual elimination of conifer species and an increase in abundance of hardwood species with winter warming scenarios → possible shift to mixed broadleaf–needleleaf tree composition.
- Evergreen forests may expand into current tundra while being replaced by grasslands or temperate forest at the biome's southern edge.
- Longer and warmer summers can increase fire frequency. → The area burned is expected to increase. → Alaska may become a net carbon source.

California

- Substantially warmer and wetter winters, somewhat warmer summers and an enhanced El Niño Southern Oscillation, direction of change in precipitation is not clear.
- Both upward and downward shifts in species’ optimum elevations.
- In tidal marshes, salinity has increased. → Increased cover of the most salt-tolerant plant species and decreased cover of the least salt-tolerant ones.
- According to a warmer and wetter scenario, expansion of forests and a net increase in evergreen conifer forest can be expected as well as the advancement of grassland.
- Under a drier and cooler scenario, the expansion of grassland is predicted along with a net decline in evergreen conifer forest, mixed evergreen woodland and shrubland.
- Significant declines in the extent of alpine/subalpine forest.
- Replacement of evergreen conifer forest by mixed evergreen forest or by woodland, shrubland or grassland.

Southwestern USA

- A warmer and drier climate is predicted.
- Changing precipitation regimes, increases in nutrient and water availability and soil disturbance may enhance the susceptibility of habitats to invasion by non-native plant species (e.g. in the Mojave Desert).
- Accelerated plant mortality due to climate warming and drought.
- Shifts in vegetation distribution are expected to be the most rapid at ecotones, e.g. between ponderosa pine forest and pinon-juniper woodland.
- Large-scale shifts in dominance from grasses to shrubs or vice versa, depending on the amount and seasonality of precipitation.
- Compositional and structural changes of grassland vegetation are predicted.

- Expected declines in stream base flows and water tables or increased flood intensity → shifts in functional types and vegetation structure.

Eastern USA

- Increases in annual temperature and precipitation in New England.
- Large-scale changes are predicted in the distribution of natural vegetation and considerable northward shift of both the northern and southern boundaries of the biomes.
- Significant reduction and upslope retreat of boreal conifer forest in New England.
- Mixed oak-hickory forests are expected to shift northward and increase in area.
- Northern deciduous hardwoods are expected to decrease in area and move upslope.
- Vascular plants have been replacing bryophytes in the alpine zone, alpine communities are in danger of regional extinction.
- Possible displacement of individual species: *Pinus taeda* may shift over 400 km northward.
- Coastal plant communities may be affected by the projected increase in sea level as well as by drought.
- Distribution patterns of shrub thickets are influenced by variations in transpiration caused by environmental changes.
- Possible drying up of bogs in the Southern Appalachian Mountains → they may become a carbon source.
- Salt marsh communities may be resilient to modest warming and large changes in precipitation.

Southeastern USA

- Future climate is predicted to become warmer and drier.
- In the Greater Everglades region of southern Florida, an increase in salinity of the vadose zone is expected due to sea level rise and storm surges. → Potential eradication of the salinity-intolerant hardwood hammocks at higher elevations and landward migration of mangroves.
- In wetlands, changes in hydrological properties (sea level, duration and depth of flooding, seasonal variation in rainfall) control plant distribution.
- In coastal ecosystems, regeneration (seed germination and seedling growth) may be dictated by disturbances related to hurricanes, water fluctuation and saltwater intrusion.
- Alteration of hydrology could limit the dispersal, germination and regeneration of short-lived woody species from *Taxodium distichum* swamps.
- Marsh loss due to scrub-shrub encroachment.
- Replacement of abandoned agricultural areas by forest.
- Potential shift of pine savannas towards a forested state, due to decreased frequency of fires and hurricanes as well as the CO_2 fertilization effect.

The Great Lakes region

- Temperature and precipitation increases are predicted.

- An overall decrease in total area for northern conifers and northern deciduous species is expected, northward shift of the current range, decline in dominance or complete extirpation.
- Southern mixed forests and southern oak-hickory-pine forests are predicted to expand northward.
- A trend toward homogenization of forest conditions due to the widespread expansion of *Acer spp.*
- In bog communities, an increase in the production and abundance of woody plants is expected due to warming and lowered water-table elevations.
- In coastal wetlands, plant community composition has shifted and become more homogeneous due to an invasion by *Typha x glauca.*

The Great Plains

- Drought and decreased fire frequency → changes in dominance from xeric fire-tolerant *Quercus* to mesic fire-intolerant tree species, rapid encroachment of *Juniperus virginiana.*
- “Savannification” of the forest on the prairie-forest border → biome boundary is predicted to shift to the northeast.

Intermontane basins and plateaus

- Major role of water availability and within-season distribution of precipitation events.
- In Colorado shortgrass steppe, the relative evenness of rainfall event size in combination with event number may have important effects.
- Shifting precipitation distribution to a spring/summer pattern has the greatest potential for altering productivity, composition and structure of *Artemisia tridentata* steppe vegetation → loss of forbs, increase in bare ground.
- A warmer environment coupled with a winter precipitation regime, greater CO_2 levels and increased fire disturbances would likely permit invasion and dominance by *Bromus tectorum.*

Rocky Mountains and the Cascades

- In Washington State, snowpack declines and warmer summers are projected. → Area of forest that is severely water-limited will likely increase.
- *Pseudotsuga sp.* is possibly one of the most climate-sensitive species.
- Areas with climatic conditions favourable for *Pinus contorta* will decrease considerably.
- The rate of forest change in response to climate change will mainly be driven by disturbances.
- An overall decrease is predicted in pine-dominated subalpine forests in the Greater Yellowstone Ecosystem.
- The upper and lower timberline appear to be particularly sensitive to climate change, the former one is likely to migrate upward in elevation, whereas the lower treeline may retreat under drier conditions or move down slope under wetter conditions.
- The extent of alpine vegetation is expected to decrease.

- Due to warming, aboveground biomass of forbs may decrease, that of shrubs may increase, whereas that of grasses may remain unchanged.

Central and South America

- In Mexico, drier conditions are predicted mainly for the northern part.
- In case of warming and reduction in rainfall, a drastic distribution contraction of *Fagus grandifolia var. mexicana* can be expected.
- Potential expansion of chaparral at the expense of temperate forest and possible extinction of high-altitude species.
- Climate gets warmer in response to urban heat islands as well. → Plant communities are expected to migrate upwards in mountains.
- Most of the tropical Andean tree genera shifted their mean distributions upslope in the first years of the 21st century.
- Shifts of the savanna–forest transition depend heavily on annual precipitation values and the length of the dry season.
- In Brazil, suitable areas for savanna tree species will be localized in the most disturbed regions, with the most fragmented and degraded habitats. → Geographical limits of *Caryocar brasiliense* are predicted to be widely reduced.
- Expansion of savanna-like vegetation in South America.
- At the southernmost limit of the Brazilian Atlantic forest, a continuous but slow process of forest expansion has been observed.
- Tropical forests might be replaced by seasonal forests or savanna over eastern Amazonia with temperature increases or precipitation decrease.
- Potential widespread dieback of Amazonian forest cover through reduced precipitation.
- Fire may have a significant role in the degradation of forest ecosystems.

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CORRELATING THE POLLENS GATHERED BY *APIS MELLIFERA* WITH THE LANDSCAPE FEATURES IN WESTERN FRANCE

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Abstract. Honey bee health depends on various factors, including the availability of food resources and chronic exposure to toxins in the foraging area. These parameters can be evaluated using indicators based on either pollen gathered to the hive or landscape features of the foraging area, including the structure, land use, or density of such specific landscape elements as hedgerows.This study examines the correlation between the diversity of pollens gathered and the landscape features in a 3-km radius using Geographic Information System technology. Palynological analyses were performed on pollen pellets collected from sixteen apiaries in western France during one year. Richness, diversity and similarity indices were calculated for land-cover features and palynological data and then compared. The land-cover analyses permitted the identification of three different landscape contexts (hedgerow, cultivated, and urban landscapes). Although the palynological profiles were highly diverse, some taxa were conserved between hives. The flower richness was greater in the apiaries from urban landscapes than in apiaries from rural landscapes, regardless of the dominant land-cover. The statistical analysis did not associate a specific flora with a specific landscape. However, it was possible to distinguish the pollen gathered by bees in urban landscapes and from pollen collected in rural areas.

Keywords: *foraging area, land-cover, palynology, honey bees*

Introduction

Profound changes in urban and farming landscapes have occurred over the last decade, and the increasing human population has led to expanding urbanization and modifications to urban and suburban landscapes (Loibl and Toetzer, 2002). Similarly, profound changes in agricultural practices induced by agricultural production methods, technological advances and government policies, have modified the landscape structure and composition (Burel and Baudry, 1990; Macdonald and Johnson, 2000; Robinson and Sutherland, 2002; Le Féon et al., 2010). This agricultural intensification has affected land-use patterns, resulting in 1) a large increase in cultivated areas, 2) fragmentation of uncultivated features including forests, hedgerows (Burel and Baudry, 1999), and natural meadows (Monteiro et al., 2011), and 3) the loss of these semi-natural elements (Agger and Brandt, 1988; Hobbs et al., 2008). Furthermore, the decrease in landscape heterogeneity has contributed to the decline of biodiversity (McLaughlin and Mineau, 1995; Krebs et al., 1999; Holzschuh et al., 2007; Le Féon et al., 2010; Potts en al., 2010) through the loss of suitable habitats and food resources for many species of wild flora and fauna (Robinson and Sutherland, 2002; Benton et al., 2003; Carvell et al., 2007; Hannon and Sisk, 2009).

The composition and structure of the landscape have strong effects on honey bees, particularly with regard to the pollen collected and the abundance of flower-visiting bees (Steffan-Dewenter et al., 2002; Steffan-Dewenter and Kuhn, 2003). Fragmentation has an impact on the distribution of plants and the distribution of animals in relation to the modification of patch size, edges, and landscape connectivity (Hadley and Betts, 2012), and the loss of habitat decreases the plant density and has a negative impact on the abundance of pollinators (Hadley and Betts, 2012). In fact, flower richness and abundance are important for the food balance of honey bees and thus for the health of the colony (Crailsheim et al. 1992; Alaux et al. 2010). Furthermore, environmental pollution in landscape contaminates bees and beehive products (Balayiannis and Balayiannis, 2008; Perugini et al., 2009; Lambert et al. 2012).

The qualification of the landscape context is therefore important to predict the food resources and toxic exposure of honey bee colonies. However, the extent to which the pollen collected around an apiary is correlated to the surrounding landscape composition and thus with the landscape context remains questionable. As an example, apiaries surrounded by high-intensity agriculture and isolated from semi-natural habitats are expected to exhibit a lower floral diversity in the collected pollen, whereas apiaries in proximity to greater proportions of urban habitats could have higher levels of floral diversity represented in the pollen stores, as related to the variety of urban ornamental species. In an attempt to address these questions, the landscape variables of a foraging area and palynological data were compared in an array of 16 apiaries within different landscape contexts. The results are discussed with respect to the particular landscape components, cultural practices and/or selective foraging that could have an impact on the diversity of the pollen returned to the apiaries.

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Materials and Methods

Study area

Sixteen apiaries owned by sixteen different volunteer beekeepers were selected for this study. The apiaries, indicated by a letter (A to P), were located in six departments in western France (*Fig.1*): nine apiaries in Loire-Atlantique (44, France), two in Vendée (85, France), two in Maine et Loire (49, France), two in Sarthe (72, France), one in Mayenne (53, France).

Figure 1. *Location of the sixteen apiaries.*

The foraging distance depends on landscape structure and food resources (Beekman and Ratnieks, 2000; Steffan-Dewenter and Kuhn, 2003) and can reach 13.5-km (to collect nectar) (Visscher et al., 1996). Nevertheless, the average foraging distance varies between 1.5-km (Steffan-Dewenter and Kuhn, 2003) and 6.1 km (Beekman and Ratnieks, 2000), with resources near the beehives being favored. As a compromise between the highest values and the average of foraging distance, a radius of 3 kilometers was chosen for the foraging area (2827 ha) in the present study.

Landscape analysis

The land-cover data used for the analysis was obtained from the European data base Corine Land Cover (2006) for the categories urban areas, woodland, and water. The identification system for agricultural plots from the Common Agricultural Policy of Europe (2008) was used for the cultivated areas of annual crops and permanent and market garden crops and grassland. Missing land-use data for agriculture were complemented by a field survey (a direct questionnaire and visit to the farmers in the foraging areas). The hedgerow networks and copses were digitized manually on the basis of satellite pictures (BD Ortho® IGN, 2004) using ArcGis 9.2. The areas, hedgerow density, and average plot size were calculated using ArcGis 9.2.

The fourteen synthetic variables describing land-use were chosen by aggregating more detailed categories (*Table 1* and *Appendix A*). The objective was to retain sufficient details to discriminate among the different landscape types.

***Table 1**. Description of the variables (*Declarative data for 2008 of the agricultural parcel identification system of Council Regulation (EC) N° 1593/2000 of 17 July 2000; †Annual crops).*

Variables	**Description**	**Source**	**Units**
Grassland	natural meadows, temporary meadows	*	ha
Fallow land	fallow land	*	ha
Forage crops†	forage, broad bean, pea	*	ha
Grain crops†	oat, wheat, maize, barley, rye	*	ha
Oleaginous crops†	colza, flax, sunflower	*	ha
Permanent crops	vineyard, orchard	*	ha
Market gardens	fruit, vegetable, aromatic plant	*	ha
Other crops†	buckwheat, hemp, tobacco	*	ha
Wood and copse		Corine Land Cover 2006 Digitized on BD ORTHO® IGN (2004)	ha
Urban area	urban infrastructure, airport	Corine Land Cover 2006	ha
Water		Corine Land Cover 2006 (51.1/51.2)	ha
Others	other utilization declared, no agricultural use, area not determined	*	ha
Hedge		Digitized on BD ORTHO® IGN (2004)	m/ha
Average plot size		Field survey among farmers in the foraging area	ha

Pollen sampling and analysis

The pollen pellets were collected from eight colonies in each apiary in 2008. The samples were collected four times during the apicultural season: at the onset of beehive activity after wintering (Period 1: end of April – beginning of May); at the beginning of honey foraging (Period 2: beginning of June – end of July); during the middle-end stage of honey foraging (Period 3: end of July – beginning of August) and during over wintering preparation (Period 4: end of September – beginning of October).

The samples were collected in pollen trap set up by the beekeepers three days before the sample was removed. The field-collected samples were placed immediately on ice and stored in a standard freezer at -20°C until analysis.

The palynological analyses of the pollen pellets were performed by the Unité de Palynologie from Montpellier SupAgro using the method of Cour (Patent CNRS-ANVAR, Cour, 1974) in accordance with the European method (Von der Ohe et al., 2004). For this study, the raw data were processed at the taxonomic level of the plant family.

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Data analysis

According to the experimental design, two datasets have been constituted: one for the landscape data and one for the pollen data. The statistical analysis managed to explore and compare the diversity of those datasets. In a first description stage, the richness and index of diversity were evaluated for species from the plant family (pollen) and for landscape from the land-cover data. Indices of diversity were calculated using Shannon's formula:

$$H_s = -\sum p_i \, ln(p_i) \qquad \text{(Eq. 1)}$$

where (i) refers to a species and $p_i = \frac{n_i}{N}$ with n_i being the number of individual species and N the overall number of individuals for all species. The Shannon indices of species on one hand and landscape in other hand were compared with a Spearman's test.

In a second description stage, the indices of similarity, Brain-Curtis index, were calculated for each data set. Then, dendrograms were generated illustrating the similarity of the apiaries for species and for landscape. The comparison of those similarity matrices was achieved by a Mantel's test performed with 5000 randomizations.

In a third description stage, a multivariate method as Canonical Correlation Analysis (CCA) was used to analyse simultaneously the plant family profiles in the pollen pellets and the land-cover features. This method explores the sample correlation between two sets of quantitative variables observed on the same experimental units (Ter Braak and Verdonschot, 1995; Gonzales et al., 2008).

The statistical analysis were performed with R software (R 2.12, R development Core Team, 2011) using the "Vegan" package for factor analysis.

Results

Landscape data

Table 2 and *figure 2* show the composition and structure of the sixteen foraging areas.

Table 2. *Characteristics of the sixteen apiary foraging areas: composition (grassland, fallow land, forage crops, gain crops, oleaginous crops, permanent crops, market gardens, other crops, wood and copse, urban, water and others) and structure (hedgerow density and average plot size).*

Apiary	A	B	C	D	E	F	G	H
Grassland (%)	38.1	12.8	16.2	21.2	5.7	45.7	14.3	19.3
Fallow land (%)	4.0	5.3	4.2	6.1	1.0	3.9	5.7	6.5
Forage crops (%)	0.9	0.6	0.6	0.2	0.0	0.0	2.7	1.1
Grain crops (%)	30.5	47.0	21.6	31.5	5.0	31.1	32.9	37.2
Oleaginous crops (%)	3.4	3.6	1.7	2.8	0.3	2.8	7.3	2.0
Permanent crops (%)	0..0	3.0	0.0	0.2	0.4	0.0	0.9	0.0
Market gardens (%)	0.0	0.4	0.0	2.4	0.4	0.3	1.9	0.3

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Other crops (%)	0.0	0.1	0.0	0.0	0.0	0.6	2.1	0.0
Wood and copse (%)	8.9	8.4	10.2	8.2	14.3	1.7	9.5	8.5
Urban area (%)	5.7	7.3	31.6	0.8	46.9	4.5	7.4	2.9
Water (%)	0.0	0.0	0.0	0.0	7.0	0.0	0.0	0.0
Others (%)	8.4	11.4	13.9	26.6	18.9	9.2	15.2	22.2
Hedges (m/ha)	82	17	34	55	39	60	24	58
Average area of plot (ha)	5.1	4.4	3.8	4.2	3.1	5.1	3.3	3.4

Apiary	**I**	**J**	**K**	**L**	**M**	**N**	**O**	**P**
Grassland (%)	32.4	19.9	0.1	28.9	42.1	1.5	45.0	9.6
Fallow land (%)	2.4	10.1	0.0	3.8	3.4	0.0	3.8	0.2
Forage crops (%)	1.3	0.8	0.0	1.1	4.8	0.0	0.9	0.0
Grain crops (%)	25.5	52.5	0.0	39.4	37.8	0.6	30.2	16.7
Oleaginous crops (%)	0.7	2.4	0.0	6.1	1.3	0.0	2.0	0.0
Permanent crops (%)	0.0	0.3	0.0	0.0	0.0	0.0	1.3	0.0
Market gardens (%)	0.2	2.5	0.0	0.6	0.0	0.0	0.3	0.0
Other crops (%)	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.6
Wood and copse (%)	2.1	3.6	3.5	8.4	1.9	5.6	2.7	14.8
Urban area (%)	12.0	1.0	75.1	6.5	4.4	78.6	6.5	42.1
Water (%)	0.0	0.0	11.9	1.2	0.0	0.0	0.0	0.0
Others (%)	23.1	6.4	9.5	4.0	4.3	13.7	7.4	16.1
Hedges (m/ha)	69	35	13	33	59	18	87	45
Average area of plot (ha)	2.8	5.1	2.3	5.1	4.9	2.5	3.8	3.4

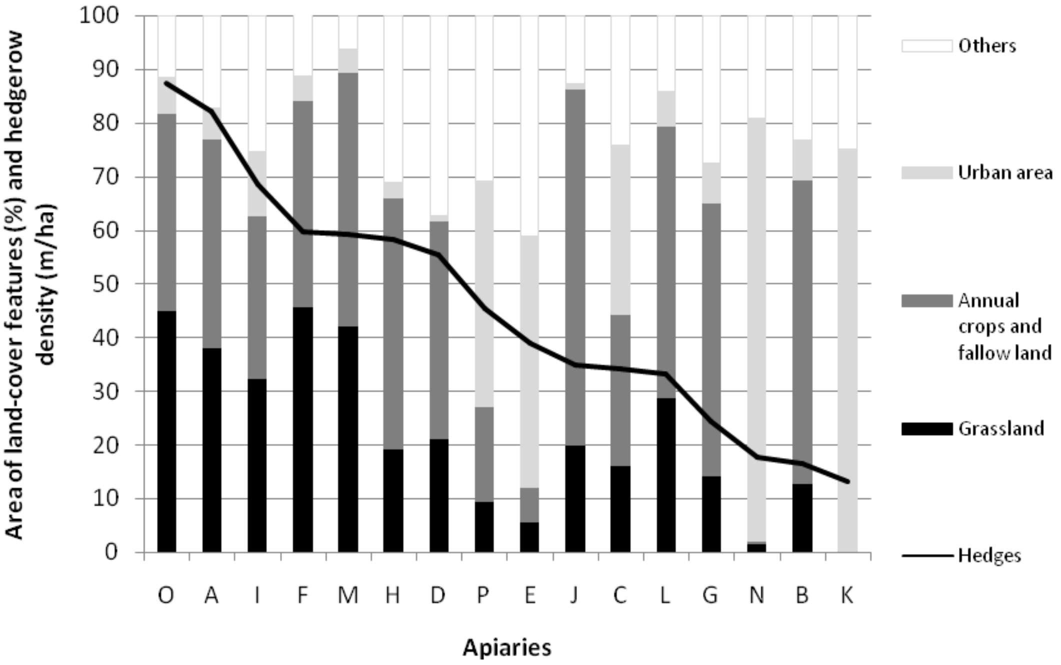

***Figure 2**. Area of land-cover features (% of total surface) and hedgerow density (m/ha) of the sixteen apiary foraging areas (apiaries ranked by hedgerows density).*

For apiaries N, K, E and P, 40% of the foraging area comprised urban areas. The grasslands were dominant in foraging areas F, O, and M, covering more than 40% (1000 ha) of the entire foraging area (*Table 2, Figure 2*). The crops were less represented in apiaries K, N, E, and P apiaries (less than 20 %) in contrast to the J and B sites, which contained more than 1500 ha of crops, covering more than 50 % of the foraging area.

The hedgerow length comprised between 13 and 87 m/ha and was more important for the O, A, I, F, M, H, and D apiaries (*Table 2, Figure 2*). The average plot size varied between 2.3 ha (K) and 5.1 ha (A, F, J, and L), with an average of 3.6 ha and a median of 3.8 ha. Apiaries C and O were situated at the median level.

The landscape richness was more important for the B, G, and J apiaries (*Table 3*) and less important for the K, M, N, and P apiaries. The landscape diversity (*Table 3*) was high for apiaries B, C, and G and low for apiaries K, M, and N.

Table 3*. Landscape richness and diversity of the sixteen apiary foraging areas*

Apiary	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	**M**	**N**	**O**	**P**
Landscape richness	9	11	9	10	10	10	11	10	10	11	5	10	8	6	10	8
Shannon index (H)	1.61	1.71	1.73	1.68	1.56	1.43	2	1.65	1.6	1.5	0.82	1.67	1.4	0.72	1.5	1.51

Figure 3 shows the similarity between the land-cover of the sixteen foraging areas. The apiaries were differentiated into four groups: a first group including the K, N, E, C, and P apiaries, a second including the J, L B, and G apiaries, a third including the A, F, M, and O apiaries, and the last including the D, H, and I apiaries.

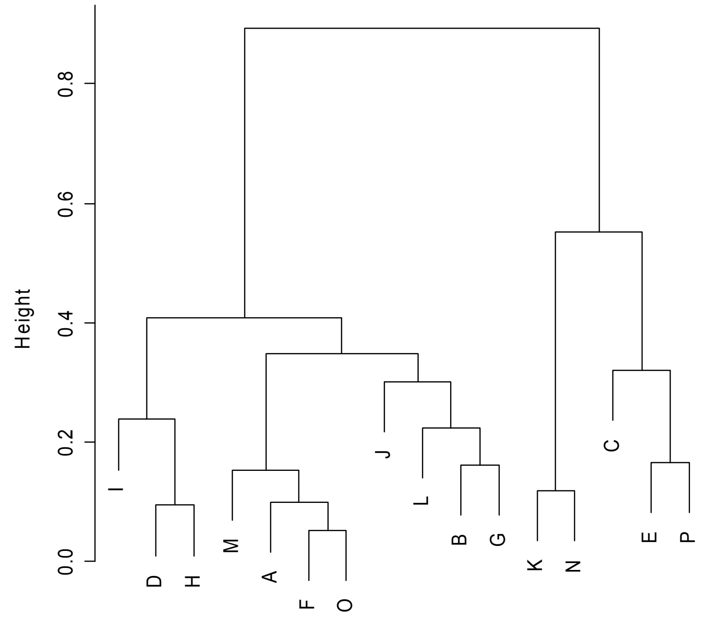

Figure 3. *Dendrogram built from a similarity index (Bray-Curtis) of land-cover data of the sixteen apiary foraging areas.*

Palynological data

Fifty-four families of wild and cultivated species were identified in the pollen pellets (*Table 4*).

Table 4. *Plant family profiles in the pollen pellets collected from sixteen apiaries (white=absence of the family; black=presence of the family). The apiaries are classified according to the number of families represented in the pollen profile, from the most important to the least important. The species are classified according to their presence in the set of apiaries.*

Apiaries	**K**	**C**	**N**	**E**	**H**	**B**	**J**	**O**	**P**	**I**	**D**	**A**	**L**	**G**	**F**	**M**
Asteraceae	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Brassicaceae	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Fabaceae	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Fagaceae	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Poaceae	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Rosaceae	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Rhamnaceae	■	■	■	■	■	■	■	■	■	■	■	■	■			■
Plantaginaceae	■	■	■	■		■	■	■	■	■	■	■	■		■	
Araliaceae	■	■	■	■		■	■	■	■	■	■			■	■	
Cistaceae	■		■	■	■	■	■	■	■	■	■		■			
Nelumbonaceae		■	■	■	■			■	■	■	■	■		■	■	
Ranunculaceae			■	■	■	■		■	■	■	■	■				■
Boraginaceae	■	■		■					■		■	■	■		■	■
Caprifoliaceae	■	■	■	■	■		■	■	■			■				
Liliaceae	■	■	■	■	■		■	■		■		■				
Papaveraceae	■	■		■	■	■	■		■					■		■
Scrophulariaceae	■	■	■	■	■		■			■				■		■
Apiaceae	■		■		■	■	■	■							■	■
Gentianaceae	■	■	■	■	■		■		■			■				
Vitaceae			■	■		■	■	■	■	■						
Convolvulaceae	■	■		■		■	■		■							
Lamiaceae	■	■			■			■		■	■					
Onagraceae	■		■	■	■	■				■						
Polygonaceae		■						■	■		■		■		■	
Salicaceae	■	■				■						■	■	■		
Euphorbiaceae	■					■	■				■			■		
Geraniaceae	■	■			■					■				■		
Sapindaceae		■	■				■			■			■			
Tamaricaceae			■			■		■	■		■					
Balsaminaceae	■				■	■			■							
Cornaceae	■		■	■		■										
Ericaceae	■	■	■												■	
Myrtaceae	■		■	■	■											
Oleaceae		■		■	■		■									
Pinaceae		■	■			■	■									
Resedaceae		■								■		■		■		
Urticaceae		■	■		■	■										
Anacardiaceae						■		■				■				
Aquifoliaceae	■										■		■			
Campanulaceae		■	■								■					
Caryophyllaceae	■				■			■								
Alismataceae					■								■			
Cucurbitaceae	■						■									
Menyanthaceae					■			■								
Plumbaginaceae	■		■													
Amaranthaceae													■			
Arecaceae	■															
Cyperaceae		■														
Linaceae				■												
Lythraceae				■												
Magnoliaceae																■
Malvaceae		■														
Nymphaeaceae				■												
Platanaceae												■				

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Some families were present in only one apiary (e.g., Arecaceae, Malvaceae) whereas others (i.e., Asteraceae, Brassicaceae, Fabaceae, Fagaceae, Poaceae, and Rosaceae) were present in all apiaries.

The pollen profiles of apiaries K and C had the highest richness (*Table 5*), in contrast to apiaries F and M, with the lowest richness. The diversity index was more important for the palynological profiles of the K, G, and N (*Table 5*) apiaries, whereas the Shannon diversity index was less important for the palynological profiles of the A, E, and M apiaries.

Table 5*. Pollen richness and diversity of the sixteen apiary foraging areas*

Apiaries	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	**M**	**N**	**O**	**P**
Pollen richness	18	24	30	19	27	13	14	26	20	23	31	16	13	28	22	21
Shannon index (H)	1.48	1.56	1.57	1.76	1.51	1.7	1.98	1.87	1.87	1.71	2.19	1.58	1.51	1.89	1.54	1.78

Figure 4 shows the similarity between the pollen species data of the sixteen foraging areas. In contrast to the dendrogram achieved using the land-cover data, no apiary groups were identified.

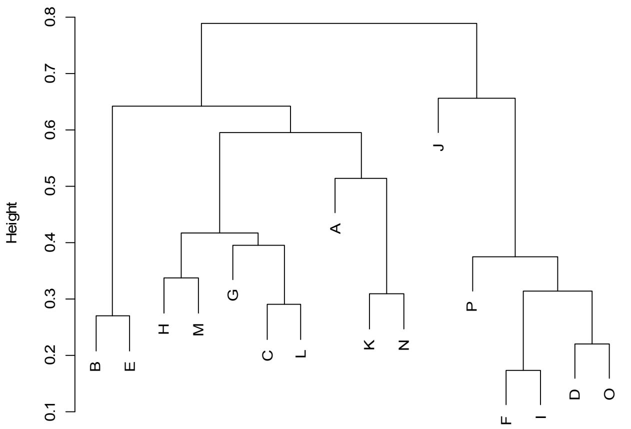

Figure 4. *Dendrogram built from a similarity index (Bray-Curtis) of pollen species data of the sixteen foraging areas.*

Pollen and landscape

The landscape richness and the pollen richness were different among the apiaries or within the same apiary. In general, the foraging areas with a low landscape richness presented a high pollen richness and *vice versa*. The landscape richness of foraging area K was equal to 5, which corresponded to the lowest landscape richness, though the pollen richness was equal to 31, which corresponded to the highest pollen richness. In contrast, the landscape richness of foraging area G was 11, and the pollen richness was 14. The foraging areas with an important urban area typically exhibited high pollen richness. Low pollen richness was observed for apiaries located in the landscapes with important grassland or crop areas.

The Spearman test based on the entire landscape and palynological diversity data (Shannon indices) did not highlight a correlation between the landscape diversity and the pollen diversity (p>0.05; r=-0.094). This result was illustrated by the foraging areas of apiaries K and N, which were characterized by a low landscape diversity and high pollen diversity. However, apiary G presented high landscape and pollen diversities, as opposed to apiary M, which was characterized by low landscape and pollen diversities.

The similarity indices were compared by a Mantel test (5000 randomizations). However, no correlation was demonstrated between the landscape data and pollen data (p>0.05; r=0.1303).

CCA provided an overview of the land-cover data and the families identified in the pollen pellets and described the proximity between the variables and apiaries. The first factorial plane is displayed in *Figure 5*.

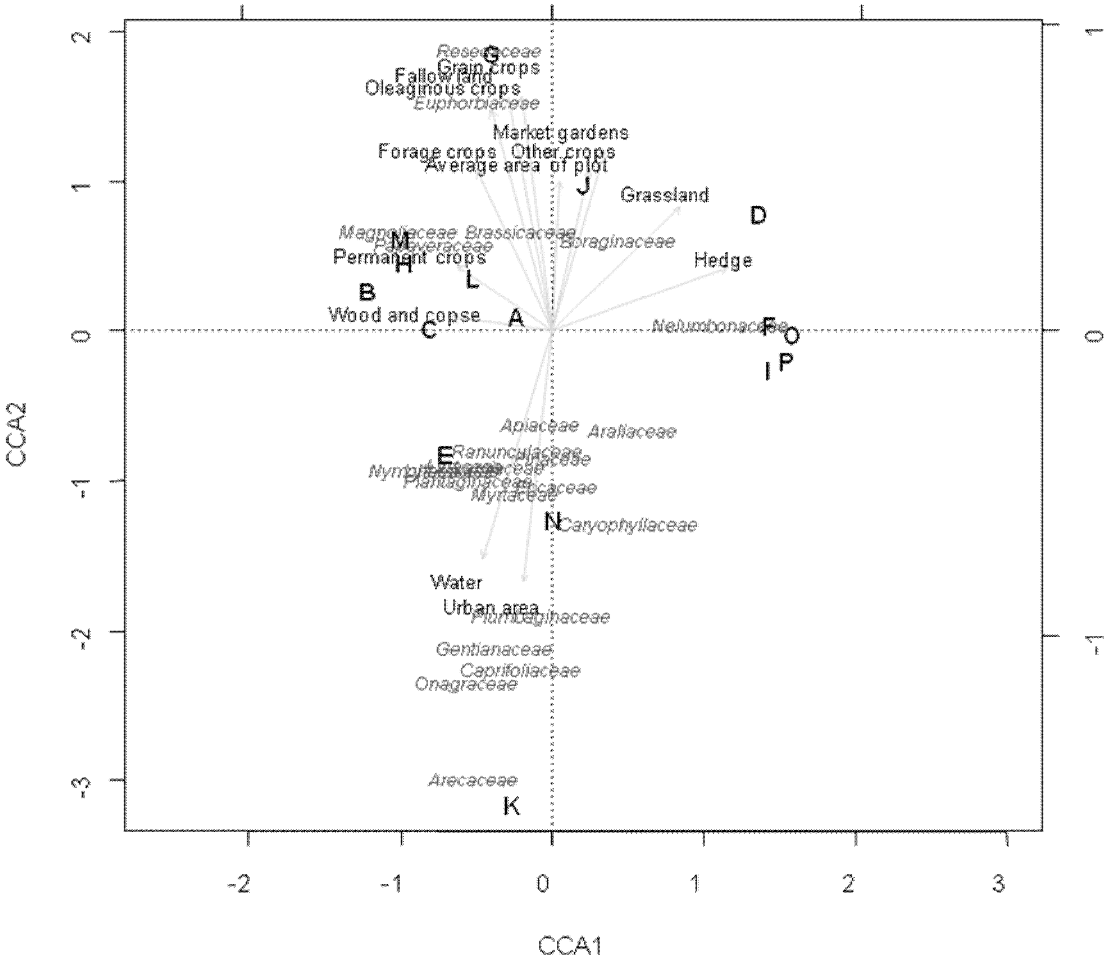

Figure 5. *Projections of the variables (landscape and pollen data) and the apiaries on the first factorial plane of CCA (the species variables placed near the center of plot were removed for better readability).*

The first CCA axis (CCA1, *Figure 5*) accounted for 31.16% of the total inertia and revealed an opposition between the combination of the variables hedge, grassland and Boraginaceae and Nelumbonaceae and the combination of the variables permanent crops, oleaginous crops, grain crops, forage crops, fallow land and Magnoliaceae, Papaveraceae, and Brassicaceae. On the second axis, we have on one side the foraging areas D, F, O, P, and I (characterized by grassland, hedge, and their associated families) and on the other side the apiaries B, H, M, C, L, A, J, and G (characterized by crops and the associated families).

The second CCA axis (CCA2, *Figure 5*) accounted for 20.23% of the total inertia and revealed a combination of variables, including urban area, water, and Arecaceae, Onagraceae, Caprifoliaceae, Gentianaceae, and Plumbaginaceae. Additionally, on this axis in Figure 5, an opposition between apiaries K, N, and E, characterized by urban area and their associated families, and the other apiaries is observed.

Many species (not represented on the graph) were not discriminative, such as Rosaceae, Asteraceae, Fagaceae, Poaceae, and Fabaceae.

Discussion

The different foraging areas were not classifiable into obvious landscape categories. The analysis revealed gradients of hedgerow density and variable proportion of grassland and crop areas. This result was because the apiaries were located in the same geographic region (western France), with a plain topography and comparable agricultural management, as characterized by a hedgerow landscape with mixed farming, in which pasture and permanent crops are present at different levels for each site (Burel and Baudry, 1990).

The land-cover data and similarity index (Bray-Curtis index) distinguished three groups of landscape contexts. The K, N, E, P, and C apiaries were characterized by an important urban area and a low crop area and were considered to be urban landscape. The other foraging areas were characterized by rural areas.

Our results demonstrated two groups of foraging apiaries within the rural landscape context according to the gradient of hedgerow networks and to the gradient of grassland and crop areas. Apiaries A, F, I, M, and O were defined by 1)a high length of hedges between 59 and 87 m/ha and 2) numerous grassland plots comprising between 49% and 58% of the grassland and annual crop areas (32% and 46% of the foraging areas), respectively. The landscape context for these apiaries would be close to a hedgerow landscape as defined by Michel et al. (2007) for western France. A second group including apiaries B, G, J, and L consisted of 1) a low hedgerow network between 17 and 35 m/ha and 2) large plots of crops, with an overall area comprising between 62% and 80% of the grassland and annual crop areas (45% and 56% of the foraging areas), respectively. This group was characteristic of a cultivated landscape (Michel et al., 2007). Two apiaries (D and H) displayed intermediate values with important hedge lengths and crop plots, and exhibited difficulty with regard to classification within the landscape context of the foraging area.

Landscape and flower diversity

The land-cover data analyses indicated that the landscape richness was highest for the foraging areas of apiaries B, G, and J and was lowest for the K, M, N, and P sites. The palynological analyses demonstrated that the pollen richness was more important for apiaries K and C, whereas apiaries F and M displayed the lowest values. However, important landscape richness was not necessarily correlated with important pollen family richness and *vice versa,* as observed for apiaries K and G. The foraging areas with important urban areas were sites that were characterized by a low landscape richness and a high pollen richness, which was linked to the flower diversity in the urban areas comprising many ornamental, cultivated and wild species (Dana et al., 2002; Acar et al., 2007; Hennig and Ghazoul, 2012). Accordingly, the pollen richness appeared less important for the apiaries surrounded by large crop and grassland areas. This finding might be explained by 1) the presence of species or varieties of the same species providing less attractive pollen (Louveaux, 1959; Pierre et al., 1999) and 2) chemical or mechanical management of the areas, reducing flower diversity and availability (Louveaux, 1959; Freemark and Boutin, 1995; De Snoo and van der Poll, 1999; Schippers and Joenje, 2002). In fact, Freemark and Boutin (1995) demonstrated that use of herbicides decreases the presence of self-propagating plants that could be attractive to honey bees (Louveaux, 1959). Intensive grazing, cutting prior to the flowering period, and fertilizer application have similar a negative impacts on flower richness (Schippers and Joenje, 2002).

Richness was associated with the different land-cover categories present in foraging areas and the different families of plant identified in the pollen. In addition to qualitative data, the diversity index takes into account quantity of the different variables. Additionally, apiary C, which showed high pollen richness, had low pollen diversity. Conversely, apiary G had low pollen richness and high pollen diversity. Overall, the diversity was more noteworthy that the quality and quantity of data combined. There was no correlation between landscape diversity and pollen diversity, a result that can be illustrated by the foraging areas of apiaries K and N, which were characterized by low landscape diversity and high pollen diversity. However, apiary G presented high landscape and pollen diversities, different from apiary M, which was characterized by low landscape and pollen diversities. These results can be explained this by the same reasons cited above.

The palynological analyses showed that the flower richness is greater in apiaries of urban landscapes than in apiaries of rural landscapes. Nevertheless, the diversity of pollen gathered by honey bees does not reflect the diversity of the landscape, which, in turn, depends on the landscape context (composition and structure) and management of the environment.

Landscape and typical flora

The similarity indices between the apiaries considering land-cover data were different from the similarity indices between the apiaries considering pollen data. Indeed the comparison of these similarity indices (the Mantel test) showed an absence of correlation. Thus, the apiary clusters built using palynological data were different from the apiary clusters built using land-cover data.

CCA permitted an overview of the land-cover and pollen data and a description of the proximity between the variables and apiaries. As was the case for the richness data, we observed an opposite trend between the urban landscape and rural landscape. The plant families associated with the pollen collected from urban areas were Arecaceae, Onagraceae, and Caprifoliaceae, and were mainly ornamental species present in parks and gardens. Although in low quantity, many ornamental species were present in parks and gardens, which partially explains the high flower richness but not necessarily the high flower diversity in the urban landscape. The foraging areas K, N and E, classified as urban landscapes, were characterized by these variables.

In the rural landscape, the apiaries were characterized by crops and three plant families: Magnoliaceae, an ornamental species well represented in this region, Papaveraceae, self-propagating plants mainly found in crops, and Brassicaceae, species widely cultivated in France.

Many wild, cultivated, and ornamental species were not found to be discriminating with regard to the landscape context, including Rosaceae, Asteraceae, and Fabaceae. These families are known for their high attractiveness to pollinators (Louveaux, 1958) and constituted the majority of the pollen identified. This concept of a main pollen source was introduced early in the study of palynology and is linked to the fact that honey bees select plants for the specific nutritional properties of their pollen (Louveaux, 1958; Hügel, 1962). This nutritional aspect most likely explains why pollen from the same families (main pollen), such as Asteraceae, Fabaceae, and Rosaceae, were reported to be selected and returned to hives in many countries, including France, the United States, and Brazil (Louveaux, 1959; Almeida-Muradian et al., 2005; Tuell et al., 2008; Boff et al., 2011).

In the rural landscapes, the pollen gathered by the honey bees was a not typical for many potential reasons: 1) the foraging areas were not homogeneous and included a mixture of grasslands, crops, market gardens, and urban areas (Burel and Baudry, 1990); 2) the pollen was sampled four times during the year and reflected a single time point, which may explain the omission of some families; 3) the palynological analyses were performed at the taxonomic level of the family and not at the species level; and 4) selective honey bee foraging is linked to pollen quality (Louveaux, 1958; Hügel, 1962; Blütghen and Klein, 2011).

Finally, Louveaux (1959) found a good correlation between land-cover, plant and pollen and considered honey bees as good investigative agent for botanical geography. However, this correlation was far from evident based on the analysis developed in the present study, as the results failed to relate a typical flora (notably flowers visited by honey bees) to a landscape context. Some explanations might include the following features: 1) our sampling method at a single time point did not reflect the dynamic pool of pollen and the complete botanical diversity over a full apicultural season; 2) our study concerned one geographical region with weakly differentiated landscapes compared to the Louveaux study performed over the entire country; and 3) many modifications in landscape structure, composition and management have occurred since the 1950s. However, our results did distinguish an urban landscape from a rural landscape based on the pollen gathered by honey bees and the dominance of ornamental species in the pollen gathered by the honey bees guides the characterization of the landscape as an urban landscape. Regardless, the scarcity or absence of ornamental species does not necessarily mean that the apiary is not located in an urban area.

Conclusion

Based on our results, it is concluded that the diversity of collected pollen is a poor indicator to employ for landscape qualification: a high landscape diversity does not necessarily entail a wider variability in the pollen gathered by honey bees. As a rule, the colonies were found to gather pollen that was not typical of the landscape defined for the apiary. The dominance of pollen from ornamental flowers may, however, have resulted in the characterization of a landscape as an urban landscape. In contrast, rural landscapes could not be discriminated by the pollen collected because honey bees presumably select pollen and favor flowers of nutritional interest. Therefore we suggest that although there is a dependency on the apiary environment and landscape context, the diversity of collected pollen is significantly influenced by additional factors, such as site management and selective foraging.

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Appendices

Appendix A. *Detailed description of the variables used in the study (* Declarative data for 2008 of the agricultural parcel identification system of Council Regulation (EC) N° 1593/2000 of 17 July 2000).*

Variables	**Description**	**Sources**	**Units**
Grassland	natural meadows, temporary meadows	*(PN, PT, PX)	ha
Fallow land	fallow land	*(GE, GB, GI, GV)	ha
Forage crops	forage, broad bean, pea	*(DH, FA, FE, GL, LP, PH, PP, SM)	ha
Grain crops	oat, wheat, maize, barley, rye	*(AC, AV, BA, BB, BD, BH, BP, BT, MA, MD, ME, MS, OH, OP, SE, SH, TR)	ha
Oleaginous crops	colza, flax, sunflower	*(AO, CH, LN, LU, TO)	ha
Permanent crops	vineyard, orchard	*(VE, VI)	ha
Market gardens	fruit, vegetable, aromatic plant	*(FP, LC, PE, PF, PM, PO)	ha
Other crops	buckwheat, hemp, tobacco	*(AT, CU, CV, CW, SR, TA)	ha
Wood and copse		Corine Land Cover 2006 (31.1/31.2/31.3) Digitized on BD ORTHO ® IGN (2004)	ha

Urban area	urban infrastructure, airport	Corine Land Cover 2006 (11.1/11.2/12.1/12.2/12.3/12.4)	ha
Water		Corine Land Cover 2006 (51.1/51.2)	ha
Others	other utilization declared, no agricultural use, area not determined	*(AU, HC, UN)	ha
Hedge		Digitized on BD ORTHO ® IGN (2004)	m/ha
Average plot size		Field survey among farmers in the foraging area	ha

RELICT BOREAL WILLOWS (*SALIX LAPPONUM* AND *SALIX MYRTILLOIDES*) AS AN ELEMENT OF PHYTOCOENOSES OVERGROWING THE WATER BODIES IN EASTERN POLAND

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Abstract: The aim of the present research, which was conducted in the years 2002 and 2012, was to determine whether and to what extent the biocenotic changes taking place in the aquatic peatland ecosystems affect the state of the populations of endangered boreal willows (*Salix lapponum* and *Salix myrtilloides*) in the Łęczna-Włodawa Lakeland (Eastern Poland). The results of this research show that the decline in population numbers of the studied species is associated with the changes that have taken place in their habitats since the 1950's. These changes manifest themselves in the species composition and structure of the phytocoenoses of which the species under investigation are components. In consequence, the intensive process of ecological succession can accelerate the rate of extinction of *S. lapponum* and *S. myrtilloides* within the area of the Łęczna-Włodawa Lakeland.

Keywords: *ecological succession, endangered species, habitat*

Introduction

In natural ecosystems, any change in the abiotic environmental conditions are usually reflected in the functioning of biocoenoses. Neither large-scale anthropogenic transformations of the environment nor seemingly unnoticeable minor disturbances caused by natural factors leave the species composition and structure of phytocoenoses unaffected. Differences in ecological tolerance of individual species play a particularly important role here. With changing habitat conditions, one can observe both the encroachment and the withdrawal of particular species. The problem of disappearance of rare taxa, frequently strongly associated with their specific habitat, from their natural stands is now common.

In eastern Poland, the area of the Łęczna-Włodawa Lakeland has been subjected to strong anthropogenic pressure since the beginning of the 20th century. This region of exceptional environmental value was originally characterized by a significant proportion of inaccessible wetlands, peatlands, and lakes. In the 1950's hydraulic improvements were initiated in this area and these works continued until the 1980's; as a result of that, a significant part of the Lakeland area was drained, the wetland ecosystems became fragmented, and major eutrophication occurred which was caused by the waters that came from the outside via a system of canals and drainage ditches

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(Bartoszewski and Michalczyk, 1996; Radwan et al.,1999). As one of the consequences of long-term anthropogenic impacts, ecological succession can be observed within this area and this process is particularly intensive in the aquatic peatland ecosystems. This process, which contributes to terrestrialization of the lakes in this Lakeland and to the changes in the nature of its peatland ecosystems, is often manifested in the encroachment and increase of population numbers of expansive species which crowd out rare species with a narrow range of habitat requirements (Radwan et al., 1999).

Since the 1950's, we have observed a decline in the number of stands and population numbers of relict boreal willow species (*Salix lapponum* and *S. myrtilloides*) which were once found in great numbers within the Łęczna-Włodawa Lakeland area (Fijałkowski, 1959). These are species associated with peatland ecosystems, with strictly defined habitat requirements and very sensitive to changes in them (Kaźmierczakowa and Zarzycki, 2001; Pogorzelec, 2008). Most of the old stands of boreal willow populations do not exist anymore due to the change in the nature of their habitats, whereas those that have survived are predominantly located in the peat bogs adjacent to different sized water bodies that are at different stages of the process of being overgrown (Pogorzelec, 2009; Pogorzelec and Banach, 2008). The succession changes in the stands of *S. lapponum* and *S. myrtilloides* are taking place with varying intensity and manifest themselves in characteristic changes in the species composition of these phytocoenoses (Pogorzelec, 2009).

The aim of the present research, which was conducted in the years 2002 and 2012, was to determine whether and to what extent the biocenotic changes taking place in the aquatic peatland ecosystems affect the state of the populations of endangered boreal willows. To test the thesis that the changes in biocenotic conditions have a significant impact on the functioning of these populations, an attempt was made to answer the following questions: How much has the quantitative and qualitative structure of the phytocoenoses in which the populations of the studied species function changed since the 1950's and over the last 10 years? Is anthropophytization of the flora taking place in the stands of downy and swamp willow? To what extent have the habitat conditions changed, which are determined based on, among others, the proportions of different ecological plant groups found in the phytocoenoses studied?

Procedures

Field investigations were carried out at the peak of the growing season in 2002, from May to August, and they were repeated in 2012 within the Łęczna-Włodawa Plain (in the Łęczna-Włodawa Lakeland), which is one of the six of the Western Polesie mesoregions (Kondracki, 1981).

The first stage of the study involved the designation of seven study plots (100 m^2 in area) in the phytocoenoses in which the occurrence of *S. lapponum* and *S. myrtilloides* populations had been observed. The study plots were established at five study sites which were aquatic peatland systems at different stages of being overgrown. The criteria of selection of these study sites primarily included the stage of terrestrialization and differences in the size of the water bodies adjacent to the phytocoenoses studied. The following peat bogs within the Polesie National Park were included in the selected study sites: the Blizionki bog (the study plot designated BZL) – a completely overgrown mid-forest water body located in Torfowisko Orłowskie (Orłowskie Bog), a peat bog by Lake Karaśne (KL) which is at an advanced stage of being overgrown, the peatlands surrounding Lake Długie (DL) and Lake Moszne (ML, MM) as well as a peat bog located outside the boundaries of the Park on the western shore of the largest of these water bodies - Lake Bikcze (BL, BM; *Fig.1-2*).

The exact numbers of the *S. lapponum* and *S. myrtilloides* populations were determined within the study plots and in their immediate vicinity due to the fact that the study plots were located within the stands of the species under investigation, but they did not always cover the whole area occupied by these populations.

