Restoration of oak forest: Effects of former arable land use on soil chemistry and herb layer vegetation

Valtinat, Karin; Bruun, Hans Henrik; Brunet, Jörg

Published in:
Scandinavian Journal of Forest Research

DOI:
10.1080/02827580802545572

2008

Restoration of oak forest: effects of former arable use on soil chemistry and herb layer vegetation

Running title: Effects of former arable use in oak forests

KARIN VALTINAT[1], HANS HENRIK BRUUN[1] and JÖRG BRUNET[2,*]

[1]Department of Ecology, Plant Ecology and Systematics, Lund University, Ecology Building, 223 62 Lund, Sweden;

[2]Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, P.O. Box 49, SE-230 53 Alnarp, Sweden

*Author for correspondence (email: Jorg.Brunet@ess.slu.se; fax: +46-40-462325; phone: +46-40-415184)

Abstract

Stands of pedunculate oak (*Quercus robur*) planted 50-80 years ago on two types of land - previously forested land and former arable fields - were compared regarding vegetation and soil. Former arable soils were characterized by a higher pH, higher nitrate concentration and a higher soil density, but had lower organic matter content and lower ammonium concentration in the top soil (0-5 cm). These differences, however, decreased with soil depth. Phosphorus concentration was consistently higher in former fields throughout the soil profile (0-45 cm). Nitrogen mineralization, determined by *in situ* incubation, showed a strong seasonal pattern with peak values in spring. NMS ordination revealed marked compositional differences in the vegetation between the two land-use categories, and also compositional turnover along gradients in soil pH and nitrogen availability. Differences in soil pH between land-use categories occurred in a range critical for the establishment of many typical forest herb-layer species. Plant indicator species were identified for the two land-use categories. The results showed that acid-sensitive forest herbs may benefit from the higher-pH soils in new woodlands in contrast to ancient forest soils with little buffer capacity towards natural and anthropogenic acidification. We conclude that former arable use has long-lasting effects on soil properties and vegetation composition in broadleaved forests. New woodlands on former fields can thus offer relatively persistent new habitats for acid-sensitive species which have suffered from reduction in habitat area during historic periods of deforestation and cultivation.

Keywords: Afforestation, ancient woodland, nitrogen mineralization, old fields, phosphorus, soil acidity, understory

Introduction

Conversion to arable fields has dramatically reduced the area of temperate broadleaved forests on productive soils in Europe during the past millennium, and the area of arable land probably reached a maximum around 1900 (Rabbinge & van Diepen, 2000). Afforestation of arable fields started in the beginning of the 20th century but was initially dominated by conifer species. From late 20th century onwards, however, establishment of new broadleaved forest has been promoted in several European countries (Stanturf & Madsen, 2002; Weber, 2005).

In comparison with ancient forest land, previous arable use commonly leads to increased levels of soil pH, nitrification, and phosphorus concentration and to a decrease in organic matter and soil porosity (Koerner et al., 1997; Bossuyt et al. 1999a,b; Honnay et al., 1999; Compton & Boone, 2000; Dupouey et al., 2002; Falkengren-Grerup et al., 2006). Soil differences increase with duration and intensity of agricultural use (Alriksson & Olsson, 1995; Verheyen et al., 1999; Ritter et al. 2003). The persistence of an arable legacy after afforestation depends also on soil type and effects of the planted tree species on soil properties (Bossuyt et al., 1999a,b; Compton & Boone, 2000; Dupouey et al., 2002; Ritter et al. 2003).

The effects of previous cultivation on soil properties are expected to be most obvious in the ploughed layer (ca 0-30 cm soil depth), but deeper layers may be affected by the influence of plant roots, soil fauna and soluble elements that are transported downwards. Examples of the latter are ploughed-down lime, which has been found to increase soil pH to a depth of 1 m (Noble & Hurney, 2000) and phosphorus, which has been found to be transported down to 0.5 m (Garz et al., 2000).

Except for the planted or sown tree species, all other forest plants must recolonize new forest stands on former fields. Establishment of plant species in secondary forests is controlled both by their dispersal capacity and by effects of site properties that influence recruitment and growth, either directly or indirectly through interspecific competition. Most previous studies have focussed on the absence of typical forest plants in isolated secondary forests due to dispersal limitation (Flinn & Vellend, 2005; Hermy & Verheyen, 2007). However, in secondary forest adjacent to ancient forest with source populations, dispersal limitation may be less important for plant colonization as compared to effects of soil conditions (Brunet, 2007a).