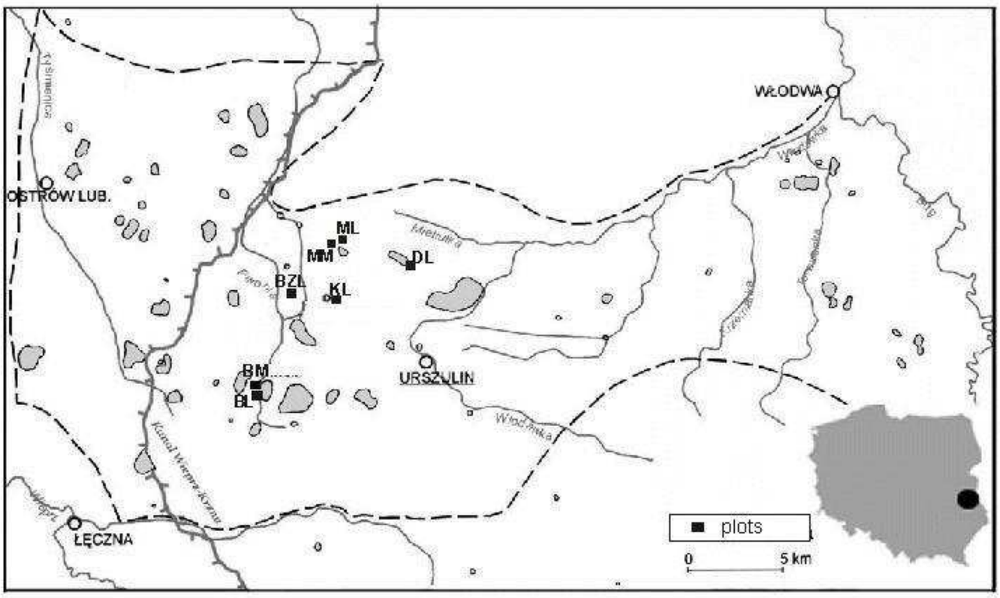

***Figure 1**. Location of the study plots in the Łęczna-Włodawa Lakeland*

In each study plot, flora observations and phytosociological relevés were made using the Braun-Blanquet method. Species were identified following Rutkowski (2006), while species nomenclature followed Mirek et al. (2002). In addition, both in 2002 and 2012 one water sample was taken for physical and chemical analysis from each of soil piezometers installed in the central part of each of the study plots. At the Central Agro-Ecological Laboratory of the University of Life Sciences in Lublin, laboratory analyses were performed using standard methods to determine the following: electrolytic conductivity (specific conductance in $\mu S*dm^{-1}$), pH, nitrogen fractions (in $mg*dm^{-3}$): total nitrogen (N), ammonium nitrogen ($N\text{-}NH_4$), nitrates ($N\text{-}NO_2$), nitrates ($N\text{-}NO_3$), phosphorus fractions: total phosphorus (P), phosphates ($P\text{-}PO_4$), sulphates ($S\text{-}SO_4$), basic cations: potassium (K), sodium (Na), calcium (Ca), magnesium (Mg).

Using desk research, the changes in population numbers of the studied species were traced, also referring to the first data on their status from the 1950's (Fijałkowski, 1958; 1958a). A multifaceted analysis of the species composition of the flora in the study plots was made in terms of the assignment of species to historical-geographical (Mirek et al., 2002), syntaxonomical and ecological groups (Matuszkiewicz, 2001; Zarzycki et al., 2002). The habitat requirements of the investigated phytocoenoses were determined using ecological indicator values (Zarzycki et al., 2002; Diekmann, 2003). On the basis of species numbers, average weighted values of the following indices were determined: light (L), soil moisture (W), trophy (Tr), acidity (R), and organic matter content (H).

The obtained results were compared with the available historical data (available only for *S.lapponum*) [12]. The habitat conditions and the changes that had taken place in the stands of the boreal willow species studied over a long (1958-2002) and short (2002-2012) time interval were characterized on this basis.

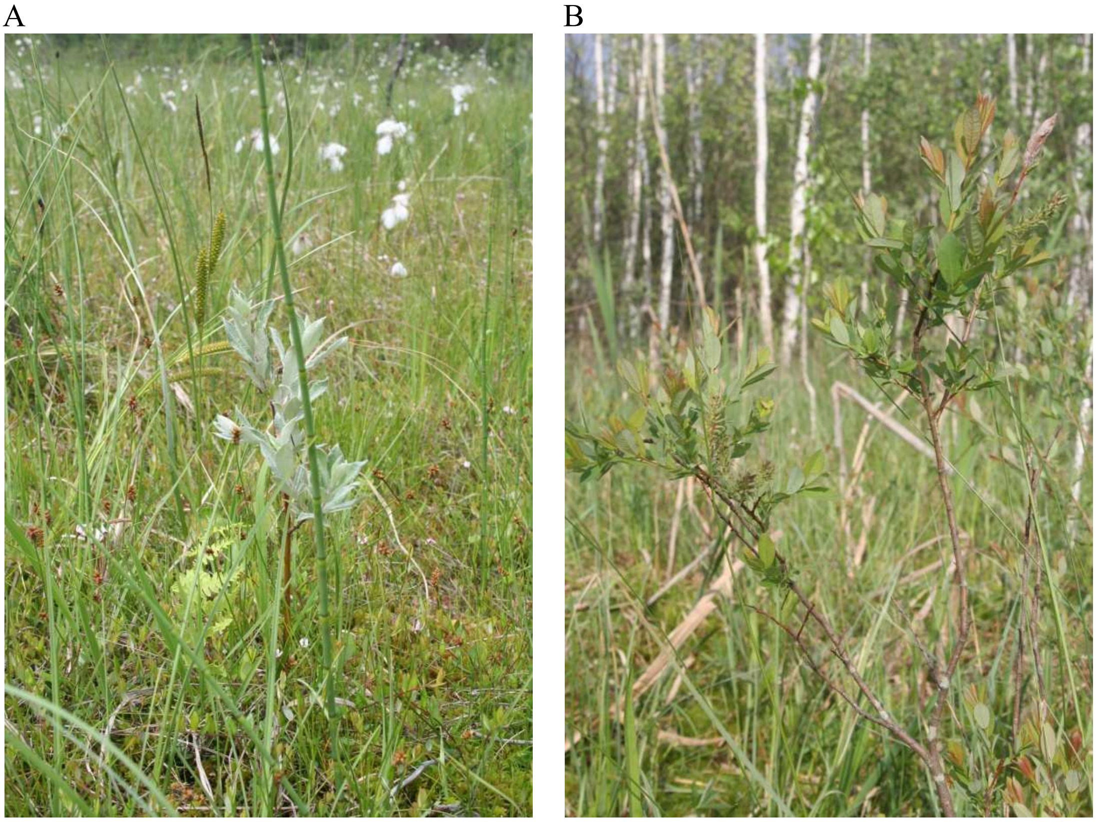

***Figure 2**. Salix lapponum (A) and Salix myrtilloides (B) in the stand located in the peat bog near Lake Moszne in the Polesie National Park (2012)*

During the first stage of statistical analysis, a comparison was made of the Shannon-Wiener indices and the evenness index for the particular phytocoenoses in the study plots. Subsequently, a non-metric multidimensional scaling (NMDS), hierarchical cluster analysis (HCA) and redundancy analysis (RDA) were performed to analyse the data set. Statistical computations were carried out using the computing environment R, version 2.15.3 (2013-03-01), packages: Vegan, MASS and MVSP (Multivariate Statistical Package), version 3.22 (Oksanen et al., 2013; Chahouki, 2011; Ter Braak and Prentice, 1988).

Results

The population numbers of the studied species changed in all the stands investigated. The most numerous population of *S. lapponum* existed in 2012 in the peat bog by Lake Bikcze, while that of *S. myrtilloides* near Lake Moszne, despite that a rapid decline in their numbers had been observed since 2002. In 2012 the population of *S. lapponum* in the Blizionki bog was found to have completely disappeared (*Fig. 3*).

The syntaxonomical analysis of the species composition (*Table 1*) of the studied phytocoenoses revealed that species characteristic of the classes *Alnetea glutinosae, Oxycocco-Sphagnetea* and *Scheuchzerio-Caricetea* were the most numerous group. An increase in the proportion of species of the alliance *Magnocaricion* and *Alno-Ulmion* could be observed, in particular in the stands located in the peat bog near Lake Bikcze.

Taking into account the species composition and proportion of the individual species throughout the study period (including the historical data), it was found that spontaneophytes had the highest number of representatives in the studied phytocoenoses (their percentage was 77% – 100%). Kenophytes, that is, alien species classified as anthropophytes, were found incidentally (the last time in 2012 in the bog near Lake Moszne).

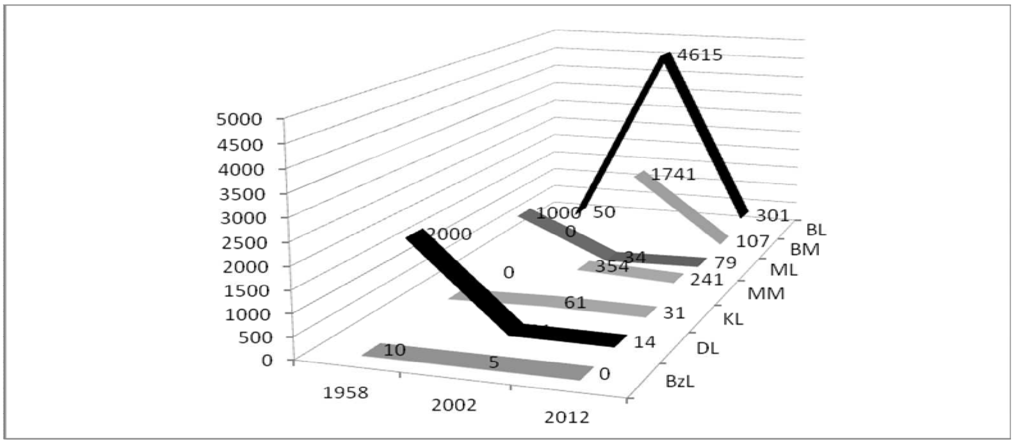

***Figure 3**. Changes in population numbers of boreal willows in the studied stands in the Łęczna-Włodawa Lakeland*

***Table 1.** Species composition of the phytocoenoses of the study plots in the years 1958 (Fijałkowski, 1958a), 2002 and 2012, taking into account the characteristic cover-abundance of individual vascular plant species (Braun-Blanquet's scale with a 10-point modification acc. to van der Maarel 1979)*

Plots	BL			BM		ML			MM		KL			DL			BZL	
Year / Species	1958	2002	2012	2002	2012	1958	2002	2012	2002	2012	1958	2002	2012	1958	2002	2012	2002	2012
Cl. Phragmitetea																		
Calla palustris	+	1	+	+	1	+					+	+						
Carex acutiformis							3		1								+	
Carex appropinquata	+					2			2									
Carex elata											+	+						
Carex grcilis											+							
Carex rostrata	+	1	1	1	1		1	1	1	1	2	1	1	+	1	1	5	
Carex vesicaria												+						
Equisetum fluviatile	3	2	2	2	1			1		1	+	1	1	+	+	1		+
Galium palustre		+	+	+	+		+	+			+	+	+					
Glyceria maxima													1					
Lysimachia thyrsiflora		+	1		1											+		
Peucedanum palustre	+	+	+			+	1	1	1	1	+			+	+	+		

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Phragmites australis	+	+	1		1	+	1	2		+			6		7	8		3
Ranunculus lingua		+			1							+						
Typha angustifolia		1	+	+					1			+						
Typha latifolia					1													
Cl. Scheuchzerio-Caricetea nigrae																		
Agrostis canina	+										+			+				
Calamagrostis stricta											+			+				
Carex chorrdorhiza	+													+				
Carex davalliana									3									
Carex diandra	+					1					+			+				
Carex echinata								1		+						1		
Carex flava	+						1											
Carex lasiocarpa	2	+	2		1	6		1		1	1		1	1		2		
Carex limosa	+					+	+	+		1	+	+	+			1		
Carex nigra	+	2	2	2	2	+		1		2	+	1	1	+	2	2		
Comarum palustre	+	3	2	+	3	1	+	1	2	+	+	1	1	+	+	1	+	+
Drosera anglica														+				
Epipactis palustris																		
Eriophorum angustifolium	+	+	1					1		1	+		+		+	1		
Eriophorum gracile	2													2				
Juncus articulatus		+																
Menyantes trifoliata	+	1	3	1	1		2	1	1	1	+	+	1		2	3	+	
Parnassia palustris						+							+					
Pedicularis palustris	0					+												
Rhynchospora alba								+										
Scheuchzeria palustris	+							+										
Stellaria palustris			+		+													
Triglohin palustre							+											
Viola palustris							+					+						
Cl. Oxycocco-Sphagnetea																		
Andromeda polifolia		+	+				+	+										
Drosera rotundifolia	+	+				+	2	1		1		+	+	+	+	+		
Eriophorum vaginatum	+	+		+		1		+				+					2	
Oxycoccus palustris		3	1		1		6	3	6	6		*3*	1	2	4	2	4	2
Cl. Molinio-Arrhenatheretea																		
Agrostis gigantea						1					+							
Carex panicea			+			1	2	1		+					2			
Cirsium palustre									+									
Dactylorhiza majalis														+				
Epilobium palustre	+						+											
Festuca rubra											1							
Galium uliginosum	+	+				+			+					+				
Juncus conglomeratus		+																
Lysimachia vulgaris	+	1	1	+	1	+	+		+	+	+	1	1		1	+		+
Lythium salicaria	+	+		+			+	+			+	+		+	+			
Molinia caerulea	+	+				+	+	+						1				
Poa pretensis						1												

Ranunculus acris						+			+									
Cl. Alnetea glutinose																		
Alnus glutinosa												2	2					+
Betula humilis	1					+	1	1			+	1	2				+	+
Calamagrostis canescens		+	+				+		+		+	+		+	+	1		3
Lycpus europeus	+					+					+							
Salix aurita							1											
Salix cinerea	+	2	1	3	1		2	1	2	1	+		2	+	+	1		
Salix pentandra		+		2			+				+	+	2					
Salix rosmarinifolia	+	2	+	2	2		+		1		2		+	+	+	+		+
Thelypteris palustris	2	+		3	1	+	4	1	4			+	1	1	3	1	+	
Other species																		
Alnus incana				1				+										
Betula pendula	+	1	3	2	2	+	1			+	+							
Betula pubescens		1	+		+		3	1	3	2		*2*	1	2	+	+	1	+
Carex curta		+	1							1						+		
Frangula alnus			+				1		1	+		1	+		+		+	+
Lemna minor					1													
Mentha x verticillata						+												
Pinus sylvestris				+			1	1	+	1						+		
Polygonum persicaria													+					
Potentilla erecta												+						
Quercus robur																+		
Salix lapponum	+	2	2			1	1	+	+	+	+	+	+	1	+	+	+	
Salix myrtilloides				2	1		+	+	+	+								
Stellaria uliginosa						+												
Urticularia vulgaris													+					+
Vaccinum uliginosum										1								

The Shannon-Wiener diversity index (the log to base 10) and the evenness index determined for the studied phytocoenoses indicate a clear division of the phytocoenoses in the investigated stands into those in which the populations of the species under study were numerous (BL, BM, MM, ML, KL) and not numerous (BzL and DL). For both habitat groups distinguished, significant differences were found (p=0.05) in the mean value of the diversity index (Wilcox test for unequal variances), the evenness index, and average population numbers (Welch two sample t-test). The assumption about the normality of distribution of the diversity and evenness indices as well as of the numbers in both groups was verified by the Shapiro-Wilk test, while the homogeneity of variances was checked by Bartlett's test.

In the next stage, non-metric multidimensional scaling (NMDS) was used to obtain an ordination in two-dimensional space. We obtained a stress value of ≈0.157 and it provides a good representation in reduced dimensions. The analysis of species composition using NMDS differentiated the study plots into three groups. The phytocoenoses investigated in 1958 were observed to be grouped together compared to the other years of the study. The analysis also showed low similarity of the phytocoenoses investigated in 2002 and 2012 in the Blizionki bog (*Fig. 4*).

The comparative analysis of the phytocoenoses of the study plots, both qualitative (Jaccard's coefficient; *Fig.5*) and quantitative (percent similarity; *Fig.6*), revealed a division of the stands into four groups. Group I included the phytocoenoses studied and described in 1958. The other clusters suggest similarity of the phytocoenoses related to their location within the study area; the stands located in close proximity are grouped close to each other. The results demonstrate distinct changes that have occurred both in the species composition and in the proportion of individual species in the phytocoenoses since the 1950's. Over the last 10 years, these changes were most evident in the Blizionki bog and on Lake Bikcze, which is evidenced by low similarity of the phytocoenoses in 2002 and 2012.

The habitat requirements of the plant patches determined based on the assignment of plant species to ecological groups indicate that over the period of the last 10 years (2002-2012) the most noticeable changes occurred in the stand in the Blizionki bog. One can observe there changes in the proportion of occurrence of species representing particular ecological groups of vascular plants for all the factors analysed. In the case of the other stands, in all time intervals minimal differences are seen in the proportions of different ecological plant groups, which does not exclude the possibility of tracing the changes in habitat conditions taking place there (*Fig.7*).

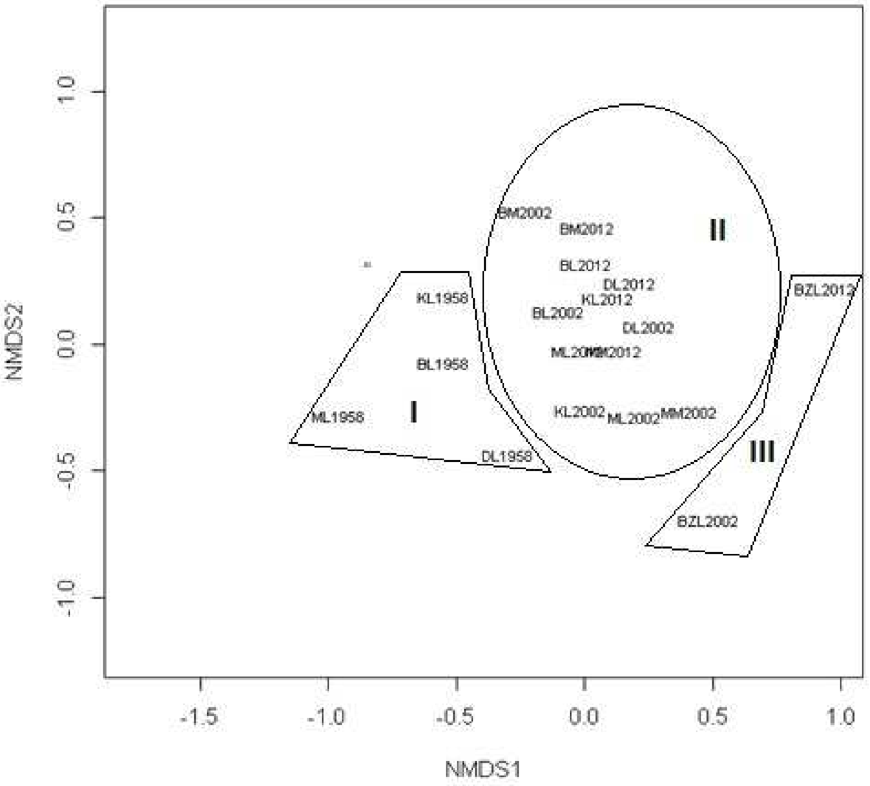

Figure 4*. Two dimensional non-metric multidimensional scaling (NMDS) plot based on Bray-Curtis dissimilarities for phytocoenosis. The stress of the diagram non-metrically scaled in two dimensions is 0.157*

The physico-chemical analysis of water samples collected from the soil piezometers installed in the study plots served as a habitat background for examination of the flora (*Table 2*) and was used for RDA ordination analysis.

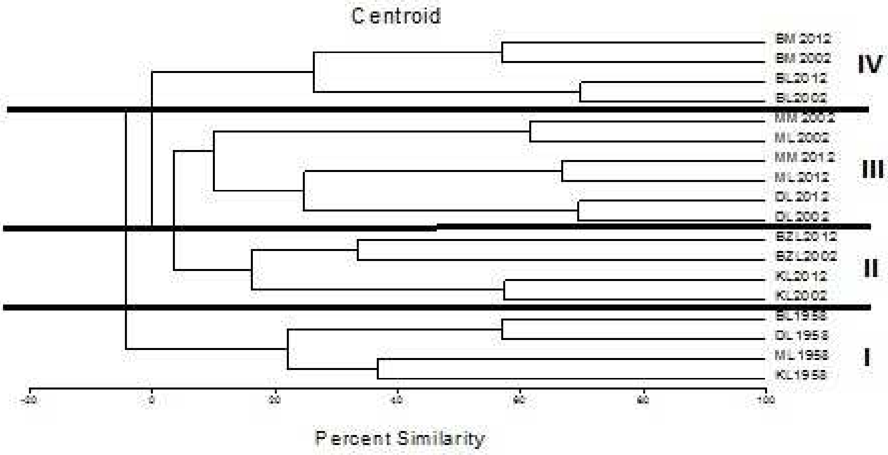

***Figure 5**. Dendrogram of hierarchical cluster analysis of 18 phytocoenoses based on percent similarity measure and centroid method.*

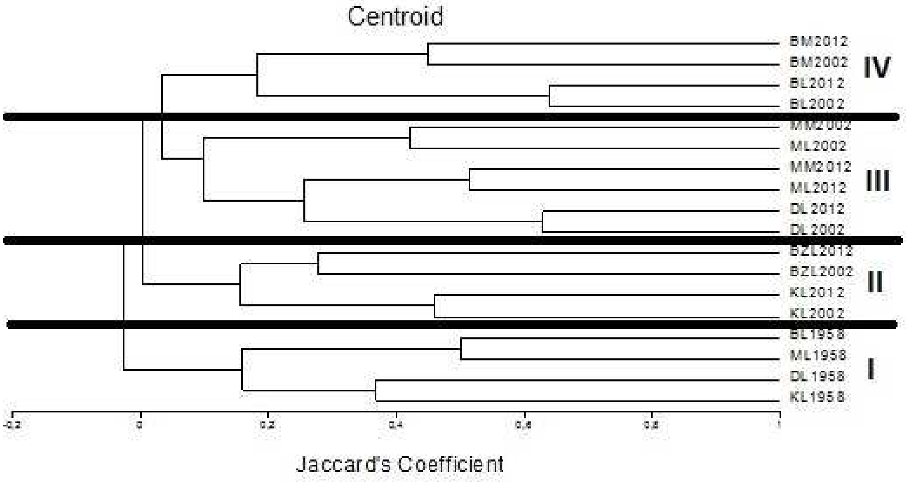

***Figure 6.** Dendrogram of hierarchical cluster analysis of 18 phytocoenoses based on Jaccard's coefficient and centroid method.*

RDA examines the relationship between environmental variables and species composition. The analysis was preceded by the determination of environmental gradient length. The obtained value of 2.49 recommends the use of redundancy analysis (RDA). Two data collections were considered: species composition and variable values of selected habitat factors. The phytocoenoses studied in 1958 were excluded from the analysis due to the lack of data.

The analysis showed that there was a strong correlation of concentration of Na ions in the water sampled from the investigated habitas with electrolytic conductivity and water pH as well as a negative correlation of Na, with NO_3 and SO_4. Likewise, there was a strong positive correlation between water concentration of PO_4, and Mg, NO_2, N, P as well as a negative correlation for PO_4 and Ca (*Fig. 8*).

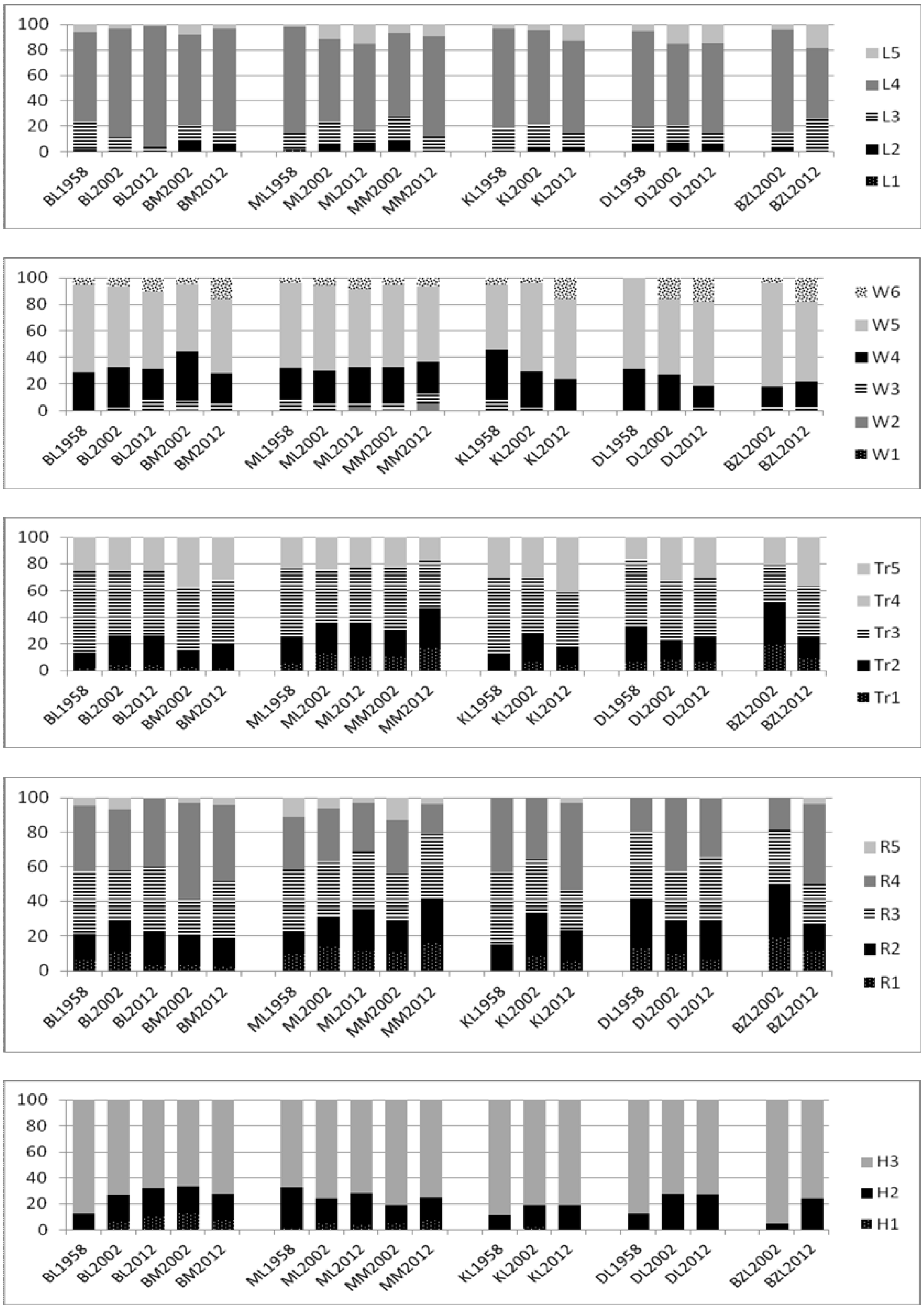

Figure 7. *Proportion of species of different ecological groups of vascular plants in the flora of the study plots in the years 1958, 2002 and 2012 (L – light value; W – soil moisture value; Tr – trophy value, R – water acidity value, H – organic matter content value; the numerical designations denote the assignment to specific ecological groups following Zarzycki et al., 2002).*

Table 2*. Values of some abiotic factors as measured in the water samples in the years 2002 and 2012.*

Plots	Year	Acidity	EC	N	NO_3	NO_2	P	PO_4	SO_4	Mg	Ca	Na	K
		pH	*(µS*dm^{-1})*	*(mg*dm-^{3})*									
BL	**2002**	5,49	147,0	8,36	0,10	0,29	3,66	7,00	1,20	4,91	13,11	6,91	15,58
	2012	5,30	74,0	6,75	0,07	0,00	1,55	2,20	0,12	3,45	15,10	34,70	6,30
ML	**2002**	6,41	175,0	1,88	0,13	0,00	0,32	0,15	3,42	0,97	33,38	1,72	2,79
	2012	5,90	102,1	1,47	0,00	0,00	0,28	0,00	0,19	2,79	26,40	22,60	4,58
KL	**2002**	6,53	154,5	4,93	0,20	0,00	0,12	0,12	9,59	0,62	16,41	9,59	11,49
	2012	6,50	293,7	5,08	0,06	0,00	0,39	0,00	0,00	3,81	75,10	35,60	5,30
DL	**2002**	6,64	163,0	6,52	0,26	0,00	0,72	1,51	0,87	0,55	6,20	3,30	10,33
	2012	5,70	107,2	2,21	0,05	0,00	0,26	0,00	0,13	3,37	25,30	35,80	5,93
BZL	**2002**	4,20	88,8	7,26	0,00	0,00	1,75	4,34	0,74	3,24	19,74	5,93	6,82
	2012	6,20	169,1	27,63	0,00	0,00	0,55	1,39	0,17	3,40	28,10	6,71	3,51
MM	**2002**	5,22	59,4	5,58	0,32	0,00	0,52	0,90	2,09	2,20	49,67	3,13	3,56
	2012	5,60	77,2	3,36	0,00	0,00	0,33	0,00	0,14	1,46	10,90	32,20	5,50
BM	**2002**	5,88	96,4	16,22	0,26	0,08	3,33	9,08	1,11	3,47	10,32	9,09	34,57
	2012	6,20	235,1	2,81	0,06	0,00	0,64	0,37	0,00	6,39	25,30	32,30	4,74

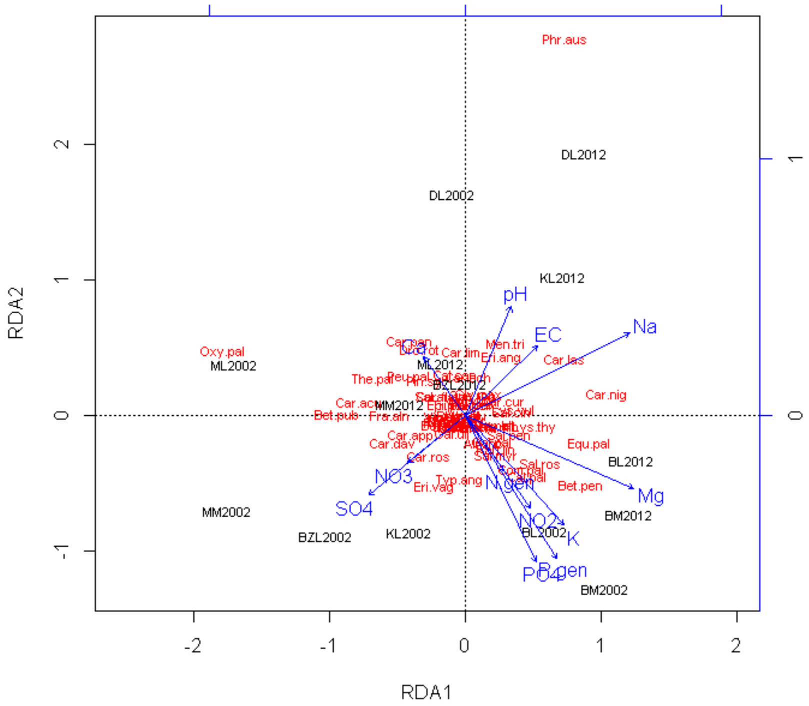

Figure 8. *Redundancy analysis (RDA) ordination diagram (showing the first and second ordination axes) displaying the relation of phytocoenoses and the correlation pattern of all environmental characteristics (arrows). Scaling method 2. Eigenvalues for constrained axes: RDA1- 11.8773, RDA2- 10.9274, sum of eigenvalues for constrained axes - 51.197, sum of all eigenvalues – 55.588*

At the next stage of the analysis, stepwise selection of environmental variables was performed (using Akaike's information criterion as the selection criterion) and a statistical analysis was made of their effect on variations in the phytocoenoses. The stepwise selection of the variables shows that only Na and PO_4 are significant ($p<0.05$) variables in the model (*Fig. 9*). The other environmental variables are not statistically significant ($p>0.05$).

The results of the significance test of the first ordination axis show that there is a statistically significant ($p\leq0.01$) gradient causing variations in the habitats. The first axis explains 17% of the total variation, while the other one 9%. Moreover, the analysis also shows a statistically significant ($p<0.05$) relationship of the occurrence of phytocoenoses with the gradient of the RDA canonical axes.

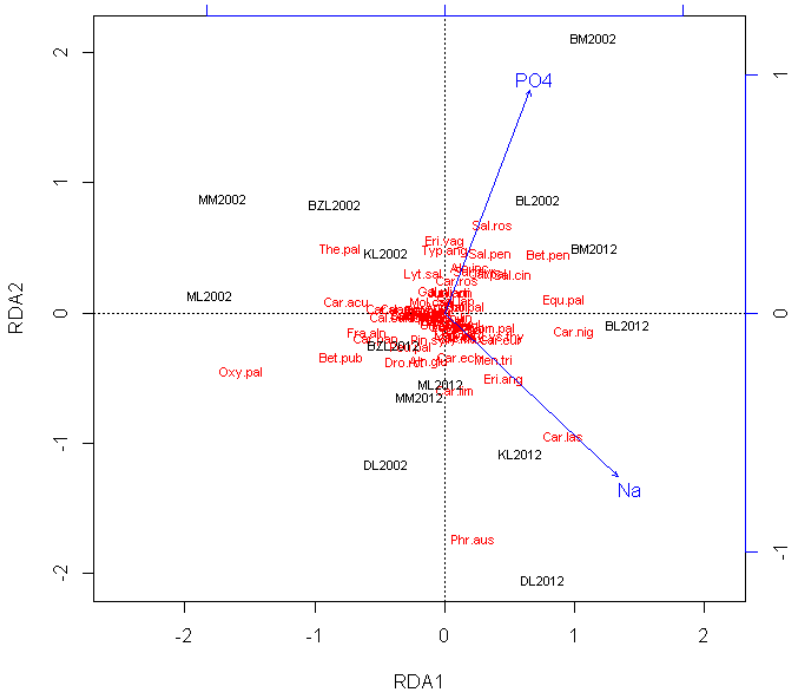

***Figure 9**. Redundancy analysis (RDA) ordination diagram (showing first and second ordination axes) displaying the relation of phytocoenoses and the correlation pattern of selected 2 environmental characteristics (arrows). Scaling method 2. Eigenvalues for constrained axes: RDA1- 9.462 , RDA2 - 5.150, sum of eigenvalues for unconstrained axes - 40.976, sum of all eigenvalues - 55.5879*

Discussion of results

In phytoindication, among different categories of indicators we find the so-called species scales in the case of which changes in the composition and proportion of species or their groups depend on the intensity of environmental factors (Solon, 2005). It is also known that individual species, due to their specific habitat requirements, can be good indicators of the state of the environment (Godefroid and Koedam, 2003; Cousins and Lindborg, 2004; Furlan et al., 2006; Pietrzykowski and Krzaklewski, 2006). Species that are particularly sensitive to environmental disturbances are often rare species or species threatened with extinction in the case of which the number of stands and population numbers are continually decreasing. In Poland such species in peatland ecosystems are, among others, *S. lapponum* and *S. myrtilloides* – relict willows whose few stands are outside the continuous species range (Kaźmierczakowa and Zarzycki, 2001).

The research conducted in Poland shows the progressive impoverishment of the populations of both species in question (Urban and Wawer, 2001; Churski and Danielewicz, 2008; Pogorzelec, 2008a; Pogorzelec, 2010). If we refer to the historical publications (Fijałkowsk,i 1958; Fijałkowski, 1958a; Fijałkowski, 1959) which provided the first data on *S. lapponum* and *S. myrtilloides* within the study area, it can be determined how much the extent and nature of the habitats in which populations of the studied species existed in great numbers have changed. Most of the populations that had survived in their stands until 2002 significantly decreased their numbers within the next 10 years. In one of its stands, the population of *S. lapponum* completely disappeared (the Blizionki bog), while in the other stands it has reached a state in which it may become impossible to restore the population if the habitat changes continue (near the lakes Długie, Moszne, and Karaśne). The population of this species is quite numerous only in the peat bog by Lake Bikcze, though the history of the rapid decline in its numbers does not bode well for the future, similarly as in the case of both studied populations of *S. myrtilloides* (quite numerous at the moment).

Habitat conditions are not the only factor determining the proper functioning and survival of populations of endangered species. Nevertheless, the analysis of the structure and ecological characteristics of the phytocoenoses in the stands of the studied willow species in 2002 and 2012 allows us to presume that in this specific case it is the habitat disturbances that will play a key role in weakening the condition of these populations. The statistical analysis shows differences in the habitats, depending on the year of the study, but the group of data collected in 1958 clearly stands out. These phytocoenoses exhibit low similarity, both in qualitative and quantitative terms, to the communities of the same area described in 2002 and 2012.

The gradual slow transformations taking place in the environment give time and possibility for species to adapt, which is quite different to quick and abrupt changes that can be destructive (Sprugel, 1991). The research carried out in 2002 and 2012 revealed that the greatest decline in numbers of the willow populations related to the stands in which the greatest changes in the species composition and structure of the phytocoenoses had occurred over the period of 10 years – the stands in the Blizionki bog and near Lake Bikcze. The habitat investigations carried out using indicator value analysis also confirmed this result.

In spite of the fact that *S. lapponum* and *S. myrtilloides* have a wide range of tolerance for the values of different abiotic environmental factors (Pogorzelec, 2008a), their populations are probably not able to resist the changes taking place in the aquatic peatland ecosystems undergoing succession. The encroachment of expansive species that win the competition for environmental resources, including related species (of the family Salicaceae) which additionally create a risk of hybridization (Pogorzelec and Nowosielski, 2006), has an adverse effect on intrapopulation processes that determine the numbers and condition of *S. lapponum* and *S. myrtilloides*.

Most of the studied stands of the boreal willow populations are within the Polesie National Park area that has been covered by area-based conservation since the 1990’s and in which active conservation of the peatlands is carried out; it involves, among others, the removal of expansive species (Różycki and Sołtys, 1999). In spite of these efforts, the populations of the studied species are on the verge of extinction. In analysing the historical data (Fijałkowski, 1958; Fijałkowski, 1958a), an observation can be made that the problem appeared in the second half of the 20th century. It is probable that the fragmentation and disappearance of the habitats of the species in question initiated a series of intrapopulation processes and changes in the habitats which have led to the present state through their impact on the biology of the studied species.

Conclusions

The decline in numbers of the populations of relict boreal willows (*S. lapponum* and *S. myrtilloides*) existing in the Łęczna-Włodawa Lakeland is associated with the changes that have taken place in their habitats since the 1950's. These changes are manifested in the species composition and phytocoenosis structure in the stands of the studied species. Over the last ten years, these changes were most evident in the stands in the Blizionki bog and near Lake Bikcze where the greatest decrease in population numbers of the studied willow species is also observed.

If the changes in biocenotic and abiotic conditions of the habitats continue with the present intensity, these species will probably become extinct without the intervention of active protection ex situ.

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CHALLENGES IN ASSESSING ECOLOGICAL IMPACTS OF CONSTRUCTION AND DEMOLITION WASTE ON WETLANDS: A CASE STUDY

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Abstract. Although wetlands are of ecological and economic importance, they continue to be lost to anthropogenic activities such as infilling. The impacts of wetland infilling with construction and demolition (C&D) waste on wetland plant and dipteran (Insecta: Diptera) communities were examined. Areas of wetland infilled with C&D waste compared to non-infilled areas had: a) higher soil pH and lower soil moisture / organic content; b) a relatively higher percentage of ruderal plant communities; c) relatively fewer dipteran families that were wetland specialist, gall-forming, parasitic and haematophagous; d) relatively lower abundances and species richness of marsh flies (Diptera: Sciomyzidae). Challenges encountered during this study included locating C&D waste sites; obtaining permission from landowners to undertake this study; frequent damage and theft of equipment due to human interference, machinery and infilling activity. Given the current paucity of data regarding the ecological impacts of infilling with C&D waste on wetlands and the considerable challenges with undertaking such studies, we make recommendations for appropriate site selection and monitoring at C&D waste infill sites.

Keywords: *Construction & Demolition waste; wetlands; ecological impacts; Diptera; surveying challenges*

Introduction

Wetlands

Wetlands are considered as some of the most ecologically and economically important habitats worldwide. Covering between seven and ten million km^2 globally, they provide many important ecosystem services (Costanza et al., 1997; Keddy, 2000; Lehner and Döll, 2004), including the provision of essential habitats for wetland plant

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and invertebrate communities, water filtration and flood control. However, wetlands have been and continue to be lost at significant rates: two-thirds of European wetlands were lost during the 20th century due to anthropogenic activities (EC, 1995) such as draining, dredging and infilling (Mitsch and Gosselink, 2007) with agriculture being one of the main driving forces behind the loss (Chen et al. 2012). This is not surprising given that wetlands are frequently perceived as land with no direct economic benefit to the landowner. Infilling with construction and demolition waste (Poon, 2001; Shen et al., 2004) is, therefore, seen as a means of creating improved agricultural grassland by covering the infill with topsoil or developing dry, elevated sites for building purposes.

Construction and demolition waste

Construction and demolition (C&D) waste can be described as waste that is produced as a result of the construction, demolition or renovation of structures (Shen et al., 2004; USEPA, 2009). It is composed of a mix of wastes from building sites, including concrete, wood and asphalt (EPA, 2009; Fischer and Werge, 2009; Poon et al., 2001; Williams, 1998). Although approximately 870 million tonnes (32.9% of total waste) of C&D waste were produced in EU countries in 2008 (Eurostat, 2011), detailed information regarding the disposal of the waste is not currently available (European Commission DG ENV, 2011) given that EU countries frequently categorise infilling as C&D waste recycling. Nevertheless, some EU countries (Spain, Hungary and Ireland) have documented problems with illegal disposal of C&D waste (European Commission DG ENV, 2011; EPA staff member, Pers. Comm.) in unregulated fill sites.

Information on the regulation of C&D waste infill in Ireland is presented in *Table 1*. Prior to 2001, municipal landfills were the only legal sites at which C&D waste could be placed. However, with the waste being viewed as mainly inert, it was often used as unregulated fill material (EPA, 1996; EPA staff member, Pers. Comm.). Post-2001 Waste Permits (WP) were obtained for many of these unregulated sites, usually without any ecological assessment, so that infilling could continue. The more recently introduced Certificates of Registration (COR) which require submission of biodiversity details of the site, give no indication of the level of ecological detail required for the granting of the permit. Given this situation, the loss, due to C&D infilling, of unprotected Irish wetlands and their associated biota is likely to be still taking place.

With the exception of a single publication by Gabrey (1997) which found that C&D waste had no significant impacts on bird populations in the USA (in the context of birds as hazards to nearby airports), the ecological impacts of infilling wetlands with C&D waste have been poorly studied. Wetland sites infilled with C&D waste are, at best, challenging sites to complete ecological investigations, for a number of reasons. Landowners may refuse requests to undertake site surveys (noted by Krause et al., 2013 when undertaking stream investigations) due to the possibility, in this case, of an ecological surveyor discovering hazardous, non-C&D waste material. On the other hand, C&D waste sites frequently have open access and are subject to constant disturbance, not only from machinery dumping and spreading the C&D waste but from illegal fly-tipping activities. While the authors quickly became aware of these challenges early in this study, we nevertheless persisted with our investigations in the belief that quantitative data, in the form of a case study, would go at least some way in highlighting the ecological effects of infilling wetlands with C&D waste, given the paucity of knowledge in this field. These data can bring to light potential ecological impacts on wetlands of C&D waste with a view to informing policy changes for future site selection and monitoring. With this in mind, we concentrated on wetland biological groups such as plants which are sensitive to chemical changes in their environment (LaPaix et al.2009; Pardo et al., 2011) and Diptera (families and morphospecies), shown to be influenced by vegetation structure (Hughes et al., 2000; King & Brazner, 1999; Whiles and Goldowitz, 2001). In particular, we identified marsh flies (Diptera: Sciomyzidae), to species level since they have been shown to reflect a range of wetland conditions (Murphy et al., 2012; Speight, 1986; Williams et al., 2009, 2010). While plants are frequently used in isolation to assess habitats, we included invertebrate groups in this study given that, apart from charismatic invertebrate species such as butterflies, policy makers can often be unaware of problems associated with general invertebrate conservation (Cardoso et al., 2011).

***Table 1**. Regulations relating to Construction and Demolition (C&D) Waste infilling in the Republic of Ireland. ta-1 = tonnes per annum. na = not applicable. EIA = Environmental Impact Assessment. AA = Appropriate Assessment.*

	C&D waste disposal permits [a, b, c, d, e, f]	**Outcomes** [a, b, c]	**Ecological survey details** [b, c, d, e, f]
Pre 2001	No C&D specific disposal sites. C&D waste was directed to municipal landfills	C&D waste often used as unregulated fill material. Many of these sites granted WPs post 2001 to continue infilling	na
2001 - 2008	<5,000 ta^{-1}: Waste permits (WP) granted by local authority	Most inert C&D waste was disposed on WP sites	Ecological information not essential - Environmental survey (no details given) decided on a case-by-case basis in situations where pollution is likely, or site is near/in Natura 2000 site
	>5,000 ta^{-1}: Waste License granted by EPA	Few Waste Licenses granted with result that most inert C&D waste was disposed on WP sites	Environmental survey (EIA) required for waste license. (See EPA Advice Notes on Current Practice[g])
2008 - present	<10,000 ta^{-1}: Certificate of Registration (COR) granted by local authority	Most inert C&D waste disposed on COR or WFP sites	Application requires details of biodiversity on site. No information on minimum level of ecological detail required. EIA required if pollution is likely - this is decided on a case-by-case basis OR if waste >25,000 tonnes. AA[h] required if there are potential impacts on NATURA 2000 site
	10,000 - 50,000 ta^{-1}: Waste Facility Permit (WFP) granted by local authority		
	>50,000 ta^{-1}: Waste License granted by EPA	Most inert C&D waste disposed on COR or WFP sites	EIA required. AA[h] required if there are potential impacts on NATURA 2000 site

[a] EPA, 1996. [b] EPA staff member, Pers. Comm. [c] Local authority staff member, Pers. Comm. [d] Statutory Instrument No. 165 of 1998. [e] Statutory Instrument No. 821 of 2007. [f] Office of Environmental Enforcement, 2008. [g] CAAS Environmental Services Ltd., 2003 [h] European Commission, 2002.

This study presents a description of nine wetland sites which have been affected by the infilling of C&D waste. The objectives of the study are to compare, for the first time, plant and dipteran communities on the C&D infilled and non-infilled portions of wetlands. Our hypothesis is that plant and dipteran community composition will be significantly different on C&D infilled and non-infilled portions of wetlands. In addition, we identify problems currently associated with ecological site investigations at C&D infill sites with a view to developing recommendations for appropriate site selection and monitoring.

Methods

Study area

Nine sites (*Table 2*), located in County Galway (*Fig. 1*) in the west of Ireland were investigated for this study. Eleven sites were originally selected for the present study. However, two of these sites had to be abandoned within weeks of starting due to repeated vandalism and theft of invertebrate sampling equipment. Sites were chosen from all County Galway sites for which permits were held for the disposal of C&D waste. They were selected on the basis of proximity to each other so that aerial invertebrate samples could be collected from all sites on the same day, thereby reducing the influence of weather conditions on invertebrate catches. Most sites were chosen in areas to the north of Galway city where there is a concentration of wetlands. Sites were selected from those wetlands which were partly infilled with C&D waste to facilitate comparisons between the infilled and non-infilled portions of the wetlands. Habitat classification was carried out on the selected sites following Fossitt (2000).

The nine sites (*Fig. 1*; *Table 2*) consisted of two (WG1 and WG2) wet grassland sites (soil pH>7), two (SW1 and SW2) reed & large sedge swamp sites (soil pH>7) and five (CB1–CB5) cutover raised bog sites (soil pH<7). Total wetland sizes ranged from 9ha to 169ha (estimated from aerial photography). One site (WG1) was situated within an EU designated Special Area of Conservation (SAC) on the River Clare. All sites had already been partly infilled with C&D waste when this study began, with varying levels of infilling activity being carried out during the study period.

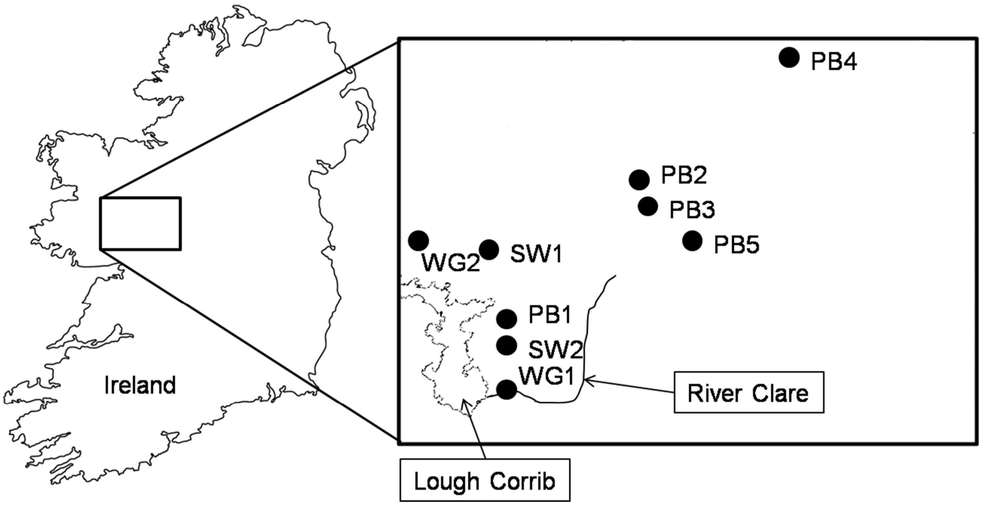

Figure 1. *Location of wetland study sites within County Galway, Ireland*

Sampling methods

Diptera were sampled in 2009 and 2010 while vegetation surveys and soil sampling were undertaken in 2010. However, due to infilling activity and discontinuation of access permission to sites CB5 and SW2 respectively at the end of 2009, vegetation surveys and soil sampling took place on seven sites only. Vegetation surveys were carried out on sites WG1, WG2, SW1 and CB1-CB4 in August 2010. Sampling in the wetland using three 0.5m x 0.5m quadrats (Bullock, 2006), 5m apart, was restricted to 5m from the edge of the infill and, in the infill, to 5m from the edge of the wetland. This sampling strategy was limited by the size of the smallest site with other sites being sampled in the same manner for comparative purposes. In addition, depth of water became greater in some of the wetlands with distance from the infill and safety considerations prevented sampling in these areas. Nevertheless, given the abrupt changes in plant communities that can be seen at the interface between the infill and wetland (*Fig. 2*), the vegetation data recorded gives a good indication of differences in plant communities at the infill and wetland interface.

All plant species within each quadrat were identified using Rose and O’Reilly (2006) and Webb et al. (1996). Percentage cover of each plant species, bryophytes (bryophytes were not identified to species level, but were dealt with as a group), dead vegetation and bare ground were recorded. Within each quadrat, four measurements were taken randomly with a ruler for both vegetation height (maximum height from ground of resting vegetation) and vegetation length (length of longest plant when stretched out), as measurements of structural complexity for use in data analysis (Williams, 2010). Ellenberg indices (Hill et al., 1999), as corrected for use in the British Isles by Hill et al. (2000), were used as additional surrogate environmental variables, and were calculated following Williams et al. (2011). Ellenberg indices are based on the plant community data and can be used to indicate soil parameters (moisture, pH and nitrogen content) and light intensity. Ellenberg values (moisture and pH) were also compared with measured field soil parameters.

Figure 2. *Example of interface between infill and wetland*

Using a Dutch auger (Eijkelkamp), soil samples at each quadrat (ca. two kilograms) were taken in 2012 to a depth of 20cm. C&D waste which was frequently compacted by heavy machinery was difficult to penetrate preventing the extraction of samples at lower depths. Moisture content (expressed as a percentage of the wet weight), mass loss-on-ignition (expressed as a percentage of the dry weight) and pH (using soil suspensions) were determined according to British Standards (BSI, 1990). Results from individual samples were averaged (mean if normal distribution obtained, otherwise median) for the infill and for the wetland zones of each site for comparison.

Aerial invertebrates (Diptera) were collected using pan traps (Southwood, 1978) at all nine sites in 2009 and from the remaining seven sites in 2010. All sciomyzids were removed and identified from these samples. In addition, aerial invertebrates collected in 2009 were identified to morphospecies level for those seven sites in which plant surveys were undertaken in 2010 to allow comparison of the plant and aerial invertebrate data. Each pan trap consisted of a white plastic container (20cm diameter x 10cm high) placed within a similar container fixed to a wooden post set at 50cm (allowing for flood events) above ground level (Southwood 1978; Campbell and Hanula, 2007). One pan trap was placed in the centre of each vegetation quadrat. While it could be argued that some dipteran species could move between infill and wetland trap areas, any differences in data for dipteran community composition are likely to be real differences reflecting the nature of the habitats. A 25% solution of ethylene glycol (preservative) was added to the pan trap (filled to two centimetres from rim) in addition to a small amount of Ecover® washing up liquid, which was used as a surfactant. The traps were emptied weekly (July 14 to October 13 in 2009; May 6 to September 30 in 2010) and trapped invertebrates were collected by straining the trap contents through a fine nylon mesh (0.5mm). All samples were then preserved in a 70% ethanol solution. Sciomyzidae were identified to species level (Rozkošný, 1984, 1987) for all dates, and all dipteran individuals were identified to family (Oosterbroek, 2006; Unwin, 1981) for three sampling dates in 2009 (14 July; 1 September; 13 October). Taxonomic minimalism reduces time spent on species identification, allowing more samples to be analysed (Beattie and Oliver 1994), while still being a useful method to assess biodiversity (Rivers-Moore and Samways, 1996). Groups with different morphological features were identified within dipteran families and treated as separate morphospecies (Beattie and Oliver, 1994). Adult sciomyzids were identified to species level since they are known to remain close to where they eclose and therefore, reflect different types of wetland conditions (Williams et al., 2010).

Aerial invertebrates were also sampled at one site (WG2) using a sweep net (50cm diameter x 67 cm bag depth and 30.5cm handle length)(Williams et al., 2009) every two weeks in 2010 (19th May to 22nd September) allowing comparison of catches caught by sweep-netting with the pan trap method. Eight parallel sweep paths (ten metres long with a two metre buffer zone between each) were marked out using bamboo canes on both the wetland and the infill. Vegetation to the east of each path was swept in the standard figure of eight motion (ca. 1m wide), and this was carried out by the same person using a consistent walking pace and sweeping speed. The invertebrates in the sweep net were euthanized for each sweep path in the field (with each sweep path being a separate sample) by placing in a kilner jar (12cm diameter x 30cm) with ethyl acetate (99.5%). Samples were preserved in 70% ethanol and sciomyzids were identified to species level (Rozkošný, 1984, 1987). Environmental variables measured at the time of sampling were vegetation height, length of outstretched vegetation (both measured

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beside each sweep path), wind speed, humidity (Skywatch® Atmos by JD Industries), light intensity (Hanna Lux meter HI97500) and nebulosity (visual percentage estimate). Uneven surface topography prevented sweep netting at the other sites.

Statistical analysis

Various statistical procedures were carried out on the collected data to assess if there was a significant difference between the biota of the of wetland area infilled with C&D waste compared to non-infilled wetland area. Multi-Response Permutation-Procedure (MRPP) was used for observing the strength of grouping variables (habitat type and site) for multivariate datasets (Meilke and Berry, 2001). Non-metric multi-dimensional scaling (NMS) ordinations which do not assume multivariate normality were used to compare plant and dipteran communities of the wetlands and C&D waste infill (Kenkel and Orloci, 1986). Indicator Species Analysis, a method for observing the association of a species with a particular grouping variable, in this case, habitat (Dufrêne and Legendre, 1997), was also undertaken. Shannon's entropy is used (instead of Shannon's diversity index) as entropy has been shown to be more useful, giving a value for the uncertainty in the data, rather than true diversity (Jost, 2006). Minitab® Statistical Software (version 16) was used for univariate statistical analysis, and PC-ORD (version 6) was used for multivariate analyses (McCune and Grace, 2002; McCune and Mefford, 1999).

Results

Soils and plant communities

Overall there were significant differences found between the soil parameters and plant communities of C&D infill and wetland. When all wetland sites were combined for analysis, mean soil pH was significantly ($t=5.71$, $P<0.05$) greater on the infill (7.94) than the wetlands (6.41). In addition, median percentage soil moisture content (*Table 2*) was significantly ($T<0.1$, $P<0.05$) lower on the infill (15.35%) than in the wetland (80.69%) as was ($t=11.34$, $P<0.05$) mean percentage soil mass loss-on-ignition (5.03% on infill and 70.95% on wetland). Although the cutover raised bog wetlands were all acidic (pH<7) with the remaining wetland habitats being alkaline (pH>7), nevertheless, for each site studied, the pH of the C&D waste substrate was significantly ($P<0.05$) greater than the median pH of the original wetland (*Table 2*).

A total of 94 plant species were recorded at the seven sites in 2010 (n=42 quadrats), with median plant species richness and Shannon's entropy being significantly ($P<0.05$) higher on the infill than on wetlands regardless of wetland type (*Table 3*). However, there was no significant difference ($P>0.05$) in plant species evenness between infill and wetland. Following separation of sites (according to wetland soil analysis) into acidic (pH<7) or alkaline (pH≥7) wetlands, the plant data show that variance in plant species composition that was attributable to habitat status (i.e. wetland versus C&D waste) was slightly higher on acidic sites (15% of variance) than on alkaline sites (14% of variance), based on MRPP (*Table 4*). *Table 2* shows the most dominant plant species for each site (wetland and C&D waste infill). Plant indicator species analysis was performed on the acidic and alkaline sites separately using the Monte-Carlo test of

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Table 2. *Brief description of the nine wetland and infill study sites in Co. Galway, Ireland. Site code explanation: WG = Wet Grassland, SW = Swamp, CB = Cutover Raised Bog, nd = no data.*

Site code	**Total site area with permission for infilling (ha)**	**Percent of total permitted area with infill**	**Mean soil pH Wetland $^{T, a}$ (Infill)**	**Mean soil mass loss on ignition % Wetland $^{T, a}$ (Infill)**	**Median soil moisture content % Wetland $^{W, a}$ (Infill)**	**Two most dominant wetland plant species ^{b}**	**Two most dominant infill plant species ^{b}**
WG1	2.87	89.89	7.65* ± 0.11 (8.10 ± 0.06)	32.61* ± 5.74 (2.01 ± 1.26)	64.23* (14.04)	*Agropyron repens,* *Deschampsia cespitosa*	*Agrostis stolonifera,* *Festuca rubra*
WG2	0.88	32.95	7.74* ± 0.06 (8.00 ± 0.04)	37.39* ± 13.89 (2.50 ± 0.03)	77.86** (14.67)	*Carex disticha,* *Cardamine pratensis*	*Agrostis stolonifera,* *Trifolium repens*
SW1	6.62	15.56	7.13** ± 0.14 (8.01 ± 0.15)	63.45* ± 14.83 (2.31 ± 0.63)	69.28* (14.02)	*Cladium mariscus,* *Iris pseudacorus*	*Agrostis stolonifera,* *Cirsium arvense*
SW2	12.87	4.58	nd	nd	nd	*Cladium mariscus* *Phragmites australis*	*Agropyron repens,* *Sonchus asper*
CB1	5.72	47.55	6.56* ± 0.63 (7.83 ± 0.15)	85.53** ± 1.77 (1.94 ± 0.60)	89.71** (16.64)	*Molinia caerulea,* *Calluna vulgaris*	*Agrostis stolonifera,* *Trifolium pratense*
CB2	9.05	4.09	5.01** ± 0.25 (7.89 ± 0.01)	95.93** ± 1.73 (6.23 ± 1.02)	84.27** (27.74)	*Calluna vulgaris,* *Carex rostrata*	*Agrostis stolonifera,* *Centaurea nigra*
CB3	4.03	70.22	6.08* ± 0.49 (7.54 ± 0.27)	94.79** ± 2.19 (12.87 ± 1.15)	89.95** (32.43)	*Calluna vulgaris,* *Eriophorum angustifolium*	*Agrostis stolonifera,* *Circium arvense*
CB4	1.53	17.00	4.53** ± 0.19 (8.21 ± 0.26)	86.91** ± 1.05 (7.28 ± 3.28)	80.68** (15.35)	*Molinia caerulea,* *Succisa pratensis*	*Agrostis stolonifera,* *Plantago lanceolata*
CB5	2.07	71.01	nd	nd	nd	*Molinia caerulea,* *Calluna vulgaris*	*Trifolium repens,* *Holcus lanatus*

* Significant difference between infill and wetland data with ($P<0.05$) and ** ($P<0.005$). ^{W} Wilcoxon signed rank test used. ^{T} paired t-test used. ^{a} Mean ± standard deviation calculated from three samples of soil from both infill and wetland areas on each site. ^{b} Most dominant species based on percentage cover.

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***Table 3.** Species richness, species evenness and Shannon's entropy of all sites (only WG2 for sweep net data) for vegetation, Sciomyzidae and dipteran families and morphospecies. na = not applicable (due to zero collections).*

Dataset	**Median species richness wetland $^{W, a}$ (infill)**	**Median species evenness wetland $^{W, a}$ (infill)**	**Median species entropy wetland $^{W, a}$ (infill)**
2010 Vegetation	10.00 ± 4.57** (17.00 ± 5.54)	0.74 ± 0.14 (0.75 ± 0.08)	1.66 ± 0.56** (2.24 ± 0.14)
2009 (pan trap) Sciomyzidae	2.00 ± 1.28 (1.00 ± 1.64)	0.45 ± 0.43 (0.00 ± 0.45)	0.56 ± 0.40 (0.00 ± 0.53)
2010 (pan trap) Sciomyzidae	1.00 ± 0.39 (na)	0.00 ± 0.37 (na)	0.00 ± 0.26 (na)
2010 (sweep net) Sciomyzidae	4.00 ± 1.30* (0.00 ± 0.92)	0.79 ± 0.09* (0.00 ± 0.46)	0.63 ± 0.05* 0.00 ± 0.28
2009 Dipteran family	24.00 ± 3.45 (25.00 ± 4.38)	0.81 ± 0.07 (0.77 ± 0.08)	2.61 ± 0.28 (2.44 ± 0.28)
2009 Dipteran morphospecies	48.00 ± 12.08 (44.00 ± 12.07)	0.81 ± 0.07 (0.77 ± 0.09)	3.26 ± 0.40 (2.91 ± 0.42)

* Significant difference between infill and wetland data with (P<0.05) and ** (P<0.005). ^{w} Wilcoxon signed rank test used. ^{a} Median ± standard deviation calculated from all sites.

***Table 4**. Multi-Response Permutation-Procedure (MRPP) for vegetation, Sciomyzidae and dipteran families and morphospecies (Distance measure: Sørensen). Chance corrected within group agreement is a measure of within group homogeneity and P-values were assessed by permutation. Alkaline = sites with wetland soil pH≥7; Acidic = sites with wetland soil pH<7. na = not applicable (analysis could not be performed as all sciomyzids for 2010 were captured on wetland area).*

Dataset	**Grouping variable**	**Chance-corrected within-group agreement (*A*)**	***P***
2010 Vegetation	Infill v Wetland (alkaline)	0.14	2 x 10^{-5}
	Infill v Wetland (acidic)	0.15	3 x 10^{-6}
	Between site (alkaline)	0.19	7 x 10^{-5}
	Between site (acidic)	0.07	0.01
2009 Dipteran Family	Infill v Wetland (alkaline)	0.04	^{a}
	Infill v Wetland (acidic)	0.06	3 x 10^{-4}
	Between site (alkaline)	0.32	5 x 10^{-8}
	Between site (acidic)	0.14	3 x 10^{-6}
2009 Dipteran Morphospecies	Infill v Wetland	0.04	2 x 10^{-5}
	Between site	0.21	10^{-8}
2009 sciomyzid pan traps	Infill v Wetland	0.07	5 x 10^{-3}
	Between site	0.11	0.03
2010 sciomyzid pan traps	Infill v Wetland	na	na
	Between site	0.02	^{a}
2010 sciomyzid sweep net	Infill v wetland	0.14	5 x 10^{-3}

^{a} not significant at P>

significance (*Table 5*). Eleven plant species were found to be significant indicators of C&D waste on acidic sites, and six on alkaline sites, with *Agrostis stolonifera* L. having the highest percentage of perfect indication on both. Of the six indicator plant species of C&D waste on alkaline sites, four (*A. stolonifera, Cerastium fontanum* Baugm, *Lolium perenne* L. and *Ranunculus repens* L.) were also listed as indicators of C&D waste on acid sites (*Table 5*). Four plant species (*Calluna vulgaris* (L.) Hull, *Erica tetralix* L., *Molinia caerulea* (L.) Moench and *Potentilla erecta* (L.) Rauschel) were significant indicators of wetland on acidic sites, with *M. caerulea* having the highest percentage of perfect indication (*Table 5*). Alkaline sites, which consisted of more variable wetland types, were without significant wetland indicator species.

Non-metric multi-dimensional scaling (NMS) ordinations after McCune and Grace (2002) were performed with the plant data (*Fig. 3a*), with soil moisture, loss-on-ignition and pH included as vectors, resulting in a 3-dimensional solution. The plant community ordination (*Fig. 4*) showed the C&D waste infill communities to be tightly clustered indicating a high similarity between these sites regardless of the type of wetland which had been infilled with C&D waste. The wetland points, however, were more dispersed suggesting a higher variation between wetland plant communities. For the plant community data, axis 1 was most strongly correlated (r^2=.446) with Ellenberg moisture indicating the importance of moisture in determining plant community composition (*Table 7*).

Table 5. *Indicator species analysis results for vegetation data from 2010 (n=42 quadrats). (Monte-Carlo randomised test, 4999 permutations). IV = percent perfect indication.*

Max. Group		**Indicator species**	**IV**	***P* (4,999 permutations)**
Acidic sites only	Infill	*Agrostis stolonifera*	99.7	2×10^{-4}
		Cerastium fontanum	69.6	0.031
		Circium arvense	70.0	0.002
		Holcus lanatus	86.1	2×10^{-4}
		Lathyrus pratensis	41.7	0.037
		Lolium perenne	66.7	0.008
		Plantago lanceolata	54.8	0.019
		Polygonum amphibium	41.7	0.037
		Ranunculus repens	73.8	6×10^{-4}
		Taraxacum officinalis	41.7	0.036
		Trifolium repens	66.7	0.002
	Wetland	*Calluna vulgaris*	58.3	0.006
		Erica tetralix	38.1	0.002
		Molinia caerulea	74.5	4×10^{-4}
		Potentilla erecta	71.2	6×10^{-4}
Alkaline sites only	Infill	*Agrostis stolonifera*	99.8	4×10^{-4}
		Bryophytes	83.8	0.001
		Cerastium fontanum	55.6	0.031
		Festuca rubra	99.4	4×10^{-4}
		Lolium perenne	66.7	0.008
		Ranunculus repens	88.9	6×10^{-4}
	Wetland	No indicators with P<0.05	-	-

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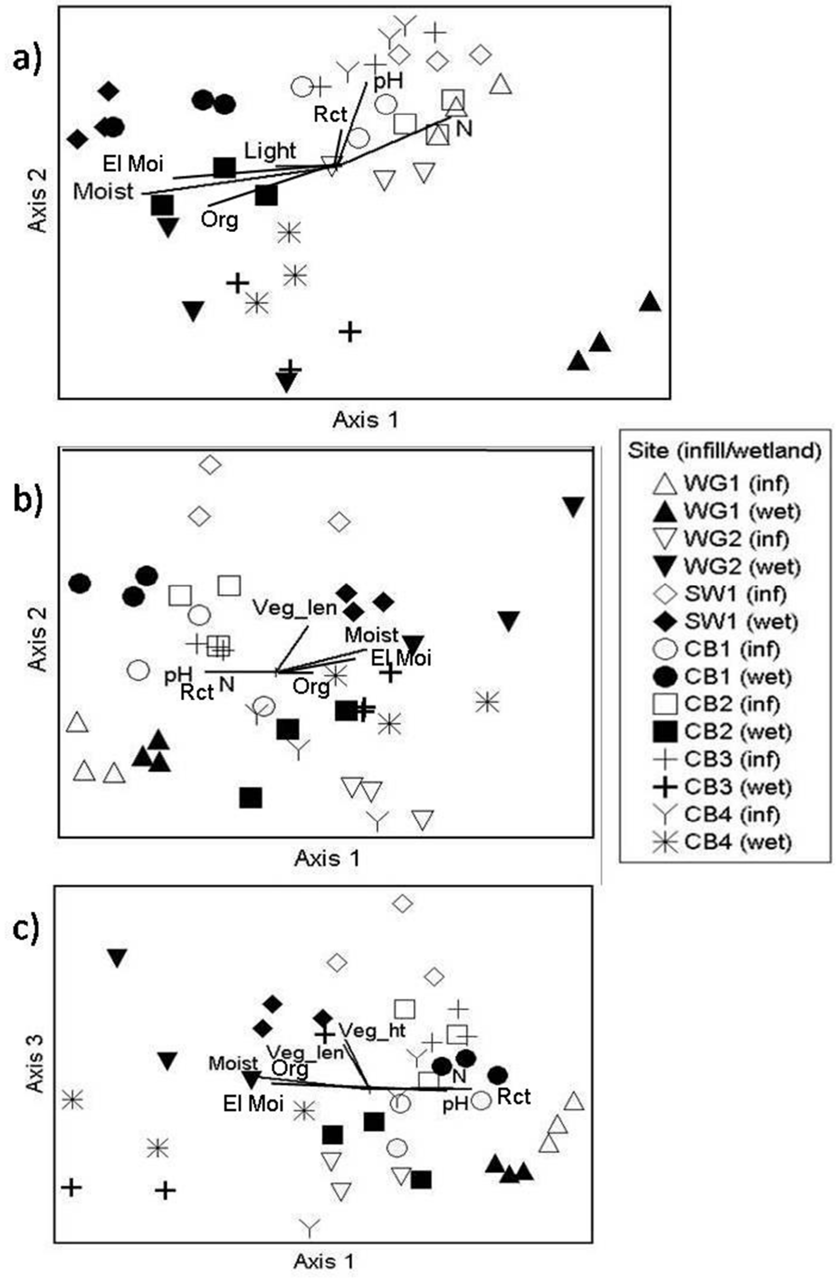

***Figure 3**. Non-metric multi-dimensional scaling (NMS) ordinations of sites in plant species space (a), dipteran family space (b) and dipteran morphospecies space (c). a) shows the 2010 plant community data (48 iterations, stress of 12.316). b) shows the 2009 dipteran family data from pan traps (45 iterations, final stress of 11.584). c) shows the 2009 dipteran morphospecies data from pan traps (47 iterations, final stress of 11.711). Distance measure: Sørensen, random starting configuration, three-dimensional solutions with orthogonality of 100%, final instability of <0.001. Coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space were: a): axis 1 = 0.287, axis 2 = 0.288, axis 3 = 0.154, b) axis 1 = 0.516, axis 2 = 0.224 and axis 3 = 0.055 and c) axis 1 = 0.565, axis 2 = 0.117 and axis 3 = 0.131. Environmental variables are overlaid as vectors. Light = Ellenberg light, N = Ellenberg soil nitrogen, El Moi = Ellenberg soil moisture, Rct = Ellenberg soil reaction (pH), Veg_len = vegetation length, Veg_ht = vegetation height, Moist = percentage soil moisture, pH = soil pH, Org = percentage soil mass loss-on-ignition (organic content), wet = wetland and inf = infill.*

Dipteran communities

Forty-four dipteran families were identified from a total of 10,688 individuals collected using pan traps on three sampling dates in 2009 (14 July; 1 September; 13 October) across seven sites (CB1 – CB4, SW1, WG1 & WG2). There was no significant difference in median morphospecies richness, evenness or Shannon's entropy for any dipteran families identified (*Table 3*). Following separation by wetland soil pH (as with plant data above), site-specific differences accounted for 32% of variation in dipteran family composition for alkaline sites, and 14% for acidic sites whereas habitat status (infill v wetland) accounted for only 4% and 6% of the variance, respectively based on MRPP (*Table 4*). *Table 6* shows the significant indicator dipteran families for C&D waste (six families) and wetlands (four families). The families Chloropidae and Phoridae had the highest percentage of perfect indication for infill at 73.7% and 66.8%, respectively. For wetlands, the two best indicators were Culicidae and Chironomidae, with values of 71.8% and 69.5%, respectively. The Family Sciomyzidae was found to have a percentage of perfect indication of 26.1% (*P* = 0.083) as indicators of wetlands. This low percentage (and higher *P* value) is likely due to low abundances, especially on the cutover raised bog sites. Similar to the plant indicator species, there was no overlap in indicator morphospecies or sciomyzids between infill and wetlands.

Table 6. *Indicator species analysis results pan trap dipteran family data from 2009 (n=42 pans), pan trap sciomyzid data from 2009 (n=54 pans) and 2010 (n=42 pans), and sweep net sciomyzid data (n=16 paths) for 2010 (Monte-Carlo randomised test, 4999 permutations). IV = percent perfect indication.*

Dataset	**Indicator species / Family**	**Max. group:**	**Abundance in Max. grp.**	**IV**	***P* (4999 permutations)**
2009 Pan trap dipteran families	Anisopodidae	Infill	17	38.5	0.040
	Carnidae		931	64.4	0.017
	Chloropidae		609	73.7	0.001
	Muscidae		286	62.6	0.032
	Phoridae		510	66.8	2×10^{-4}
	Sepsidae		78	62.4	0.010
	Cecidomiidae	Wetland	113	67.7	0.003
	Chironomidae		421	69.5	0.036
	Culicidae		144	71.8	0.001
	Tachinidae		24	47.9	0.015
	Sciomyzidae[a]		23	26.1	0.083
2009 Pan traps sciomyzid	No indicators with P<0.05	Infill	-	-	-
	Tetanocera robusta	Wetland	82	61.4	0.048
2010 Pan traps sciomyzid	No indicators with *P*<0.05	Infill	-	-	-
	Tetanocera robusta	Wetland	12	52.4	0.001
2010 Sweep net sciomyzid	No indicators with *P*<0.05	Infill	-	-	-
	Pherbina coryleti	Wetland	41	97.6	2×10^{-4}
	Ilione albiseta		39	83.2	8×10^{-4}
	Tetanocera ferruginea		11	80.2	0.006

[a] Although Sciomyzidae were not a significant indicator family, some sciomyzid species were.

Two hundred and seven dipteran morphospecies were identified. Site specific factors were the most important factor in accounting for differences among morphospecies (ca. 21%) based on MRPP analysis of all seven sites (*Table 4*). The habitat status (i.e. infill versus wetland) accounted for ca. 4% of morphospecies compositional differences among the data-sets. There were seven significant indicator morphospecies for C&D waste (within Calliphoridae, Carnidae, Chloropidae, Muscidae, Phoridae and Sepsidae) and nine for wetlands (within Cecidomyiidae, Chironomidae, Lauxaniidae, Psychodidae, Sciaridae and Tachinidae). There was a lack of obvious clustering in the dipteran family and morphospecies NMS ordinations (*Fig. 3b* and *Fig. 3c*). This suggested little advantage to using morphospecies, when compared to family data alone. For dipteran family (*Fig. 3b*) and morphospecies (*Fig. 3c*) data-sets, soil moisture (r^2=0.298) and Ellenberg moisture (r^2=0.466) respectively were strongly correlated with axis 1 (*Table 7*).

Table 7. *Pearsons'correlation coefficients between environmental variables and axes of NMS ordinations a) 2010 plant community data-set, b) 2009 dipteran family data-set, c) 2009 dipteran morphospecies data-set, d) 2010 sciomyzid data-set.*

Data-set	**a) 2010 plants**			**b) 2009 dipteran family**			**c) 2009 dipteran morphospecies**			**d) 2010 sciomyzid**
Axis	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**
Vegetation height	.094	.033	.213	.123	.201	.077	.094	.032	.216	.045
Vegetation length	.104	.017	.198	.118	.254	.138	.103	.016	.200	.205
Ellenberg light	.001	.006	.003	.004	.018	.095	.001	.007	.003	.088
Ellenberg moisture	.466	.000	.058	.288	.113	.000	.466	.000	.057	.043
Ellenberg reaction (pH)	.408	.001	.006	.266	.010	.017	.407	.002	.006	.011
Ellenberg nitrogen	.331	.000	.010	.195	.000	.000	.330	.000	.010	.000
Measured soil pH	.288	.014	.005	.137	.013	.020	.287	.013	.006	.043
Measured soil moisture	.448	.000	.012	.298	.004	.001	.447	.000	.012	.039
Measured soil organic	.390	.004	.035	.284	.004	.018	.390	.003	.036	.002

Sciomyzid communities

There were 192 sciomyzid individuals (seven species) collected using pan traps in 2009 (*Fig. 4*) and 19 individuals (three species) in 2010 (*Fig. 5*). *Tetanocera robusta* Loew accounted for 50% (n=96) and 63% (n=12) of the total sciomyzid abundances in 2009 and 2010, respectively. This was followed by *Tetanocera ferruginea* Fallén which represented 43% (n=82) and 32% (n=6) of the sciomyzid catches for 2009 and 2010. In 2009, ca. 11% of variation was attributable to site-specific differences, and ca. 7% of variation could be attributed to habitat status, for pan trap sciomyzid data (*Table 4*), following MRPP analysis. *Tetanocera robusta* was found to be a significant indicator species of wetlands in both 2009 and 2010 (*Table 6*). There were no significant indicator sciomyzid species for infill. A useful NMS ordination could not be constructed from the 2009 sciomyzid data-set due to high variation in abundance data. The 2010 sciomyzid data-set, however, resulted in a 1-dimensional ordination and showed that axis 1 had the strongest correlation (r^2=.205) with vegetation length (*Table 7*).

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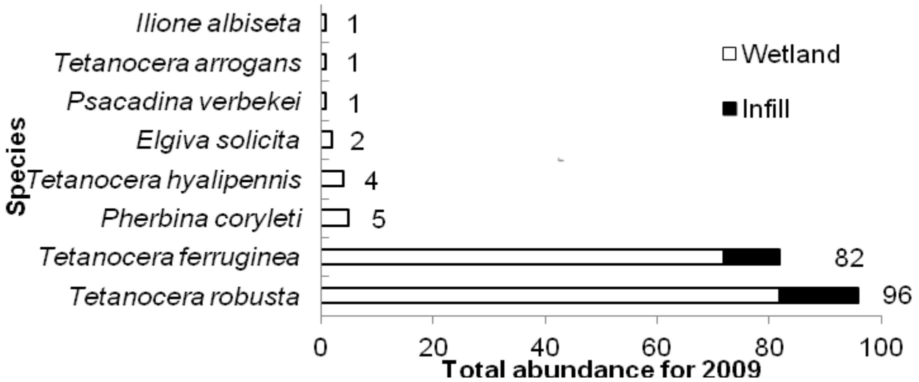

Figure 4. *Total sciomyzid species abundances from 2009 (14th July to 13th October) pan trap (n=54) data across all 9 study sites.*

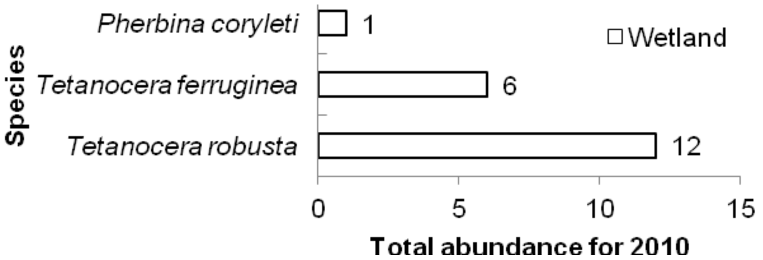

Figure 5. *Total sciomyzid species abundances from 2010 (6th May to 30th September) pan traps (n=42) data across 7 study sites.*

A total of 110 sciomyzids (12 species) were collected by sweep net in 2010 at WG2 with 105 (11 species) and five individuals (three species) collected on the wetland and infill, respectively (*Fig. 5*). Of the 12 species collected in total, *Pherbina coryleti* Scopoli and *Ilione albiseta* Scopoli were the two dominant species, representing 38% and 37% of the total catch, respectively (*Fig. 6*). The dominant species collected using sweep nets (*P. coryleti* and *I. albiseta*) were also different to the dominant species collected with the pan traps (*T. robusta* and *T. ferruginea*) at the same site (WG2). The 2010 pan trap data (*Fig. 4*) for WG2 also showed a higher median abundance of sciomyzids on the wetland (n=5) than the infill (n=0). None of the measured environmental variables showed any significant influence on the sweep net results. For the sweep net sciomyzid data, median abundance of all sciomyzid species was significantly greater ($P<0.01$) on the wetland (n=9.5) than the infill (n=0). Median species richness and median Shannon's entropy were significantly ($P<0.05$) higher on the wetland than the infill, whereas species evenness was higher on the infill (*Table 3*). MRPP on the 2010 sciomyzid data (collected using sweep nets on site WG2), showed that ca. 14% of variation in the data could be attributed to habitat status (*Table 4*). Although MRPP sometimes indicated a low proportion of explained variance, all tests were highly statistically significant for sciomyzids (*Table 4*). Indicator species analysis on sciomyzid data from sweep net samples identified three species that were indicative of wetlands (*Table 6*): *P. coryleti* (97.6%), *I. albiseta* (83.2%) and *T. ferruginea* (80.2%).

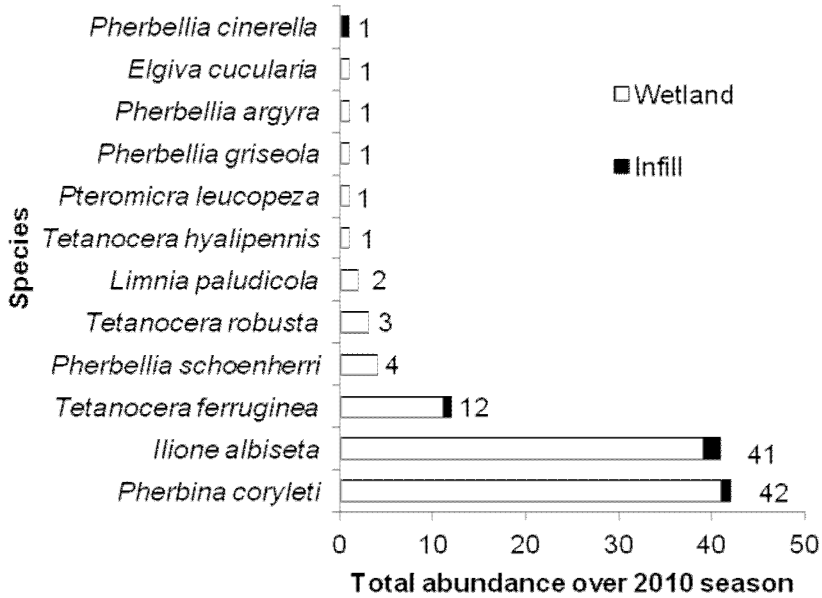

Figure 6. *Sciomyzid total abundances (2010 sampling season) for infill and wetland at site WG2 using sweep nets.*

Discussion

Soils and plant communities

C&D waste infill substrate on wetlands has significantly different properties (pH, moisture and organic content) in comparison to the non-infilled wetlands and this is likely to be responsible for its impact on plant communities as soil properties (including pH, moisture and nitrogen content) are known to be important factors in their composition (Critchley et al., 2002; Gough et al., 2000; Schultz et al., 2011). In addition, substrate disturbance during the process of infilling likely affects plant communities, allowing ruderal species which have the ability to colonise disturbed ground rapidly, to become more dominant (Grime et al., 1996). In this study indicator species analysis has proven to be a useful tool in identifying the impacts that the soil properties of C&D waste have on plant communities. *Agrostis stolonifera, Cirsium arvense* (L.) Scop, *Festuca rubra* L., *Holcus lanatus* L., *R. repens* and *Trifolium repens* L. are recognised as species associated with areas of moderate disturbance and soils with a higher (>5) pH (Grime et al., 1996). In this study these were, unsurprisingly, among the most significant indicator species of C&D waste infill. *Molinea caerulea* (L.) Moench and *Potentilla erecta* (L.) Rauschel, both described by Grime et al. (1996) as being positively associated with low pH soils and undisturbed ground, were significant indicators of acidic wetland areas for this study, having been found extensively on cutover raised bog wetlands. *Cladium mariscus* (L.), although not a significant wetland indicator species, was the dominant species (*Table 2*) in site SW1 (wetland only), and is a species found in wet, neutral to alkaline soils (pH>6), occurring mostly on limestone soils (Conway, 1942), a description befitting this site. As expected there is a strong similarity between the vectors for measured soil properties (pH and percentage moisture content) and estimated values using Ellenberg indices (pH and moisture) in the NMS ordinations (*Fig. 3* and *Table 7*).

The disposal of C&D waste on wetlands significantly increased the plant species Shannon's entropy, but it is important to note that common ruderal species accounted for most of this increase. Based on Grime et al. (1996), some 57% of all species found on C&D waste infill in this study are known to have a ruderal strategy compared with just 25% of species on the wetlands. Given that the ruderal plant species found in this study are common, their replacing of wetland habitat, and all the ecosystem services associated with it (Mitsch and Gosselink, 2007), is less than desirable. When all sites were analysed together, 10% (*Table 4*) of the variation in plant communities was attributable to habitat status (infill v wetland). Similarities between infill and wetland are likely due to bare ground, bryophytes, dead vegetation and a small number of species (*Epilobium hirsutum* L., *Juncus effusus* L. and *Rubus fruticosus* L.) which were found to be present in both C&D infill and wetland quadrats, although not necessarily at the same site, along with the variety of wetland plant communities. This variation can be seen on the NMS ordination (*Fig. 3a*) where the infill plant communities are more clustered than the plant communities of wetland areas. The points for WG1 are likely to be isolated as the dominant species *Elymus repens* (L.) was almost exclusively found on that site. Interestingly, the points for the wet grasslands (wetland area) WG1 and WG2 are at almost opposite corners of the ordination, although they classify as the same habitat under Fossitt (2000). This highlights the limitations of using such a broad habitat classification, which takes abiotic factors into account as well as floristic composition. Following separation of sites according to their pH, MRPP shows that plant communities of acidic wetlands are affected to a greater degree (as shown by higher percentage difference attributed to habitat status) than those of alkaline wetlands by the alkaline C&D waste (*Table 4*). This was expected as there was a greater difference in pH between infill and wetland on acidic sites than alkaline sites. Differences between alkaline and acidic site-specific variation could be explained by the variety of alkaline wetland habitats, compared with acidic wetlands.

Dipteran communities

The impacts of C&D waste on dipteran communities is less clear than the impacts on plant communities (*Fig. 3*) where there is less obvious clustering of sites in the NMS ordination. The C&D waste may have had no significant impact on median dipteran (family and morphospecies) richness, Shannon's entropy and evenness on the infill compared to wetland areas. However, there were significant differences (albeit explaining a low proportion of variance) between community compositions according to the habitat status and among sites. This is likely due to the wide variety of ecological associations within many dipteran families (Keiper et al., 2002; Oosterbroek, 2006). As shown in *Table 6*, there are a number of dipteran families and morphospecies that were significant bioindicators of both infill (six families and seven morphospecies) and wetland (four families and nine morphospecies). These indicator families changed from generally wetland specialist (Chironomidae, Culicidae), parasitic (Tachinidae), haematophagous (Culicidae) and gall-forming (Cecidomiidae) groups to saprophagous (Anisopodidae, Carnidae, Phoridae, Sepsidae), phytophagous (Chloropidae), haematophagous (Muscidae) and coprophagous (Muscidae, Phoridae) groups, based on published descriptions of the ecology of these families by others (Brake, 2011; Cranston, 1995; McAlpine et al., 1981; Oosterbroek, 2006).

The loss of aquatic microhabitats in the infill is the most likely cause for the lower abundances of Chironomidae and Culicidae. The change in plant communities is likely to be the cause of the loss of Cecidomiidae and the gaining of Chloropidae as indicator families after infilling. Although Tachinidae can be found in many habitat types, many species may be habitat-specific due to their host species (phytophagous insects such as Lepidoptera) specificity (Stireman III et al., 2006). As a result, their occurrence on the infilled sites may be limited. The family Chironomidae was found to be a significant indicator of wetlands, a finding that is supported elsewhere (Cranston, 1995). The MRPP results also suggest that infilling with C&D waste may be more detrimental to acidic wetland dipteran communities than those on an alkaline wetland, as higher proportion of variation in dipteran composition can be attributed to habitat status (*Table 4*) for the dipteran communities of the acidic sites (6%) than for alkaline sites (4%) regardless of site-specific differences being higher in the latter (32% in alkaline sites versus 14% in acidic sites).

Sciomyzid communities

Fifty nine species of Sciomyzidae are currently known in Ireland (Speight and Knutson, 2012), 14 of which were collected during this study. The C&D waste appears to have had a significant impact on sciomyzid communities. Pan trap data showed significant (P=0.005) differences between the sciomyzid communities of the infill and wetland areas even though the distance between the pan traps of each area was only ten metres. *Tetanocera robusta* was a significant (P<0.05) indicator species for wetlands in both years. Sweep net sampling also showed a significant (P=0.005) difference between infill and wetland, with *P. coryleti* being a significant (P<0.005) indicator species for wetland. These findings support previous studies showing that sciomyzids display limited movement and are habitat specific (Speight, 2004; Vala & Brunel, 1987; Williams et al., 2009, 2010).

The most dominant species caught using the pan traps (for 2009 and 2010) was *T. robusta*, followed by *T. ferruginea*. The dominance of *I. albiseta* and *P. coryleti* in the sweep net data when compared with pan traps, supports previous findings (Williams, 2007). At site WG2 sweep nets and pan traps gave very different results. Pan traps collected only *T. robusta* and *T. ferruginea*, whereas the sweep nets collected 12 species. This difference between trapping methods should be considered if using sciomyzids as bioindicators. The significant wetland indicator sciomyzid species (*T. robusta* and *P. coryleti*) are known to prey and feed on multiple aquatic snail species from several genera as larvae (Speight and Knutson, 2012) as are all sciomyzids found on C&D waste (with the exception of *Pherbellia cinerella* Fallén which preys upon a range of terrestrial and semi aquatic gastropods). Interestingly, although these aquatic snails usually prefer alkaline water and the C&D waste is more alkaline than the wetlands, there was a decrease in the abundance of sciomyzids collected on the C&D waste. This was likely due to a shortage of appropriate aquatic microhabitats on the C&D waste for the aquatic snails and sciomyzid larvae.

Pherbellia cinerella was the only species to have been collected (one individual with sweep net) solely on the C&D waste infill. This was not surprising given its known occurrence on dry habitats (Speight and Knutson, 2012). All of the other sciomyzid species collected are associated almost exclusively with ‘wet’ habitats (Speight and Knutson, 2012). The observation here that these species were all either exclusively found on wetlands, or had a large majority on the wetlands, highlights their sedentary

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nature and usefulness as bioindicators of wetland habitat change. The low number of sciomyzid individuals collected is a trait of the family which is not unknown, although there are some species (such as *I. albiseta*) that are often found in high numbers (Williams et al., 2009; Williams et al., 2010).

Problems encountered

From the start of this study, it was found that wetlands were often perceived by landowners as valueless land, especially if peat had already been cut away from bogs, or if they were too wet to graze with livestock. Landowners sought to improve the land by covering the infill with topsoil to produce agriculturally productive grasslands. Permits specifically for the disposal of C&D waste have been available from local authorities in Ireland since 2001.

The almost complete absence of published information on ecological impacts of infilling wetlands with C&D waste is not aided by the problems associated with studying these sites. Permission to undertake ecological work has to be obtained from the landowner and this permission is likely to be refused at any time given the nature of the activity, as happened on site SW2 at the start of year two. The disturbance of sites by heavy machinery and the process of infilling had been anticipated as a potential problem at the beginning of the study, but this is very difficult to predict as sites that appear 'dormant' can become active at any time (as happened with site CB5 at the beginning of year two), depending on the volume of waste being produced in the locality. Two more otherwise suitable sites had to be removed from the study at the beginning of Year 1 (in addition to the loss of individual samples from several sites over the study) as a result of human interference with equipment being stolen and broken repeatedly. As these (usually poorly fenced) sites were frequently located near rural-urban interfaces and major roads, they were highly visible to members of the public. Shortly after our studies commenced at some of the sites, sampling was compromised by members of the public moving or emptying traps and/or flattening vegetation and non-permissible waste items were observed on more than one occasion. There were also unforeseen restrictions regarding invertebrate sampling, in particular, the limitations of using sweep nets caused by the hazardous topography of infilled sites.

Currently, some inspections of waste composition at C&D waste sites are carried out by the local authority but daily inspections of waste are the responsibility of the waste haulier and landowner. Although the waste permits were almost always granted to landowners with the condition of using the land for agricultural purposes afterwards, it was frequently found in this study (particularly for sites owned by building developers) that these sites were left without topsoil or had been further developed (residential or commercial buildings or yards). There is a possibility that this type of permit could provide a route for such surreptitious development of wetland areas, for which it would be difficult to get permission directly.

Recommendations

Our results indicate that the infilling of wetlands in this study with C&D waste has resulted primarily in the replacement of wetland plant communities with ruderal plant species and a reduction in wetland specialist Diptera. Given these dramatic changes, it is likely that the wetland ecosystem function of the sites studied has been impaired. However, the degree and significance of impairment will depend on the resilience of the wetland which in turn depends, *inter alia*, on the wetland type, the size of the wetland, its connectivity with other wetlands and the proportion of the wetland infilled with C&D waste. While it could be argued that any loss in wetland ecosystem function should be avoided at all costs, the reality is that, in the absence of complete C&D waste recycling, wetlands, particularly those not included in Natura 2000, will continue to be infilled for the foreseeable future. With this in mind, we would make the following recommendations:

- All future waste permits (regardless of site size or C&D tonnage) should require either an independent Environmental Impact Assessment or an Appropriate Assessment. These assessments should include, as a minimum, surveys of plants, wetland invertebrate assemblages and wetland vertebrates in addition to the collection of physical data on soils and hydrology. If permission is granted, these surveys will provide baseline data for future monitoring of the sites.
- Annual ecological surveys should be undertaken by local authorities or a third party authorised by them, to monitor changes in the wetlands after infilling has commenced and to ensure that licensing agreements are adhered to.
- Invertebrate baseline monitoring stations, protected by security fencing to avoid damage by vandalism, should be set up (prior to and during infilling). Once these secure stations are in place, more visible invertebrate sampling methods such as malaise, emergence and pitfall traps could be employed.
- The above increased ecological monitoring could contribute to a database used to inform decisions regarding appropriate site selection for C&D infilling, thereby preserving those wetlands which are most vulnerable.
- At least part of the wetland sites used for C&D infill should be protected from future infilling activities. The initial ecological assessment could be used to determine the most ecologically valuable area to protect.

Conclusions

The infilling of wetlands in this study with C&D waste has had an impact on soil properties and plant communities. Dipteran communities were also affected by the C&D waste infill, probably as a result of the changes in plant communities and the loss of 'wet' areas. There are many potential problems with carrying out such studies and recommendations have been given to overcome these. Given the paucity of research in this area, this study highlights that the infilling of wetlands with C&D waste can have serious consequences for wetland ecology.

Future research should focus on C&D waste infill sites of different waste composition and in areas of different geographical, geological, topographical and meteorological settings. Following further research, this information could be used by planning authorities to aid in future policy making and in the development of sustainable C&D waste management strategies.

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STRUCTURE AND COMPOSITION OF EDAPHIC ARTHROPOD COMMUNITY AND ITS USE AS BIOINDICATORS OF ENVIRONMENTAL DISTURBANCE

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Abstract. We analyzed arthropod community structure and composition among different anthropogenic systems. The study was conducted in areas of secondary forest (control system), *Eucalyptus* plantation and pasture, where we sampled arthropods using pitfall traps. The systems did not differ in mean richness and mean abundance of arthropods, however, eucalyptus presented the highest total richness. The systems supported different arthropod communities in relation to structure and species composition. Pasture was the most simplified and different system in comparison to the others, probably because it is more open and presents low complexity. Our results demonstrate that different anthropogenic systems exhibit communities that reflect its characteristics, corroborating the evidence that human impacts are capable of changing community composition and structure. Our study serves to understand arthropod response in face of environmental disturbance, selecting indicator morphospecies and orders of arthropods for different anthropogenic systems and providing valid information for the development of conservation strategies.

Keywords: *Atlantic Forest, Eucalyptus, Habitat change, Pasture, Vegetation complexity*

Introduction

The introduction of different anthropogenic systems in natural ecosystems can reduce biodiversity and alter the functioning of these environments (Chapin et al., 2000; Sala et al., 2000). Biodiversity loss occurs by the simplification of complex and diversified ecosystems, since environments with high habitat heterogeneity present higher species diversity (Pianka, 1983). Therefore, the evaluation of biological communities is essential, due to the growing need to maintain ecological integrity of natural and anthropogenic systems (Basset et al., 2008).

In this context, soil arthropods have been widely used as bioindicator organisms in order to quantify and qualify the conditions of an environment (e.g. Dufrêne and Legendre 1997; Maleque et al., 2009; Almeida et al., 2011; Gerlach et al., 2013). Soil arthropods are considered good bioindicators because of their high diversity, easy and

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low sampling cost, wide spatial and temporal distribution, rapid response to environmental changes and participation in several ecological processes of ecosystems maintenance (Lavelle, 1996; Knoepp et al., 2000; Nakamura et al., 2007). The bioindication of these organisms enables to infer about an ecosystem condition, providing scientific basis for environmental management and conservationist strategies (Suthar, 2009; Gerlach et al., 2013).

Several studies have used the diversity of a single taxon as a bioindicator, however the evaluation of different taxonomic groups is necessary (Schulze et al., 2004), because each taxon can present a specific response to environmental modifications. Studies that use various taxa allows to reach more concrete conclusions, as well as to reduce the costs that are involved in the execution of a scientific project (Barlow et al., 2007; Gardner et al., 2008).

This work aimed to evaluate the structure and composition of soil arthropod communities in areas of secondary forest, *Eucalyptus* plantation and pasture and also to identify possible indicators of each system. We tested the hypothesis that arthropod fauna will respond negatively to the decrease of system complexity, reducing their abundance, species richness and evenness, and increasing their dominance patterns. We also expect that each anthropogenic system will sustain distinct arthropods communities according to structure and species composition and that they will possess specific indicators.

Material and methods

Study sites

The study was conducted at the Universidade Federal de Lavras, in areas of secondary forest, *Eucalyptus* plantations and pastures. The municipality of Lavras is located in Minas Gerais state (21º 14’S 45º 00’W), at an altitude of 919 m. It presents a mesothermal climate (Cwa), according to Köppen classification, with a dry winter and rainy summer, average annual temperature of 20.4 ºC and a rainfall of 1460 mm (Dantas et al., 2007).

The landscape of our study site is composed by Atlantic Forest remnants surrounded by an agro-silvo-pastoral matrix of agricultural crops, pastures and monocultures such as *Eucalyptus* plantations (Oliveira-Filho et al., 1994). Most of the forests are secondary formations in different successional stages with less than 10 ha (Oliveira-Filho et al., 1994). Therefore, this area provides excellent conditions to generate information on how the edaphic arthropod community responds to different agro-silvo-pastoral land use systems.

Arthropods sampling

The present work was carried out in April 2011, when we sampled three areas (replicates) of each anthropogenic system: secondary forest, *Eucalyptus* plantation and pasture. Secondary forest was considered the control system in order to understand the consequences of habitat change for edaphic arthropods.

We sampled edaphic arthropods using pitfall traps without baits. A transect of 80 m was delimited at each anthropogenic system, at least 20 m distant from the edges. At every 20 m of the transect we placed a pitfall trap, corresponding to a total of 5 traps per area, totalizing 15 pitfalls per anthropogenic system. Pitfall traps were left in the field for 24 hours.

We identified arthropods at family level whenever possible and specimens were grouped in morphospecies. Specimen's identification was based on Borror et al. (1989).

Data analysis

We generated a species accumulation curves according to the number of samples to evaluate sampling effort and to compare the patterns of total species richness among the studied anthropogenic systems. This analysis was performed in EstimateS 7.5.2 (Colwell, 2005).

To verify if arthropods' mean abundance and mean species richness (response variables) are different among the different anthropogenic systems (explanatory variables), we used generalized linear models (GLM) with Gaussian error distribution. All models were submitted to residual analysis to verify their suitability to error distribution. These analyses were conducted in the R (R Development Core Team, 2012).

In order to observe dominance patterns in arthropod community of each anthropogenic system, we constructed abundance distribution curves. Abundance data was (log + 1) transformed. We also calculated the evenness of each anthropogenic system through the software Species Diversity and Richness 3.0. Evenness values were statistically compared using the null model approach developed by Solow (1993).

To evaluate if there were significant differences in community structure (abundance) and composition (presence/absence) we performed an analysis of similarity (ANOSIM). Bray-Curtis index was used as a similarity measure for the abundance data and Raup-Crick index for species composition (presence/absence). The analysis was carried out using software R (R Development Core Team, 2012), package Vegan (Oksanen et al., 2013).

In order to identify morphoespecies and orders of arthropods that are indicators for each anthropogenic system, we conducted an IndVal analysis (Indicator Species Analyses), using software R, package labdsv (R Development Core Team, 2012 – Roberts, 2013).

Results

We collected 981 arthropods of 92 morphospecies distributed in 14 taxonomic groups: Acari, Aranae, Blattodea, Coleoptera, Diptera, Embioptera, Formicidae, Hemiptera, Hymenoptera, Isopoda, Isoptera, Orthoptera, Trichoptera and Thysanoptera.

Species accumulation curves did not reach an asymptote in any of the studied systems (*Fig. 1*). These curves also showed that total richness of forest and pasture was not different between each other and *Eucalyptus* exhibited the highest total richness.

We captured 45 morphospecies and 267 individuals in *Eucalyptus*; 36 morphospecies and 261 individuals in the forest and 35 morphospecies and 451 individuals in the pasture. However, these anthropogenic systems did not differ in relation to the mean number of arthropod morphospecies ($F_{2,15} = 2.02$; $p = 0.21$) and mean abundance ($F_{2,15} = 0.61$; $p = 0.58$).

Forest and the *Eucalyptus* presented similar evenness indexes ($p = 0.75$), 0.56 and 0.58, respectively. Pasture showed the smallest evenness index (0.48), differing from the forest ($p < 0.001$) and *Eucalyptus* ($p < 0.001$).

The systems presented similar abundance distribution curves, where some species showed numeric dominance over the other relatively less abundant (*Fig. 3*). In all the systems, the four morphospecies with higher abundance were representatives of the family Formicidae, except for the Diptera sp. 1, which was the fourth most abundant of the forest (*Fig. 2*). However, the species that dominate each anthropogenic system is different.