In the regional species pool of forest-dwelling vascular plants, a majority is restricted to base-rich soils (Ellenberg et al., 1991; Ewald, 2003). Growth of these species on acid forest soils can be inhibited by low pH itself (H-toxicity), Al-toxicity, nutrient deficiency (Ca, Mg, K, P) or an unfavourable nitrogen source (Marschner, 1991). On the background of a large historical loss of broadleaved forest area and acidification of the remaining forests by atmospheric deposition (Falkengren-Grerup, 1995), the question arises whether forests on former arable fields have soils that are better buffered against acidification and can provide new suitable habitat for basiphilous forest plants.

In the south Swedish province of Skåne/Scania, broadleaved forests have been planted on former arable fields since the 1920'es on certain larger estates. Transect studies across three woodland ecotones in the Torup-Skabersjö area in southwestern Skåne have previously shown that certain basiphilous species are more frequent in oak plantations on former fields than in adjacent ancient woodland (Brunet et al., 2000). A later comparison of soil chemical conditions in other oak plantations in the same area showed significant higher soil pH and phosphorus levels on former fields (Falkengren et al., 2006).

The objective of the present study was to link differences in soil chemical properties due to former land use directly to vegetation patterns and plant species distributions. We compare stands of pedunculate oak (*Quercus robur*) planted 50-80 years ago on both ancient woodland sites and on former arable fields. We focus particularly on some aspects that are rarely studied, but may improve our understanding of herb layer differentiation: soil chemical gradients in different layers of the top soil and the seasonal variation of nitrogen mineralization.

We assume that the stands subjected to different former land-use originally had similar soil conditions. Differences in soil characteristics due to land-use should therefore be most pronounced in the top soil and decrease downwards. We further hypothesize that former arable use has resulted in higher pH, faster nitrification and higher P-concentration. Therefore, basiphilous and nitrophilous forest species should be more abundant in these new broadleaved stands than in ancient forest, given that our sampling design minimizes the effects of dispersal limitation.

Materials and methods

Study stands

The study was conducted in oak stands within the 2000 ha large forest-dominated landscape on the estates of Skabersjö and Torup in the south Swedish province of Skåne (55°32´N, 13°11´E). The area is situated in the nemoral vegetation zone, and deciduous hardwood forests typically occur on deep, well-drained dystric cambisols. During the period 1920-50, a large number of oak stands were planted on both arable and previously forested land (hereafter referred to as *former fields* and *ancient forest land*). The study area is documented in a database on land-use history showing that the ancient forest land has a documented continuity of forest vegetation during the past 300 years (Brunet, 2007b). However, most stands have probably been woodland for a much longer time. Historical sources from 1694 and onwards indicate that these forests were managed by selective cutting.

Temperature and precipitation data were collected from the weather station in Lund, ca 20 km north of the studied area. The summer and spring periods were 2.2 °C and 1.3 °C, respectively, warmer than the average of the reference period 1961-90, and the autumn and winter periods had about average mean temperatures. The autumn and spring periods had a precipitation deficit of 18 mm and 22 mm, respectively, per month, whereas summer and winter precipitation was close to average. The total precipitation in the area was 586 mm during the studied period as compared to an annual average of 666 mm.

Stand selection

Based on the historical data we chose ten oak stands planted on each of the two land-use category (stand size 0.7-6.6 ha). Ten stands, five of each land-use category, have been studied previously by Falkengren-Grerup et al. (2006). The remaining stands of this study were selected in order to minimize differences in stand age. All stands were adjacent to or situated in a matrix of other forest stands. Stands of both land-use categories were often situated close to each other and had similar topography and soil origin (glacial till type). The ancient forests of the Torup and Skabersjö estates were primarily kept as hunting areas and as a timber source, although the sites were potentially suitable for arable use (Brunet, 2007b). It is thus reasonable to assume that the former fields initially had similar soil conditions as the ancient forest sites.

The stands studied on ancient forest land were beech forests (*Fagus sylvatica*) prior to oak plantation except two stands with oak in the previous state. The stands on former fields represent the first forest generation after arable abandonment, and all sites were under cultivation in 1915 according to a detailed survey map (scale 1:20.000). The stands on ancient forest land had a mean stand age of 62 years (range 50-83 years) and those on former fields of 70 years (range 57-77 years) according to current management plans.