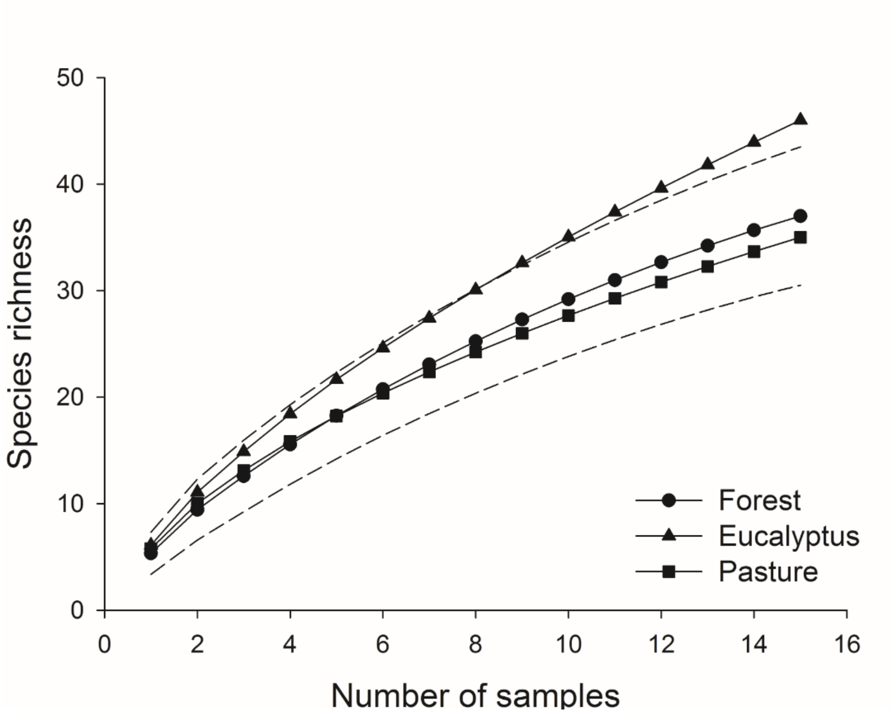

Figure 1. *Species accumulation curve of soil arthropods sampled in forest, Eucalyptus and pasture areas located at Lavras, state of Minas Gerais, Brazil. Dashed lines represent the confidence interval (95%) of the forest.*

The anthropogenic systems exhibited different arthropod community structures and compositions (*Table 1*). Of the 92 collected morphospecies, only seven were common to all of the systems, and these include one Diptera species and six of ants. Forest and *Eucalyptus* plantation shared 8 species between each other, while forest and pasture just presented one species in common and *Eucalyptus* plantation and pasture just one species in common too. *Eucalyptus* presented the highest number of exclusive species (29 morphospecies - 64.4% exclusive species), followed by the pasture (26 morphospecies - 74%) and forest (20 morphospecies - 55%).

Only one species was indicator of the forest (Diptera sp. 1). Two species were considered indicators of the *Eucalyptus* (Diptera sp. 4 and Isopoda sp. 1). In the pasture, there were three indicator species: Acridiidae sp. 2, Formicidae sp. 3 and Formicidae sp. 6 (*Table 2*). Considering a higher taxonomic level (arthropods order) forest did not show any indicators, while *Eucalyptus* showed two (Isopoda and Diptera) and pasture two indicator groups (Hemiptera and Orthoptera) (*Table 3*).

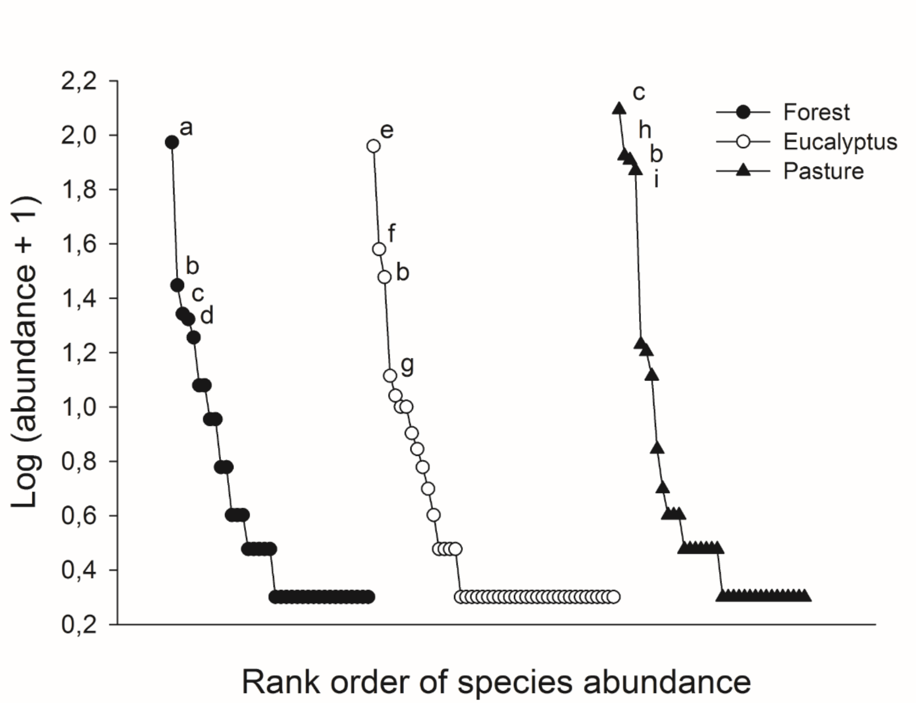

Figure 2. Rank abundance distribution of arthropod species sampled in three different landscape uses (Forest, Eucalyptus plantation and Pasture) of south Minas Gerais, Lavras, Brazil. a) Formicidae sp. 13; b) Formicidae sp. 5; c) Formicidae sp. 8; d) Diptera sp. 1; e) Formicidae sp. 1; f) Formicidae sp. 12; g) Formicidae sp. 4; h) Formicidae sp. 3; i) Formicidae sp. 6.

Table 1. *R and p values from the similarity analysis (ANOSIM) implemented to evaluate possible differences in arthropods community structure (abundance) and community species composition (presence/absence) between the forest, Eucalyptus and pasture areas (Lavras, Minas Gerais, Brazil). Levels significance $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$ are represented by *, **, *** respectively.*

Systems	**Community structure**		**Community composition**	
	R	**P**	**R**	**P**
Forest x *Eucalyptus*	0.13	0.005**	0.2	0.0005***
Forest x Pasture	0.25	< 0.001***	0.44	< 0.001***
Eucalyptus x Pasture	0.27	< 0.001***	0.38	< 0.001***

In relation to the number of different arthropod orders captured in each anthropogenic system, forest exhibited 12, *Eucalyptus* 11 and pasture eight (*Fig. 3*). The species richness and the abundance of individuals of each taxonomic group were different among the systems. Of the 14 groups, only five were common to all systems (Aranae, Diptera, Coleoptera, Formicidae and Hymenoptera). Two groups were exclusive to the forest (Embioptera and Trichoptera) and none was exclusive to

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Eucalyptus and pasture and these last systems shared two groups, Acari and Hemiptera (*Fig. 3*).

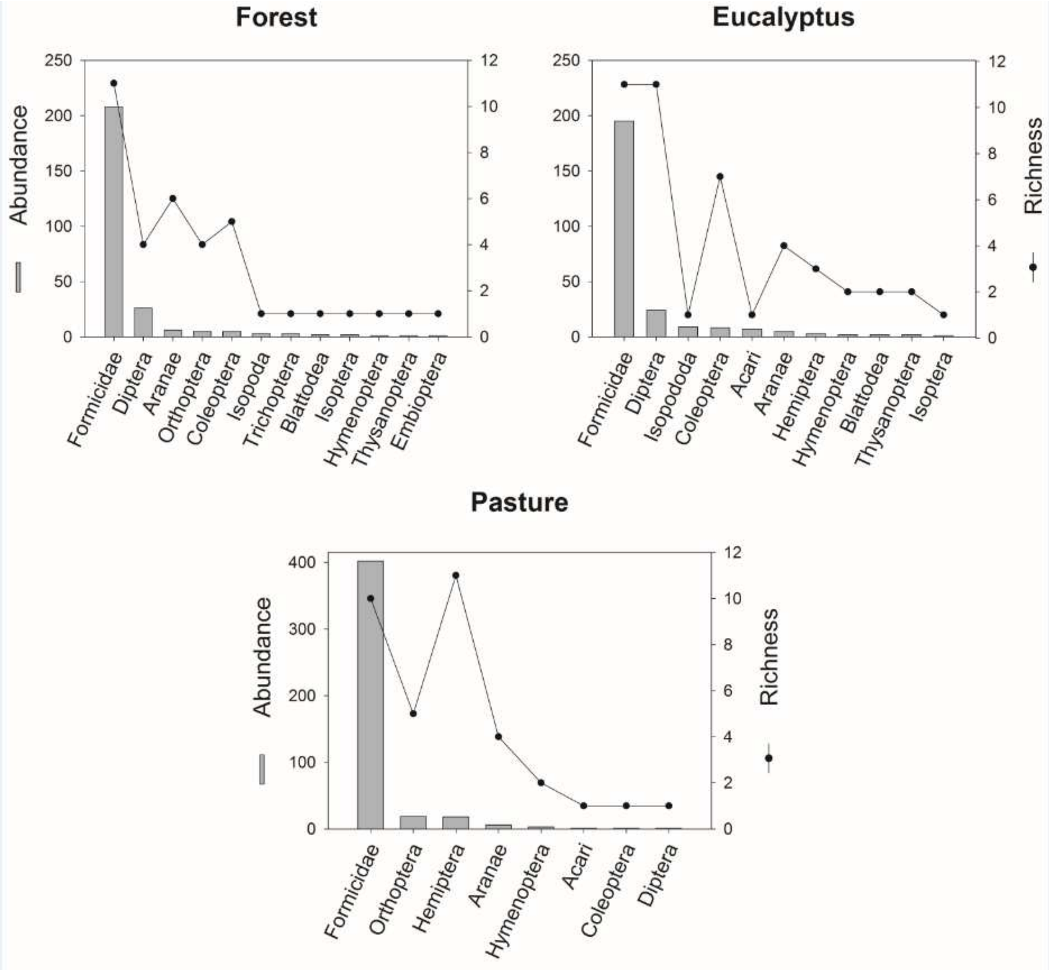

Figure 3. *Abundance and species richness of the taxonomic groups sampled in forest areas, eucalyptus plantations and pastures of south Minas Gerais, Lavras, Brazil.*

Table 2. *Arthropod morphospecies with significant values of IndVal ($p < 0.05$) sensitive to the different anthropogenic systems (Forest, Eucalyptus and Pasture) inserted in the municipality of Lavras, state of Minas Gerais, Brazil. IV: indication value. Significance levels: $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$ are represented by *, **, *** respectively.*

Morphospecies	Systems	IV	P
Diptera sp. 1	Forest	56.4	0.0004***
Diptera sp. 4	Eucalyptus	48	0.0006***
Isopoda sp. 1	Eucalyptus	30	0.02*
Acrididae sp. 2	Pasture	53.3	0.0002***
Formicidae sp. 3	Pasture	32.2	0.02*
Formicidae sp. 6	Pasture	57.3	0.001***

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Table 3. *Arthropod orders with significant values of IndVal (p < 0.05) sensitive to the different anthropogenic systems (Forest, Eucalyptus and Pasture) inserted in the municipality of Lavras, state of Minas Gerais, Brazil. IV: indication value. Significance levels: p ≤ 0.05, p ≤ 0.01 and p ≤ 0.001 are represented by *, **, *** respectively.*

Arthropod orders	**System**	**IV**	**P**
Isopoda	*Eucalyptus*	30	0.02*
Diptera	*Eucalyptus*	40.8	0.04*
Hemiptera	Pasture	51.4	0.0008***
Orthoptera	Pasture	52.8	0.0008***

Discussion

Several studies have already shown that arthropod diversity is highly affected by the modification of natural ecosystems and implantation of different anthropogenic uses (e.g. Basset et al., 1998; Lawton, 1999; Schulze et al., 2004; Basset et al., 2008), due to the changes in vegetation structure (e.g. Siemann et al., 1998; Wettstein and Schmid, 1999; Gardner et al., 2008).

Natural environments tend to sustain higher arthropod diversity because of their higher spatial heterogeneity, since they possess more species richness of trees and an understory usually developed (Elton, 1973). This complex vegetation structure creates a larger amount of micro-habitats and more resources availability for the arthropods (Ribas et al., 2003; Tews et al., 2004). However, our results do not corroborate with these theoretical expectations, because mean arthropod richness and abundance did not differ among the systems, despite having extreme differences in vegetation structure. Likewise *Eucalyptus* total richness was higher than the observed in the forest.

However, these two parameters of the arthropod community (richness and abundance) by themselves cannot reflect the reality of the studied systems, as confirmed by several studies (e.g. Hoffmann, 2010; Gollan et al., 2011; Ribas et al., 2012). Furthermore, Fleishman et al. (2006) reported that richness is not an appropriate metric for conservation planning strategies, because do not provide information about the identity of species. Abundance also cannot be considered a good indicator of habitat quality, since several species increase their populations in face of a disturbance (Hillebrand et al., 2008; Blaum et al., 2009), altering dominance structure in the community (Vasconcelos, 1999; Loyola et al., 2006). Thus, Barlow et al. (2007) recommended that to obtain more robust responses about how biological communities resist to disturbances, the use of metrics based on the similarity among communities is more reliable.

Our results showed that forest, *Eucalyptus* and pasture sustained highly dissimilar arthropod communities both in structure and species composition. Loyola et al. (2006) found this same pattern when studying the invertebrate community in areas of forest and pasture in Pantanal wetlands, while Ferreira and Marques (1998) verified low similarity between litter arthropod communities of secondary forest and *Eucalyptus* monoculture, as well as, arthropod richness and diversity of secondary forest and *Eucalyptus* monoculture. All these results, therefore, corroborate with the evidences, that modifications of natural ecosystems caused by human activities generate changes in composition and structure of biological communities (Hillebrand et al., 2008).

Pasture showed a simplified arthropod community, because of its lowest evenness, number of taxonomic groups and absence of exclusive arthropod orders. According to Hillebrand et al. (2008) alteration of ecosystems by humans is capable of strongly affect community evenness, being this metric very important to understand the response of the organisms to anthropic impacts. Low evenness can influence the interaction of species in a community, ecological processes and community resistance and resilience, because of the dominance of few species that are more resistant to the loss of vegetation covering (Hillebrand et al., 2008; Sobek et al., 2009). Thus, the lowest evenness found in the pasture is an indication of how much this system presents a more altered biological community in relation to the forested systems. Furthermore, among the landscape studied, pasture presented the most distinct community of arthropods, since 74% of the species found in this environment were exclusive to it, leading to a low number of species shared with the forest and *Eucalyptus*.

The substitution of forest areas by pastures represents an abrupt change in the environment, since removal of forest cover leads to a decrease in the amount of soil organic matter, the occurrence of erosive processes, higher soil compaction, litter loss and microclimatic alterations (Gash and Nobre, 1996; Alves et al., 1999; Mathieu et al., 2005; Loyola et al., 2006; Bernarde and Macedo, 2008). All these factors can be unfavorable for the survival of some species, mainly for those associated with forest environments (Howden and Nealis, 1975; Larsen et al., 2008). Thus, pasture does not maintain the same conditions of forest system in order to allow the establishment of similar fauna. Therefore, species found in pasture are in general those common of opened environments or habitat generalists. Following the changes in ant assemblages in different stages of vegetational succession, from cultivated fields up to forest environments, Gómez et al. (2003) found major changes including the increase of cryptics species and cold-climate specialists. They also reported a decrease of opportunists species as well the hot-climate specialists, followed by a decrease in ant species richness.

Forest and *Eucalyptus* were different in relation to arthropod species composition, probably as a reflection of the structural differences of these vegetational formations. *Eucalyptus* plantation consists of an environment with a single plant species and individuals with similar ages, besides the absence of an understory, promoting a discontinuous canopy cover favorable to a greater incidence of light. In this context, they are less complex environments when compared with the primary forest areas.

All anthropogenic systems exhibited indicator species, however, in relation to arthropod orders, just the *Eucalyptus* and pasture showed it. Most of these species and orders entered in the category of detectors, according to McGeoch et al. (2002) and Verdú et al. (2011), because they had an indication value between 45% and 70%. Detector species just reflect preferences for a certain habitat type, but these species can also be found in adjacent systems, mainly when their habitat conditions are under change. None of our species presented an indication value above 70%, which according to the above mentioned authors, is what characterizes real habitat indicators. In this study the forest, although being the most complex system, presented the lowest number of indicator species, it did not have indicator arthropod orders and sustained the lowest number of exclusive species. This might have occurred due to the degree of degradation and small size of the secondary forest fragments, which may not present the conditions inherent to more intact forest environments and may not represent the reality of well-preserved forests. Nevertheless, it was the system with higher number of exclusive arthropods orders.

In conclusion, human activities change the composition and the structure of biological communities. Our results enable us to know the response of the arthropod community facing the implantation of different anthropogenic systems, selecting indicator species and orders of each system, which currently dominates the scenario of the south of Minas Gerais. The selection of bioindicators is of unquestionable importance, since with this information it is possible to choose and evaluate sites for the establishment of nature reserves, to create conservation management plans and to evaluate the ecological impacts generated by human activities. Such studies enable us to understand the processes that govern the disassembly of biological communities and to elaborate conservation strategies to minimize the impacts upon biodiversity.

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SHIFTS ACROSS TROPHIC LEVELS AS EARLY WARNING SIGNALS OF COPPER SULFATE IMPACTS IN PLANKTON COMMUNITIES

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Abstract. Intensive agricultural practices have been characterized by an overuse of agrochemicals. The inputs of chemicals in a watershed are likely to alter trophic interactions affecting its ecological integrity. This ecotoxicological study aims to identify warning signals of agrochemicals effects on a plankton community. Eighteen outdoor microcosms were used to establish an experiment with 2 concentrations of copper sulfate above and below the legal limit with six replicates lasting two weeks. Phytoplankton and Zooplankton structure changes were studied. Chlorophyll-a concentration was used as a functional indicator. A rapid change in phytoplankton structural features, abundance and size classes, was detected after both, below and above legal, concentrations. Similarly, Zooplankton structural changes showed an effect of copper exposures on abundance and composition. As Phytoplankton response was so rapid, it could be used as an early and direct warning signal, but also to warn of future indirect effects on zooplankton structural features owing to a change of food resources. In summary, the shifts across both trophic levels could be use as warning signals. Moreover, even legal limits do not protect the plankton community, which emphasises the need of a more ecotoxicological and realistic approach to achieve a balance between agriculture development and ecosystems conservation.

Key words: *Copper; Microcosms; Plankton; Warning*

Introduction

Current main environmental pressures are highly linked to human exponential population growth (United Nations Population Division 2000). One of the main consequences of population growth is an increase in food demand; therefore, agricultural practices intensify with the consequent increased use of agrochemicals (Valavanidis & Vlachogianni 2010). The socio-economic value of agriculture cannot be denied, however, its integration with environmental criteria must be a priority. The improper use and / or application in excess of pesticides, herbicides and fertilizers generate an impact on the ecological integrity of ecosystems, affecting their structure and function (Troncoso et al. 2002, Parra et al. 2005). In this sense, there is enough bibliographic information which shows that intensive agriculture is causing the disappearance and / or pollution of wetlands (Casado & Montes 1995, Troncoso et al. 2000, Parra et al, 2005, García-Muñoz et al. 2011). These impacts have consequences at different hierarchical levels: from the individual by morphological, physiological and biochemical alterations, to the community level through the loss of diversity, and impairing the value and services that healthy ecosystems provide (Montes & Sala 2007).

Ecological indicators are tools which detect changes on ecosystems that are likely to impact ecological integrity and so then the community structure and function, and

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consequently ecosystem services. Structural features have been usually used alone to monitor and assess impacts on the ecosystem ecological integrity, focusing on communities assemblages and their resources. Structural attributes are easiest to visualize and they are, by far, the most commonly used. Examples are species numbers, dominant species, guild composition, taxonomic representation, abundances, size composition, and others (Bain et al. 2000). For instance, crustacean zooplankton size has been shown to be more strongly correlated with lake water quality than community taxonomic structure (Sprules 1984). In addition to structural levels, ecosystem functional aspects are gaining more importance in the evaluation of ecosystem integrity. Functional indicators assess rates and patterns of ecosystem processes and are considered to be an essential complementary aspect to assess ecological integrity due to their different sensibility from structural levels to environmental pressures (Gessner & Chauvet 2002). However nowadays, society is demanding this to go further, with the intent of detecting, as soon as possible, the negative effects on ecosystems. In this sense, a warning signal is an important component of the integrated approaches that are needed to acquire a general knowledge of toxic impact, and which will allow predictions and early mitigation measures (Schmitt-Jansen et al. 2008).

The study is focused on the effects of a fungicide (copper sulfate) on trophic levels in wetlands which are surrounded by intensive olive tree agriculture. The aim was to evaluate how this toxic substance could alter structural and functional characteristics of the plankton components, and if these changes could be used as early warning signals. In the present study two different concentrations were used, the first above the legal limit, in order to find clear effects on the plankton community features. The second concentration, below the legal limit, in order to check if the changes could be detected even before the community was highly altered.

Materials and methods

Microcosms

Eighteen microcosms were set, based on, and adapted from, OECD (2006), and were placed outdoors in a specific installation at the University of Jaén (HUMEXPUJA, experimental wetland infrastructure in the University of Jaén, which were exposed to the same environmental conditions). Microcosms length, height and width were 0.34-0.28-0.24 cm respectively, 22.8 liters in volume and placed 15 cm apart from each other. Microcosms were filled with 18 liters of water and 5 cm of sediment. Water came from an artificial pond supply free of contamination and zooplankton (HUMEXPUJA). Sediment came from a natural wetland [Casillas wetland, UTM 30SVG1084 with a surface area of 2.2 ha. (Ortega et al. 2003)], it was homogenized and distributed among the microcosms. Microcosms were established in November 2011 and the experiment was finished in January 2012. There was a stabilization period of 7 weeks before adding copper to the microcosms in order to favour the development of the planktonic communities from the resistant structures present in the sediment. The experiment lasted 21 days, with a single pesticide spike on day 0.

Disturbance

Control and two treatments of copper sulfate, with six replicates each one, were used in the experimental design. The first one, called high treatment (H: 0.2 mg l^{-1} Cu), represents a concentration of copper sulphate over the limit established by both the Water Framework Directive (WFD 2000/60/CE) and its application into the Spanish National legislation (DMC 2000/60/CE) (0.04 mg l^{-1}). The second one, low treatment (L: 0.02 mg l^{-1} Cu) shows a lower concentration than those legal limits previously mentioned. Therefore, our L treatment falls within legal limits, while the H treatment is one order of magnitude higher. Nominal dosages of copper sulfate were directly added and stirred over the water surface of the microcosms as an only pulse on day 0 for the whole experimental period. The criteria to establish the concentration of the treatments was not based on lethal concentration data of the species involved because the aim of the study focused on studying the effect over the entire plankton community. Water samples to control the fate of copper sulphate were taken every week and analyzed by ICP Mass Spectrometry.

Physical-chemical variables

Each microcosm was surveyed every seven days. Each time, physical-chemical measurements (temperature, pH, % dissolved oxygen and conductivity) were taken using field probes. At the same time, water samples were taken, cold stored and transported to the laboratory to perform nitrogen dissolved nutrients (nitrate) and alkalinity analysis. Alkalinity was measured in the lab using a 848 Tritino Plus device. Nitrate was determined following the reduced column Cadmium method (Keeney & Nelson 1982).

Biological variables

Abundance and changes in phytoplankton size distribution were evaluated with flow cytometry. Water samples were taken weekly, preserved in glutaraldehide (4%), frozen in liquid nitrogen and stored at 80ºC until running the analysis with BD- LSR Fortessa flow cytometer. Calibration spheres were used to obtain a cell size regression curve: y = 0.011 x – 14,388, where “x” represents the mean of the Forward Scatter (FSC), and “y” represents the cell size of the cells in μm^3. Three cell size populations were determined characterized by a mean volume of 58 μm^3 (small), 304 μm^3 (medium) and 749 μm^3 (high). Population cells abundance were determined from an acquisition time of 180 s at a rate of 60 µL min^{-1}. Data analysis was performed using the FACSDIVA software.

Chorophyll-*a* concentration was measured weekly with a field fluorometer (Aquafluor deTurner Design). Chlorophyll-a (Chl-a) concentrations were later calculated using a previously obtained calibration curve determinate by fluorometry. Calibration samples were filtered through Whatman GF/C glass microfibre filters (1.2 µm pore-size), and extracted in 90% acetone for 24 h at 4ºC (Strickland & Parsons 1968).

Zooplankton in microcosms was sampled weekly during the study through water-integrated samples of 100 ml. Water integrated samples were collected, then filtered through a plankton net of 30 µm, and preserved *in situ* with formalin (4%). The filtered water was returned to the microcosm. Zooplankton was identified to the lowest practical levels and abundance estimated.

Physical-chemical, plankton and Chl-*a* variables were compared among microcosms using univariate and multivariate analyses with SPSS 19 software. Repeated measures of ANOVA were used to test for time and time x treatment effects. An univariate ANOVA and a post hoc Tukey test at the sampling date were used to determine the significance of differences between treatments. Prior to analysis, data were tested for normality and homoscedasticity. Zooplankton data could not be treated with a parametric test due to its low abundance or even complete disappearance in some microcosms. Therefore, total zooplankton abundance, rotifera abundance, and copepod abundance were analyzed with the non-parametric test of Friedman to test for differences due to time and treatment. Wilcoxon post hoc test was also used to determinate which treatments were significantly different from one another. Ordination of treatment and control of physical-chemical parameters and biological variables, except phytoplankton cell size populations, were made considering a Principal Component Analysis (PCA) (CANOCO v4.5 software). PCA aimed understanding the main factors influencing microcosm's responses.

Results

Copper nominal concentrations were achieved with the spike on day 0. The degradation was very low, therefore the average concentration exposure over the whole experiment matched the intended nominal concentrations (*Table 1*).

***Table 1**. Mean ± standard deviation (S.D.) of copper sulfate after pulse, by the end of the experiment and the average concentration exposure.*

Nominal concentration (mg L^{-1})	Concentration (mg/l) after pulse application (day 0) ± S.D.	Concentration ((mg/l) after pulse (day 14) ± S.D.	Average concentration exposure (mg/l) ± S.D.
0	0.01± 0	0.01 ± 0	0.01 ± 0
0.02	0.03 ± 0.01	0.09 ± 0.04	0.06 ± 0.05
0.20	0.11 ± 0.09	0.18 ± 0.04	0.14 ± 0.07

Temperature ranged from 9ºC to 13ºC during the experimental period. Dissolved oxygen (% DO), pH, conductivity and alkalinity presented significant differences between treatments and controls, while nitrate concentration did not present significant differences among them, independently of the treatment (*Table 2*). At the same time, pH was higher in H treatments in day 0 (F = 396.820, P = 0.000) and in L and H treatments in day 7 (F = 236.197, P = 0.000). Dissolved Oxygen (%) was lower in L and H treatments from day 0 (F = 148.684, P = 0.000) till the end of the experiment in day7 (F = 143.703, P = 0.000). Average oxygen content in controls, L and H treatments were 16, 13 and 12 mg l^{-1} respectively. Conductivity was higher in L and H treatments from day 0 (F = 4.104, P = 0.038) till the end of the experiment in day7 (F = 6.273, P = 0.010). Alkalinity was higher in L and H treatments in day 7 (F = 43.707, P = 0.000). PCA shows that those differences were not relevant enough to discriminate among treatments. PCA of physical-chemical and biological variables discriminate the controls (to the left) from the treatments (to the right) (*Fig. 1*). The two main axes explain 89% of the variance, x-axis explains 69% and y-axis explains 20% and they are correlated to conductivity and copper concentration and to rotifera and zooplankton abundance, respectively.

The results obtained show a negative effect of both copper sulphate concentrations tested on the plankton community under study. Even legal limits do not protect the plankton community. The plankton community was affected by a decrease in phytoplankton and zooplankton abundances under both copper concentrations.

***Table 2**. Physical-chemical and biological parameter measurements (mean ± SE) in treatments and controls microcosms along the whole experiment period. *Denotes statistical significant differences with the controls.*

Treatments	Controls			Low			High		
Parameters / Days	0	7	14	0	7	14	0	7	14
Temperature	14.23 ± 0.59	7.26 ± 0.08	10.44 ± 0.08	13.73 ± 0.53	7.68 ± 0.14	11.72 ± 0.29*	14.19 ± 0.61	9.20 ± 0.21*	12.50 ± 0.31*
pH	9.01± 0.03	8.81 ± 0.01	8.81 ± 0.03	8.92 ± 0.05	7.91 ± 0.04*	7.87 ± 0.04*	8.86 ± 0.03	7.49 ± 0.03*	7.99 ± 0.02*
% DO	149.81 ± 1.47	133.81 ± 2.36	133.46 ± 1.25	150.81 ± 8.92	98.75 ± 0.62*	101.86 ± 1.67*	141.66 ± 2.90	108.81 ± 0.77*	110.90 ± 1.07*
Conductivity (µS cm^{-1})	0.80 ± 0.03	0.83 ± 0.03	0.82 ± 0.03	0.84 ± 0.04	0.93 ± 0.04	1.09 ± 0.17*	0.85 ± 0.03	0.98 ± 0.02	0.97 ± 0.03*
Alkalinity	48.33 ± 10.33	58.00 ± 4.35	63.00 ± 5.10	60.00 ± 6.77	63.67 ± 20.97	131.67 ± 6.93*	58.67 ± 12.84	79.67 ± 7.73	121.33 ± 4.46*
Nitrate (µg N-NO_3 l^{-1})	0.09 ± 0.00	0.09 ± 0.00	0.09 ± 0.00	0.09 ± 0.00	0.09 ± 0.00	0.09 ± 0.00	0.09 ± 0.00	0.09 ± 0.00	0.09 ± 0.00
Rotifera abundance (ind l-1)	0	15.00 ± 8.46	6.67 ± 3.33	8.33 ± 3.07	0	3.33 ± 3.33	30.00 ± 20.49	8.33 ± 8.33	0
Copepoda abundance (ind l-1)	33.33 ± 22.46	1.67 ± 1.66	13.33 ± 8.81	18.33 ± 8.72	0	0	16.67 ± 14.75	0	0
Total zooplankton (ind l^{-1})	33.33 ± 22.46	16.67 ± 8.02	20.00 ± 7.30	26.67 ± 6.66	0	3.33 ± 3.33*	46.67 ± 20.92	8.33 ± 8.33	0*
Total phytoplankton (cells l^{-1})	17 $*10^4$	98 $*10^3$	79 $*10^3$	27 $*10^3$	35 $*10^2$ *	16 $*10^3$ *	38 $*10^3$	24 $*10^1$ *	61 $*10^1$ *
Small size phytoplankton (cells l-1)	15 $*10^2$	23 $*10^2$	17 $*10^2$	14 $*10^2$	64 $*10^1$	46 $*10^2$	34 $*10^2$	1.8 $*10^2$	21 $*10^2$
Medium size phytoplankton (cells l-1)	17 $*10^4$	95 $*10^3$	77 $*10^3$	24 $*10^3$	26 $*10^2$	12 $*10^3$	34 $*10^3$	20 $*10^1$	40 $*10^2$
High size phytoplankton (cells l-1)	13 $*10^2$	13 $*10^2$	59 $*10^1$	18 $*10^2$	37 $*10^1$	43 $*10^1$	97 $*10^1$	2.4 $*10^1$	25 $*10^1$
Chl *a* (µg l-1)	1.98 ± 0.29	1.97 ± 0.40	3.94 ± 0.76	1.89 ± 0.27	0.78 ± 0.10	1.57 ± 0.14	1.25 ± 0.12	1.60 ± 0.79	2.00 ± 0.93

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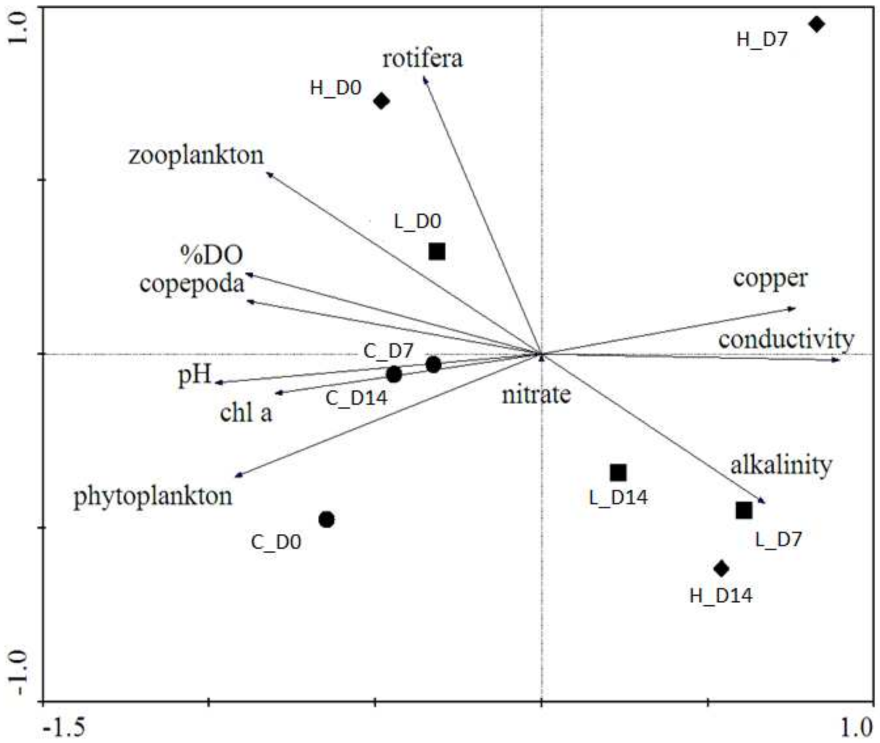

***Figure 1**. Physical-chemical PCA ordination graph. Arrows represent the lineal combination of zooplankton variables with the first and second axes. C, L and H stand for control, low and high copper treatments respectively. D indicates the sampling days.*

Phytoplankton presented differences in population abundance among microcosms (F = 5.447, P = 0.045, *Table 2*). A drastic decrease of phytoplankton populations can be observed after the copper application in the treatments with respect to the control (*Fig. 2* a). Chlorophyll *a* did not show significant differences (day 0, $\chi^2 = 2.648$, P = 0.104; day 7, $\chi^2 = 2.406$, P = 0.124; day 14, $\chi^2 = 2.351$, P = 0.129;) even though it was lower in microcosms treated with copper (*Table 2*). Our functional indicator, Chl *a*, decreased but not significantly under both copper concentrations, in accordance with phytoplankton abundance decrease. In addition, variation of phytoplankton size classes of small, medium and high phytoplankton cells showed that copper treatment led to an increase in the small size group (*Fig. 2*).

Total zooplankton abundance was negatively affected mainly at the end of the experiment. The average abundance of total zooplankton during the study period was 23, 10 and 18 ind l^{-1} in the control, L and H treatments, respectively. The zooplankton community was represented by the presence of rotifera (*Euclanis sp., Brachionus sp. and Monostila sp.*) and copedoda (Calanoida). Zooplankton abundance (Table 2) showed statistical differences among the controls and treatments at the end of the experiment ($\chi^2 = 9.500$, *P* = 0.009) and was lower in L treatment (Wilcoxon test Z = -2.060, *P* = 0.039,) and H treatment (Wilcoxon test, Z = -2.060, *P* = 0.039) than in controls. There were not statistically significant differences among zooplankton groups in control and treatments but they behaved in different ways. Copepods disappeared at the end of the experimental period, while the rotifers increased their abundance.

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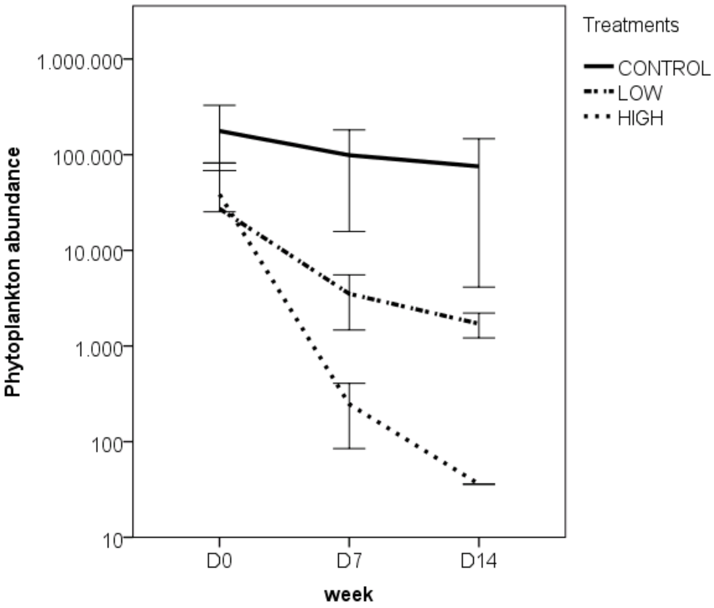
a)



b)

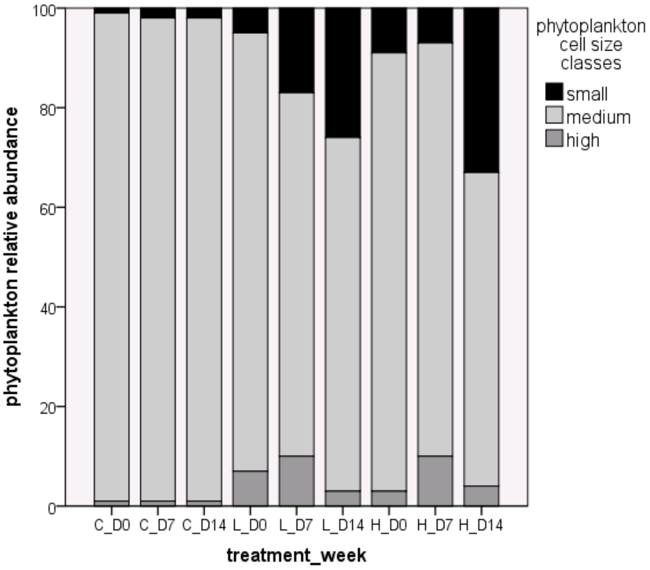


Figure 2. *a) Phytoplankton abundance (cells L-1) and, b) cell class proportion (%) along the experiment.*

Discussion

Even though there are some specific differences in physical-chemical parameters during the experiment, PCA shows that those differences were not relevant enough to discriminate among treatments. Therefore, all microcosms were under the same water quality and an environmental condition which allows us to refute that community differences are neither related to water quality and environmental-induced differences among microcosms, but owing to treatment effects.

Phytoplankton was highly affected during the whole experiment in both low and high treatments. Even working under legal copper concentrations, there are negative impacts on the aquatic community since phytoplankton abundance in treatments differed from the control abundance. Phytoplankton sensitivity to copper has been reported in other studies (Santos et al. 2002, Nayar et al. 2004). Moreover the changes in cell size group distribution showed by cytometry give information about the impairment in the plankton community and can be used as an early warning signal. Besides this fact, small size populations increased in microcosms treated with copper (Fig. 2 b). This implies a variation of predator-prey mass ratio. Body size relation is important in trophic interactions owing to its influence in growth efficiency. Growth efficiency depends on the relative body size of the prey, and on the prey density (Kerr & Dickie 2001), and copper sulfate treatments have affected both aspects. Therefore, phytoplankton cell size changes towards smaller sizes may have indirect effects upon the zooplankton community through a reduction in its growth efficiency. Phytoplankton structural features showed the first warning signals: these were a drastic decrease of phytoplankton abundance and changes towards smallest cell sizes after copper application; hence, its measure could be used as a simple and efficient tool to identify an early impairment signal. In this sense, flow cytometry has been shown as a very rapid and useful technique. As has been mentioned before, a warning signal is an important component of the integrated approaches that are needed to acquire a general knowledge of toxic impact allowing predictions and early mitigation measures (Schmitt-Jansen et al. 2008) and flow cytometry could be easily incorporated in the assessment and biomonitoring programs.

The delay in zooplankton response could be related to an indirect effect of copper on trophic interactions. The direct effect of copper on phytoplankton affected zooplankton food availability. Therefore food resources decreased for zooplankton but the effect on zooplankton was not detected right away after copper application. Moreover, this different response timing is also related with the different life span of phytoplankton and zooplankton, being faster in phytoplankton. Even though there were no statistically significant differences among zooplankton groups in control and treatments, they behave in different way. For instance, the copepoda disappearance in some treatment microcosms suggest a specific impact in that group's ability to face the experimental conditions, and consequently in its potential recovery capacity. At the same time, rotifera responded differently to copper treatments, increasing its abundance in treatment microcosms, which implies that there had been a community shift both in L and H treatments that could not be observed at total zooplankton abundance level. In fact, the control microcosms had more than double that of the zooplankton in both L and H treatments, showing the importance of analyzing changes at a lower hierarchical level in order to better understand the changes at a higher hierarchical level. Going deeper into zooplankton shift, it has been shown in other studies that rotifera are more tolerant immediately after copper application than other organisms even up to 20 mg l^{-1} of copper, however after 8 days under copper exposure from 0.5 mg l^{-1} to 20 mg l^{-1} its population was dramatically affected (Källqvic & Meadows 1978). Large-bodied zooplankton also is more sensitive to environmental stressors including pesticides than their smaller congeners (Havens & Hanazato 1993). Further, copedoda and rotifera play a different role in the ecosystems and in the food web structure. For instance, macrozooplankton, as copedoda, grazing pressure has a stronger role than rotifera in regulating phytoplankton which is an important function to control eutrophication

(Miracle et al. 2007). Kasai & Hanazato (1995), using experimental ponds, observed that the herbicide simetryn caused a decrease in zooplankton density due to indirect effects related to a decrease of algae. But picking up the changes in phytoplankton size, it is interesting to note that at the end of the experiments, both L and H treatments, showed higher proportion of small phytoplankton cells than control. The smallest filter-feeders could take advantage exploiting the mentioned small food resources, increasing their abundances. In addition, the community shift could be a response caused not only by the apparent higher rotifera tolerance to copper but also by other indirect situations. The main indirect effect is the decrease of competence for food resources due to copedoda reduction that allows the increase of rotifera population. Miracle et al. (2007) found an inverse relationship among rotifera and cyclopoida copepod abundance under perturbation. This inverse relationship of rotifera and copedoda under perturbation has been found in other studies. For instance Richard et al. (1985) observed how under herbicide treatment there were shifts from copedoda and copedoda-cladoceran dominated communities to rotifera and small cladoceran dominated communities. A similar relationship was found by Gagneten & Paggi (2009), under heavy metals treatments (Pb and Cu) rotifera increased while copedoda and cladocera decreased. Both studies used such relationship as a tool to characterize the water bodies under study: in the first case the trend towards rotifera was identified as an indicator of eutrophy impairment and in the second case as a tool to determinate heavy metals impairment. In this study, an inverse relationship between rotifera and copedoda matches with other observations that indicate copper impairment as the decrease of total zooplankton in the treatments. Therefore, it supports its use as an easy and cost-efficient indicator and warning signal of contamination in aquatic systems as Gagneten & Paggi (2009) also suggested. The negative impact that has been showed during this short term experiment on the poorest food resources could be intensified, in the long term, to the zooplankton community. The impairment in trophic relationships observed due to copper exposition, allows considering both, phytoplankton and zooplankton changes, as early warning signals. In nature, loss of species at basal trophic levels can affect production at higher levels and thus can also lead to decreased energy transfer efficiency (Gamfeldt et al. 2005). Undoubtedly, further studies must be developed to confirm these results in long term exposition, with different toxic substances, and this with holistic approaches that can detect indirect effect and alarm signals as the phytoplankton did.

Chlorophyll content is used to highlight stress due to a single environmental factor or to a combination of different environmental factors, but it also constitutes potential biomarkers of anthropogenic stress (Ferrat et al. 2003). However, in the present study Chlorophyll-*a*, as a functional indicator, has not been shown as effective as structural changes indicating alterations in plankton community.

This study works towards a deeper understanding of the agrochemicals negative effects on plankton communities at concentrations above but also below their legal limits. Surprisingly, even legal limits do not protect the plankton community. This result emphasizes the need of more ecological and realistic approaches to ensure adequate regulation limits in order to achieve a balance between development and conservation.

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CAN LIFE HISTORIES PREDICT THE EFFECTS OF HABITAT FRAGMENTATION? A META-ANALYSIS WITH TERRESTRIAL MAMMALS

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Abstract. Anthropogenic fragmentation of habitats has been identified as one of the primary drivers of mammalian declines and extinctions. Previous research has implicated five life history traits as being predictive of the impacts of habitat fragmentation on mammalian abundances: potential growth rate, sociality, mass, home range, and niche breadth. In order to systematically test if these five life histories correlated with mammalian abundances across a gradient of habitat fragmentation, we conducted a meta-analysis. We systematically collected data from 68 studies, encompassing 232 mammalian species within 143 genera, 50 families, and 17 orders. We found that mammals with lower growth rates, paternal care of offspring, greater mass, larger home ranges, and increased niche specialization had significantly lower abundances in fragmented habitat. These results could provide land managers and conservationists with a coarse tool for predicting the impacts of habitat fragmentation across a wide taxonomic breadth of terrestrial mammals.

Keywords: *abundance, mixed-effects model, specialists vs. generalists*

Introduction

Humans have fragmented most continuous habitats on the planet, causing large changes in population sizes of many species (Turner, 1996; Ferraz et al., 2003). Anthropogenic fragmentation is the primary cause of mammalian declines and extinctions worldwide (Wilcove et al., 1998; Grelle, 2005), and has increasingly isolated parks and refuges created to protect wildlife (Janzen, 1983; Newmark, 1995). Despite their conservation status, these fragmented habitats frequently support fewer species, and the species that remain often maintain lower densities when compared to contiguous landscapes (Newmark, 1995).

Despite a large body of literature on the effects of fragmentation, it has been difficult to generalize results across studies because the research focus has typically been the *effects* of fragmentation on a species, and not *why* the species is affected by fragmentation (Funk & Mills, 2003; Banks et al., 2007). In other words, most studies addressed *how* a species is affected by fragmentation (for example, changes in demography or population size), and not what aspects of the species life-history caused the species to be vulnerable (e.g. Ceballos & Brown, 1995; Newmark, 1995; Brashares, 2002).

Proactive, strategic conservation necessitates an evidence-based framework that can be used to predict the impact of anthropogenic disturbances. To accurately target conservation efforts, land managers need to know which species are most threatened by anthropogenic fragmentation and why (Doak & Mills, 1994; Turner, 1996). Several life-history traits have been proposed as predictive of the effects of fragmentation across species (e.g. Laurance, 1994; Ganzhorn & Eisenbeiß, 2001; Laurance et al., 2002), but the predictive capacity of these traits have not been systematically tested (Dale et al., 1994; Peters & Herrick, 2004; Banks et al., 2007), or applied systematically to predict impacts and aide management (Ferguson & Larivière, 2002; Funk & Mills, 2003).

To test whether selected life history traits predict mammal responses to fragmentation, we conducted a meta-analysis of all published literature linking fragmentation and mammals (Englund et al., 1999; Gurevitch & Hedges, 1999; Osenberg et al., 1999). Previous research has proposed that the potential growth rate, sociality, mass, home range, and niche breadth may each predict a directional change in mammal abundances due to fragmentation (*Table 1*). To assess whether the use of these life histories in management is warranted, we tested both the validity and strength of each of the following hypotheses.

Potential Growth Rate

Those species that have the greatest potential growth rate may be more capable of compensating for losses of individuals due to fragmentation (Laurance, 1991; Viveiros de Castro & Fernandez, 2004).

Sociality

Social mammals require groups in order to maintain populations or colonize fragments. Thus social mammals may be less likely to colonize a fragment and more prone to local extirpation than solitary species (Lawes et al., 2000; Swihart et al., 2003). Fragmentation can also have a negative effect on social species by reducing group size and therefore restricting fitness enhancing social strategies (Banks et al., 2007).

Mass

Mammals with heavier body mass require more resources. Because fragments provide a lower quantity of resources, mammals with large body masses may negatively correlate with fragmentation (Marquet & Taper, 1998; Cullen et al., 2001; Michalski & Peres, 2007; Okie & Brown, 2009).

Home Range

Wide ranging species are notably absent from small habitat fragments and may be particularly susceptible to habitat loss (Noss et al., 1996; Woodroffe & Ginsberg, 1998; Feeley & Terborgh, 2008). Thus as the home range of a species increases, the size of the fragment needed to support a viable population increases.

Niche Breadth

Specialists and generalists may respond differently to fragmentation. Specialists, compared to generalists, use fewer resources and thus have fewer alternatives when habitats are constricted. Specifically, specialization of diet, denning, and locomotion could predict a mammal's vulnerability to fragmentation (Laurance, 1990; Laurance,

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1994; Swihart et al., 2003; Viveiros de Castro & Fernandez, 2004; Prugh et al., 2008).

Table 1. *List of life histories and the predicted changes in mammal abundances in response to habitat fragmentation.*

life history	effect of fragmentation	citations
low potential growth rate	negative	Laurance (1991) Viveiros de Castro & Fernandez (2004)
highly social	negative	Lawes et al. (2000) Swihart et al. (2003) Banks et al. (2007)
heavy mass	negative	Marquet & Taper (1998) Cullen et al. (2001) Michalski & Peres (2007) Okie & Brown (2009)
wide home range	negative	Noss et al. (1996) Woodroffe & Ginsberg (1998) Feeley & Terborgh (2008)
specialist	negative	Laurance (1990) Laurance (1994) Swihart et al. (2003) Viveiros de Castro & Fernandez (2004) Prugh et al. (2008)

Materials and Methods

Data Acquisition

On January 27th, 2010 we performed a literature search on Web of Science using three separate groups of phrases in order to avoid biases associated with selection criteria (Englund et al., 1999): 1) “fragment” and “mammal” and “patch,” 2) “fragment” and “mammal” and “habitat,” 3) “fragment” and “mammal” and “disturbance.” Because Web of Science detects word-fragments, a search for “fragment” returns all results for “fragmentation” as well. The results from these three groups of phrases were summed for a total of 1101 studies, and each study’s abstract was read. Based upon the abstracts, we read 304 studies in detail (see *Appendix 1* for the PRISMA flow diagram). Studies were selected for inclusion in the database if they assessed the abundances of terrestrial mammals within at least two unaltered fragments of different sizes. If a study had assessed abundances in fragments but did not include either the abundance estimates or fragment size, we contacted the author and requested the information for inclusion in this study. A total of 68 studies (*Appendix 2*) encompassing 232 mammalian species within 143 genera, 50 families, and 17 orders, were included in our meta-analysis.

Effect Statistic

We were interested in predicting shifts in mammalian abundances in response to anthropogenic fragmentation. To assess whether the aforementioned life history traits could predict changes in mammalian abundance, we needed to first quantify the impact of fragmentation on abundances in the form of an effect statistic. In the traditional meta-analysis, the effect statistic is calculated as the standardized difference between two treatments (*d* in Hedges & Olkin, 1985) or the correlation coefficient (*r* in Osenberg et al., 1999). However, nearly all the studies collected for this meta-analysis assessed abundances in more than two habitat fragments; many species abundances were estimated in more than one study; and the goal of our research was to measure the magnitude of the effect of fragmentation on abundances; thus we needed an alternative statistic (Osenberg et al., 1997).

To accommodate these data, we used the regression coefficient from linear mixed-effects models as an effect statistic. By regressing the estimated abundances against the habitat fragment size within each species across studies, the resulting regression coefficient indicated both the strength and the direction of the effect for each species. We compared regression coefficients from linear and exponential regressions and found 127 of 203 species showed a better fit with a linear model. Given that the abundances of 85 species were estimated in two or more studies and given the need for one effect statistic per species in order to avoid pseudoreplication (Hurlbert, 1984), we included study as a random predictor with a fixed slope. Since both the fragment size and abundance estimates varied widely within and across studies, we used their respective logarithmic values (Michalski & Peres, 2007). In order to include abundance estimates of continuous forests in the model, we set their values equal to 10,000 ha (Vieira et al., 2009).

The effect statistic for each species is the negative of the regression coefficient ($-\beta_1$) from the following equation:

$$\log(\text{area}) \sim \beta_0 + \beta_1 * \log(\text{abundance}) + (1|\text{study}) \qquad \text{(Eq. 1)}$$

The (1|study) term allowed the various studies to have different intercepts, but also forced all the studies to have the same slope.

Life History Traits

To quantify a mammal's life history traits, we extracted values from encyclopedic references (Emmons & Feer, 1999; Nowak, 1999; Foresman & McGraw, 2001). If we could not find a given value, we searched for primary literature in Web of Science and in the IUCN Red List of Threatened Species (IUCN 2009). We defined potential growth rate as the litter size multiplied by the number of litters per year and then divided the total by generation time (Pianka, 1970). Each species' sociality received an ordinal score of 0 to 4, with asocial species scored as 0, rudimentary sociality as 1, matrilineal lineages but no male care as 2, monogamous species as 3, and communal groups with cooperative foraging as 4 (as in Swihart et al., 2003). Niche breadth was an ordinal value from 0 to 3 as calculated by the sum of a mammal's specialization across three axes, diet, denning, and locomotion. For each of these three traits, mammals received a 0 if they were a generalist and a 1 if they were a specialist. A generalist was defined as possessing an omnivorous diet, terrestrial locomotion, and terrestrial or fossorial denning (Laurance, 1994; Swihart et al., 2003; Viveiros de Castro & Fernandez, 2004; Prugh et al., 2008), and a specialist was anything else.

Statistical Analyses

To assess the predictive value of potential growth rate, mass, home range, and niche breadth, we used linear regressions. Potential growth rate, mass, and home range were continuous variables and niche breadth was an ordinal variable. Since land managers frequently do not know all five life histories for a given species, and since the goal of this research is to inform management, we regressed the effect statistic ($-\beta_1$ from Eq. 1) against each predictor individually. To assess possible inverse trends within order, we evaluated individual scatterplots with each taxonomic order. We also regressed the effect statistic against life histories for each taxonomic order represented by at least 10 species. Investigation of Cook's distance revealed fitted values with an influence greater than the 20th percentile for potential growth rate, mass, and home range. Thus we log-transformed these predictors (Kutner et al., 2005), and each of the regressions were as in the following equation:

$$\text{effect} \sim \beta_0 + \beta_1 * \text{life history} \qquad \text{(Eq. 2)}$$

We also compared ordinary linear models to linear mixed-effects models within which the individual slopes and intercepts were allowed to vary according to taxonomic order. Visual investigation of effect values as predicted by sociality revealed a discernible break point as differentiated by an absence (0, 1, 2) or presence (3, 4) of male care for offspring. To assess whether the presence or absence of male care predicted the effect of fragmentation on mammalian abundances, we performed a Wilcoxon rank sum test. All statistical analyses were run in R 2.10.1 (R Development Core Team, 2009).

Results

All five life history traits had a significant impact on the predicted effects of fragmentation on mammalian abundances. Higher potential growth rates reduced the impact of habitat fragmentation (*Table 2, Fig. 1a*; positive correlation with effect statistic), and species with paternal care were more negatively affected by fragmentation than those without paternal care (*Fig. 1b*; Wilcoxon rank sum, W = 2947.5, $p = 0.017$).

***Table 2**. Effect of fragmentation on mammalian abundances as predicted by life history traits. Below are results from the linear regression of the effect statistic against each predictor as in equation 2.*

predictor	**β_1**	**(±SE)**	***p*-value**	**R^2**
log (potential growth rate)	0.0209	(0.0062)	0.001	0.054
log (mass)	-0.0119	(0.0045)	0.009	0.029
log (home range)	-0.0100	(0.0043)	0.022	0.029
niche breadth	-0.0678	(0.0259)	0.009	0.030

Mass, home range, and niche breadth all showed significant negative correlations with the effect statistic (*Table 2*), indicating that species with heavier mass, larger home

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range, and greater degree of specialization had lower abundances in habitat fragments (*Fig. 1c, d, e*).

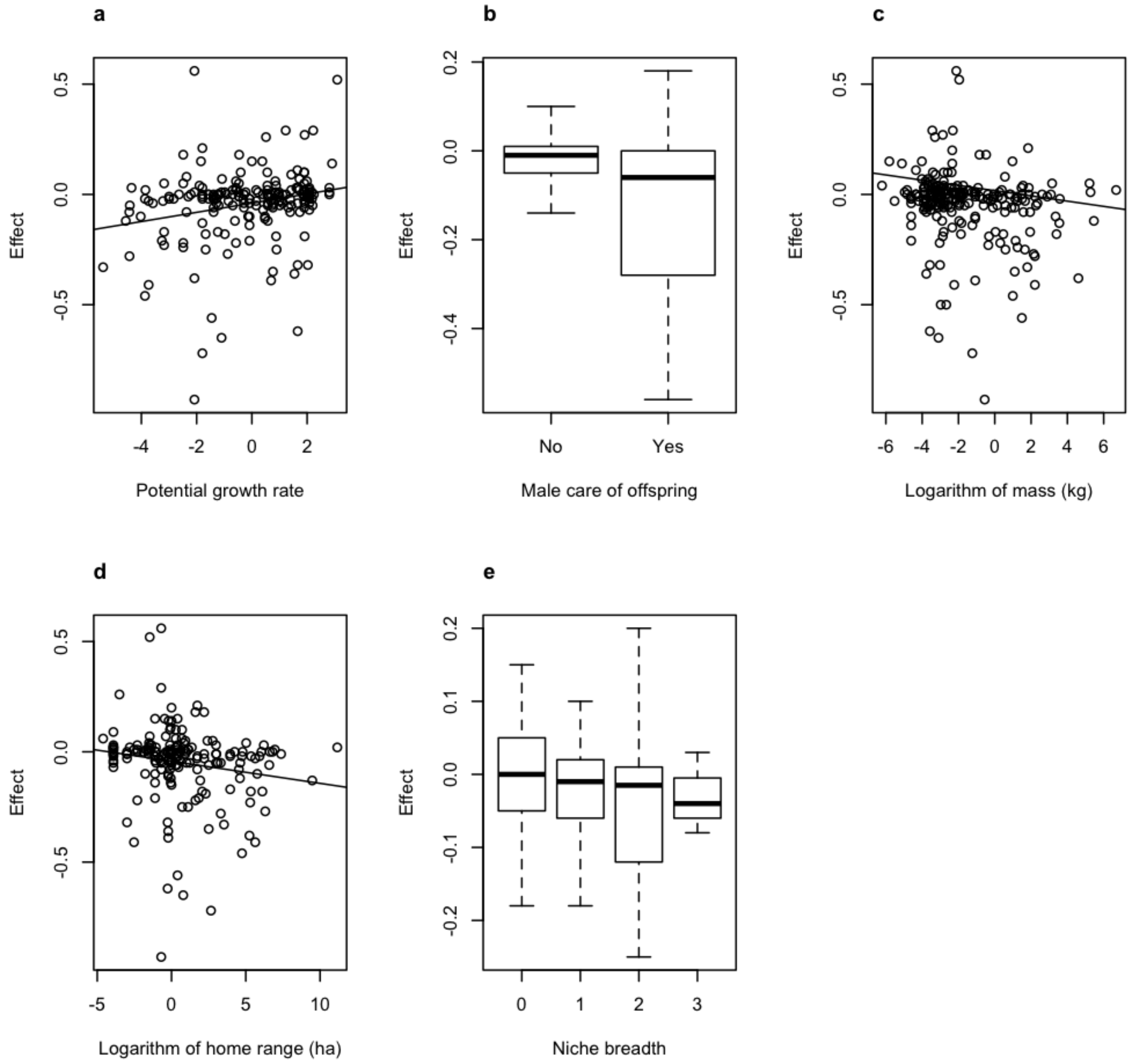

Figure 1. *Effect of fragmentation on mammal abundances as predicted by (a) potential growth rate, (b) mammals with and without paternal care, (c) mass, (d) home range, and (e) increasing specialization across niche breadth.*

The addition of taxonomic order as a random effect did not alter the interpretation of the results. With all five of the life histories, the coefficient and standard error for each regression changed less than 0.0003 with the addition of order as a random effect.

Linear regressions of the effect of fragmentation against life histories within taxonomic orders containing greater than 10 species revealed no significant trends (*Table 3*). We found no inverse trends within any of the five life history predictors indicating the trends found were not caused by over representation of any one order.

Discussion

In accordance with previous predictions, all five life history traits predicted mammalian abundances across a gradient of habitat fragmentation, and each of these correlations were significant. Thus the theorized tenets of mammalian life history as applied to the impacts of fragmentation appear sound, and generalizations found in a host of more specific studies appear to be substantiated by this meta-analysis.

Potential growth rate has been shown to correlate with Australian mammal abundances across a fragmented landscape, where species with lower growth rates had lower abundances in habitat fragments and vice versa (Laurance, 1991). Our research also indicates that mammals that are slow to mature and have few offspring are most likely to experience declines due to fragmentation (*Table 2, Fig. 1a*).

Social mammals can respond to fragmentation differently than asocial species. For example, the tree hyrax (*Dendrohyrax arboreaus*) and blue duiker (*Philantomba monticola*) do not exhibit parental care and had gradual declines due to fragmentation whereas the samango monkey (*Cercopithecus mitis*) has parental care and experienced dramatic declines in abundance (Lawes et al., 2000). The differences in abundances across these species were attributed to their social structure (Lawes et al., 2000). Our meta-analysis supports the observation that mammals with paternal care are more negatively affected by fragmentation than those without (*Fig. 1b*).

Several studies have found that larger mammals have lower abundances in habitat fragments than smaller species. In the Brazilian Atlantic forest, five common mammals of mass greater than 1 kg had average densities in 20,000 ha habitat fragments nearly triple that found in 200 ha fragments (Chiarello, 2000). On the Sunda shelf islands of Indonesia and Malaysia mammals of large body sizes were absent from smaller islands (Okie & Brown, 2009). Body size also accounts for carnivore abundances across coastal southern California with larger species having lower abundances in habitat fragments (Crooks, 2002). In the Chiquitano forests of Bolivia, mammals with a body mass less than 6 kg were found to have greater abundances in habitat fragments than in contiguous forests (Kosydar, 2010). Our results agree that mammals of greater mass are more susceptible to fragmentation (*Table 2, Fig. 1c*).

Mammals with larger home ranges need larger habitat fragments in order to support viable populations. Since people hunt mammals, the edges of habitat fragments can serve as a sink, thus rendering species with wide ranges especially susceptible to fragmentation (Woodroffe & Ginsberg, 1998). A study of ten carnivores found that mammals with large home ranges are more likely to go extinct than mammals with small home ranges (Woodroffe & Ginsberg, 1998). We found that this trend appears to hold true across taxa and that species with larger home ranges have lower abundances in fragmented habitats (*Table 2, Fig. 1d*).

The conservation literature points out differing responses of specialists and generalists to fragmentation. For example, a meta-analysis of amphibians, reptiles, invertebrates, birds and mammals in habitat fragments found that the specialization of diet and locomotion could predict the presence or absence of a species (Prugh et al., 2008). Results from the Biological Dynamics and Forest Fragments Project indicated that generalist herbivores and omnivores have stable or increasing abundances, whereas specialist predators have declined (Laurance et al., 2002). In Queensland, Australia specialization along the axes of diet, denning, and locomotion strongly correlated with abundances of five mammals with specialists nearly extirpated from habitat fragments (Laurance, 1990). The results of this meta-analysis indicate that resource specialization in general – spanning all three of these axes – indicates a species response to fragmentation (*Table 2, Fig. 1e*).

Table 3. *The effect of fragmentation as predicted by life histories within mammalian orders with at least 10 species represented.*

order	**potential growth rate**		**sociality**		**mass**	
	β_1 (±SE)	*p*-value	W	*p*-value	β_1 (±SE)	*p*-value
Carnivora	-0.05 (0.06)	0.41	5	0.50	-0.01 (0.01)	0.93
Cetartiodactyla	-0.03 (0.05)	0.55	12	0.36	-0.01 (0.03)	0.80
Didelphimorphia	-0.04 (0.07)	0.59	no paternal care		-0.04 (0.02)	0.11
Diprotodontia	-0.05 (0.13)	0.69	10	1.00	0.04 (0.08)	0.66
Eulipotyphlya	0.02 (0.01)	0.10	no paternal care		-0.01 (0.01)	0.46
Primates	-0.01 (0.06)	0.82	11	0.43	0.00 (0.05)	0.92
Rodentia	0.01 (0.01)	0.24	308	0.54	-0.02 (0.01)	0.15

order	**home range**		**niche breadth**	
	β_1 (±SE)	*p*-value	β_1 (±SE)	*p*-value
Carnivora	0.01 (0.03)	0.80	0.06 (0.08)	0.50
Cetartiodactyla	0.00 (0.02)	0.96	-0.04 (0.10)	0.72
Didelphimorphia	-0.04 (0.02)	0.08	0.03 (0.07)	0.70
Diprotodontia	0.00 (0.15)	0.98	0.13 (0.20)	0.54
Eulipotyphlya	-0.01 (0.01)	0.67	0.01 (0.05)	0.81
Primates	-0.02 (0.04)	0.65	0.03 (0.09)	0.74
Rodentia	-0.01 (0.01)	0.60	-0.06 (0.04)	0.09

The above findings must be interpreted with care. Given that the trends we found were across taxonomic orders and not within taxonomic orders, we suggest that in the absence of additional research, these results should not be used to compare species within one order. Secondly, although we found a significant effect of fragmentation on abundances and we predicted this effect based upon a mammal's potential growth rate, sociality, mass, home range, and niche breadth, we also found a large degree of stochasticity with each of these predictors. Thus these results are best interpreted as suggestive of a mammal's potential response to fragmentation. Yet the stochasticity is not random. Given that we attempted to make global generalizations across a wide taxonomic array, a large amount variation should be expected.

Our findings indicate that the previously proposed theories generally hold and that each of the five life histories correlated with a mammal's response to fragmentation. For managers attempting to assess which mammals are most susceptible to habitat fragmentation, these life history traits can serve as a predictive tool. When developing plans about which species to monitor, this framework is likely to yield results allowing managers to focus limited resources on mammals that are prone to declines, specifically, mammals with slow growth rates, paternal care, large mass, wide home ranges, and specialized niches. These five life history traits could provide a relative risk index that managers could use to help predict changes in abundances due to habitat fragmentation.

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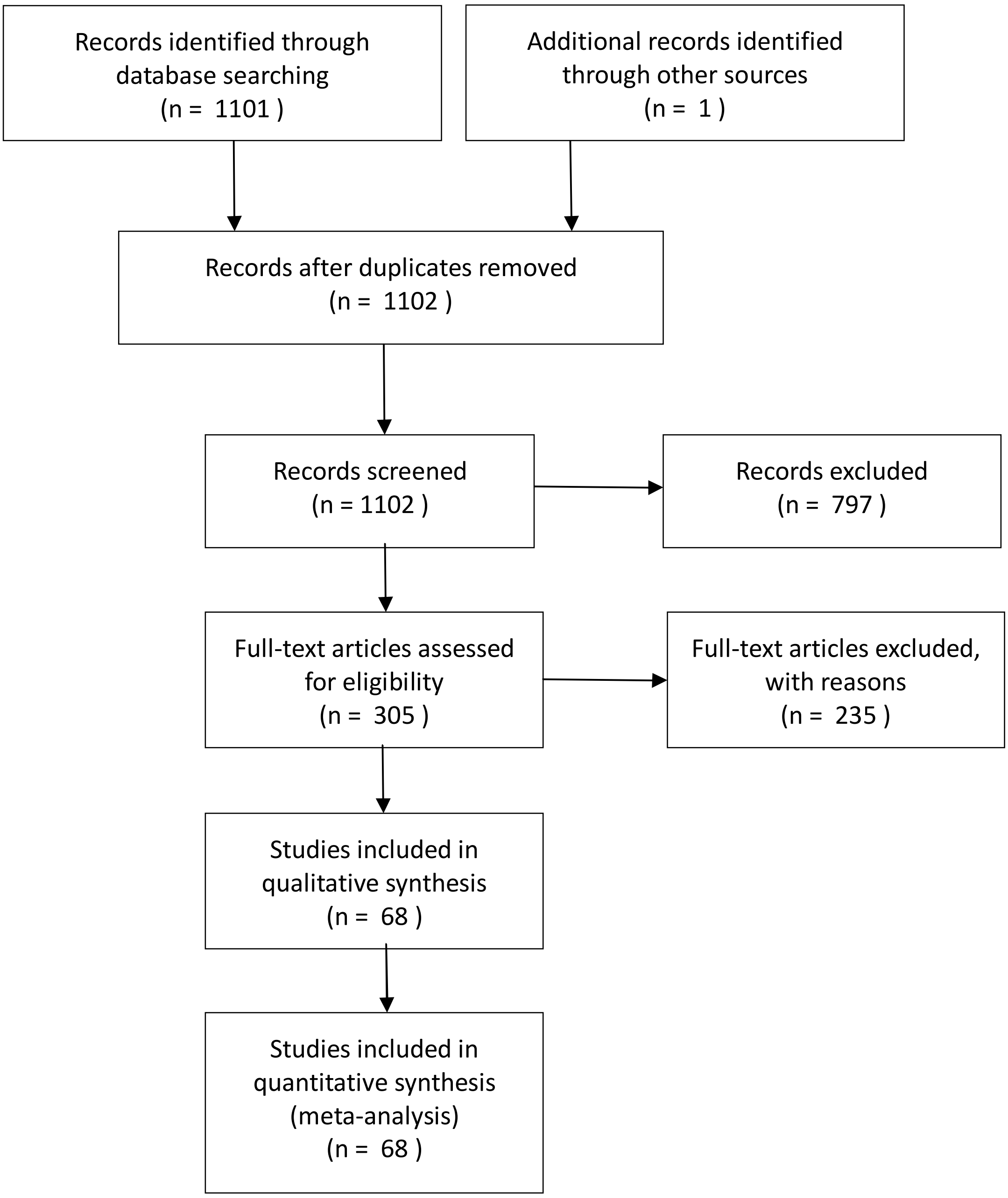
Appendices

Appendix 1. *PRISMA Flow Diagram (Moher et al., 2009) detailing the flow of information through the different phases of the meta-analysis. This flow diagram maps out the number of records identified, included and excluded, and the reasons for exclusions.*



Appendix 2. *List of 68 studies from which data was extracted for the meta-analysis. An asterisk (*) in front of the title indicates that the author(s) of the study shared additional data for inclusion in this meta-analysis.*

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THE CHANGES IN PRECIPITATION DURING 124 YEARS AND ITS INFLUENCES ON THE PHYSICAL CONDITIONS OF HERNÁD RIVER

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Abstract. Natural factors affect not only surroundings on River Hernád, but the appearance of people and their activities as well. These factors have significant effect on both the natural landscape and the river meandering processes. Recently, an intensive destruction level was measured concerning river banks in the selected area. By the comparison of historical maps and the GPS measurements in that region, the movements of the river basin have been reconstructed. The results show a displacement volume of 4-6 meters in some places within few years. The natural factors (precipitation, water levels) were examined as well as anthropogenic factors and their relationships. Research results demonstrate interaction of certain environmental elements. This study compares daily changes of precipitation data for hundred and twenty-four years through analysing the recorded water level of River Hernád. The high amount of river bank destruction is mainly caused by water level fluctuations, significant decrease in regional precipitation, and both type and intensity of cultivation.

Keywords: *precipitation, water level, meandering, River Hernád*

Introduction

In the floodplain of the river's Hungarian sections approximately 30 settlements face a constant threat of floods. Next to overflow, floods have a strong effect on the river's running line. On the other hand changes in the running line itself have knock-on effects on posterior flood-incidents that they provide a positive feedback. It is also important to define that directly or indirectly the same factors can cause flowages dissolved in the area where sporadic high banks are along the river-bed. Sometimes, this can result catastrophic damages or disasters. Devastating effects do not only appear on high bank-descents. By slipping into the river-bed mass of soil the running line of the river is changing next to causing damages in some gardens or other parts of local habitations. It can even block the total river-bed.

Therefore, monitoring the development of a river with mainly meandering sections in Hungary and forecasting their prospective changes are crucial for both theory and practice. Lately, geomorphologic research work in Hernád valley has been focused on the development of river banks. Important investigations were carried out by authors of recent study parallel with a research team of geomorphologists at the University of Szeged. Common research and consulting were often applied (Kiss et al., 2009; Blanka

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& Kiss, 2010; Szabó, 2008; Kozma, 2008; Kozma & Puskás, 2012; Kalmár & Kozma, 2012).

Concerning regulation on Hernád several activities were implemented in the Hungarian part of the river valley over last hundred years. They have interfered with natural processes-related to the river-bed as well as with its surroundings. Join of streams as Kis-Hernád and Bársonyos-creek has been providing a good example for this theory. Its building-up took place at the end of the 18th, early 19th century. Earlier, moorland surrounded this area where water streams of Hernád could have expanded. This phenomenon disappeared completely after having established the Bársonyos mill-channel. Afterwards its side-streams also become regulated and their waters were directed into the river entirely. The regulation of left-side streams (Gönczi-creek 1928-30, Becsali-creek 1930) took place from 1930 to 1931, ones of right-side (Vasoncza-creek and Vadász-creek (1928-30), a Bélus-brook and Garadna-creek (1930-31) from 1928 to 1931 (Trummer, 1933). In Slovakia some significant water storages and damming plants were built up in the last century having a profound impact on the regime of the river (*Fig. 1, Table 1*).

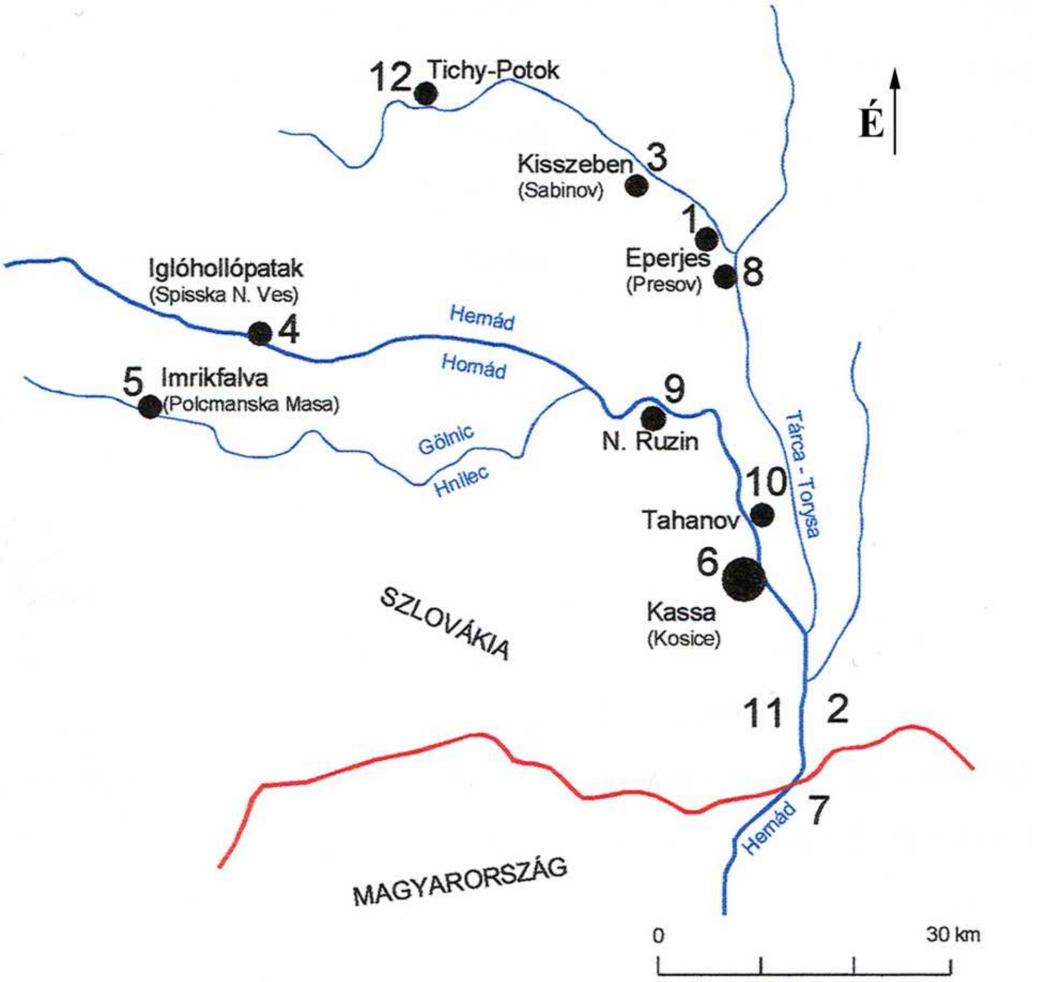

Figure 1. *Location of the reservoirs and weirs on the catchment area of Hernád in Slovakia (on basis SHMÚ Pozsony/Bratislava and RVT 1998)(The numbers show the water facilities (Table 1)*

Table 1. *Data of water facilities on Hernád in Slovakia*

	Facilities	**Construction**		**Stream**	**Settlement**	**Function**	**Important data**
		start	**end**				
1.	hydroelectric power		1904	Tárca (Torysa)	Eperjes (Presov)	E	-
2.	channelization		1910	Hernád		A	cut across 10 meander
3.	hydroelectric power		1912	Tárca	Kisszeben (Sabinov)	E	-
4.	hydroelectric power (HP)		1914	Hernád	Iglóhollópatak (Spisska N. Ves)	E	-
5.	reservoir	1948	1954	Gölnic (Hlinec)	Imrikfalva (Polcmanska Masa)	E, Ip, Iv	T=11.046+ HP
6.	weir	1956	1961	Hernád	Kassa (Kosice)	E	-
7.	channelization	1962	1963	Hernád	Hidasnémeti	A	-
8.	weir	1967	1969	Tárca	Eperjes	E	-
9.	reservoir		1972	Hernád	Óruzsin (Nad Ruzin)	E, A	+ HP
10.	reservoir	1962	1973	Hernád	next to Kassa	E, Ip, Iv	T= 59.0
11.	river bank protection		1975	Hernád		A	-
12.	reservoir	1979	1982	Tárca	Tichy Potok	Iv	T= 19.6

A= flood prevention, E= energy production, Ip= industrial water supply, Iv= drinking water supply, T= reservoir volume ($10^6 m^3$)

Now there are four dams in the Hungarian sections of river. Three of them (Hernádszurdok, Gibárt and Felsődobsza) are located in top and middle river sections. However hydro-electric generators are operated with water flow, they do not have an enormous impact on their direct surroundings. They do not have any significant impacts on flood processes either (Konecsny, 2011). Researchers investigated meandering activities of river more as a “natural” function over last fifty years. These investigations took the artificial intervention-related modifications into consideration (Szabó, 2008; Kozma, 2008; Kiss et al., 2009; Blanka & Kiss, 2010; Szabó et al., 2011; Kozma & Puskás, 2012; Kalmár & Kozma, 2012). With the appearance of extreme flood situations a new space for research work has been created concerning the river. A great number of studies have been published focusing on river’s meandering activities applying a morphological approach for research objectives. Nevertheless, there have been such incidences lately that researchers should not avoid. For example the land use in this territory, which turned into the intensive agriculture or the extreme weather events usually experienced. The enormously transformations of both factors could evoke significant changes concerning natural processes of the river.

There are extreme variations in climate not only global or on nationwide level but some smaller regions are also involved recently. The volume of changes can turn into extreme posing indirect effects on other natural processes (Drégelyi-Kiss et al., 2008). Last few decades high precipitation amounts became more frequent, a quarter or even a third of national average of 600 mm could be falling within a single month (Rakonczai & Ladányi, 2010). Moreover all that rain can happen within a simple hour. According to an IPCC report, this growing frequency of extreme precipitation conditions could risk both climate and agriculture in several regions. Studies published by Bartholy & Pongrácz (2005, 2008) described such changes in the Carpathian Basin that reflected to these facts. They concluded that the "high" precipitation proportion on rainy days was significantly increasing by the fourth quarter of twentieth century however the number of rainy days was lower than before.

The meandering activity of River Hernád has been posing lots of questions and it is giving researchers a constant work. One of the researched areas is the field of dams in Slovakia that have a significant impact on its total passage. Authors do not have concrete data neither about the number of dam-ups nor its volume. Therefore a model-situation was performed taking into consideration the characteristic factors and indicators related to river sections in Hungary. The quantity of precipitation concerning the Hungarian river sections was analysed in the period of 1890-2013 as well as the elevations of water in the relevant field between 1946 and 2011. The main objectives of these analyses were to identify substantial changes in terms of key factors and indicators as well as to determine effects on river-related natural processes. Furthermore, the different land-uses in the relevant areas were also investigated to be able to realise their impacts.

Materials and Methods

The Hernád valley - located in North-Hungary - shows a unique character. Not only the tectonic movements in the Quaternary and Tertiary periods contributed to geomorphic evolution, but fluvial action also had an important role, which intensively shape the landscape of the river and its surroundings.

The length of the Hungarian section of the River Hernád is 118 km. 22 % of the total length of the river is channelized. Our study area is about 20 kilometres long along the lower river section (*Fig. 2*). This territory was chosen, because the effects of river regulations between 1908 and 1972 did not influence this reach. The study area still has natural conditions, because it can be experienced only negligible effects of river regulation. Further reasons of our selection is that this territory is sparsely populated and it do not influence the natural conditions there. The bank collapses are very spectacular along this section of the river.

Our examination methods consist of field measurements and in addition, processing regular data precipitation, facts and figures with daily and monthly bases were registered and analysed embracing a total period of a hundred and twenty-four years. Graphically described results have become available as well. Concerning precipitation data of Hidasnémeti, the issues of National Meteorological Service (Hajósy et al., 1975) until 1970 provided a great source, from 1971 daily meteorological reports were used, which were published by National Meteorological Service.

Annual precipitation volumes and tendencies had been analysed from 1890 to 2013, and monthly precipitation were evaluated as a result. With appraisal work data over a hundred and twenty-four years were divided into four smaller sections, each of them involving thirty years. This kind of sectioning was based on the definition of WMO (World Meteorological Organization) that counted a period of 30 years to be compatible with character references of climate (IPCC, 2007). Data from last sixty-five years in terms of the daily elevation of water were added to these results applying Minitab v14 statistic software for data processing.

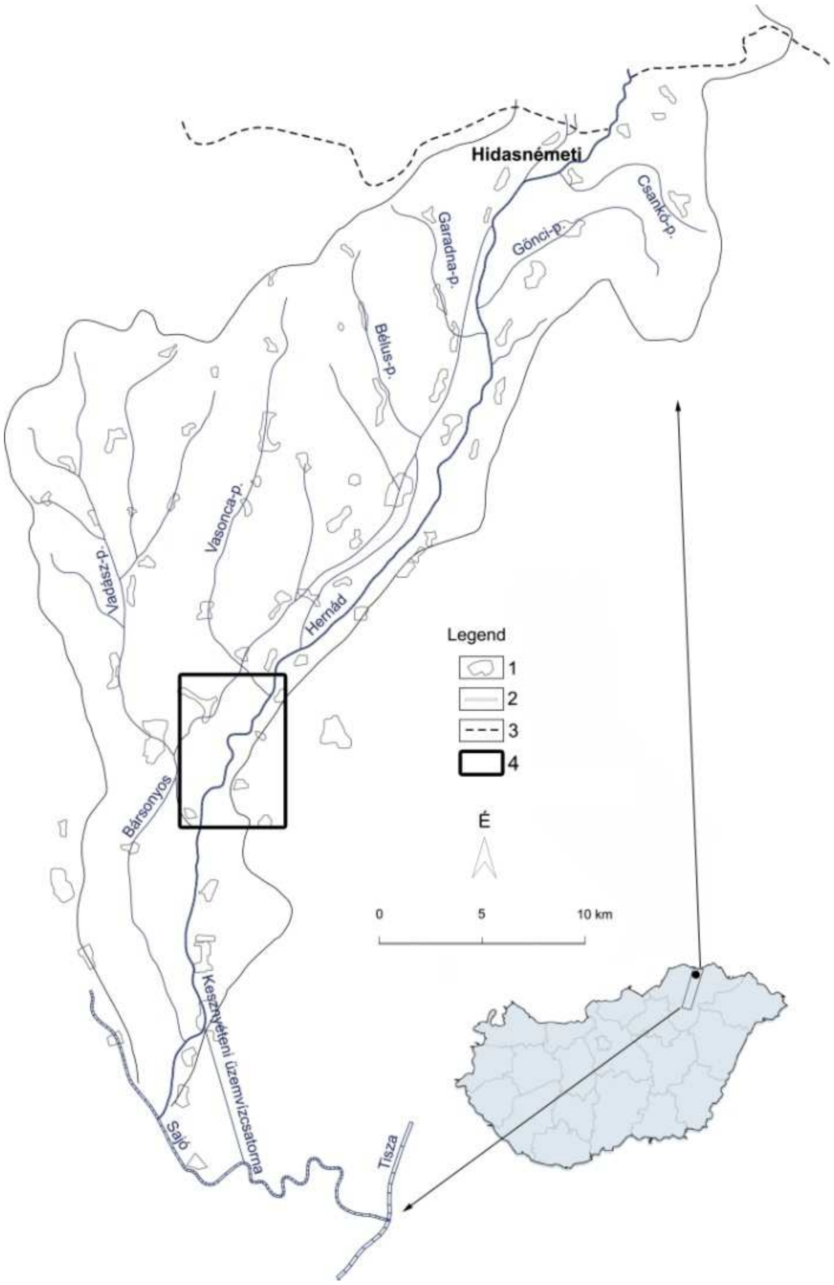

Figure 2. Catchment area of the river Hernád
1. *settlement, 2. watercourse, 3. Hungarian border, 4. research area*

Results

Based on the evaluation of precipitation data over more than a hundred years it is evident that total amount shows a declining tendency. The quantity of precipitation has been reduced by 0.23 mm a year (*Fig. 3*). These results are in accordance with the hypothesis that a slow dry-up period has begun in the Carpathian Basin (IPCC 2011; Bartholy & Pongrácz, 2008; Horváth, 2009). Szász (1994) had some similar conclusions in his work. He expressed a definite descending tendency while he was analysing it in Hungary by assembling and comparing precipitation data of major meteorological sampling sites.

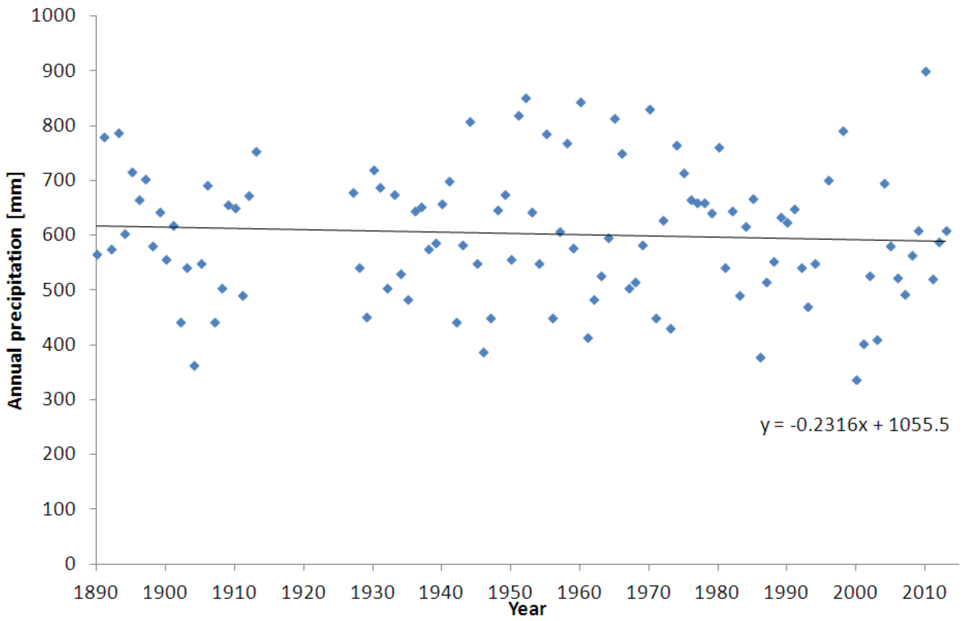

Figure 3. *Amounts of annual precipitation between 1890 and 2013 in Hidasnémeti*

On the analogy of annual precipitation amounts monthly precipitation from 1890 to 2013 were calculated and tendencies were verified (*Fig. 4*). As the graphically described monthly sectioning represents there is a certain decrease in precipitation volume besides of two separate months, February and June. Aridity in August and winter months catches everyone's eye. Thus, in accordance with former graph a reduction in precipitation amounts is clearly observable.

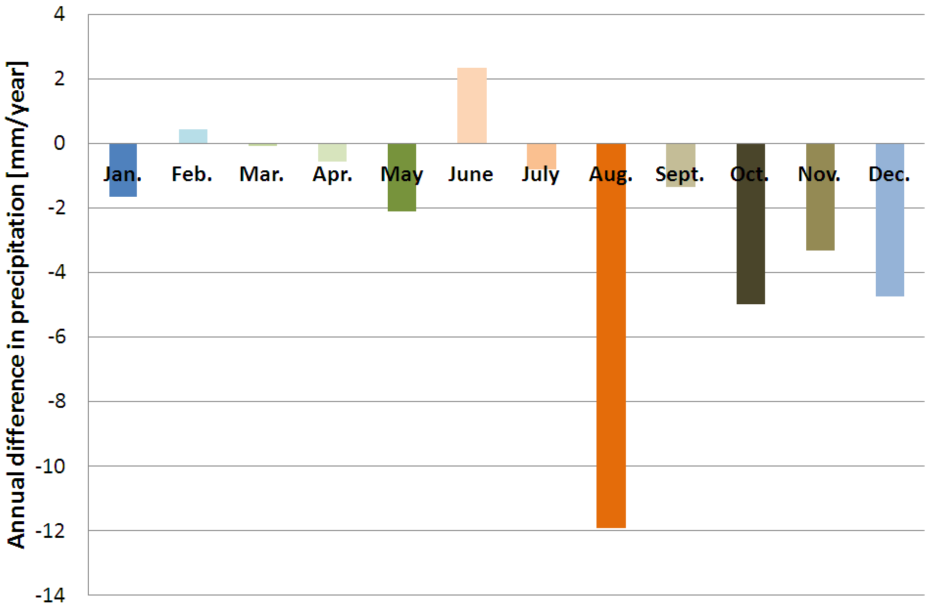

Figure 4. *Total change of the amount of precipitation on monthly basis, between 1890 and 2013 in Hidasnémeti*

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To study this tendency, this research was extended with one more aspect. The investigations related to reduction in precipitation amounts and tendency-analysing were carried out by adopting the WMO sectioning where each period includes 30 years. The gradients of the precipitation for the 30-year examination period were calculated, which were the degree of the variation in precipitation [mm/yr]. The gradient values were plotted against the beginnings of the examination period, separately for the months (*Fig. 5*). First period concerns a time frame 1890-1919, the next one 1981-1920, etc. Each study period appear in one-year offset. The last examined 30 years includes the years from 1984 to 2013, because of this, the last points can find above 1984 on the diagram. The graph below (*Fig. 5*) compares the figures for quantity changes in precipitation-periods of 30 years and the precipitation changes self. Regarding the investigated time period of a hundred and twenty-four years the reducing tendency in precipitation is obvious it does not matter from what directions graph data are analysed. Decrease began early 1930s touched the bottom in the middle of 1970s approximately, and after a certain stagnation period it started growing towards zero. The local intensity was remarkable however the for last few years characteristic tendencies in terms of extreme weather conditions could not be recognised in this tendency as significantly.

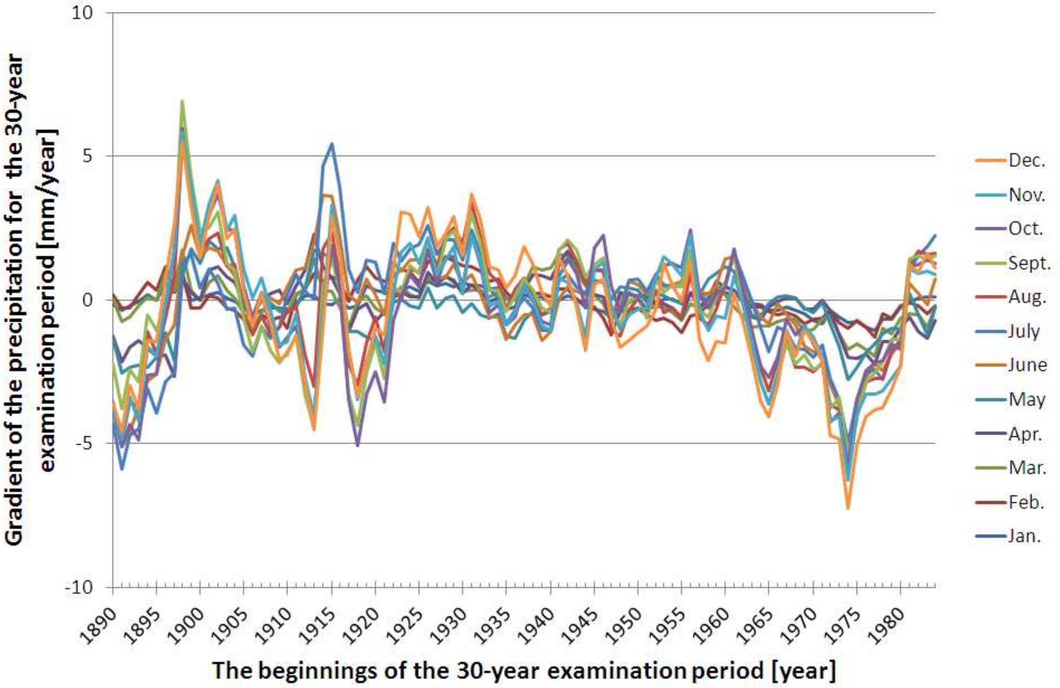

Figure 5. *Tendencies of changes of precipitation on monthly basis*

The experienced results by analysing precipitation amounts have been compared to values of water level-values of the relevant area. Data bases from the investigated sections have served as research pull to analyse daily water levels over last sixty five years. This period has offered sufficient sources to collect representative facts and figures.

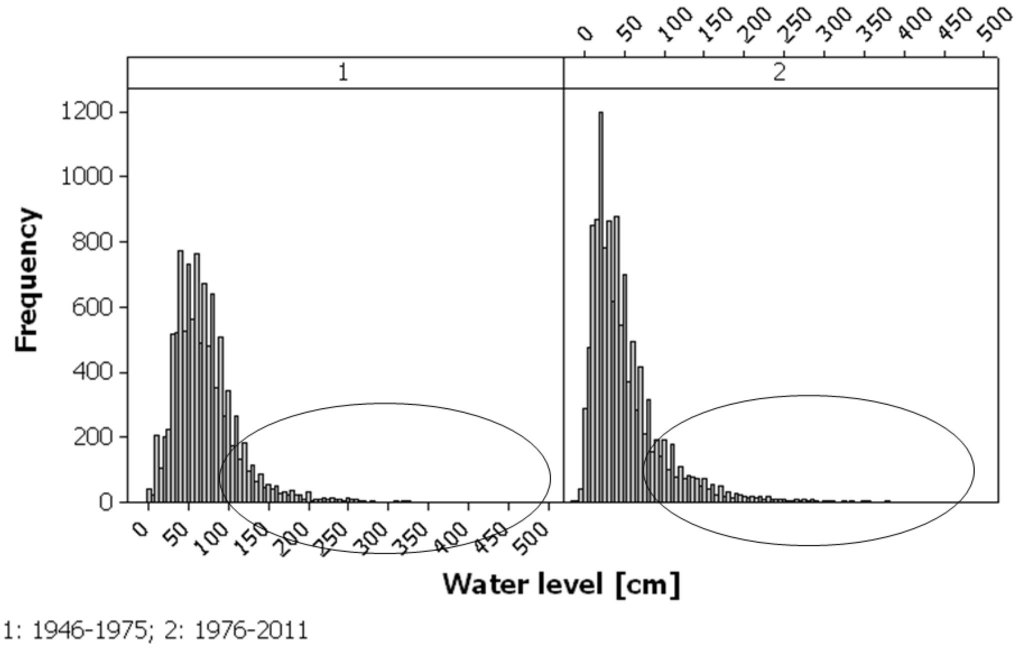

Figure 6. *Changes of values of water level on Hernád during the last 66 years*

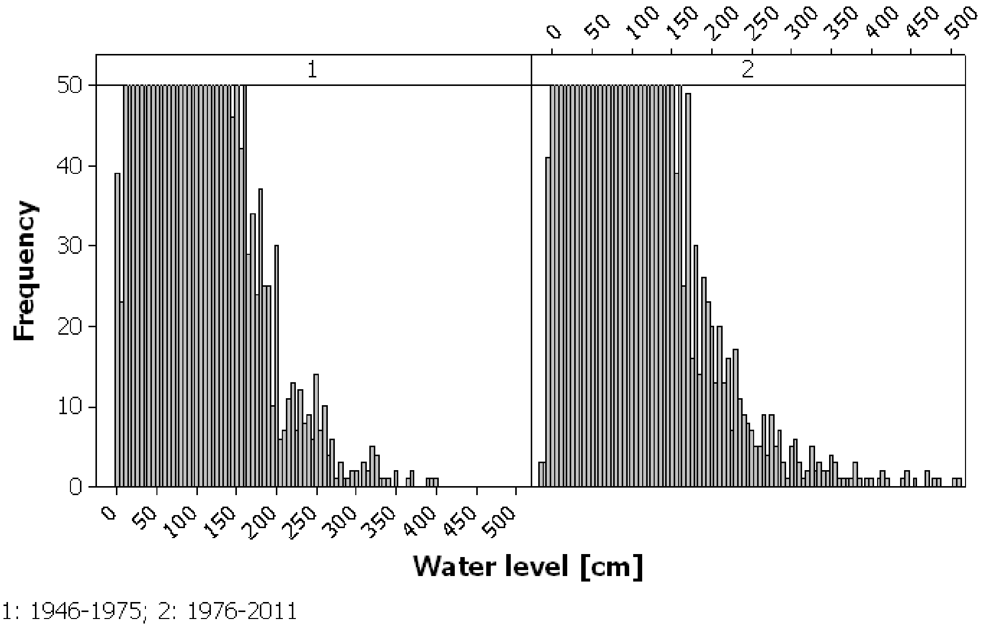

Figure 7. *Changes of maximum values of the water level on the Hernád (enlarged part of the circled part of Figure 6)*

A histogram was created on the basis of daily water-levels and it indirectly generated an excellent tracking way to realize climate changes. Necessary data were divided into two periods, each of 30 years just as in the case of precipitation amounts. In comparison of data from 1946, the evaluating of chart data shows (*Fig. 6-7*) that water levels-values have been moved towards extremities in time. The applied statistic program offered space for new unique domains while processing data. This option performed as a single classification itself. Thenceforward, it was authors' duty to verify results. Taking a daily basis into consideration, the following water level-classifications were created: (-5)-5 cm, 5-10 cm, 10-15 cm, etc. Results clearly show that water regime in first period (1946-75) is more balanced compared to the second period (1976-2011) when it moves towards more extreme values. Therefore, values of low water have remarkably grown just as the frequency of water-levels above 350 cm. While comparing the results to locally experienced-climate variations, in terms of water-levels a significant movement has been approved towards low values (*Fig. 6*). The extremities of last fifteen years have been manifested in a growing frequency of high water (*Fig. 7*).

Concerning the relevant river sections both frequency and grades of flood-prevention measurements were investigated in the course of data-analysis. Especially those tendencies were examined, where changes in number of measurements and their grades reflected water-level modifications. In case of River Hernád, there are three categories or grades related to flood-prevention: first grade is suitable for the case when water level is 250 cm or above, second grade is necessary for water-level of 350 cm or above, and third, the highest grade is commanded in case of 450 cm water level or above (*Fig.8*). Changes are remarkable. The frequency of first grade has been decreased. Nevertheless, commands for second and third grades have been increased significantly.

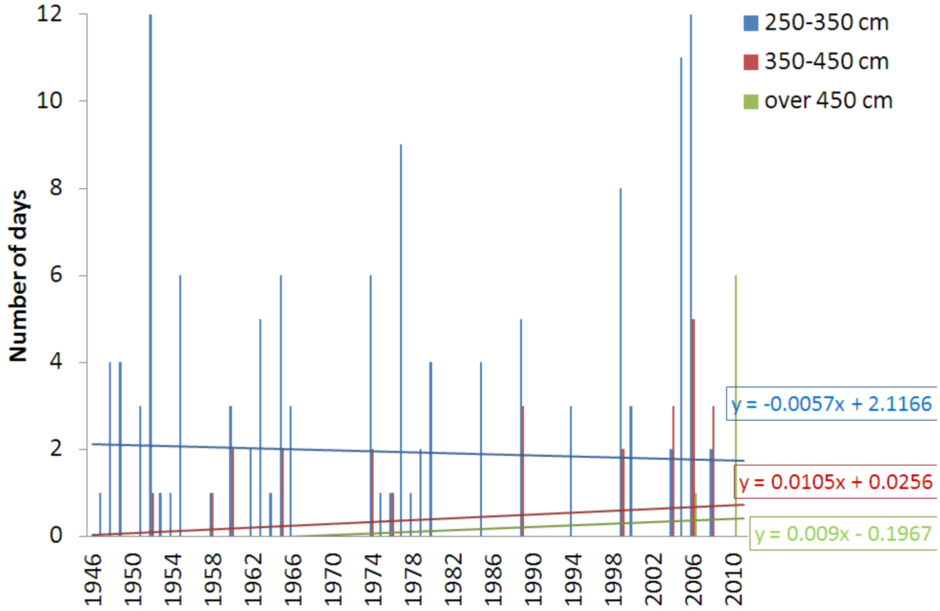

Figure 8. *Changes of ordered flood gradation numbers during the last 65 years near Gesztely I.grade of flood prevention is 250-350 cm, II. grade of flood prevention is 350-450, III: grade of flood prevention over 450 cm*

This is in direct ratio to authors' results whereas the suddenly descending precipitation has a devastating impact by causing floods with a high water-level in a short time. The examinations rapport to an analysis performed in the area of Hidasnémeti a hundred years ago that figures of water outputs analysed. In essence, that had similar results (Konecsny, 2011; Szabó et al., 2011). The evaluations of data related to the river's water-level and water output have not resulted important differences in

Hidasnémeti or Gesztely indeed, the same trends had been realized there. Consequently, the annual water-level minimum can be characterized with a descending tendency (approx. 1 m) while the number of high waters is growing. Sziebert & Zellei (2009) has been verified in a statement that the annual trend for high waters is slowly increasing. Last hundred years the flood level of river increased by approximately 2 meters. (According to a study published in 1933, the highest flood on Hernád took place in 1893. It was 306 cm. In 2010, at time of great flood, a water-level of 503 cm was measured in Hidasnémeti and one of 517 cm in Gesztely.)

The decreasing tendencies in quantity of precipitation also appears in data concerning elevation of water, its moving average for 5 and 10 years indicates a strong correlation between precipitation values and water-levels (*Fig. 9a-b*). It is evidently established that the quantity of precipitation in the area has a direct or indirect impact on the elevation levels. That might powerfully influence even the shape of river-bed.

After having carried out morphologic researches in this area, authors were allowed to have some similar conclusions. In the course of examining the development of river-bed, the largest bank collapses (3-6 m) were rather experienced at a descent, shorter (about 3-4 weeks) water-level fluctuation (50-60 cm). In case of high water-levels, after extreme rainy periods, they were not as important (approx. 0.5 m or even zero). (Kozma, 2008; Kalmár & Kozma, 2012), (*Fig. 10*) Regarding these results it can be concluded that a flood with a short descent period while remaining in river basin is increasing the speed of river. Thereby it destroys large parts of river banks. Sudden flood often undercuts, even washes away them and later on when, after a sudden water level-descent, their supporting function disappears, risks of leaning and collapsing become higher. Since the water-level changes generated by instantaneous floods are more frequent recently, degradation rates of river banks appear more significant.

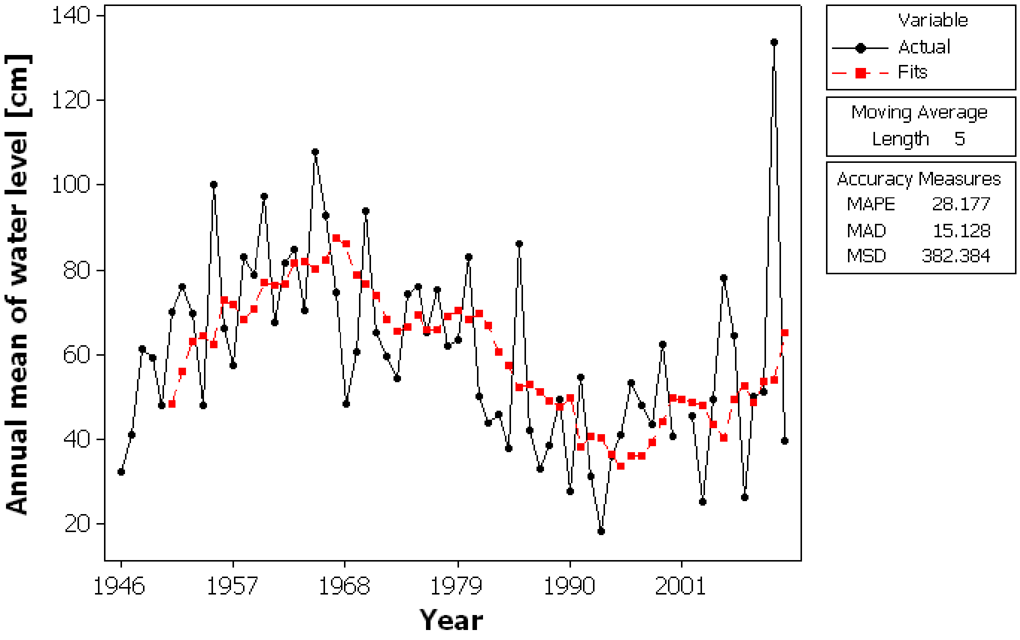

Figure 9/a.

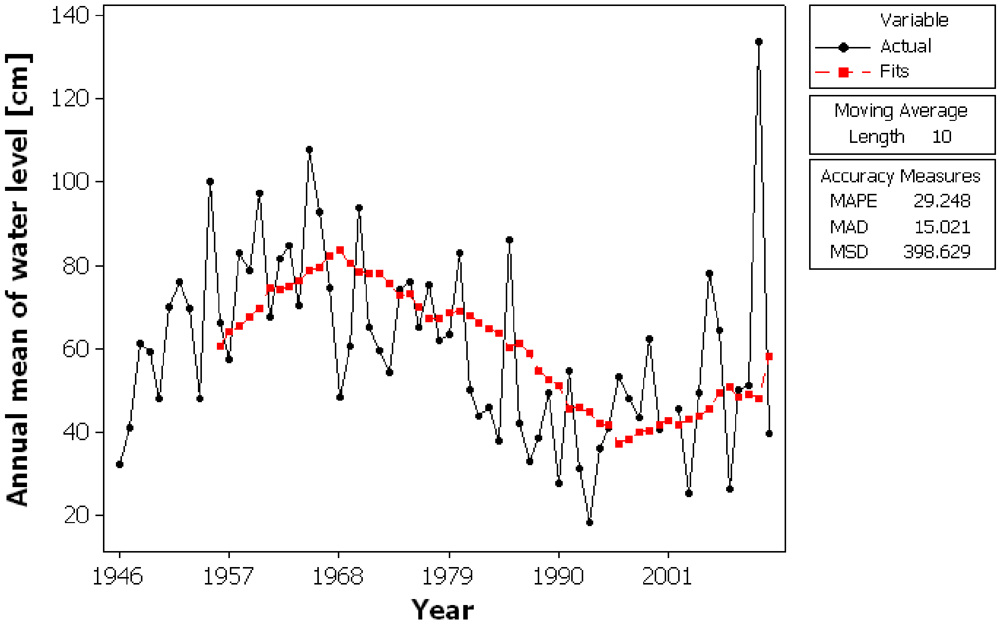

Figure 9/b

Figure 9/a-b. *Moving average of water levels of river Hernád from 1946*

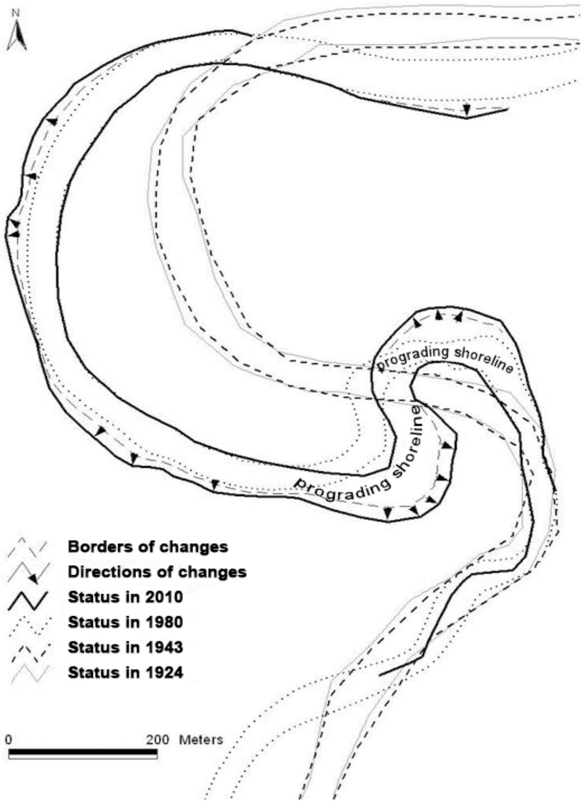

Figure 10. *Developing of the meander on the research area*

The represented incidents and their effects are also strengthened by a modified land-use in the region. Last decades there was a strong transformation related to use of land in investigated areas. Territories used for pasturage or as meadowland, and orchard became stages for intensive agricultural activities. Nowadays, some parcels are reaching the riverside. Due to breaking natural vegetation, the “fastening” function of river banks perishes and it results in faster and larger devastation (*Picture 1*). On the other hand at those river sections where natural vegetation could remain and still covering river banks, a devastation process evoked by the river has had smaller dimensions (*Picture2*).

Picture 1. *Block collapses along the river bank which covered by natural vegetation*

Picture 2. *Strongly degrading river bank along the intensively cultivated agricultural land*

According to results of recent study, modifications occurred in use of land have even accelerated it. In such areas where land-uses are different, not only the intensity of devastation has been changed, also its forms can vary. In case of lands under a more intensive cultivation along high, steep river-banks, sudden bank-collapses or inclinations are more characteristic. This means that some coherent blocks or even whole vertical walls belonging to river-banks can break off suddenly and parts of the decaying blocks can fall into the river. Whereas in river sections with bank tracks and extensive bluffs, and covered by natural vegetation, massive river banks are more likely to collapse. In general, the longer fragmentation prepares their slower decay.

Discussions

Many influencing factors and their contributions have been studied while investigating the meandering activities of River Hernád. However, this circle should be extended for the sake of more appropriate results in terms of study topic. In case of River Hernád with its mainly meandering sections in Hungary, a great importance is attached to the examination of river-bed development as well as to tracking meteorological events and characteristics in the Hernád valley. Not only questions of theoreticians could be replied with more exact forecasts of prospective changes, but also flood prevention could become more efficient.

In general, a strong negative effect can be experienced across the whole Carpathian Basin namely there is a significant decrease in rainy days. In addition, this tendency can last longer (Horváth, 2009). Results of this study are likely to confirm these statements by analysing both direct and indirect effects on natural processes in the region.

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SOIL SEED BANKS IN LOESS GRASSLANDS AND THEIR ROLE IN GRASSLAND RECOVERY

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Abstract. Loess grasslands are among the most species-rich grasslands in Europe. In many regions only species-poor degraded fragments of formerly species-rich loess grasslands remained due to the agricultural intensification in the last century. To preserve and restore loess grasslands it is necessary to understand, how soil seed banks can contribute to the maintenance of diversity. We studied the vegetation and seed banks of (i) a loess grassland in a semi-natural state and (ii) a degraded loess pasture. We found that species richness was significantly lower in the degraded loess pasture (10.2 species/m^2) than in the semi-natural loess grassland (27.0 species/m^2). Mean seed bank densities were quite similar in the two grassland types (22,800 and 20,200 seeds/m^2, respectively). Out of the frequent graminoids in the vegetation, only *Poa angustifolia* possessed considerable dense seed banks. Forb species having considerable seed banks were mainly disturbance-tolerant species (e.g. *Euphorbia cyparissias*, *Galium verum* or *Hypericum perforatum*). Most characteristic forb species possessed only sporadic seed banks (e.g. *Filipendula vulgaris, Pimpinella saxifraga* and *Salvia nemorosa*). Our results suggest that seed banks have only a limited role in the recovery of loess grasslands.

Keywords: *grazing; grassland restoration; plant traits; propagule limitation, seed density*

Introduction

Grasslands contribute with a significant part to the biodiversity of Europe harbouring a very diverse flora and fauna at multiple spatial scales (Kovács-Hostyánszky et al., 2011; 2013; Valkó et al., 2012). The extension and diversity of grasslands is in a constant decline in Europe in the past decades, thus, conservation and restoration of species-rich grasslands is an urgent task nowadays (Penksza et al. 2010, 2013; Török et al., 2011, Házi et al. 2011, 2012; Szentes et al., 2011a, 2011b; Zimmermann et al., 2011, Kiss et al., 2011). For an effective planning of conservation, it is vital to understand mechanisms sustaining grassland biodiversity (Drobnik et al., 2011, Malatinszky et al. 2013, Valkó et al., 2013).

The maintenance and recovery of species diversity in grasslands can be supported by local propagule sources preserved in the form of persistent soil seed banks (Bossuyt & Honnay, 2008; Valkó et al., 2011). There are contrasting views on the role of soil seed banks in sustaining grassland biodiversity. Several studies stress that soil seed banks form an important source for re-colonization, especially when species dispersal is limited (Simmering et al., 2006). Persistent soil seed banks of characteristic grassland species enable fast grassland recovery after degradation or disturbances (Bossuyt & Honnay, 2008). However, other studies found that target species often lack persistent seed banks (Kalamees & Zobel, 1998; Bossuyt & Honnay, 2008). Still there is a shortage of seed bank records, especially for species of high conservational value. Underrepresentation of target species in databases might also hamper the understanding of seed banks' role in grassland recovery (Csontos, 2001; Valkó et al., 2011). To design

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conservation and restoration measures in grasslands it is necessary to study soil seed banks as potential propagule sources for grassland recovery.

The species composition and density of seed banks varies considerably across grassland types and regions, thus it is necessary to have seed bank analysis and persistency records for each grassland type of high conservation value. Published seed bank type records are available for approximately 50% of the Hungarian flora (Csontos, 2001). Hungarian seed bank studies were mainly published from sandy grasslands (Halassy, 2001; Matus et al., 2003, 2005; Török et al., 2009), mountain hay-meadows (Valkó et al., 2011), native alkali (Valkó et al., 2013) and restored alkali and loess grasslands (Török et al., 2012a), rocky grasslands on dolomite (Csontos et al. 1996a), oak forests and clearcuts (Csiszár 2004; Koncz et al., 2010, 2011; Csontos 2011), and pine plantations (Csontos et al. 1996b). Seed bank studies are especially crucial in very fragile and threatened species-rich steppic grasslands, like loess grasslands (Kelemen et al., 2013; Török et al., 2012b). The seed banks of loess grasslands were formerly studied by Virágh and Gerencsér (1998), but in this study for the detected species no seed bank classification was provided.

Loess grasslands are among the most species-rich communities in Europe and harbour many threatened plant and animal species (Török et al., 2011; Török et al., 2012b). The area of historically characteristic loess grasslands become fragmented in lowland areas in Central-Europe because of the agricultural intensification in the last century (Molnár and Botta-Dukát, 1998). In many regions, only species-poor degraded fragments of formerly species rich grasslands remained surrounded by croplands and other intensively managed agricultural lands (Török et al., 2012c, Vida et al., 2010). In spite of the high conservation value of loess grasslands, only sparse seed bank data is available for their characteristic species. To preserve and restore loess grasslands it is necessary to understand how soil seed banks can contribute to the maintenance of species diversity. A crucial question is whether target species already missing from aboveground vegetation of degraded stands are still present in the soil seed banks.

Aims of the study

In the present study, we evaluate the seed bank composition of two types of loess grasslands in relation with aboveground vegetation. Vegetation and seed bank composition of (i) a semi-natural loess grassland (Salvio nemorosae – Festucetum rupicolae) traditionally managed by mowing and (ii) a degraded, abandoned loess pasture (Cynodonti – Poëtum angustifoliae) were studied. We asked the following study questions: (i) How dense are the seed banks of loess grasslands? (ii) Which species of the vegetation possess persistent seed banks? (iii) Is the regeneration from seed banks feasible after degradation of loess grasslands?

Material and methods

Study sites

The studied grasslands are in the Hortobágy National Park (East-Hungary), near the village Hortobágy (Nyírőlapos, degraded loess pasture, N 47°34’47”, E 21°15’30”) and the town Balmazújváros (Magdolna Puszta, semi-natural loess grassland, N 47°35’01” E 21°17’54”). The vegetation in the region is characterised by alkali grasslands, scattered alkali marshes at the lowest and loess grassland patches at the highest elevations (Török et al., 2010, Kelemen et al., 2013). The region is characterized by a moderately continental climate. The mean annual temperature is 9.5 C, while the mean annual precipitation is 550 mm with high among-year variations. The yearly maximum precipitation is typical in June (mean 80 mm) with high year-to-year fluctuations (Molnár, 2004).

Nyírőlapos site was formerly an overgrazed species-poor loess pasture (Cynodonti – Poëtum angustifoliae) till the 1980's. We studied vegetation and seed banks of enclosures established in the 1980's, where no management have been applied.. Abandoned, degraded loess pastures (Cynodonti – Poëtum angustifoliae) are characterised by a high cover of grazing-tolerant grasses, sedges (*Cynodon dactylon*, *Poa angustifolia*, *Festuca pseudovina*, *F. rupicola* and *Carex stenophylla*) and forbs (*Convolvulus arvensis, Galium verum* and *Euphorbia cyparissias*). At heavily grazed sites, thistles dominate (*Eryngium campestre* and *Ononis spinosa*).

In the study region, only small stands of less degraded semi-natural loess grasslands (Salvio nemorosae – Festucetum rupicolae) have remained. The semi-natural grassland in Magdolna Puszta is one of these remnants. The site is traditionally managed by mowing. The characteristic grasses for species-rich loess grasslands are *Festuca rupicola*, *Bromus inermis*, *Koeleria cristata*, *Stipa capillata*, *Alopecurus pratensis* and *Poa angustifolia*. They are rich in perennial forb species, including several characteristic loess-specialist species (*Filipendula vulgaris, Fragaria viridis, Pimpinella saxifraga, Salvia nemorosa, Thymus glabrescens, Trifolium striatum* and *Veronica prostrata*).

Vegetation and seed bank sampling

In each grassland stand, twelve 1-m×1-m plots were marked randomly, and the percentage cover of vascular plants was recorded in June 2009. In the forthcoming spring (2010) three soil cores (4-cm in diameter and 10-cm in depth, 126 cm^3 per core,) were drilled from each plot for seed bank analyses (in total 36 soil cores per grassland). Two vertical segments (0-5-cm, 5-10-cm) were separated; then identical segments from the same plot were pooled. Samples were concentrated by sieving using the method of ter Heerdt et al. (1996). After bulk reduction, samples were spread in 3-4 mm thick layer on surface of trays filled with steam-sterilised potting soil. Germinated seedlings were regularly counted, identified and removed from the trays. Unidentified seedlings were transplanted and were grown until identification. Accidental airborne seed contamination was detected using sample-free control trays filled with steam-sterilised potting soil. Trays were placed in a greenhouse under natural light conditions and watered regularly from April to October. Watering was stopped in early July (when no seedlings emerged) to mimic natural drought conditions during summer. Watering was re-started in late August, and was continued until the early days of November.

Data processing and analysis

Species were grouped into 'graminoids' (i.e. Poaceae, Cyperaceae and Juncaceae) and 'forbs', i.e. dicots and non-graminoid monocots (including Typhaceae). Species were classified into seed bank types (SBT) based on the classification criteria of Csontos (2001) and Thompson et al. (1997). For seed bank types classification, we used vegetation records and vertical distribution data of the seed bank (seed density scores for the 0-5 and 5-10-cm layers). We assigned species to the following seed bank types: T – transient, SP – short-term persistent, LP – long-term persistent (Thompson et al., 1997). Seeds of transient species remain viable in the soil seed bank for less than one year, while seeds of persistent species can survive longer. Generally, short-term persistent seeds remain viable for 1-5 years, while long-term persistent ones can germinate even after being more than 5 years in the soil (Thompson et al., 1997). We assigned those species to SBT types which were either (i) present with at least 3 germinated seedlings (corresponding with a seed density of 66 seeds/m^2) or (ii) were detected in 50% of the plots in the aboveground vegetation (possessing frequency score of at least 6) in at least one grassland stand. Seedlings of *Carex praecox* and *C. stenophylla*; *Juncus bufonius* and *J. ranarius*; *Trifolium angulatum* and *T. retusum* and *Typha angustifolia* and *T. latifolia* were pooled because of identification difficulties. Greenhouse weeds detected in control trays were excluded from analyses. Means of species richness of grassland stands were compared using t-test (Zar, 1999). Similarity between the species composition of aboveground vegetation and seed banks was calculated by the Jaccard index. Vegetation and seed bank composition was compared using DCA ordination (Legendre and Legendre, 1998). Nomenclature follows Simon (2000) for taxa and Borhidi (2003) for syntaxa.

Results

Vegetation composition

We detected altogether 94 species in the vegetation and seed banks of the two study sites. We found altogether 58 species in the vegetation of the study sites: 24 species in the vegetation of degraded loess pasture and 52 species in the traditionally managed loess grassland, while 18 species were present in the vegetation of both study sites.

We detected significantly lower species numbers in the plots of the degraded loess pasture (Nyírőlapos – a mean of 10.2 species/m^2) than in the semi-natural loess grassland (Magdolna Puszta – a mean of 27.0 species/m^2; t-test, $p < 0.001$). The vegetation of the degraded loess pasture was characterised by the high cover of *Festuca rupicola;* only two other species possessed cover scores higher than 5% (*Galium verum* and *Poa angustifolia*; see *Table 1* and *Table 2*). Loess-specialist forb species (e.g. *Filipendula vulgaris* and *Salvia nemorosa*) were missing or only present with low cover scores in the degraded loess pasture (*Table 2*). The vegetation of the semi-natural loess grassland was also characterised by a high cover of *Festuca rupicola*, and there were four species present with cover scores higher than 5% (*Cynodon dactylon*, *Filipendula vulgaris*, *Poa angustifolia* and *Thymus glabrescens*). For detailed species composition, see *Figure 1*. In the DCA ordination, the aboveground vegetation and seed banks of the two loess grassland stands were clearly separated. A higher patchiness of species composition was detected both for the vegetation and seed banks of the degraded loess pasture compared to the semi-natural loess grasslands (*Figure 1*).

We detected altogether 68 species in the seed banks. In the seed bank of degraded loess pasture 52 species, in the semi-natural loess grassland 44 species were found, respectively. We detected 28 species in the seed banks of both study sites. We were able to classify 56 species into seed bank types (Thompson et al. 1997; *Table 1, Table 2*). Total density of seed banks in the two grassland types did not differ significantly; a mean seed density of 22,800 seeds/m^2 in the degraded loess pasture, and 20,200 seeds/m^2 in the semi-natural loess grassland were detected, respectively. No significant differences were found in seed bank species numbers in the two grassland types (means were 17.0 species/ m^2 in the degraded loess pasture and 15.4 species/ m^2 in the semi-natural loess grassland; t-test, P = 0.299). The Jaccard similarity of aboveground vegetation and seed banks were 0.31 in the degraded loess pasture and 0.35 in the semi-natural loess grasslands, respectively. In the degraded loess pasture 76%, while in the semi-natural loess grassland 46% percent of species detected in the aboveground vegetation possessed at least short-term persistent seed banks.

Table 1. *Percentage cover and seed density of graminoid species in the degraded (Nyírőlapos) and semi-natural (Magdolna Puszta) loess grasslands. Notations: VC: mean cover scores in the aboveground vegetation (%); VF: frequency scores in the aboveground vegetation; SN: seedling number; SF: frequency scores in the seed bank. SBT: seed bank type: T – transient, SP – short-term persistent, LP – long-term persistent (Thompson et al. 1997). One germinated seedling corresponds with a seed density of 22 seeds/m2. Species with a frequency score of more than six, or more than three germinated seedlings detected in one grassland stand were listed.*

	Degraded grassland				**Semi-natural grassland**				
	VC	**VF**	**SN**	**SF**	**VC**	**VF**	**SN**	**SF**	**SBT**
Agropyron intermedium					1.1	8			T
Agropyron repens	0.8	9							T
Alopecurus pratensis	0.5	6	7	1	0.4	2	2	2	T
Bromus mollis					0.2	9			T
Carex praecox/stenophylla			113	11	2.8	11	16	6	SP/LP
Cynodon dactylon	0.3	3			7	12	26	10	T
Echinochloa crus-galli							5	1	LP
Festuca rupicola	44.6	11	5	3	33.9	12	31	8	SP
Juncus bufonius/ranarius			5	4			6	4	LP
Juncus compressus			9	6			45	8	LP
Koeleria cristata	0.1	1			0.6	7	6	4	T
Poa angustifolia	7.2	11	43	11	6.1	11	48	11	SP

Out of the most frequent species in the vegetation of the degraded loess pasture, only two forbs, *Galium verum* (4268 seeds/m^2) and *Achillea collina* (2090 seeds/m^2) possessed considerable dense seed banks (higher seed density than 1000 seeds/m^2; *Table 2*). Graminoids present in the aboveground vegetation with high cover scores (like *Festuca rupicola* and *Poa angustifolia*) possessed only low-density seed banks (*Table 1*). Several species sporadically found in the aboveground vegetation, possessed dense seed banks in the degraded loess pasture, like some short-lived weeds (*Carduus acanthoides*, 860 seeds/m^2 and *Conyza canadensis*, 6764 seeds/m^2), sedges (*Carex praecox* and *C. stenophylla*, 2486 seeds/m^2) and wind-dispersed hygrophytes (*Epilobium tetragonum*, 575 seeds/m^2). Loess-specialist forbs detected with low cover scores in the vegetation possessed only sparse (*Salvia nemorosa*, 66 seeds/m^2) or no seed banks (*Filipendula vulgaris*).

Among the most frequent graminoids in the vegetation of the semi-natural loess grassland, only *Poa angustifolia* possessed considerable seed banks (1061 seeds/m^2). Other frequent graminoids of the aboveground vegetation possessed lower seed densities (e.g. *Festuca rupicola* - 685 seeds/m^2, *Cynodon dactylon* - 545 seeds/m^2; *Table 1*). In the seed bank of the semi-natural loess grassland, eight forb species had higher seed density than 500 seeds/m^2; these were *Euphorbia cyparissias* (685 seeds/m^2), *Hypericum perforatum* (6,233 seeds/m^2), *Myosotis stricta* (1,967 seeds/m^2), *Plantago lanceolata* (1,017 seeds/m^2), *Potentilla arenaria* (1,304 seeds/m^2), *P. argentea* (1,326 seeds/m^2), *Stellaria graminea* (862 seeds/m^2) and

***Table 2**. Percentage cover and seed density of forb species in the degraded (Nyírőlapos) and semi-natural (Magdolna Puszta) loess grasslands. For notations, see Table 1.*

	Degraded grassland				**Semi-natural grassland**				
	VC	**VF**	**SN**	**SF**	**VC**	**VF**	**SN**	**SF**	**SBT**
Achillea collina	2.6	8	95	11	1.7	10	11	6	SP
Arenaria serpyllifolia			7	4					LP
Carduus acanthoides	0.1	4	39	12	0.1	1	2	2	SP
Centaurium minus			4	1					LP
Chenopodium album			5	2			1	1	LP
Chenopodium strictum			4	3					LP
Cirsium arvense			5	4					LP
Convolvulus arvensis	0.2	5	4	2	0.1	4			T/LP
Conyza canadensis	0.1	1	307	12					SP/LP
Cruciata pedemontana			8	2	0.1	2			T/LP
Cynoglossum officinale	1.7	8	5	2					T
Daucus carota			2	2	0.7	9	3	3	T
Epilobium tetragonum	0.1	1	26	9			6	3	SP
Euphorbia cyparissias	0.2	5	4	3	0.3	6			T/SP
Filipendula vulgaris	0.4	12			5.5	12			T
Fragaria viridis	1.1	8	3	1	7	11	1	1	T
Galium verum	22.9	12	194	10	4.4	11	3	2	SP
Gypsophila muralis			13	6			7	5	LP
Hypericum perforatum					0.3	5	283	12	SP
Inula britannica	0.1	1	8	2	0.1	3	1	1	SP
Lotus corniculatus					0.6	7	4	3	T
Medicago falcata					1.6	7			T
Medicago lupulina			2	2			5	5	LP
Myosotis stricta			20	5	0.1	4	89	12	SP/LP
Pimpinella saxifraga					1.2	8			T
Plantago lanceolata					0.5	10	46	10	SP
Polygonum aviculare	0.1	2	6	4	0.1	1	6	4	SP/LP
Potentilla arenaria	0.1	2	8	4	1.3	12	59	12	SP
Potentilla argentea	0.2	4	4	3			60	11	LP
Salvia nemorosa	3.6	7	3	3	5.2	11			T
Sonchus asper			6	3					LP
Stellaria graminea	2.6	4	1	1	0.1	1	39	11	T/SP
Thymus glabrescens					7	12	3	3	T
Trifolium angulatum/retusum			8	4					LP
Trifolium striatum			5	3	0.6	6			T/LP
Typha angustifolia/latifolia			4	1			8	5	LP
Verbascum phoeniceum			9	4	1.3	12	10	4	SP/LP
Veronica persica			22	6			55	12	LP
Veronica prostrata			1	1	0.6	8	1	1	T
Veronica verna					0.3	10			T
Vicia angustifolia					0.5	6			T
Vicia lathyroides					0.4	4	13	8	SP

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Veronica persica (1,216 seeds/m^2). Several forb species characteristic to loess grasslands like *Knautia arvensis*, *Pimpinella saxifraga*, and *Salvia nemorosa* had no or at most very sparse seed banks (*Table 2*).

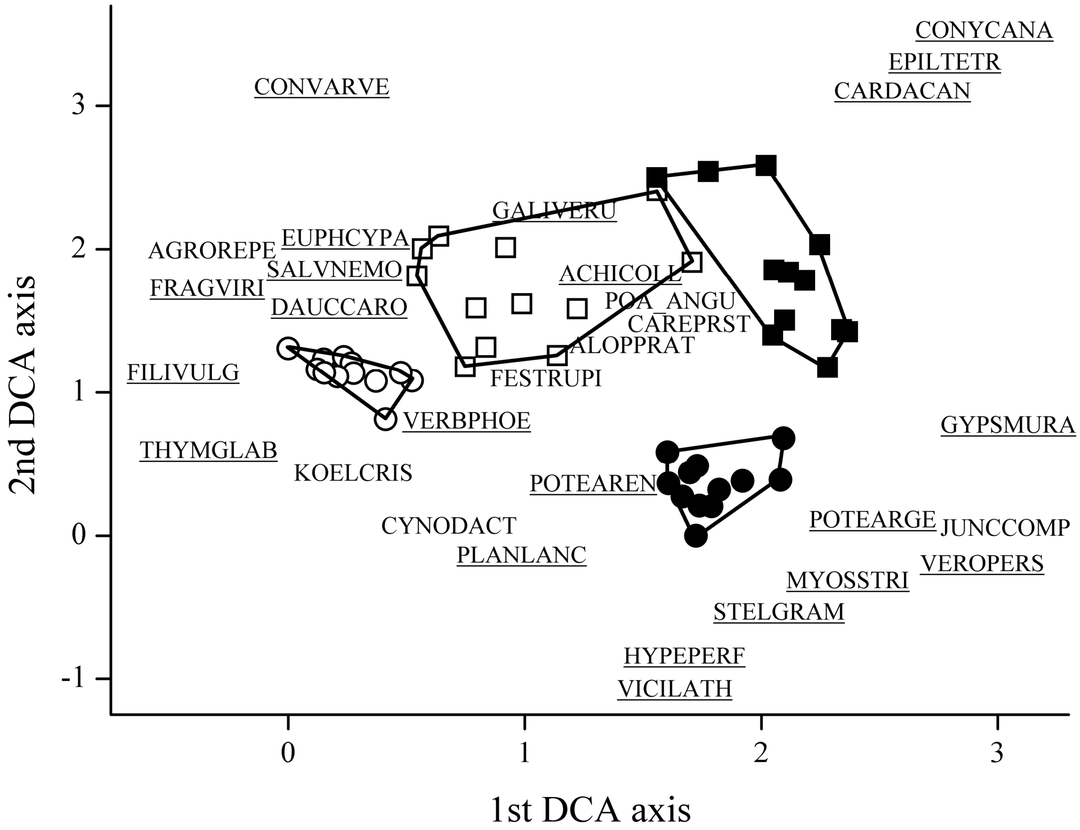

Figure 1*. Species composition of vegetation and seed banks of the studied grasslands displayed by a DCA ordination based on presence-absence datasets. Notations: □ – degraded loess pasture, vegetation; ■ – degraded loess pasture, seed bank; ○ – semi-natural loess grassland, vegetation; ● – semi-natural loess grassland, seed bank. The most frequent 30 species are shown, using four letters of their genus and four letters of their species names. Forbs were marked with underlines.* ***Seed bank composition***

Discussion

Seed banks of loess grassland species

No significant differences were found between the mean seed bank densities of the two types of loess grasslands. Seed bank densities were higher than in other species-rich dry grassland types, like dry calcareous grasslands (200-900 seeds/m^2; Bossuyt et al., 2006 Kalamees and Zobel, 1998) or chalk grasslands (6000-7000 seeds/m^2; Poschlod and Jackel, 1993).

We found that most characteristic species of loess grasslands possessed at most sparse seed banks. For most of the characteristic graminoids in the aboveground vegetation, persistent seed banks were not detected in the two types of loess grasslands. Former seed bank studies in grasslands found that in case of perennial grasses, seed bank formation is often subordinated to clonal reproduction (Bossuyt and Honnay, 2008). In our study, the only perennial grass species with considerable seed densities was *Poa angustifolia*. This generalist grass species was found in high desities in several grassland types (e.g. sandy grasslands, Török et al., 2009), or restored secondary grasslands (Török et al., 2012a).

We found that forb species typical in the aboveground vegetation of the semi-natural loess grassland (e.g. *Fragaria viridis*, *Salvia nemorosa* and *Thymus glabrescens*) possessed no or only sparse seed banks in both loess grassland types. Forb species with considerable seed banks were mainly disturbance-tolerant species (*Euphorbia cyparissias*, *Galium verum*, *Hypericum perforatum* and *Potentilla argentea*).

Similarity of vegetation and seed banks

In former studies, low to medium similarity was found between vegetation and seed banks in temperate grasslands (Bossuyt & Honnay, 2008; Hopfensperger, 2007). This result was also supported by our study: mean Jaccard similarity scores were raging between 0.31 and 0.35 in the studied grassland types. There are several explanations for this phenomenon: (i) Perennial grasses of the aboveground vegetation often lack persistent seed banks (Bakker et al., 1996, Bekker et al., 1997). (ii) Seed banks are mainly characterised by weedy and disturbance-tolerant species missing or underrepresented in the aboveground vegetation in most semi-natural grasslands (Valkó et al., 2011). (iii) For rare species with aggregated seed banks, the probability of detection is low (Thompson et al., 1997). (iv) There is also a high chance for non-detection of short-lived species with high fluctuations in aboveground cover (Török et al., 2009).

Implications for restoration

Loess grasslands are among the most fragile and vulnerable grasslands harbouring high species diversity (Somodi et al., 2008). In a recent study, Kelemen et al. (2013) found that loess grasslands are especially threatned by degradation, because even a slight change in total biomass production can result in a decrease of species richness in these grasslands. Abandonment or inappropriate management by overgrazing alter biomass conditions in loess grasslands, leading to fewer and less suitable microsites for the germination and establishment of target species (Deák et al., 2010; Miglécz et al., 2013). Our results suggest that the local seed banks have only a minor contribution to the maintenance of diversity in both degraded and semi-natural loess grasslands. Irrespective of the state of degradation, only a small number of species characteristic to loess grasslands built up detectable seed banks. Therefore, loess-specialist species can become locally extinct if they disappear from the aboveground vegetation. Restoration of former species richness is therefore not possible from local seed banks in loess grasslands. Our results underline the importance of the traditional management for the species-rich loess grasslands.

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THE GROUND VEGETATION MANAGEMENT OF WOOD-PASTURES IN ROMANIA – INSIGHTS IN THE PAST FOR CONSERVATION MANAGEMENT IN THE FUTURE

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Abstract. Wood-pastures are important elements of the European natural and cultural heritage, fulfilling several ecological functions at local and landscape scale (e.g. providing a valuable habitat for a wide range of species, as well as a link to traditional landscape management practices), but are nowadays in decline especially due to land-use changes begun in the 20th century and lack of legal recognition. Wood-pastures are relatively common in Southern Transylvania (Romania), and, contrary to the majority of similar habitats from Europe, are not threatened mainly by abandonment and subsequent secondary succession, but by modifications in the traditional management regime. Using a wide range of historical documents, this paper presents an overview of the traditional and the current management of the ground vegetation in wood-pastures. These habitats were traditionally grazed mainly by cattle and pigs, sheep being often subject to regulations. Regular mowing was also practiced. Nowadays sheep are the main grazers and mowing has practically disappeared, while the incidences of burning are increasing. Analyzing the differences between the present situation and those described in old publications provides valuable information for conservation management and potential restoration of similar, degraded habitats throughout Europe.

Keywords: *traditional practices, grazing, mowing, pasture burning, Transylvania*

Introduction

Animal husbandry adapted to the landscape is a historical determinant of the character of the European vegetation (Behre, 1988). As scientific data accumulates regarding the high biodiversity and conservation value of semi-natural habitats (Halada et al., 2011), traditional management practices that created and continue to maintain these exceptionally biodiverse areas, and the associated historical, social and psychological factors, tend to be considered as integral elements of conservation management in the present context of biodiversity loss (Fischer et al., 2012; Middleton, 2013; Whiteman and Copper, 2002, Szentes et al., 2011, 2012; Saláta et al., 2011). Attention is turned towards landscapes and regions that still retain their traditional usage, both because of the high number and diversity of species they harbor, and because of their potential role as reference sites for conservation management and restoration (Babai and Molnár, 2014).

Farmland biodiversity is exceptionally rich in the Transylvanian region of Romania, due to the ongoing use of traditional practices, and a substantial part of the region is represented by high nature value farmland, retaining biodiversity in good conservation status (Akeroyd and Page, 2006; Mikulcak et al., 2013; Schmitt and Rákosy, 2007).

Agro-silvo-pastoral systems, the deliberate combination of growing trees and agriculture (mainly pasturing) are recognized for delivering economic benefits (e.g.

agricultural and non-timber forest products) and valuable ecosystem services (Bergmeier et al., 2010; Rigueiro-Rodríguez et al., 2009; Rois-Díaz et al., 2006).

Wood-pastures are one example of such systems. Due to their transitional character and structural diversity, emerging from the presence of (veteran) trees (Lindenmayer et al., 2012) scattered (Manning et al, 2006; Fischer et al., 2010) across an open landscape maintained by a long-established tradition of grazing (Stiven, 2009), wood-pastures are providing conditions for the maintenance of both open habitat and forest-dependent species and play an important role in enhancing biodiversity (Bergmeier et al., 2010; Rich et al., 2005). Wood-pastures are deliberately shaped mosaic-like areas, bearing a characteristic biodiversity and representing living documents of land-use and cultural history (Rotherham, 2013). These semi-natural habitats require specific and active management, the seizure or modification of the maintaining practices leading to major changes in their character (Bugalho et al., 2011; Rotherham, 2013).

Wood-pasturing was widespread also in Central-East Europe until few decades ago, when it was gradually abandoned following changes in agricultural and forestry regulations, as a consequence of increasing demand for crop and timber production (Saláta et al., 2009). National inventories are scarce, and those that exist (ex. Haraszthy et al., 1997 for Hungary) have confirmed that wood-pastures are one of the most threatened habitats in Europe, having lost their complex usage and being present nowadays only as a historical or neglected land-use (Bergmeier et al., 2010). Albeit these general trends, wood-pastures are shown to be relatively common in Southern Transylvania, Romania (Hartel et al., 2013), and, contrary to the majority of similar habitats from Europe, are not threatened by abandonment and subsequent secondary succession or intensification (Bergmeier et al., 2010), but by modifications in the traditional management regime (Hartel et al, 2013; Öllerer, 2013).

In a time when wood-pastures are of increasing relevance due to their integration of ecological, economical (mainly agricultural) and social interests, the management methods and experiences shared by the contemporary practitioners, or by those from older times, represent an invaluable source of information. A great amount of information regarding the creation and use of wood-pastures lies in old documents and publications dating from the period when this land-use was still valued and widely practiced. This study relies on field observations and on such old publications.

The aim of this paper is twofold. First, it intends to contribute to the general knowledge regarding wood-pastures by discussing the social-historical, economical and ecological aspects of the management of this habitat type, through the case study of Southern Transylvania. Second, it brings in attention the scientific and conservation importance of traditional management practices that are relevant for the management of this habitat type. The paper concludes with implications for conservation management by stressing out the importance of creating the necessary conditions (e.g. policies, economical regulations, transfer of knowledge underlying traditional land-use) that promote the maintenance of traditional practices on which relies the future of these unique and highly biodiverse habitats.

Material and methods

Study area

General description of the study area

The study was conducted in the southern part of the Transylvanian Plateau, Romania. The region is ethnographically distinct, being inhabited from the 12th century onwards by the Transylvanian Saxons. They were granted administrative and religious autonomy upon their arrival, which was mostly maintained up to the 18th century, however they continued to be a rich and influential population segment up to the second decade of the 20th century (Gündisch, 1998). The landscape management practices applied by the colonists were those brought from the present-day Germany and Luxembourg and were based on strict rules (Nägler et al., 1994; Schuller, 1895), a result of which Saxon farming and forestry was seen as exemplary and sustainable as soon as the accelerated pace of land-use change reached Transylvania in the 19th century (Dorner, 1910).

The study area is partially overlapping with the Natura 2000 Sighişoara-Târnava Mare Site of Community Importance (SCI), the largest representative of the continental biogeographical region in Romania (EEA, 2008; *Fig. 1*). The region is predominantly rural, settlements being scarce and mostly villages. Habitats are generally well-maintained but locally threatened by abandonment, over-grazing, illegal loggings and spring pasture burnings etc. (Akeroyd and Page, 2006; Fischer et al., 2012).

The predominant geomorphological units are the gently rolling, mainly forested hills of about 550 m a.s.l. mean altitude. The climate is continental, with a mean annual temperature of 8.8 °C, indicating a relatively low temperature potential. Annual rainfall is about 650–700 mm/sqm, with peaks in the May–June period (Oroian, 2009).

The characteristic primary vegetation is represented by mixed Oak (*Quercus petraea*) and Hornbeam (*Carpinus betulus*) and mixed Beech (*Fagus sylvatica*) and Hornbeam forests. The former can be found mainly on flat areas (hilltops, plateaus) and on slopes with southern exposition, while the latter are predominant on slopes with northern exposition (Coldea, 1992). The secondary vegetation installed after the removal of these forests, therefore the potential vegetation of wood-pastures is characteristically *Festuco rubrae-Agrostetum capillaris* Horvat (1951) 1952 and *Anthoxantho-Agrostietum capillaris* Sillinger 1933 on hilltops, respectively *Agrostio-Festucetum valesiacae* Ardelean on the more sunny slopes 1983 (Coldea, 1992).

Wood-pastures

Recent studies have shown that wood-pastures are common in this region (Hartel and Moga, 2010 reported 37; Hartel et al., 2013 reported 42; while the latest list comprises 55 wood-pastures: Roellig et al., 2013; *Fig. 1*). 31 out of the 42 wood-pastures surveyed by Hartel et al. (2013) were classified as ancient (contained veteran trees), showing the historical character of these sites. 31 out of the 55 wood-pastures are covered by Natura 2000 regulations and the entire study area is included in the High Nature Value (HNV) farming systems category. Wood-pastures have an average area of 100 ha (Hartel et al., 2013), are characteristically situated on slopes with low inclination (2-15 %) and mainly northern exposition (NE, E, NV, V, N), and sometimes on plateaus (Holban, 2011). From a land-use and legal perspective, most wood-pastures are included in the pastures and meadows category as “pastures with trees” and “wooded pastures” (Law 46/2008,

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Law 2014/2011), but without any recognition of the keystone role of the scattered trees (Manning et al., 2006), or recommendations for their maintenance and recruitment.

The best known and most studied wood-pasture is the Breite, located approximately at the centre of the overall study area (*Fig. 1*). Tree cover is characteristic for open wood-pastures, accounting for less than 7 % of the 133 ha area (Moga et al., 2009). The reasons for addressing the Breite more in detail were the existing detailed knowledge regarding ground vegetation and management history (Öllerer, 2012; 2013), and availability of data on its biodiversity (see Hartel et al., 2013 for a synthesis of studies and species numbers). The number of species identified up to date considered threatened, rare or protected at national (Red Lists) and international level (IUCN, EU Birds and Habitats Directives) is about 140.

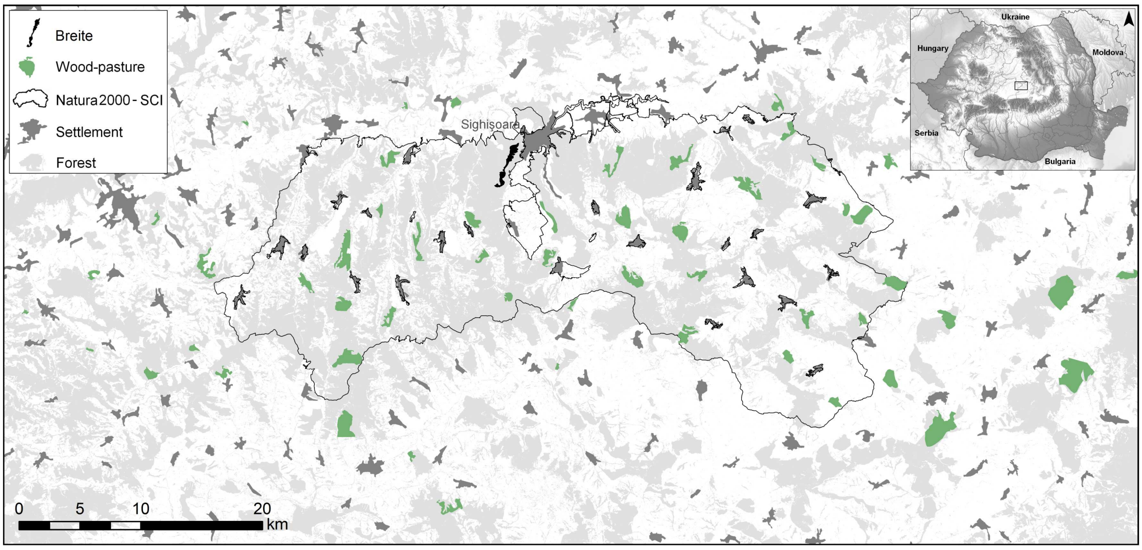

Figure 1. *The distribution of wood-pastures in Southern Transylvania, central Romania based on Hartel et al. 2013 and Roellig et al. 2013. The location of the Breite is highlighted.*

Documenting land-use history and traditional management practices

Several sources were used to reconstruct the management history and to obtain a clear picture regarding the former management practices applied in wood-pastures, and the Breite wood-pasture in particular. (i): Land registers, namely the 1st Ordnance Survey (OS) of the Habsburg Empire, also known as the Josephinian land register (1769–1773, scale 1: 28 800) and the 3rd OS of the Habsburg Empire (1869–1873, scale 1: 25 000), in order to determine the approximate period of appearance of present-day wood-pastures. (ii) Publications based on the analysis of a relatively large number of historical (16-19th c.) common land management rules and regulations applied by the Transylvanian Saxons and kept in archives (Dorner 1910; Nägler et al., 1984; Oroszi, 2004; Schuller, 1895; Siegmund, 1948). (iii) Papers from the period when wood-pasturing was still widespread in the region (Belházy, 1888; Bíró, 1910; Földes, 1895; Zsarolyáni, 1897). (iv) Books, papers and reports discussing the management practices applied in European wood-pastures in general (Bergmeier et al., 2010; Crofts and Jefferson, 1999; Haraszthy et al., 1997; Rackham, 1980; Rich et al., 2005; Rotherham, 2013; Stiven, 2009; Vera, 2000). (v) Oral evidence – personal communication of locals.

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Results and discussion

History and development of wood-pastures

Although wood-pasturing was probably applied by Saxons already upon their arrival in the 12th-13th c., as it was a widespread practice in Europe in those times (Rotherham, 2013; Vera, 2000), the first regulations regarding grazing in woodlands in this region are from the 16th c. (Oroszi, 2004). For example, the Breite was already an established common grazing area in the early-18th c. (the first written record dates from 1721 – Siegmund, 1948), but is shown on the 1st OS (18th c.) still as closed canopy woodland. However, on the 3rd OS (19th c.) it is depicted as an open grazing area with scattered trees (Öllerer, 2013), meaning that it gained its present open wood-pasture character by the second half of the 19th century. The comparison of the two land cover maps shows that the history of many wood-pastures from the study area is similar, their present open character being relatively recent, dating most probably from the second half of the 19th c. However, it is plausible to assume, based on the study of the Saxon land-use regulations (Dorner 1910; Nägler, 1984; Schuller, 1895), and of the management history of the Breite (Öllerer, 2013) that the majority of these sites were developed following the opening up of previously grazed woodlands, which shows the continuity of this practice in Southern Transylvania.

Importance for the local community

Most wood-pastures are located in close distance to villages (around 1.2 km, Hartel et al., 2013) and the majority of villages in the area have at least one wood-pasture, showing the importance of this land-use for the traditional Saxon communities.

As pasturing and certain types of forest uses, wood-pasturing was also done together by the inhabitants of individual communities, being part of the *allmende* (the common land) and their use was governed by the communal authorities (Dorner, 1910). Adherence to the rules was given much importance, providing a strict frame for everyday life (Dorner, 1910; Nägler, 1984; Schuller, 1895); no one could use the land against community interest, ensuring what we call nowadays “sustainable use” of land.

Trees from wood-pastures were grown not for their timber, but for their fruits (mainly acorns, but wild fruit trees were also widespread) (Dorner, 1910) and for maintaining the soil quality of pastures (nutrients and moisture) in order to provide sufficient fodder for livestock (Belházy, 1888). This explains why trees were left to grow old and that nowadays the majority of veteran trees in Southern Transylvania can be found in wood-pastures (Hartel et al., 2013). Such old trees were named “mother-tree”, “seed-tree”, while stand continuity was ensured by sapling protection through temporary prohibition of grazing, fencing, scrub management and by plantings (Belházy, 1888; Dorner, 1910). A part of the acorns were collected in October, just before the pannaging season (October–December, around St. Nicholas’s Day) and transported to manor game parks and nursery gardens, seedlings being planted in order to secure stand regeneration of these forests (Földes, 1895).

Different management practices were finely tuned in order to allow the regeneration of pasture plants, and were therefore applied only in certain periods, in close connection with several feast-days, adapted yearly to the particular weather conditions (*Fig. 2*), showing how land management was an integral part of the spiritual and cultural aspects of life in Saxon communities (Dorner, 1910; Nägler, 1984; Schuller, 1895;).

Nowadays the management system is much simplified (*Fig. 2*), and wood-pastures are often maintained by individuals who rent the land, raising several socio-economical questions regarding their sustainable use in the future (Sutcliffe et al., 2014).

The practice of ground vegetation management in the past and the present

Grazing

In the times when present-day wood-pastures were still closed canopy grazed forests, pigs were the main grazers, followed by cattle and horses (Dorner, 1910; Oroszi, 2004). When acorn production was seen as insufficient for renewal, pigs were not allowed to graze in the forest (Oroszi, 2004). Contrary to the traditional practice when common grazing was usually restricted to the period between the feast of St. George - 24th April and St. Martin - 11th November nowadays the grazing period is longer (*Fig. 2*).

Stocking rates (numbers and proportions) also went through major changes. Unfortunately we have no clear data regarding previous stocking rates in any of the wood-pastures in particular, however, there are several sources listing the overall number of grazing animals that were allowed out in pastures, including wood-pastures. For example, these were the following in Feldioara in 1887: buffalos and cattle – 1600, pigs – 700, horses and foals – 560, sheep – 400 (Oroszi, 2004). Therefore Saxons preferred traditionally cattle, buffalo, horses and pigs, while sheep were also present, but in a considerably smaller amount (Dorner, 1910). Even at the beginning of the 20th century, large scale grazing with sheep was present only in marginal areas in Southern Transylvania (Dorner, 1910). On several occasions, grazing with sheep was allowed only before St. George's Day (24th April) and from the end of August, but often only after St. Michael's Day (29th September), the period in between the areas were mowed or grazed with cattle and horses (Dorner 1910; Schuller, 1895; Siegmund, 1948, *Fig. 2*). The number of goats increased significantly for the first time at the turn of the 18-19th century, henceforward this species became subject to several restrictions, being even banned from several localities (Oroszi, 2004).

Wood-pastures were therefore grazed by mixed livestock, mainly cattle and pigs, while sheep and goats were often subject to regulations. However, stocking rates recorded in the study region show that sheep became the main grazers. The recent survey showed that nowadays 60 % of wood-pastures are grazed only by sheep, 21 % only by cattle and only 14 % by mixed (cattle, sheep, buffalo) livestock (Hartel et al., 2013, *Fig. 2*). In the 2008–2010 period, the following stocking rates of grazers (average numbers) have been recorded in the Breite wood-pasture during the vegetation season: sheep – 150, goats – 30 (up to 120 according to personal communication of the local ranger); cattle – 10; horses – 3.

Between 1995 and 2010 the number of cattle dropped by about 38 % whereas the number of sheep increased approximately by 25 % in the region, and sheep outnumber cattle by 9.62 times (Romanian National Institute of Statistics, reports for the 1995-2009 period). Farmers in Romania have the opportunity to receive agri-environment payments, which favor the increase in the number of sheep. On the other hand, the modifications of regulations regarding dairy-products made cattle husbandry unprofitable for local farmers, resulting in the decrease of cattle stocking rates. This situation is in accordance with the general trend reported for wood-pastures (Rotherham, 2013) and pastures in general across Europe (Isselstein et al., 2005) and started more than a century ago (Földes, 1895).

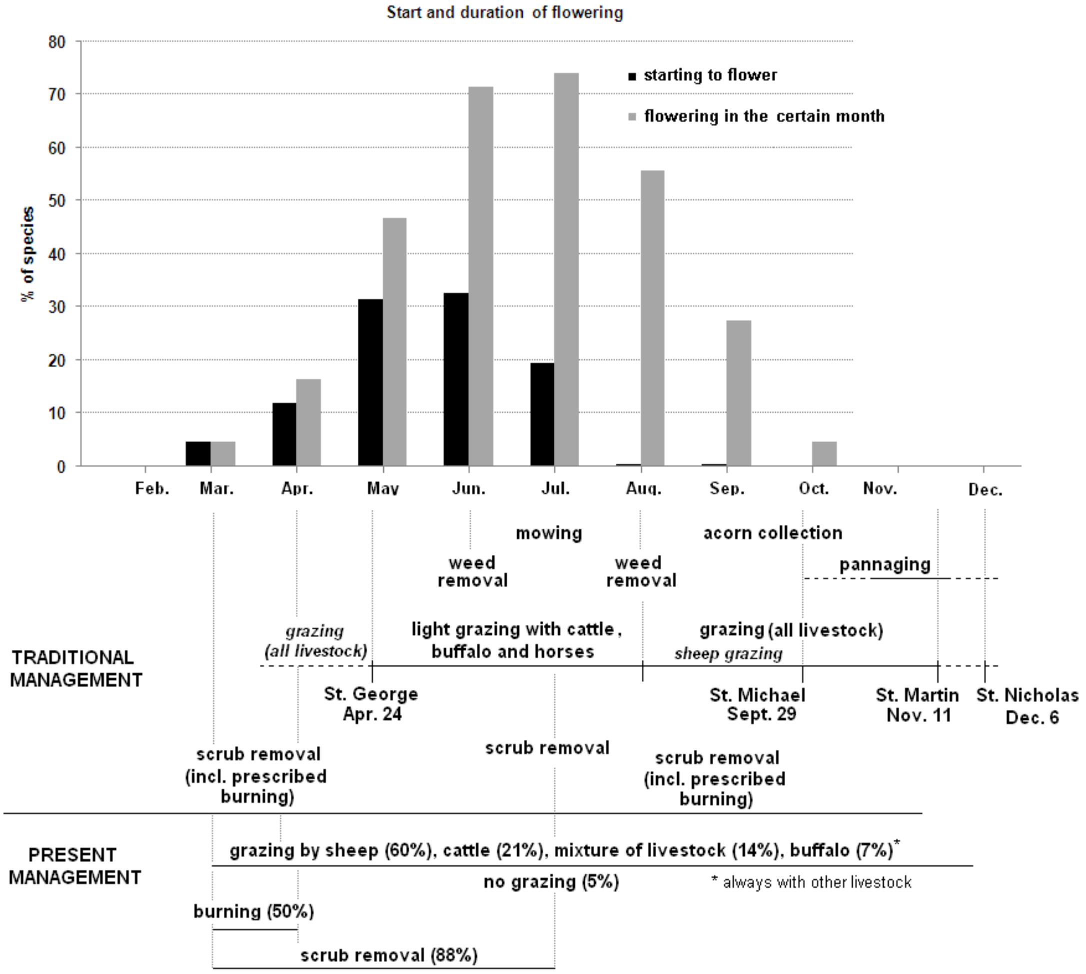

Figure 2. *The percent of vascular plant species identified in the Breite wood-pasture flowering in different months and the traditional and present management regimes applied in the wood-pastures from Southern Transylvania. Complete species list is available in Öllerer (2012). Data on flowering periods were obtained from Ciocârlan (2009). Numerical data on present management were obtained from Hartel et al. (2013).*

Saxons had strict rules also regarding the order in which animals were allowed to graze, determined by the economic importance of the different herds and their feeding habits. Cattle and horses, selective grazers, were left to graze first, followed by buffalos (upon their introduction in the 18th c.) and pigs. Sheep and goats were considered livestock of secondary importance in the Saxon society (Dorner, 1910). Besides, both are less selective grazers, causing large damage to the herbaceous vegetation and tree saplings, therefore they were the last allowed to graze, and only in certain periods, but often were completely banned out from wood-pastures (Dorner, 1910, *Fig. 2*).

Mowing and scrub removal

Although the characteristic management practice of the ground vegetation in wood-pastures is grazing, it was regularly completed by mowing (Siegmund, 1948). This practice is nowadays practically abandoned; the occasional events do not have an accountable influence on the ground vegetation. However, there are certain factors that seem to favor the reintroduction of mowing. Traditional mowing was done relatively late in the year (end of June–July, the latter being known as the *Heumonat*, meaning "hay month", *Fig. 2*), which corresponds with the recent regulations prescribed for HNV farming systems, that allow mowing only after the 1st of July (Agency for Payments and Intervention in Agriculture, Romania). Discussions with local farmers showed that they believe that the species potential of the ground vegetation of wood-pastures could be brought out only by combining grazing and mowing. They also noted that mowing and hay gathering for fodder would allow maintaining the animals in stables for longer periods, therefore decreasing the number of situations when animals have to be taken out to graze before the traditional start of the grazing season (Holban, 2011), situations which often damage the sprouting plants.

Several species with relatively low palatability (ex. *Cirsium arvense*, *C. vulgare*, *D. caespitosa* and *Juncus effusus*) showed major expansion in the last years in the Breite wood-pasture, following the abandonment of regular mowing and shift of grazing regime from the traditional system (Öllerer, 2012, pers. comm. of locals), a trend observed also in other sites (Öllerer, unpublished). This brings into attention the importance of combining grazing with mowing (Matejkova et al., 2003), which is in accordance with the traditional practices applied in wood-pastures in general (Crofts and Jefferson, 1999) and also in the study area (Siegmund, 1948).

Ground vegetation was regularly cleared of shrubs in order to allow free movement for animals (Belházy, 1888). In order to avoid encroachment due to secondary succession, saplings were cut off periodically in the middle of the summer, when the regeneration capacity is decreased due to the torrid weather. In this situation new shoots were too weak at the beginning of the cold season and would freeze; besides, young shoots are more easily consumed by grazing animals (Bíró, 1910). Removed shoots and branches were gathered and laid over the shrubs, this cover hampering the development of new shoots. Weeds grown in more intensely grazed areas were cut with a spade or hoe twice a year (in June and August) before flowering. Cattle droppings were left to dry out and later spread across the area in order to avoid the concentration of nutrients (Bíró, 1910). Well-rotted farmyard manure was periodically applied in spring and autumn for pasture improvement (Dorner, 1910; Nägler, 1984). Because fallen leaves have a high mineral content that is essential for herbaceous plants, cattle were left to walk across the area during humid days in late autumn in order to trample the leaves, helping in this way the formation of a thick humus layer (Zsarolyáni, 1897).

The practice of scrub removal is nowadays reactivated due to the agri-environment financial incentives for cleaning pastures, evidence of which were noticed in 88 % of the inventoried wood-pastures (Hartel et al., 2013; *Fig 2*).

Pasture burning

The results presented above show that in the traditional management system the ground vegetation of wood-pastures was subject to various disturbances. This extensive and complex management lead to the biodiversity that is aimed to be conserved nowadays by including the area under Natura 2000 regulations and considering it as of high nature value, biodiversity which is potentially threatened by the ongoing changes in stocking rates, extended grazing period and abandonment of certain practices.

One of the main changes in the management regime is represented by the increasing incidence of spring pasture burnings. Although pasture burning was traditionally applied for the removal of unwanted vegetation (Dorner, 1910), it was done in closely controlled conditions, whereas spring pasture burnings encountered in 50 % of the wood-pastures from the study region were uncontrolled fire events (Hartel et al., 2013). A recent study on the effects of spring pasture burnings showed that the negative effects prevailed among species belonging to *Asteraceae* and *Poaceae* (Ruprecht et al., 2013), two of the most common plant families of Transylvanian open habitats, including the study region (Öllerer 2012; Oroian, 2009) and called for caution in the use of fire as a management tool.

Pasture burnings are seen as a cost-effective and potential alternative management method to the traditional labor-intensive grazing and mowing (Valkó et al, 2014). Although burnings can contribute to the maintenance of the open character of grasslands by preventing shrub encroachment and accumulation of dry biomass, they often cause undesired changes in species abundance and composition, including the favoring of weeds and invasive species (Ruprecht et al., 2013; Deák et al, 2014; Valkó et al, 2014 and references therein). Albeit being often applied for shrub control, burning can still have a positive feed-back also on woody species (Deák et al, 2014), favoring the development of new shoots (e.g. on hornbeam – Öllerer, pers. obs, one of the main species encroaching wood-pastures in the study region – Öllerer, 2013). Besides, burning only removes biomass, whereas grazing and mowing have more complex effects on the ground vegetation due to the various associated disturbances (*Table 1*).

Table 1. *Summary of characteristic effects of different management practices on factors influencing grassland and habitat diversity of wood-pastures in Southern Transylvania based on field observations. The situations when fire can cause undesired changes from a conservation management perspective are marked with *.*

Factors influencing grassland and habitat diversity in wood-pastures	**Management practice**			
	extensive cattle grazing	extensive sheep grazing	mowing	burning
phytomass removal	selective	less selective	unselective	less selective
litter accumulation	negative	negative	negative	negative
creation of vegetation gaps / mosaics	positive	positive	no / positive	no / positive
spatial and temporal heterogeneity	positive	positive	positive	positive
shrub encroachment *	negative	negative	negative	negative / positive
spread of weed and invasive species *	negative	negative	negative	negative / positive
seed dispersal *	positive	positive	no / positive	positive/ negative
available nutrients	positive	positive	no / negative	positive
soil disturbance (trampling, hollows, temporary water bodies)	positive	positive, less considerable	no / positive	no
survival of veteran oaks *	positive	positive	positive	negative
oak regeneration *	positive	negative in the lack of fencing	positive	negative

Mowing results in a relatively uniform foliage removal (plants that exceed certain height are cut at the same level) and favours the development of a more or less stable species pool while selective removal through grazing implies also other disturbances (trampling, soil compaction, urine and dung deposition etc.), which results in a greater species dynamics (Herben and Huber-Sannwald, 2002).

Cattle movement and grazing favor the appearance and maintenance of ephemeral wetlands. Vegetation removal through grazing or mowing increases the hydroperiod (length of inundation), while exclusion of grazers leads to the decline of plant species diversity and increasing abundance of non-native species (Marty, 2005). In the lack of a permanent water source excepting rainfall, such ephemeral wetlands are essential for the maintenance of mesophile meadows, which are characteristic for the wood-pastures from the study region (Hartel et Moga, 2010), and have been shown to support vascular plant species and communities of conservation interest (Öllerer, 2012; 2013). Temporary water bodies contribute substantially to the overall biodiversity (Boix et al., 2012) of wood-pastures and of the wider region, several species and communities being limited to these habitats (Hartel et Moga, 2010; Öllerer, 2013).

Besides, uncontrolled pasture burnings have a strong negative impact on the keystone (Manning et al, 2006) veteran trees, which usually die after such events. Therefore, albeit it has a good potential in controlling undesired vegetation, pasture burning in its present form is not a viable substitute for grazing and mowing in wood-pastures.

Conclusions and implications for biodiversity conservation

This study showed that traditional uses of wood-pasture in Southern Transylvania correspond to the general practice applied in other regions (Bergmeier, 2010; Rotherham, 2013; Vera, 2000), and main uses included cattle and pig grazing, mowing, while sheep were subject to strict regulations (Dorner, 1910; Oroszi, 2004).

Field experience and discussions with local herders showed that traditional practices are gradually disappearing. However, only 5 % of the surveyed wood-pastures lacked grazing (Hartel et al., 2013), which can be seen as a sign of ongoing interest for this habitat type, albeit present management lacks much of the complexity of previous uses.

Although wood-pastures per se are not legally recognized for their key ecological role, more than half of those from the study region are covered by Natura 2000 regulations regarding management and maintenance of biodiversity, therefore it is important to stress out that it is less economically demanding to continue the practices that maintain high species richness than to apply costly conservation measures, since farmers with high traditional practices and underlying knowledge have positive attitudes towards conservation (Shen et al., 2012). Similarly to other traditionally managed regions (Babai et Molnár, 2014), local farmers have the willingness to continue traditional management, unless if it is economically disadvantageous (Holban, 2011).

Besides the economical reasons, the gradual disappearance of the traditional management regime applied in wood-pastures from Southern Transylvania is also the result of the loss of knowledge rooted in the understanding of site history, due to the disrupted social structure following the mass emigration of Saxons in the 20th century (Gündisch, 1998). This situation creates an identity-gap between land(scape), its history and the new owners, changes in the structure of the local populations leading to transmission failures (Ostrom, 1994). The general European trend towards individual management of the commons represents nowadays a social and economical challenge for the future development of this region, including the biodiversity conservation issues (Sutcliffe et al, 2014). Therefore, mediated transfer of knowledge underlying traditional land-use practices is essential.

A proactive management approach is needed that supports learning initiatives for farmers and shapes and promotes their attitude towards valuing and maintaining traditional ecological knowledge and the ecosystem services provided by traditional landscapes. Therefore, the integration of biodiversity conservation, rural development and agricultural policy is seen as the way forward in the attempt of maintaining the social, cultural and biodiversity values of such landscapes (Fischer et al., 2012; Babai and Molnár, 2014; Schmitt and Rákosy, 2007; Mikulcak et al., 2013).

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EFFECT OF GRAZING AND MOWING ON THE MICROCOENOLOGICAL COMPOSITION OF A SEMI-ARID GRASSLAND IN HUNGARY

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Abstract. Grasslands play an important role in carbon sequestration. Different management regimes may change the species composition of plants in grasslands, thus may affect the carbon sequestration potential. Therefore, we investigated if short-term changes in species composition occurred in response to shift in grazing to mowing in a semi-arid grassland in Hungary (Bugac). Species abundances were recorded as frequencies of species in contiguous 5 cm × 5 cm quadrates along six (5 meters long) permanent transects at adjacent grazed and mowed sites in the spring and fall of 2012. High variation of vegetation characteristics was found within the management units at patch scale (at few m scale). The species richness, relative abundance of species, species density, Shannon diversity index, and forage quality differed among transects; however, no differences were observed between the two managements regimes at site scale (at hectar scale) (ANOVA, $p>0.05$). The average species abundance of the grazed and mowed sites were very similar (Poa spp.: 13.48±5.34%, 14.67±6,9%; Carex spp.:12.46±8.75%, 14.24±10.16%; Cynodon dactylon: 10±8.52%, 16.01±3.49%., respectively). Our results suggest that species composition differences can not be the main factors explaining short-term differences in carbon sequestration in natural semiarid grasslands.

Keywords: *diversity, management, vegetation structure, species composition changes, species abundance*

Introduction

Due to climate change the greenhouse gas (GHG) emission should be reduced in all sectors of economics including agriculture (IPCC 2007). Therefore, new adaptation and mitigation technologies are being developed in this sector to reduce GHG's emission (Smith el al., 2008). The "AnimalChange" project of the EU's 7th framework program (http://www.animalchange.eu/) is taking a major part in achieving these goals. Our research group has participated to this project, with a special focus on the effect of management (grazing vs. mowing) on the carbon dioxide balance of grasslands.

Grasslands cover approximately 11% of Hungary and are an important sink for carbon dioxide (Haszpra et al., 2011, Nagy et al., 2011). However, changes in the management usually result in changes in carbon sequestration potential (NIR, 2010) and changes in species composition of grasslands (Moog, 2002, Jantunen, 2003). For example decreasing carbon storage capacity coupled with degradation of species

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composition was reported when intensive grassland management (fertilized and irrigated) in Hungary changed to extensive management (decreased stocking rate) (NIR, 2010).

Changing management affects several structural and functional attributes in vegetation. Therefore, it is hard to separate the direct effects of species composition change from other related effects (changes of leaf area index, soil bulk density, and soil water holding capacity) on carbon sequestration (Klumpp et al., 2011). Management regime shifts from grazing to mowing could have a significant, but varying (negative vs. positive) effect on species composition (Fritch et al., 2011, Jacquemyn et al., 2011, Socher et al., 2012). In general grasslands mostly benefit from light grazing and mowing and degrade in terms of species composition from frequent mowing and intense grazing but the direction of change also depends on the initial status of the grassland (Jantunen, 2003, Socher et al., 2012). However, comparative studies on the effects of mowing and grazing in the same areas are rare (Jantunen, 2003) and studies are mostly focusing on the changes in species richness (Jantunen, 2003, Pykälä, 2005, Socher et al., 2012), rather on fine scale structural changes in the grassland, which could early indicate the direction of changes (Virágh et al., 2000, Bartha et al., 2008).

Our initial question was whether management change from grazing to mowing influences carbon sequestration potential. Our hypothesis is that management change has an effect on carbon sequestration. If the species composition of the grazed and mowed sites differs then it could be a potential driving factor for carbon sequestration differences. Therefore, to answer the initial question, first we needed to investigate the coenological composition of grazed and mowed areas. We assumed that the two sites have similar species composition, because we wanted to start the mowed and grazed experiment on the carbon balance on sites having similar species composition. We predicted that if the two sites will have similar species composition then the species richness, the abundance of species, species density, Shannon diversity index, and forage quality will be similar at the two sites. In this paper we investigated the species composition of the grazed and mowed sites, which provides a baseline to further microcoenological and eco-physiological surveys of mowed and grazed sites.

Materials and methods

Microcoenological investigation

To investigate the effect of grazing and mowing on the species composition of grassland we performed repeated microcoenological surveys in a semi-arid sandy grassland of Hungary (Bugac, N46°41'28", E19°36'42"). The grassland (500 ha) has been grazed by cattle for a minimum of 20 years (Nagy et al., 2011). The average annual precipitation at the area is 562 mm and the annual mean temperature is 10.4°C (Nagy et al., 2011). The grazing period of cattle (1.02 cattle/ha) on the grazed site in the previous year of the present survey lasted from June to July and from October to December in 2011. In 2012, the grazing period of cattle (1.87 cattle/ha) lasted from the middle of June to August and from September to November. The mowed area (1 ha) was fenced from the grazed area in March 2011 (Figure 1). The first mowing occurred on August 10th, 2011. The second mowing was on June 22th, 2012 (for both years with a mowing height of 6 centimeters above ground). After drying for a few days the hay was removed from the site. No other treatments were applied on the sites (e.g. watering or fertilization).

The microcoenological surveys occurred on June 13-14th and October 11-13th, 2012. The microcoenological surveys consisted of 6 permanent transects of 5 meters starting at 40 meters from a climate station and where separated by 60 degrees (*Figure 1*). 5 × 5 centimeter contiguous quadrates were spaced by 5 cm distance along each transects. Within each transect the presence of all rooting plant species was recorded in the 100 contiguous microquadrats to determine species abundances and composition. Species nomenclature followed Király (2009).

The experiment was designed for the carbon sequestration survey. Carbon sequestration is studied through biomass sampling at the vicinity of the climate stations and through carbon balance measurement based on eddy covariance methods at the climate stations on both sites. Therefore, we tried to match the heterogeneity of both sites surrounding the climate stations in a 1 ha area where the carbon balance and biomass data are originating.

We used permanent transects for microcoenological survey as it provides an objective and precise baseline record to follow fine-scale changes in species abundances and composition (Bartha, 2008). Microquadrates were used to avoid subjective bias from cover estimate and also because vegetation appeared to be very compact and dense though line-intercept method could not have been used.

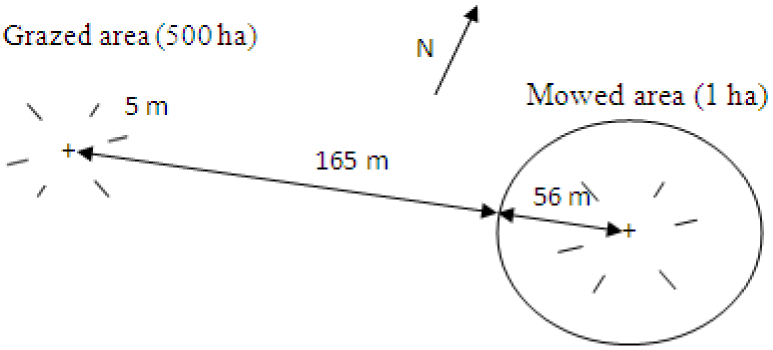

Figure 1. *The experimental design of the microcoenological survey conducted at the grassland of Bugac, Hungary (climate station: +; microcoenological transects: –) (N46°41', E19°36')*

Statistical analysis of microcoenological indicators

Grasslands were characterized by species richness, relative species abundance, species density, Shannon diversity index, and by forage quality. Identification to species level was not always possible due to the lack of flowers, seeds or to the lack of the main part of stem; therefore for the analysis we combined certain species at genus level (e.g. *Achillea* spp., *Carex* spp., *Poa* spp. see in Appendix 1.). Relative abundance of species was calculated by equitation (1):

$$A_i = \frac{a_i}{T} * 100 \qquad \text{(Eq. 1)}$$

A_i is the relative abundance of species i (%) where a_i is the number of presences of species i along the transects, T is the total number of presences of all species along the

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transect. To calculate the average species abundance for a given species at site level the average of the six transects were calculated. Coefficient of variation (CV) was calculated for all species based on the six transects, and the average of all species level coefficients was compared between sites and seasons (Equation 2). The coefficient of variation of species abundance at site level shows the relation of the standard deviation of species abundance to the mean. If it is higher than one than the standard deviation is higher than the mean.

$$CV_a = \sum_{i=n}^{n} CV_i/n \qquad \text{(Eq. 2)}$$

Where CV_a is the average coefficient of variation of species abundance for species i at site level, CV_i is the coefficient variation of species i, and n is the total species number encountered at the site.

Species density was calculated as the average number of species found within a microquadrate per transect (Equitation 3). To calculate the average species density at site level the average of the six transects were calculated.

$$SD = \sum_{i=n}^{n=100} s_i/100 \qquad \text{(Eq. 3)}$$

Where SD is the average species density (species per microquadrate), s_i is the species number within one quadrate.

To estimate the quality of forage at site level the average of transect's forage quality was calculated. Even if the two sites has similar species abundance, still the forage quality could differ as species with high forage quality values weight more in calculating the total quality of forage. Thus, little differences in the abundance of valuable forage species could lead to larger differences in total forage quality between sites. The average quality of forage was estimated at site level by a modified equitation of Klapp (1953) (Equitation 4). The quality values for species were from Balázs (1960). Equitation 4 (modified from Klapp et al., 1953):

$$Q = \sum_{i=1}^{n} \frac{f * A}{100} * \bar{A} \qquad \text{(Eq. 4)}$$

Where Q is the quality value of the forage (dimensionless index) at site level, f is the forage quality of species i, A is the abundance of the species i, and $\bar{A}$ is the average abundance of all species, instead of the total cover of plants (%) as by Klapp et al. (1953), because the total abundance here would be always 100%.

Differences in species richness, relative species abundance, species density, Shannon diversity index, and forage quality between grazed and mowed sites and between spring and fall were compared by the average values of the six transect's with ANOVA (post hoc analysis with Tukey test, where random effects were the managements regimes and seasons), and also with paired t-test between spring to fall for the same managements.

To demonstrate the overall level of similarity between mowed and grazed sites and to show the dissimilarity of individual transects cluster analysis was used (single linkage, Euclidean distance). All statistics were performed with Minitab Inc (2006).

Results

Species richness, relative abundance of species

We found 67 species on the grazed site, while 62 species on the mowed site (for a total of 83 different species) (Appendix 1). Out of these 21 species were found only on the grazed site with a very low average abundance (0.15±0.43%). The total abundance of these 21 rare species on the grazed site was 3.34%. The most abundant among these rare species on the grazed site were *Inula britannica* (0.64±1.51%, found at the same spot during spring and fall), *Cerastium* spp. (0.62±1.57%, found only during fall), and *Trifolium repens* (0.40±0.99%, found at the same spots during spring and fall) (Appendix 1). Conversely, 16 species were not found on the grazed site, but rather on the mowed site with an average abundance of 0.08±0.23%. The total abundance of these 16 rare species on the mowed site was 1.36%. The most abundant among these rare species on the mowed site were *Veronica* seedlings (0.5±1.37%, found both during spring and fall), *Verbascum phoeniceum* (0.15±0.37%, found both during spring and fall), and *Buglossoides arvensis* (0.14±0.26%, found only during spring) (Appendix 1).

The most abundant species found at the grazed site during spring and fall were *Poa* spp. (13.45±5.28%, 13.45±4.94), *Festuca pseudovina* (12.44±7.14%, 9.14±4.32%), Carex spp. (12.38±8.64%, 12.54±7.79%) and *Cynodon dactylon* (11.38±9.94%, 8.64±5.55%) (Appendix 1). At the mowed site the average species abundance for spring and fall was very similar; *Cynodon dactylon* (17.51±4.45%, 14.5±2.52), *Poa* spp. (15.56±7.77%, 13.69±5.02), *Carex* spp. (15.35±11.35%, 13.14±7.69%), and *Festuca pseudovina* (9.43±9.36%, 8.85±6.6%) (Appendix 1). The species abundance was highly variable among the six transects within the grazed and mowed sites as shown by the large standard deviations (Appendix 1) and by the large coefficients of variation for species abundance (*Table 1*). Coefficients of variation for species abundance showed that the ratio of the standard deviation to the mean is higher than one, which indicated a high variability of species abundance between transects. Differences among transects resulted from the mosaics' of different vegetation patches. Transects crossed patches where the species richness was low and a few frequent species dominated the patch (*Festuca pseudovina* and *Cynodon dactylon*), whereas other transects crossed patches having high species richness with more variable dominant species (*Poa* spp., *Carex* spp., *Elymus* spp., *Medicago falcata*). The two sites appeared to be equally patchy as coefficient of variation in species abundance was not significantly different between sites (*Table 1*). Also, relative species abundance differed only in a few instances between the grazed and mowed sites. Strong significant differences observed in species abundance only in case of *Arenaria serpyllifolia* in spring ($p<0.05$, where species abundance was higher at grazed site), and a weak difference in case of *Cynodon dactylon* in fall ($p<0.1$, where species abundance was higher at the mowed site) (*Figure 3*). For all of the rest of the species the abundance did not differ significantly between the grazed and mowed sites (for the ten most abundant species see *Figure 2* and for all species see Appendix 1). The total abundance of ten most abundant species at the

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grazed and mowed site at spring (84.01±30.36%, 82.74±28.44%) and at fall (73.30±27.49, 81.31±30.89%, respectively) was similar.

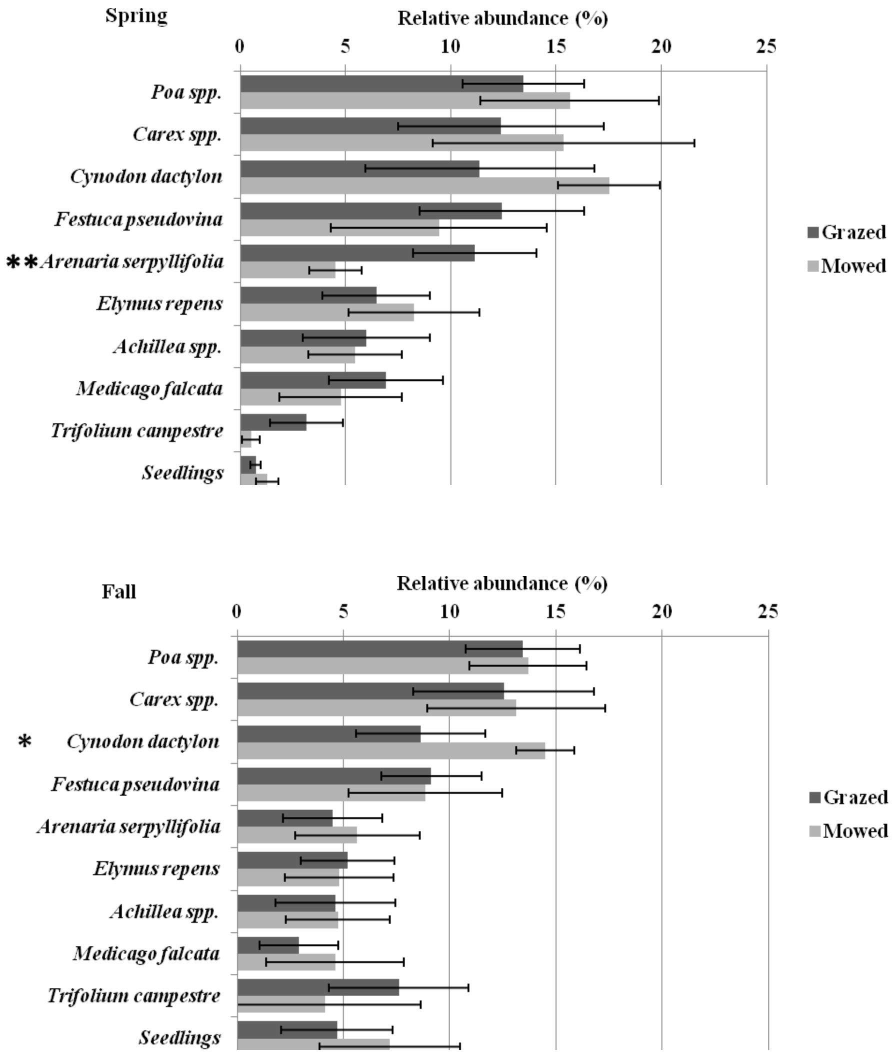

***Figure 2**. Relative species abundance (%) of grazed and mowed sites at the grassland of Bugac at spring and fall (**indicates significant differences between grazed and mowed site at p<0.05 and *at p<0.1 level, t-test)*

Between spring and fall we found significant differences (p<0.05) only at two cases. At the grazed site the abundance of *Medicago minima* and the *Geranium pusillum* was higher during fall compared to spring (Appendix 1). The abundance of *Medicago minima* was also higher on the mowed site at fall compared to spring, but the difference was weak (p<0.1). The abundance of seedlings was also higher during fall for both sites compared to spring at low significance (p<0.1).

Species density, Shannon diversity index and forage quality

The average species density found within one microquadrate (5 cm × 5 cm) did not differ between grazed and mowed site and between spring and fall (ANOVA, post hoc

Tukey test). Between season difference was also tested by paired t-test, which did not reveal differences as well in species density. The Shannon diversity index and forage quality did not differ as well between grazed and mowed sites and between seasons (*Table 1*). Since very little differences observed between the abundance of species between the grazed and mowed sites, therefore it had no effect on differentiating the average values of forage quality between the two sites and seasons (*Table 1*).

Table 1. *Mean and standard deviation (std in parenthesis) of species richness, species density, Shannon diversity and average forage quality of grazed and mowed sites at the grassland of Bugac (no significant differences observed among groups, ANOVA, Tukey test, p>0.05)*

	Spring		**Fall**		**p value**
Management	**Grazed**	**Mowed**	**Grazed**	**Mowed**	
Species number	21.17	22.17	23.83	18.33	0.46
	(6.49)	(8.21)	(4.49)	(3.61)	
Species density	3.85	3.46	3.84	3.74	0.69
	(0.78	(0.52)	(0.50)	(0.72)	
CV for species abundance (Eq. 2)	1.78	1.83	1.80	1.87	0.48
	(0.69)	(0.68)	(0.67)	(0.67)	
Shannon diversity index	2.31	2.14	2.43	2.23	0.73
	(0.50)	(0.56	(0.31)	(0.44)	
Forage quality (Eq. 4)	15.71	17.31	13.93	16.87	0.87
	(5.60)	(12.12)	(6.43)	(4.13)	
n (transects)	6	6	6	6	

Overall similarity between management regimes

The average relative species abundance was very similar for the grazed and mowed sites at spring and at fall for all species (ANOVA, Tukey, p>0.05) (Table 2).

Table 2. *Species abundance differences between the grazed and mowed sites (p values for ANOVA)*

	Spring		**Fall**	
	Grazed	**Mowed**	**Grazed**	**Mowed**
Grazed vs. mowed	0.75		0.44	
Among all groups	0.88			

Overall similarity between the grazed and mowed sites was proved by cluster analysis, as treatments did not separate into groups of grazed and mowed sites (*Figure 3*). The main dissimilarity was due to the variability between transects (*Figure 3*). A few transects differentiated from the rest of the transects e.g. transect number 1 and 5 at the grazed site was distinct from other transects during spring and fall. These transects were characterized with high species richness.

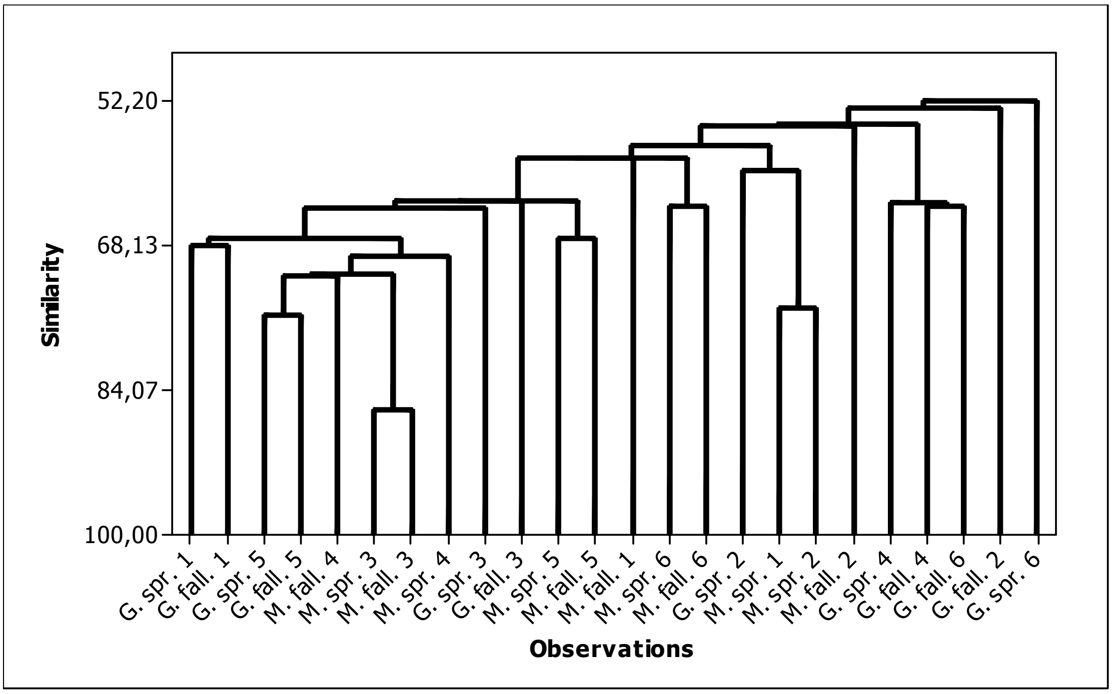

Figure 3*.Classification of transects (1-6) on grazed (G.) and mowed (M.) sites during fall and spring (spr.), 2012 at the grassland of Bugac. (Cluster analysis, single linkage, Euclidean distance) (2006 Minitab Inc.)*

Discussion

Present survey provides a baseline to follow the changes in species composition due to management change from grazing to mowing in a long-term experiment. Management change could alter the species composition and carbon sequestration potential of grasslands (Moog, 2002, NIR, 2010). Therefore, we investigated the vegetation attributes of adjacent grazed and mowed sites in semi-arid grassland of Hungary (Bugac) parallel with carbon sequestration survey (unpublished results). Species composition was investigated on both sites with microcoenological methods and described by the species richness, relative abundance of species, species density, Shannon diversity index and by the average forage quality. Within both sites the variability of these microcoenological indicators was high, which indicated the patchiness of the vegetation. Also, the grazed and mowed sites had a number of different, unique species. As these species were rare in our observations, we might have increased the abundance of these species if we had used more transects. Interestingly, the vegetation at fall was similar to spring, which was maybe due to rainy fall in 2012. Therefore, many species was germinating and growing at the both site during fall (e.g. *Geranium pusillum*, *Arenaria serpyllifolia*, *Veronica arvensis* and also seedlings), which are usually present at spring. We assumed that due to rainy fall in 2012 many species grew again (seedlings and other species usually present at spring) filling the gaps in the structure of the grassland and increased the species density to the same level as it was at spring.

In contrast to the considerable heterogeneity observed within sites, no differences were found in community level attributes when the analyses were performed at site level (comparing average attributes between sites). Species richness, relative abundance

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of species, species density, Shannon diversity index and forage quality did not differ significantly between the grazed and mowed sites. Cluster analysis also supported the similarity of the two sites.

In summary we can assume that the management change from grazing to mowing had no effect on the vegetation patterns of the mowed site, and also we can conclude that the two sites were similar in species composition. Had there been a difference in species composition between the two sites then it was assumed to be either due to the initial differences of the two sites or to the effect of management. Depending on management intensities grazing and mowing found to change the species composition in long-term studies.

Due to management change species composition could either remain unchanged or change into a negative (loss of species or increase of unfavourable species condition in terms of conservation purposes) or positive direction as found in other studies. Depending on stocking densities and grazer species, more unpalatable species might benefit from grazing while others are suppressed (Jacquemyn et al., 2011). In a study under continuous grazing no change was observed in species richness (Jacquemyn et al., 2011). In contrast, grazing was found to increase (due to light grazing of cattle, Fritch et al., 2011) or decrease (due to overgrazing by horses, Penksza, 2005) the species richness compared to the mowing treatment (Fritch et al., 2011, Penksza, 2005, respectively). Mowing found to decrease the abundance of disturbance sensitive species, while increased the disturbance-tolerant ruderal species by frequent destruction of above-ground plant organs (Socher et al., 2012). Enrichment of species or recovery after mowing might be due to enhanced seedling germination by the removal of litter and above-ground biomass, which creates gaps that act as suitable micro-sites for the establishment of small-seeded species (Socher et al., 2012). The species richness could change even during a short period of three years of mowing (once per year), however with unfavourable effects on the original dry grassland community (Jantunen, 2003). Still, grazing and mowing found to be better management regime then leaving the site abandonment as species richness was higher compared to the abandonment site (Hejcman et al., 2010). A 25 year study of light mowing and grazing from an initial homogenous state also showed that mowing and grazing were the most suitable management regimes than abandonment for conservation purposes (Moog, 2002). As species composition changes due to management change it could affect carbon sequestration potential. In a similar study contrasted management (intense vs. extensive grazing of heifers) led to distinct plant communities, which had an indirect effect on carbon fluxes as different communities respond differently to precipitation and soil drying in terms of CO_2 exchange (Klumpp et al., 2011). However, species composition change is usually a consequence of management change and it is a hard to identify the main factor responsible for changes in carbon sequestration (Klumpp et al., 2011). Besides species composition drivers could be differences in topography, phenology, direct and indirect effect of management (biomass removal, vegetation recovery, lack of fertilization on mowed sites) or even local soil properties. Our study provided evidence that if there is a difference in carbon sequestration between the grazed and mowed sites at the studied area then species composition differences can not be a leading factor for differences in carbon sequestration.

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Appendices

Appendix 1. *Mean and standard deviation (std) of relative species abundance (%) on the grazed and mowed sites during spring and fall at the grassland of Bugac*

		Spring				**Fall**			
		Grazed		**Mowed**		**Grazed**		**Mowed**	
#	**Species**	%	Std	%	Std	%	Std	%	Std
1.	*Achillea* spp.; *A. setacea*, *A. collinea*, *A. pannonica*	5.99	5.52	5.47	4.05	4.63	5.12	4.74	4.49
2.	*Alopecurus pratensis*	0	0	0	0	0.34	0.56	0	0
3.	*Alyssum alyssoides*	0.51	0.72	0	0	0	0	0	0
4.	*Anchusa officinalis*	0	0	0.04	0.09	0	0	0	0
5.	*Anthemis ruthenica*	0.07	0.15	0.11	0.24	0	0	0	0
6.	*Arenaria serpyllifolia*	11.15	5.37	4.51	2.28	4.50	4.27	5.65	5.35
7.	Asteraceae spp.	0	0	0	0	0.14	0.31	0	0
8.	*Astragalus cicer*	0.15	0.33	0	0	0	0	0	0
9.	*Astragalus onobrychis*	0	0	0.04	0.09	0	0	0	0
10.	*Berteroa incana*	0.10	0.22	0.23	0.52	0.23	0.51	0	0
11.	Brachythecium spp.	0.65	1.46	0	0	0.88	1.69	0.12	0.27
12.	*Bromus hordeaceus*	0.46	0.50	1.02	1.12	0.42	0.53	1.14	1.86
13.	*Bromus inermis*	0	0	0.11	0.24	0	0	0	0

14.	Bryophytes	0.86	1.44	1.95	3.61	0.09	0.20	0	0
15.	*Buglossoides arvensis*	0	0	0.29	0.30	0	0	0	0
16.	*Capsella bursa-pastoris*	0	0	0.10	0.23	0	0	0	0
17.	*Carduus nutans*	0	0	0.15	0.24	0	0	0	0
18.	*Carex* spp.; *Carex stenophylla*, *C. divisa*, *C. liparicarpos*, *C. Praecox*	12.38	8.94	15.35	11.35	12.54	7.79	13.14	7.63
19.	Caryophyllacea spp.	0	0	0	0	0.04	0.08	0.89	1.98
20.	*Centaurea* spp.	0	0	0	0	0.09	0.12	0	0
21.	*Cerastium* spp.; *C. pumilum, C. semidecandrum*	0	0	0	0	1.25	1.95	0	0
22.	*Chenopodium album*	0	0	0.05	0.12	0	0	0	0
23.	*Cirsium* spp. Seedling	0	0	0	0	0.11	0.25	0	0
24.	*Convolvulus arvensis*	0.84	0.87	0.76	1.00	0.39	0.31	0.20	0.46
25.	*Conyza Canadensis*	0.04	0.08	0	0	0.09	0.20	0	0
26.	*Cruciata pedemontana*	0.45	0.73	2.18	2.31	0.80	1.78	0.04	0.09
27.	*Cynodon dactylon*	11.38	9.94	17.51	4.45	8.64	5.55	14.50	2.52
28.	*Dactylis glomerata*	0.24	0.37	0.17	0.37	0.21	0.22	0.16	0.36
29.	*Descurainia sophia*	0	0	0	0	0.09	0.20	0	0
30.	*Draba nemorosa*	0.11	0.16	0	0	0	0	0	0
31.	*Elymus repens*	6.45	4.65	8.25	5.66	5.20	4.06	4.79	4.66
32.	*Erodium cicutarium*	0	0	0.37	0.72	0.85	1.91	2.32	4.72
33.	*Eryngium campestre*	0.69	0.56	1.27	2.21	0.81	1.27	1.21	1.97
34.	*Erysimum diffusum*	0.04	0.08	0.19	0.23	0	0	0	0
35.	*Euphorbia cyparissias*	0.04	0.09	0	0	0	0	0	0
36.	*Falcaria vulgaris*	0.44	0.99	0.32	0.52	0.25	0.56	0.31	0.60
37.	*Festuca pseudovina*	12.44	7.14	9.43	9.36	9.14	4.32	8.85	6.60
38.	*Galium verum*	2.56	2.95	1.43	1.71	3.34	4.02	1.75	1.95
39.	*Geranium pusillum*	0.21	0.28	0.58	1.03	1.64	1.22	1.05	1.67
40.	*Herniaria incana*	0.16	0.37	0	0	0.04	0.09	0	0
41.	*Inula Britannica*	0.63	1.40	0	0	0.67	1.50	0	0
42.	*Knauita arvensis*	0.04	0.09	0	0	0	0	0	0
43.	*Koeleria cristata*	0.16	0.37	0	0	0.14	0.20	0.17	0.37
44.	*Lamium amplexicaule*	0	0	0	0	0.13	0.28	0.09	0.20
45.	*Lamium purpureum*	0	0	0	0	0.09	0.20	0	0
46.	*Leontodon hispidus*	0	0	0.08	0.17	0	0	0	0
47.	*Marrubium peregrinum*	0.15	0.33	0	0	0.08	0.19	0	0
48.	*Medicago falcate*	6.92	4.95	4.77	5.30	2.90	3.39	4.62	5.91
49.	*Medicago lupulina*	0	0	0.17	0.37	0.39	0.77	0	0
50.	*Medicago minima*	0.31	0.44	0.17	0.37	2.72	1.64	2.10	2.29
51.	*Medicago* spp.	0	0	0	0	0.04	0.09	0.64	1.43
52.	*Medicago* spp. Seedling	0	0	0	0	1.02	2.16	0.27	0.61

53.	*Plantago lanceolata*	0.04	0.08	0.78	1.36	0.08	0.19	0.63	0.79
54.	*Poa* spp.; *P. angustifolia*, *P. bulbosa*, *P. humilis*	13.45	5.28	15.65	7.77	13.45	4.94	13.69	5.02
55.	*Podospermum canum*	0	0	0.16	0.24	0.07	0.17	0	0
56.	*Polygonum aviculare* agg.	0	0	0.20	0.35	0	0	0	0
57.	*Polygonum bellardii*	0	0	0	0	0	0	0.03	0.08
58.	*Potentilla arenaria*	0.20	0.36	0.12	0.28	0.41	0.91	0.22	0.49
59.	*Potentilla argentea* agg.	0.37	0.82	0.59	1.21	0.12	0.27	0.37	0.84
60.	*Potentilla spp.*	0.92	2.06	0	0	0.42	0.83	0.04	0.09
61.	*Scirpoides holoschoenus*	0	0	0.08	0.19	0	0	0.04	0.09
62.	*Securigera varia*	0	0	0	0	0.34	0.75	0	0
63.	Seedlings	0.73	0.46	1.28	0.96	4.69	4.78	7.18	6.04
64.	*Silene alba*	0.11	0.25	0.40	0.69	0.58	0.74	0.93	1.62
65.	*Silene otites*	0	0	0.05	0.12	0	0	0	0
66.	*Stellaria media*	0	0	0	0	0.55	1.23	0	0
67.	*Taraxacum laevigatum* agg.	0.03	0.08	0.12	0.19	0.08	0.11	0.04	0.10
68.	*Taraxacum officinale*	0.07	0.15	0	0	0	0	0.66	0.81
69.	*Teucrium chamaedrys*	0	0	0	0	0	0	0.11	0.24
70.	*Thlaspi perfoliatum*	0.04	0.09	0	0	0	0	0	0
71.	*Tortula ruralis*	1.39	2.07	0.96	1.23	3.68	6.61	0.05	0.10
72.	*Trifolium arvense*	0	0	0	0	0.14	0.31	0	0
73.	*Trifolium campestre*	3.13	3.18	0.51	0.75	7.61	5.98	4.15	8.18
74.	*Trifolium repens*	0.77	1.24	0	0	0.04	0.09	0	0
75.	*Trifolium* spp.	0.03	0.08	0.05	0.11	0	0	1.73	3.31
76.	*Verbascum phoeniceum*	0	0	0.20	0.44	0	0	0.11	0.24
77.	*Veronica arvensis*	0.46	0.68	0.79	0.83	1.31	1.58	0	0
78.	*Veronica prostrata*	0.97	0.85	0.65	0.64	0.31	0.44	0.23	0.33
79.	*Veronica* spp.	0.18	0.41	0.04	0.09	0.63	1.40	0.12	0.18
80.	*Veronica* spp. seedling	0	0	0.22	0.49	0	0	0.78	1.75
81.	*Vicia angustifolia*	0.39	0.56	0.05	0.12	0.55	0.86	0.09	0.13
82.	*Vicia* spp.	0	0	0	0	0	0	0.05	0.10
83.	*Viola arvensis*	0.11	0.18	0.04	0.09	0	0	0	0
	Total	50		51		56		44	

THE IMPACT OF THE LESSER BLIND MOLE RAT [*NANNOSPALAX* (SUPERSPECIES *LEUCODON*)] ON THE SPECIES COMPOSITION AND DIVERSITY OF A LOESS STEPPE IN HUNGARY

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Abstract. Our aim was to investigate the species richness and diversity of a loess grassland influenced by the digging of the lesser blind mole rat [*Nannospalax (*superspecies *leucodon*)] and to study the effect of this disturbance to diversity. The study was conducted in the Külső-gulya loess grassland (Körös-Maros National Park), which is unique in Hungary due to its excellent soil quality and the large spatial extent of natural loess meadow steppe.

We recorded the cover of species in 50x50 cm plots. Altogether 12 plots were sampled on mounds of mole rat and 12 plots as a control in the area with no mounds. Differences in species richness, Shannon-diversity, evenness and total cover between disturbed and control plots were tested by One-Way ANOVA. There were no significant difference neither in the number of species, nor in the Shannon-diversity and evenness. There were differences in the species composition detected by PCO ordination. We can conclude that the presence and disturbance of the mole rat influence the composition of the grassland significantly but it does not cause a difference in the species richness, diversity and total cover. Our results suggest that this grassland has adapted to these natural disturbances.

Keywords: *loess grassland, diversity, disturbance, subterranean rodents, Nannospalax (superspecies leucodon)*

Introduction

Grasslands in Europe are among the most diverse ecosystems (Habel et al., 2013). Dry grasslands can be emphasized within this group (Janišová et al., 2011) because of their high importance in biodiversity conservation in Hungary (Kun, 1998; Valkó et al., 2013a). Grasslands evolved with herbivores, burrowing animals and experienced recurrent fire and adapted to natural disturbances by various life forms and plant behavioural types (Knapp et al., 1998; Strauss and Agrawal, 1999; Gibson, 2009, Valkó et al., 2013b). Several studies concluded that high diversity of grasslands is positively related to the complexity of the disturbance regime (e.g. Collins and Barber, 1986;

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Collins, 1987; Belsky, 1992; Noy-Meir, 1995; Savadogo et al., 2008). The most diverse semi-natural grasslands have been found in Europe in traditionally landscapes with complex and patchy pattern of grazing, mowing and burning (Bartha, 2007; Wilson et al., 2012).

To maintain the high diversity of dry grasslands, in particular loess steppes, it is essential to ensure proper management mainly by grazing and mowing (Illyés and Bölöni, 2007; Kiss et al., 2011). Grazing and other natural disturbances help for sustaining high diversity (Olff and Ritchie, 1998; Hickman et al., 2004). Several studies reported degradative vegetation changes in the absence of such natural disturbances (Virágh and Bartha, 1996; Somodi et al., 2004; Enyedi et al., 2008). Recently Hungarian grasslands are strongly affected by the abandonment of traditional grazing managementdue to the decreasing number of sheep and cattle since the 1960s (KSH, 2012).

The strictly protected Külső-gulya loess grassland (also known as Kis-gulya, Tompapusztai-löszgyep) is one of the largest ancient loess grasslands remained in Hungary. Its unique nature conservation value has been reported by several botanical and zoological studies (Csathó, 1985, 1986, 2005; Csathó and Csathó, 2007, 2009; Csathó and Jakab, 2012; Herczeg et al., 2011; Kertész, 1996; Molnár, 1997; Molnár et al., 2007). The area is covered by loess steppe grassland community (*Salvio nemorosae-Festucetum rupicolae* Zólyomi ex Soó 1964) characterised by high species diversity and structural richness (Bartha et al., 2011a). The published flora list (Csathó and Csathó, 2009) contains 272 vascular plant species. Based on former studies in dry grasslands we assumed that the extraordinary diversity developed at Külső-gulya loess steppe is a consequence of the complex land-use history of this site (McNaughton, 1985; Collins, 1986; Knapp et al., 1998; Bartha, 2007). It was revealed that the site was managed by low intensity cattle grazing and regular mowing (Bartha et al., 2011b; Bartha et al., 2012). Nowadays only the regular mowing once a year has been continued. However it was revealed that this management not enough to maintain high diversity.

The presence of the lesser blind mole rat (mole rat hereafter) and its mounds are characteristic to the area (Németh et al., 2009). Both its mowing activity and mounds might contribute to preserve diversity an patch dynamics in loess grasslands. Mole rats are considered as serious pests for agriculture in the Mediterranean region due to their foraging of underground organs of vegetables (Moran, 1998). However, no information about the magnitude of such damage has been reported for the natural vegetation.

Ecosystem engineers are organisms which modify, maintainor create habitats for other species (Jones et al., 1994). Subterranean rodents like mole rats also belong to this group (Huntly and Inouye, 1988; Reichman and Seabloom, 2002; Zhang et al., 2003; Hagenah and Bennett, 2013). These species can modify vegetation composition (Ellison and Aldous, 1952; Foster and Stubbendieck, 1980; Reichman and Smith, 1985; Huntly and Reichman, 1994; Nosal et al., 2010; Case et al., 2013), microtopografical features of the soil (Inouye et al., 1997) and bulk density (Kerley et al., 2004). Furthermore they can also change the structure, organic matter and moisture contents of the soil (Mielke, 1977), and they can even reduce the proportion of available soil nitrogen (Inouye et al. 1987).

The *Spalacinae* subfamily (which has two genus, the small *Nannospalax* and the gross *Spalax*) consists of several populations with different chromosome numbers (Nevo, 1961; Savić and Soldatovic, 1984; Savić and Nevo, 1990; Nevo et al., 2001, Hadid et al., 2012). In Hungary four endemic forms exist (Németh et al., 2009) that belong to the lesser blind mole rat species complex [*Nannospalax* (superspecies *leucodon*)]. The study area is inhabited by the Hungarian blind mole rat (*Nannospalax* (*leucodon*) *hungaricus*) (Németh et al., 2009, Németh, 2011). This species leads a subterranean lifestyle (Watson, 1961) with excavating burrows (Heth, 1989).

Very scarce research (in particular about Asian and African mole rat species) focused on the effects of mole rat mounds on the vegetation (but see Cox and Gakahu, 1985; Reichman and Jarvis, 1989; Hongo et al., 1993). There are some other subterranean rodents with similar way of living, which can be used as reference and can help to understand the disturbing impact caused by the mole rats. For example prairie dogs (*Cynomys* spp.) change the species composition of their habitats (Agnew et al., 1986; Whicker and Detling, 1988). Pocket gophers (*Geomys* spp.) also alter some vegetation characteristics like species composition (Inouye et al., 1987; Huntly and Inouye, 1988). Bartha (2001) detected a negative relationship between the mound of pocket gophers and the amount of litter and dominant grass species in regenerated grasslands. Williams et al. (1986) and Martinsen et al. (1990) detected higher diversity on pocket gopher mounds than in their surroundings. Hagenah and Bennet (2013) also found that the presence of the mole rats enhanced species diversity.

Our aim was to study the species richness and diversity of the grassland influenced by the mound forming of the lesser blind mole rat and study the effect of this disturbance to the diversity.

Our hypotheses were the followings:

(i) The species composition of the mounds differs from the control area.
(ii) Diversity is higher on the mounds than in the control areas.

Material and methods

Description and land-use history of the study site

The research was done in Külső-gulya loess steppe which is located in the south-eastern part of Hungary, in Battonya-Tompapuszta (46º21'N, 20º58'E). The 20.9-ha-sized area is characterised by a continental climate with 600 mm mean annual precipitation and 10.6ºC mean annual temperature and with a high number of sunny hours (2000 hours/year). The soil type is chernozem developed on loess bedrock (Barczi et al., 2011).

The map of the first military survey shows Külső-gulya loess steppe as a grassland (Anon., 1785). The area was marked as a part of a large pasture in the map of the second military survey (Anon., 1869). The third military survey showed Külső-gulya grassland in its current size, as it can be seen that it was still used as a pasture (Anon., 1887). The Külső-gulya grassland in Battonya-Tompapuszta has been a nature conservation area since 1989, and its status changed to strictly protected in 1997. It is the part of the Körös-Maros National Park.

Sampling methods and data analysis

The sampling was made in 50×50 cm quadrats where the cover scores of species were recorded on the basis of the modified method of Braun-Blanquet (1964) using cover scores estimated by a percentage (%) scale. In determining quadrat size the extent of the mounds of a mole rat was taken into consideration. This size reflects the inner heterogeneity of the community (Virágh and Bartha, 1996). Altogether 12 plots were made on mounds (disturbed) and 12 plots in the area with no mounds (control).

The scores of Shannon-diversity and evenness were calculated as well as the total cover and the number of species in each of the plots. Rank-abundance curves based on the relative abundance of the species were also calculated. To compare the community parameters (total cover, diversity, evenness, number of species) between disturbed and control plots One-Way ANOVA and Tukey-test were used. These analyses were made in the R statistical environment (R Development Core Team, 2008). Species composition was analysed with PCO ordination with SYNTAX 5.0 program package (Podani, 1993) using Bray-Curtis similarity.

Results

The mean number of species (p=0.163) and the mean total cover (p=0.487) did not showed significant differences between the disturbed and the control sites (*Fig. 1, Table 1.*).

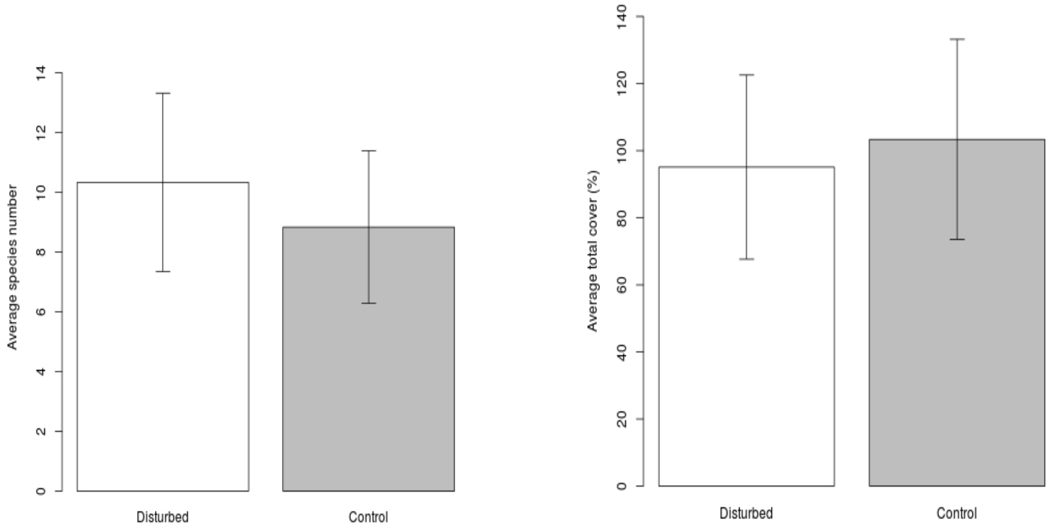

Figure 1. *The average number of species and the average cover values on the disturbed and control sites (mean±SE)*

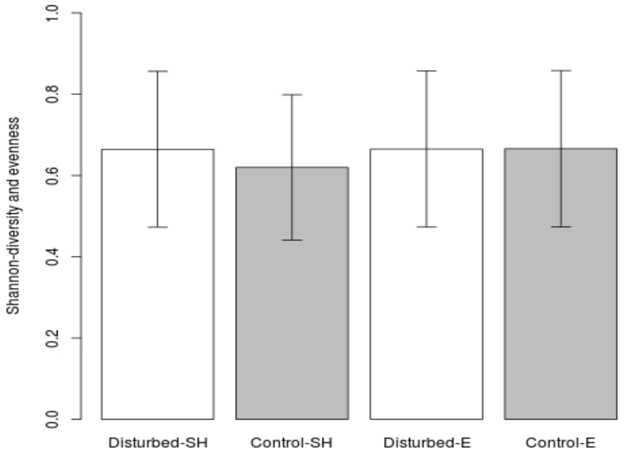

Figure 2. *The Shannon-diversity (SH) and evenness (E) on the disturbed and control sites (mean±SE)*

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There was also no significant difference (*Fig. 2., Table 1.*) neither in the Shannon-diversity (p=0.373) nor in the evenness (p=0.44).

Table 1. *Results of the One-Way ANOVA of the species number, total cover, Shannon-diversity, evenness and the cover of grass species, legumes, litter and Teucrium chamaedrys*

Source	**Df**	**MS**	**F**	**P**
Species number	1	13.5	2.0867	0.1627
Total cover	1	416.67	0.4989	0.4874
Shannon-diversity	1	0.011989	0.8263	0.3732
Evenness	1	0.0086398	0.6184	0.44
Grasses	1	12553.8	41.405	1.788e-06 ***
Legumes	1	119.707	3.0464	0.09487 .
Teucrium chamaedrys	1	6337.5	12	0.002206 **
Litter	1	5787.7	8.6561	0.007538 **

The comparison of the rank-abundance curves did not reveal distinctions between the sites (*Fig. 3.*).

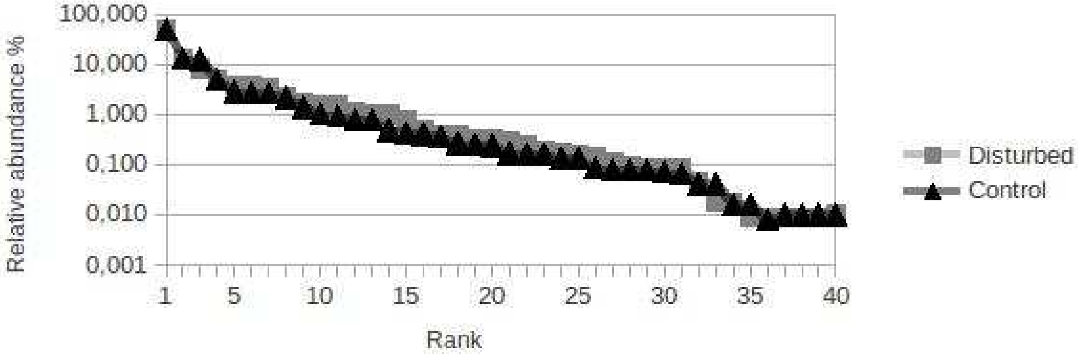

Figure 3. *Rank-abundance curves based on the relative abundance of the species*

The control and disturbed plots differ significantly based on the the PCO ordination (*Fig. 4.*). But if we have a closer look at the proportion of certain species groups (legume species, grasses) and the litter, the difference is remarkable (*Fig. 5.*). Legume species (*Astragalus cicer, Genista tinctoria, Lathyrus pratensis, Lathyrus tuberosus, Vicia angustifolia*) characterised the mounds (p=0.095) whilst the cover of the grasses (*Festuca valesiaca, Poa angustifolia, Carex praecox*) were much higher on the control sites (p=1.788e-06). The accumulation of the litter was more pronounced on the control sites as well (p=0.0075). Some dicots (*Teucrium chamaedrys* – p=0.0022, *Galium verum*, *Fragaria viridis, Thymus glabrescens*) occurred in higher cover on the mounds.

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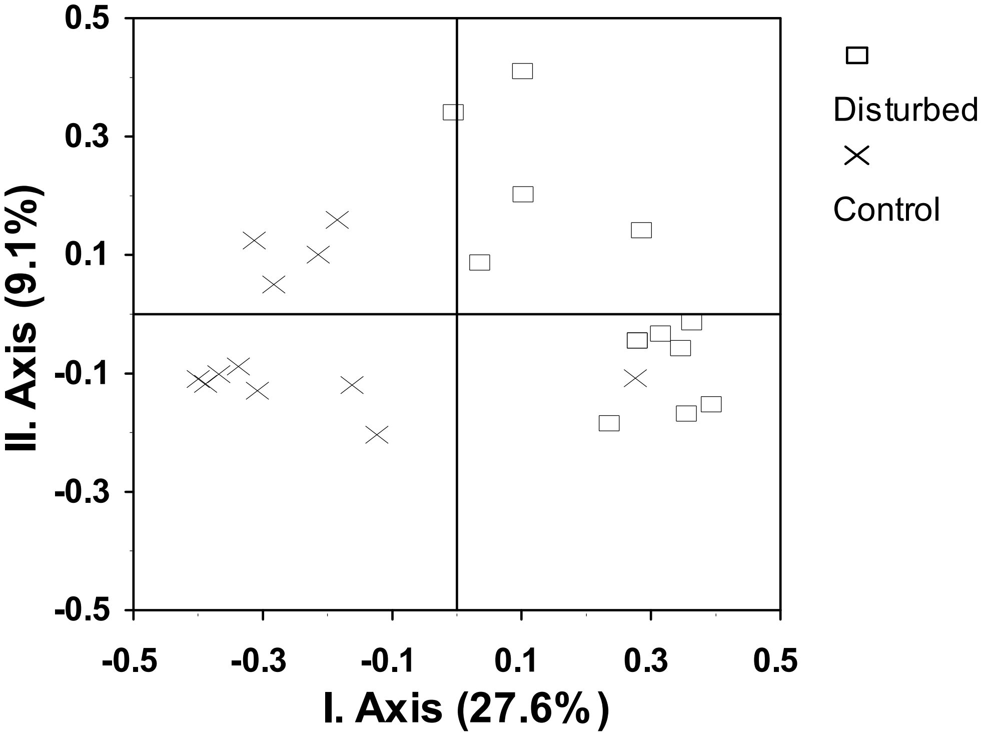

Figure 4. Compositional differentiation between disturbed and control plots analysed by PCO ordination

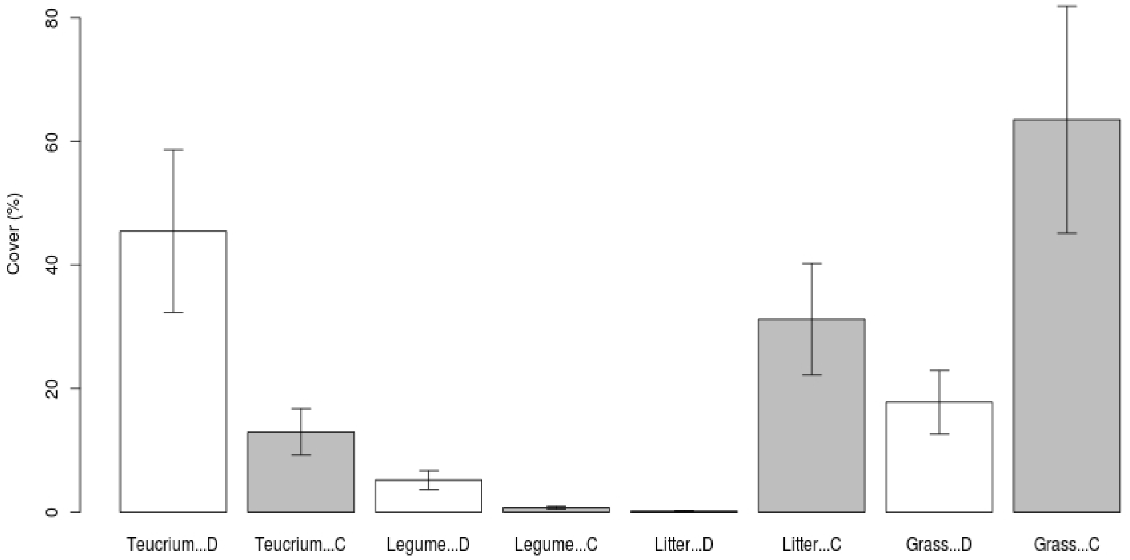

***Figure 5.** The cover of particular species (Teucrium chamaedrys) and and functional groups (legume species, grasses and litter) on the disturbed (D) and control (C) sites (mean±SE)*

Discussion

Our first hypothesis was confirmed by the results as remarkable differences were detected in the species composition between the disturbed and the control plots. The distinction is caused probably by the traits of dominant matrix species. Open surfaces are formed due to the activity of the mole rats and colonized by legumes as Hagenah and Bennett (2013) also confirmed. These open spaces also suitable for species with high seed production, and high vegetative and generative dispersal capacity (Bartha, 2007). We found that the cover of grasses was significantly lower on the mounds as it was also detected by Sigler et al., (2011). The disturbance of fossorial rodents can increase the amount of dicots (Spencer et al., 1985). It was found that the amount of litter also decreased on open surfaces, while litter accumulated in grass dominated swards. These patterns were also confirmed by a former study (Rebollo et al., 2002) analysing *Microtus* species' mounds. They found that the amount of total cover, litter and perennial species was also lower on the mounds than in the surroundings.

Although we found cleardifferences at the population and functional group levels, the community-level characteristics (total cover, species number, diversity) did not show significant differences. Thus, our second hypothesis was not supported. Other research related to pocket gophers (*Geomys bursarius*), having similar lifestyle to mole rat, showed higher species number on mounds (Deets et al., 2010). Sherrod et al. (2005) and Case et al. (2013) found higher species diversity on mounds while in contrast Rezsutek and Cameron (2000) and Rogers et al. (2001) did not find significant differences between the diversity of the disturbed and control plots.

The presence of the mole rats and their disturbance is characteristic to the area. This type of disturbance is a natural process which can highly contribute in maintaining diversity in dry grasslands (Sousa, 1984; Pickett and White, 1985). Disturbance was obtained by the foraging and trampling of the grazing animals for a long time. On the basis of our results the activity of the mole rats can supplement the lack of the grazing animals after the abandonment of grazing.

The abundance of rodents usually fluctuates in time. In case of a drastic increase in their population size they can have a negative effect on the vegetation composition and cover. Hagenah and Bennet (2013) detected such decrease of species diversity due to the increasing disturbance by the mole rats. The mole rat is a valuable species from the nature conservation point of view, thus it is important to state based on our results that their mounds do not affect negatively the diversity of the protected steppe grassland. Moreover, they enrich the disturbance regime and converge it to the complex disturbance regime of the natural grasslands.

In the studied grassland the only grassland management activity is mowing once a year. According to former studies, mowing once ayear should be appropriate to preserve diversity in dry Pannonian grasslands (e.g. Illyés and Bölöni, 2007). We found that mowing once a year was not effective to prevent litter accumulation, which was considerable even in dry years. Thus, especially in abandoned or not properly managed grasslands diversity generated and maintained by the disturbance of mole rat can be very important.

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Appendix

Nomenclature: Király (2009) for taxa, Borhidi (2003) for syntaxa

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EFFECT OF N FERTILIZER FORMS AND SOIL MOISTURE LEVELS ON THE N GASEOUS LOSSES

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Abstract. In a pot experiment using brown forest soil with clay eluviation (40 kg soil/pot) from Keszthely the gaseous losses of nitrogen (total N, N_2, N_2O NO NO_2) caused by denitrification were tested. Gas-collecting traps were placed at a depth of 20 cm in the soil. At the same fertilizer N input (6250mgN/pot, 150mg N/kg soil), the effects of two fertilizer forms (KNO_3, NH_4Cl) and two soil moisture levels (field water holding capacity, WHC= 65% and 100%) were evaluated to the gaseous losses of nitrogen with and without sowing of maize hybrids (two Stira and two Mv 355/pot) as test plants. The composition of the N-containing gases was determined by gas chromatography. From the soil-atmosphere the gas samples were taken 8 times, the sampling times were on the 2, 16, 30, 54, 68, 82, 110, 138-th days of the experiment. Statistical evaluation of the results was performed by analysis of variance. The N gaseous loss in the planted pots was the 12% of the applied fertilizer dose, while in unplanted pots it was nearly the double of it (22%) Consequently, there was a 50% decrease in the denitrification gaseous losses of fertilizer N due to plant N uptake. The N-gaseous loss was significantly higher in cases of KNO_3 applications and at the WHC=100% soil moisture than in NH_4Cl treatments and at the WHC= 65%, probably due to more intensive denitrification. In the unplanted pots the amount of N_2 and N_2O increased the most (by 95% and by 70%) compared with planted pots. It can be concluded that the improperly applied fertilizer causes significant GHG emissions in the absence of plants.

Keywords*: N-gaseous losses, nitrous-oxide, GHG emission, fertilizer treatment, soil moisture*

Introduction

The relative contributions of the three main greenhouse gases (GHG): CO_2, CH_4 and N_2O to overall global radiative forcing are 63.5%, 18.1% and 6.2%, respectively. Soils are one of the major sources of GHG contribution both to anthropogenic emissions due to land use change and agricultural management (up to 22.5% of all anthropogenic sources) (Blagodatsky and Smith, 2012). Yienger and Levy (1995) estimate for annual above-canopy emissions is 5.5Tg N (NO_x) with a range of 3.3-7.7 Tg N. Globally the strongest emitters are agriculture, grasslands, and tropical rain forests, accounting for 41%, 35% and 16% of the annual budget, respectively."Pulsing" (the emissions burst following the wetting of a dry soil) contributes 1,3 Tg N annually. In temperate regions, agriculture dominates emission, and in tropical regions, grassland dominates. By the

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year 2025, the increasing use of nitrogen fertilizer may raise total annual emissions to 6.9 Tg N with agriculture accounting for more than 50% of the global source. The agriculture is a significant contributor to the increasing N_2O concentration of air (Delmas et al., 1997; Hellebrand et al.,2003; Ruser et al., 2006). The agriculture is estimated to contribute more than two-thirds of total anthropogenic N_2O emissions (Pattey et al., 2007). The agricultural soils emit 3.3 Mt N_2O per year (Mosier et al.,1998). As the global warming potential of N_2O is 298 times as strong as that of CO_2, N_2O emissions from soils thereby exert an important impact on the environment. Soil microbial processes, nitrification and denitrification contribute significantly to the agricultural N_2O emission (Stange and Döhling, 2005). N-gaseous emissions from agricultural soils, speciation of predicted gas N flux into N_2O and N_2 depend on the N-fertilizer dose and type, the soil type and pH, the soil moisture, the oxygen supply and the C/N ratio of the soil, application practice, the vegetation and the temperature (Ma et al., 2007; Chu et al., 2007, Gu et al, 2009). Field response to fertilizaton is variable; some plots have enhanced emissions for prolonged periods, whereas others have sharper initial increases that decay over time. In general, however a positive linear correlation seems to be between fertilizer use and emission, and over the course of a growing season, total NO_x emissions change between 1-10% of added nitrogen fertilizer (Williams et al., 1992; Shepard et al., 1991, Cardenas et al., 1993). The exact fertilizer form which is more stimulatory depends on the site, although evidence suggests that a mixed form, such as NH_4NO_3, generates strongest emission (Sanhueza, 1992). In a pot experiment the total N gaseous losses were higher at KNO_3 treatment than NH_4Cl treatment in brown forest soil with clay eluviation (Debreczeni et al. 1998). The N_2O emissions from NH_4^+-N fertilizer were higher than from urea and NO_3^--N fertilizers in coarse- textured soils (Gu et al, 2009). Kramer et al.(1999) studied greenhouse gas emissions of Dutch agricultural crop production by using a life cycle approach. It was determined that the emissions of N_2O are mainly caused by the production and application of synthetic nitrogen fertilizer. The use of other nitrogen sources manure, compost or limiting the use of synthetic nitrogen could positively influence the emissions of N_2O. In contrast, Jones et al. (2005) found that during growing season the cumulative total N_2O flux from manure treatments was 25 times larger than that from mineral fertilizers. Large inputs of manure N have a potential to contribute a very high N_2O emissions, particularly in wet soil conditions. The ratio of NO_x gases depends on the soil moisture. In an experiment testing the tropical rain forest ecosystem during dry periods the NO-N: N_2O-N ratio was as high as 60:1, whereas for wetter periods it decreased to <7:1. (Butterbach et al, 2004). In Hungary, where the proportion of agricultural area to the total area of the country is quite high (63%) it is essential to investigate agricultural contribution to greenhouse gas emission.

Material and methods

Brown forest soil with clay eluviation from Keszthely (pH_{KCl} =7.7, C=1.1 %, NO_3-N = 17.5 mg kg^{-1}, NH_4-N = 12 mg kg^{-1}, humus = 1.9 %) was filled in large plastic pots (40 kg soil/pot). N fertilizers (KNO_3, NH_4Cl) were applied at a high rate of approx. 150 mg N kg^{-1} soil (6 250 mg N/pot) to trace the precise transformation processes of N, P fertilizer in all treated soils, and K fertilizer in NH_4Cl treatments was also used (N:P:K= 1:1:3.35). All experiments were carried out at two soil moisture levels (field water holding capacity, WHC= 65 % and 100 %) with and without sowing of maize as test plants (two Stira and two Mv355 plants/pot) (Table1). For statistical calculations, results of maize hybrids were taken as replicates. The plants were grown until full ripening. Maize (*Zea mays L.*) was sown in 48 pots, and 32 pots were left without plant.

***Table 1**. Setting up of the experiment*

		With maize						**Without maize**					
Maize hybrid	**Treatment**	**Control**		**KNO_3+P**		**NH_4Cl+PK**		**Control**		**KNO_3+P**		**NH_4Cl+PK**	
Stira	**WHC %**	**100**	**65**	**100**	**65**	**100**	**65**	**100**	**65**	**100**	**65**	**100**	**65**
MV 355													

All treatments were replicated four times. Gas-collecting traps of 1800 cm^3 capacity with silicon pipe outlets were placed at a depth of 20 cm in the soil. The traps collected the N gaseous losses (NO, NO_2, N_2O, N_2) released during the denitrification process. Gas samples were taken 8 times by syringe (5 cm^3) in 3 replicates from the soil atmosphere. For soil atmosphere analysis the composition of the N-containing gases (N_2, NO, NO_2, N_2O) was determined by a Carlo Erba 2350 type gas chromatograph. From these data the total gaseous N losses were calculated (mg N /pot or mg N/1800 cm^3) for each sampling point. At the end of the experiments the cumulative gaseous N losses and N_2O-N losses were also calculated by the difference method (N content difference between treated and control gas samples) and by the calculations of the relative % gaseous N losses. Results were analyzed by the means of analysis of variance (MANOVA). The statistical analyses were performed with a Microsoft Excel Macro (Aydinalp et al., 2008; Vágó et al., 2008)

Results and discussion

The total N and total N_2O gaseous losses were found to depend significantly ($LSD_{5\%}$=16,7 and 5,1) on the presence or absence of the plants (*Table 3*). In control samples in the planted pots the total N gaseous losses were 1,4 times higher (at 65% and 100% WHC), the N_2O gaseous losses were 1,6 times (at 65%WHC) and 1,9 times (at 100 %WHC) higher than in the unplanted pots (*Table 2*). Similar results were obtained by Heltai et al. (2013) in a pot experiment in control samples. In contrast to the control, in the unplanted pots treated with fertilizer the total N and N_2O gaseous losses were higher (1,4-1,7 times) than in the planted pots. Calculated by difference method the total N gaseous losses were higher in the unplanted pots by 78-84% at KNO_3 treatment and by 71-73% at NH_4Cl treatment while the total N_2O gaseous losses were higher by 67-72% and by 62-63% compared with planted pots.

The total N and total N_2O gaseous losses were significantly higher in the N-fertilizer treatments than in control samples (*Table 3*: $LSD_{5\%}$=20,5 and 6,3). The difference of total N gaseous losses was 7 times higher in KNO_3 and NH_4Cl treatment in the planted pots while in the unplanted pots it was 16-17 times higher than in the controls (*Table 2*). The difference of N_2O gaseous losses was 5-6 times higher in the planted pots and 14-15 times higher in the unplanted pots in fertilized pots than in the controls. The total N and total N_2O gaseous losses were more intensive in case of KNO_3 treatment than in NH_4Cl treatment (*Table 3:* $LSD_{5\%}$=20,5 and 6,3).

Table 2. *Total N and total N_2O gaseous losses (Nmg/1800cm^3)(+ with plant, - without plant)*

Treatment	Maize	WHC %	∑N	$\sum N_2O$
Control	+	**100**	**131,5**	**20**
		65	**119,5**	**16,5**
KNO_3	+	**100**	**921**	**107**
		65	**868,5**	**96**
NH_4Cl	+	**100**	**907,5**	**102**
		65	**868,5**	**93,5**
Control	-	**100**	**91,5**	**10,5**
		65	**85,5**	**10**
KNO_3	-	**100**	**1494**	**156**
		65	**1461,5**	**146,5**
NH_4Cl	-	**100**	**1438**	**144,5**
		65	**1369**	**135**

Table 3. *Analysis of variance of total N and total N_2O gaseous losses according to plant presence, soil moisture and treatment (N and N_2O mg/1800cm^3)*

Plant presence	∑N	$\sum N_2O$
Maize +	636	73
Maize -	990	100
$LSD_{5\%}$	**16,7**	**5,1**

Soil moisture (WHC%)	∑N	$\sum N_2O$
100%	831	90
65%	795	83
$LSD_{5\%}$	**16,7**	**5,1**

Treatment	∑N	$\sum N_2O$
Control	107	14,3
KNO_3	1186	126
NH_4Cl	1146	119
$LSD_{5\%}$	**20,5**	**6,3**

The difference was significant in the unplanted pots only (*Table 4:* $LSD_{5\%}$=29 and 8,8). Similar results were obtained in other pot experiments using same soil samples from Keszthely by Debreczeni et al.(1995, 1998) and Nótás et al. (2003).

Table 4. *Analysis of variance of total N and total N_2O gaseous losses according to plant presence x treatment, plant presence x soil moisture and treatment x soil moisture (N and N_2O mg/1800cm^3)*

Plant presence X Treatment		∑N	$\sum N_2O$
Maize +	Control	126	18,3
	KNO_3	895	102
	NH_4Cl	888	98
Maize -	Control	89	10,3
	KNO_3	1478	151
	NH_4Cl	1404	140
$LSD_{5\%}$		**29**	**8,8**

Plant presence X Soil moisture		∑N	$\sum N_2O$
Maize +	100%	653	76,3
	65%	619	68,7
Maize -	100%	1008	103,7
	65%	972	97,2
$LSD_{5\%}$		**23,6**	**7,2**

Treatment X Soil moisture		∑N	$\sum N_2O$
Control	100%	111,5	15
	65%	102,5	13
KNO_3	100%	1207	132
	65%	1165	121
NH_4Cl	100%	1173	123
	65%	1119	114
$LSD_{5\%}$		**29**	**8,8**

The total N and total N_2O gaseous losses were higher at 100%WHC than 65%WHC (*Table 3*: $LSD_{5\%}$=16,7 and 5,1). This difference of total N loss was equally significant in the planted and unplanted pots (*Table 4*: $LSD_{5\%}$= 23,6), but the total N_2O gaseous loss was significantly higher only in the planted pots (*Table 4*: $LSD_{5\%}$= 7,2). The effect of the soil moisture was significant in the fertilized samples only, in the control samples it was not (*Table 4:* $LSD_{5\%}$=29 and 8,8). The differences were dependant on the presence or absence of the plants in control samples 7-10% and 5-20%, these are not significant; while in KNO_3 treatment 2-6% and 7-12%, in NH_4Cl treatment 5% and 7-9%, these are significant.

Figure 1 and *2* (on the basis of *Table 5*) show the rate of total N gaseous losses increase in the planted pots (*Fig. 1*) and in the unplanted pots (*Fig. 2*). Results of maize hybrids were averaged.

Table 5. *Total N gaseous losses in the sampling time, ∑Nmg/1800cm3 (- unplanted pots)*

Treatment	Maize hybrid	WHC %	Sampling time (day)							
			2.	**16.**	**30.**	**54.**	**68.**	**82.**	**110.**	**138.**
Control	**Stira**	**100**	47	70	96	126	127	130	123	122
		65	37	62	7	108	113	122	112	115
	Mv 355	**100**	48	71	91	126	124	133	121	116
		65	31	65	80	101	105	117	100	109
KNO_3	**Stira**	**100**	150	344	480	616	719	931	918	876
		65	110	305	448	587	619	848	836	844
	Mv 355	**100**	124	365	504	615	743	911	903	863
		65	116	337	474	589	692	889	858	874
NH_4Cl	**Stira**	**100**	121	337	475	589	604	918	894	855
		65	107	297	426	546	587	846	827	844
	Mv 355	**100**	119	333	492	595	701	893	897	870
		65	102	303	475	579	624	850	839	891
Control	**-**	**100**	40	47	58	76	84	94	86	89
		65	38	40	52	78	75	89	73	82
KNO_3	**-**	**100**	108	345	651	911	971	1156	1494	1493
		65	101	304	614	829	895	1125	1343	1473
NH_4Cl	**-**	**100**	108	342	658	891	956	1114	1415	1461
		65	93	300	614	824	852	1096	1352	1386

It can be established that the sampling time significantly influences the production rates of total N gaseous losses. The change of total N gaseous losses growth can be characterized by two peaks, in the planted pots *(Fig.1)* on the 16th and 82nd day of the experiment and in the unplanted pots *(Fig.2)* later, on the 30th and 110th day. This differerence was probably caused by the increase of microbiological activity due to the effect of root secretion in the planted pots. Similar results were obtained in other pot experiments using the same soil type from Keszthely Debreczeni et al.(1995). The minimum values were received on the 68th day in the planted and unplanted pots equally. The N gaseous emission fluctuations may be caused by periodic changes of soil bacteria's microbiological activity, life cycle and temperature.

In our experiment with maize the total N gaseous losses changed between 749-789 mgN/1800 cm^3 in the planted pots and between 1304-1408 mgN/1800 cm^3 in the unplanted pots (*Fig. 3*). The total N gaseous losses in the planted pots were 12-13% of the applied fertilizer N while in the pots without maize it was about twice as much, 21-22%.

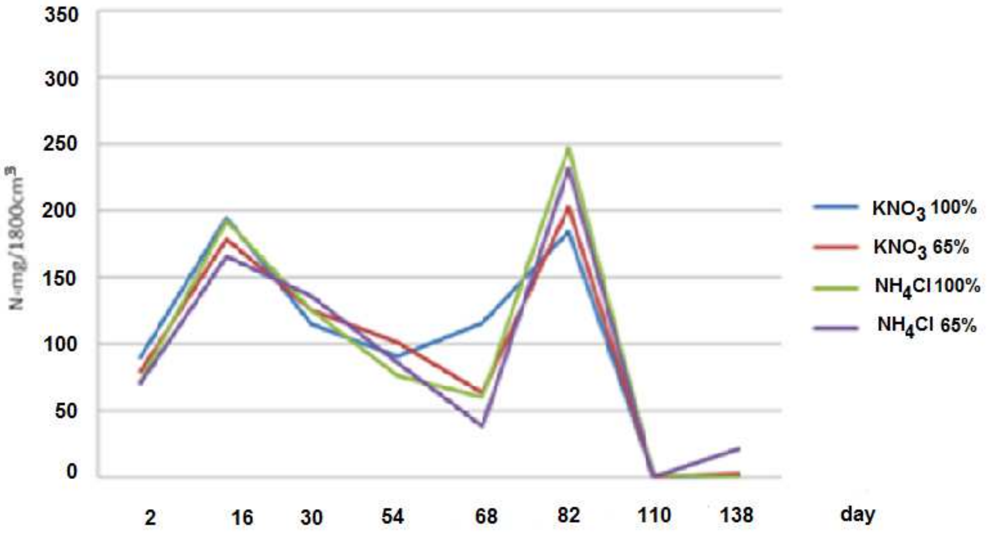

Figure 1. *The change of total N gaseous losses increase in the planted pots in the function of sampling time*

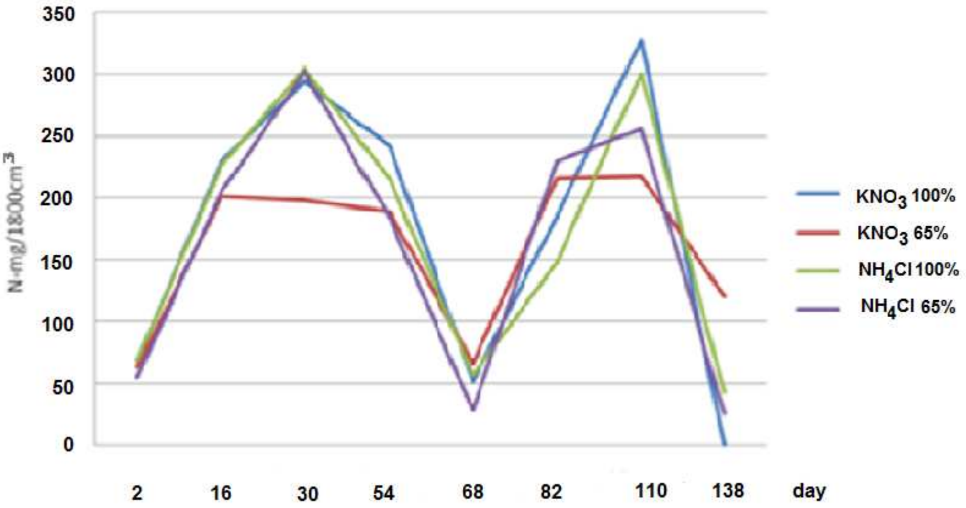

***Figure 2**. The change of total N gaseous losses increase in the unplanted pots*

The change of the relative total N gaseous losses (*Fig.4*) was found to be highly influenced by the presence of maize, the fertilizer treatment and soil moisture. It was higher at KNO_3 treatment and 100% WHC soil moisture (except 30th day), than NH_4Cl treatment and at 65% WHC. Between the 2nd and 68th day the 100%WHC increased more intensively the total N gaseous losses in unplanted pots than with maize compared to 65%WHC while KNO_3 treatment enhanced the gaseous N losses stronger in planted pots than without maize compared to NH_4Cl. The forms of the curves are similar among the 2nd and 68th sampling times. The effect of KNO_3 and 100%WHC is the strongest at

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the start of the experiment (2^{nd} and 16^{th} day) and on the 68^{th} day compare to NH_4Cl and 65%WHC.

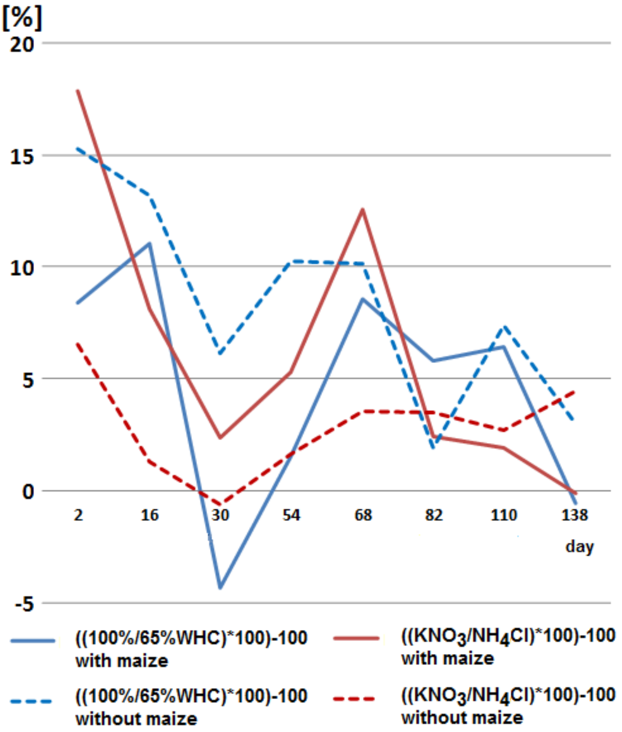

Figure 3. *The total N gaseous losses (+ planted pots, -unplanted pots)(LSD5%= 41mgN/1800 cm3)*

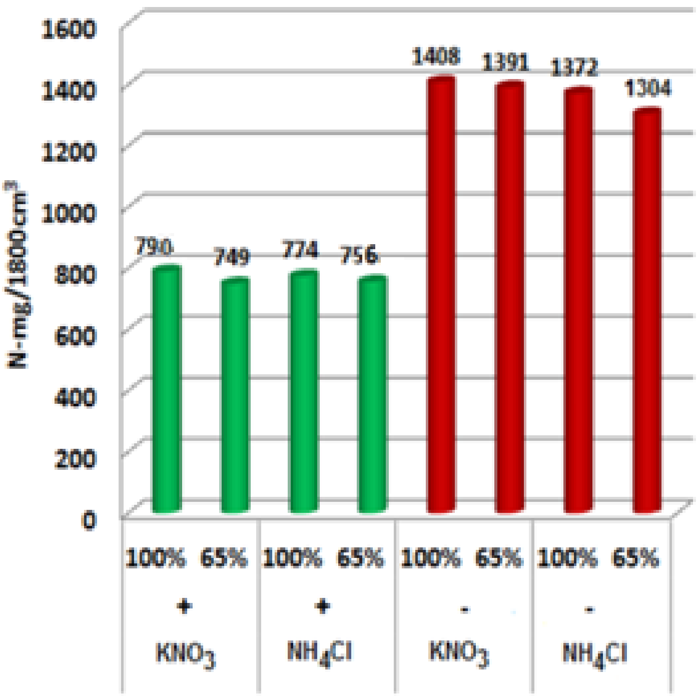

Figure 4*. Distribution of the relative total N gaseous losses in the planted and unplanted pots*

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The ratio of NO_x gaseous losses was different in the planted and unplanted pots (*Fig.5*). In the unplanted pots the ratio of N_2 gas was higher (78%) while the ratios of N_2O, NO_2 and NO were lower than in planted pots. The N_2 and N_2O gaseous losses were higher by 95% and by 70% in the unplanted pots than in the planted pots (N_2 and N_2O: $LSD_{5\%}$= 17 and 5,1 N and N_2O mg/1800cm^3) (*Fig.6*).

Figure 5. *The % distribution of N gaseous losses in planted (left) and unplanted pots (right)*

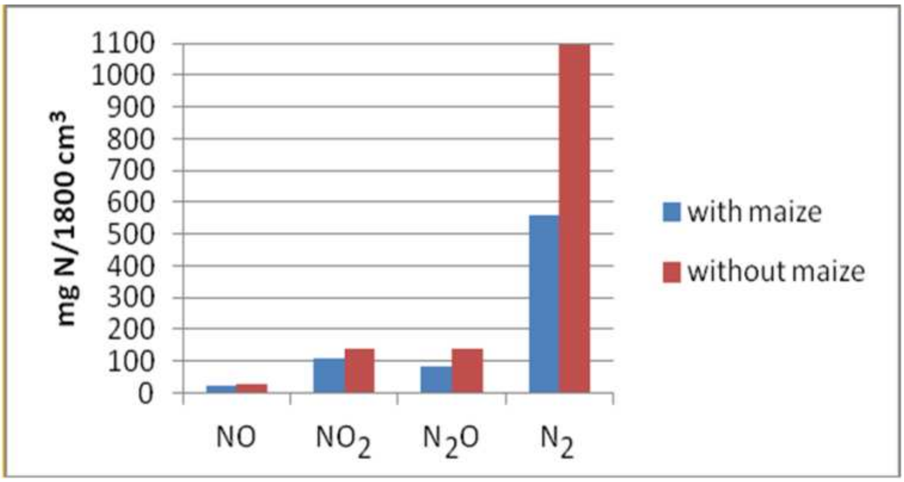

Figure 6. *The distribution of N gaseous losses in the planted and unplanted pots*

After the 16th day of the experiment the N_2O gaseous losses were much higher in the unplanted pots than in the planted pots and reached the maximum value (140 mgN/1800 cm^3) on the 82nd and 110th day of the experiment depending on treatment (*Fig.7*) and soil moisture (*Fig.8*) while in the planted pots the maximum value (about 80 mgN/1800 cm^3) was measured on the 82nd day. The N_2O gaseous losses were significantly higher at KNO_3 treatment than NH_4Cl treatment in the unplanted pots between the 54th -110th day while in the planted pots between the 2nd – 30th day and on the 82nd day (*Fig.7*). It was found that at WHC=100% soil moisture the N_2O gaseous losses were significantly higher than at WHC= 65% in all pots in most of the sampling time (*Fig.8*).There are two exceptions: in the unplanted pots on the 82nd day when same values were measured at both soil moisture and in the planted pots on the 54th day when the N_2O gaseous loss was significantly higher at WHC= 65% than at WHC=100% soil moisture.

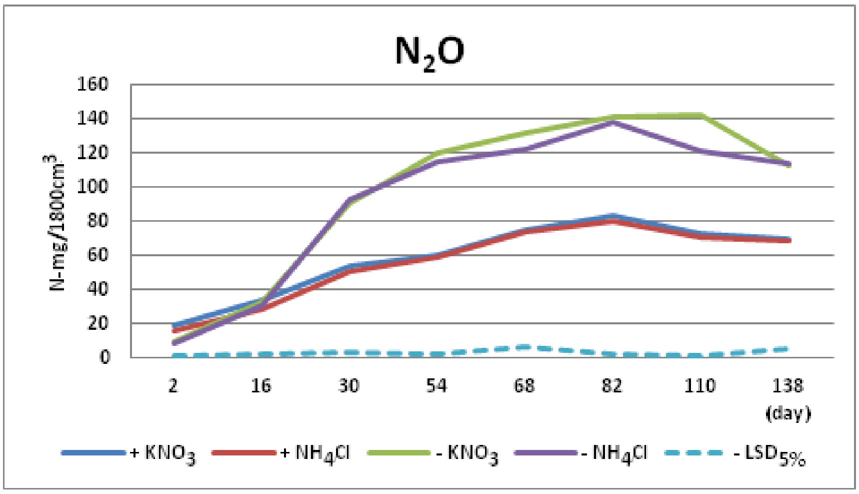

Figure 7. *Change of N2O gaseous losses in the sampling time depend on N fertilizer forms (+in planted pots, - in unplanted pots)*

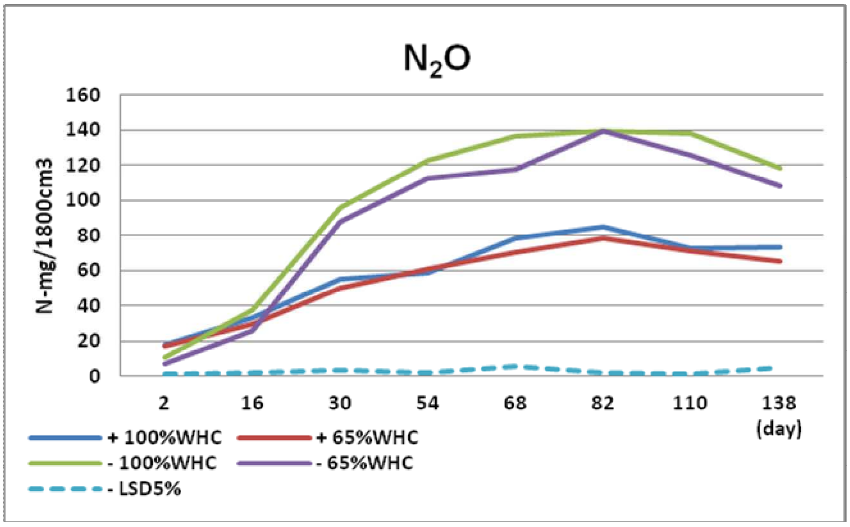

Figure 8. *Change of N2O gaseous losses in the sampling time depend on soil moisture (+in planted pots, - in unplanted pots)*

Conclusions

The total N and N_2O gaseous losses were significantly higher in the unplanted pots than in the planted pots in treated samples. In our experiment with maize the total N gaseous loss was 12-13% of the applied fertilizer N while in the pots without maize it was about twice as much 21-22%. Plant N uptake reduced the N gaseous losses by about 50%.

In contrast to the treated samples in control samples in the planted pots the total N and N_2O gaseous losses were higher than in the unplanted pots due to soil drying-rewetting intensifying microbiological activity, which is more intensive in the rhizosphere around roots (Kuzyakov et al.2000).

The total N and N_2O gaseous losses were significantly higher in the N-fertilizer treatments than in control samples due to the increased activity of bacteria, accelerated

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mineralization and release of nutrients by the large fertilizer N dose (Kuzyakov et al.2000).

The total N and N_2O gaseous losses were more intensive in case of KNO_3 treatment than in NH_4Cl treatment in most cases as an assumed consequence of the intensive denitrification.

The total N and N_2O gaseous losses were significantly higher at 100%WHC than 65%WHC due to more intensive denitrification processes.

In the unplanted pots the ratio of N_2 gas was higher (78%) than in the planted pots (72%). The N_2 and N_2O gaseous losses were higher by 95% and by 70% in the unplanted pots than in the planted pots due to the absence of plants and more intensive denitrification processes.

It can be concluded that the improperly applied fertilizer causes significant GHG emissions in the absence of plants.

The gaseous N losses were found to be influenced significantly by the presence or absence of plants, the N fertilizer form and the soil moisture.

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