Soil sampling

A well drained, flat area of 25 × 20 m was selected within each stand and five 1 × 1 m plots were marked in the centre and at the corners, leaving a 4 m corridor along the borders, to be used for repeated soil sampling over one year. All plots were placed >1 m from tree bases. The five soil samples from each plot were bulked to give one composite sample. We studied the soil at depths of 0-5 cm and 5-15 cm below the litter layer with respect to pH, organic matter and net potential N mineralization in intact soil cores.

To estimate the available N we sampled two intact soil cores using a PVC cylinder (diameter 6.8 cm, length 15 cm). One was used for the *in situ* incubation and one was taken to the laboratory for analysis of pH, C, N and moisture. The cylinder used for the *in situ* incubation was immediately put in a plastic bag and returned to its position. At the end of the incubation period the soil core was separated into segments representing 0-5 cm and 5-15 cm soil depth. Incubation was performed in the summer (June-August 2003), autumn (August-October 2003), winter (October 2003-March 2004) and spring (April-May 2004).

Five profiles, one in each 1 × 1 m plot, were dug in each stand in May 2004 and the samples were bulked and analysed regarding pH and total N, P and C at 0-5, 5-15, 15-30 and 30-45 cm soil depths. This was done to establish whether differences between land-use categories decreased with increasing soil depth.

Soil analysis

Soil analysis was performed on fresh soil <6 mm or soil dried at 105 ºC for 48 hours. Soil moisture was calculated as the difference in weight between the fresh soil and the dried soil divided by the weight of the fresh soil. The pH was measured using 10 g fresh soil extracted with 50 ml 0.2 M KCl. The organic matter content was determined as loss of ignition (LOI) at 600 ºC for the seasonal data and as total C by dry combustion (LECO CR-12) in the soil profiles sampled in May 2004. Total N and P were analysed by Kjeldahl digestion followed by flow injection analysis (FIA).

Nitrogen mineralization rates were calculated by subtracting the initial from the final amounts of ammonium (NH_4^+) and nitrate (NO_3^-), measured with FIA (10 g fresh soil and 50 ml 0.2 M KCl), and dividing by the number of days of incubation.

Vegetation sampling

A survey of species composition and species cover in the 20 stands was made in 10 plots of 1 × 1 m. These plots were systematically placed without overlap with plots for soil samples and were >1 m from tree bases. The vegetation was surveyed during the summer 2004 (July and August) and in spring 2005 (April). The spring survey included species flowering in spring or early summer. Herbaceous vascular plants <1 m, and shrubs between 1 and 5 m were recorded within a 1 × 1 m frame and each species' contribution to the ground cover was estimated on the scale 0.5, 1, 2 … 5, 5-10 … 45-50, 50-60 … 90-100 %. Average cover of each species across the ten 1 × 1 m plots was used for further analysis. For species recorded in both spring and summer, the season with the higher average cover was used. Additional species within the 20 × 25 m area were noted with 0.05 % cover.

Statistical analysis

Statistical tests were carried out on soil data normalised to soil volume (mol m^{-2} per 0-5 or 5-15 cm depth) and not on concentrations per gram soil (mol g^{-1}). One-way repeated measures analysis of variance was used to test for differences in soil chemical variables for the factors season and land use (R ver 2.7.1, R Development Core Team, 2008). Student's t-test was used to test for differences between land-use categories, and regression analysis to show relationships between soil moisture and soil organic matter (SPSS for Windows, 12.0.1). We analyzed pH and organic matter content at the start and end of the *in situ* incubation, but these two values did not provide more information than their mean, which was therefore used in all calculations related to a particular season.

Plant community data were subjected to indirect gradient analysis by Non-metric Multidimensional Scaling (NMS) as implemented in PC-Ord (McCune & Mefford, 1997). We used the Sørensen index as a dissimilarity measure. We tried different starting configurations to avoid local minima, but results were very stable. We chose a two-dimensional NMS solution based on its low final stress and its high correlation between distances in ordination space and distances in the original species-dimensional space. In order to reveal significant relationships between species composition and the environment, we used Kendall rank correlation between stand scores on the two NMS axes and soil variables at 0-15 cm depth during four seasons.

Species characteristic of stands on either ancient forest land or former fields were identified using Indicator Species Analysis (Dufrêne & Legendre, 1997) with the binary land-use variable as *a priori* classification factor. We used 999 permutations of the classifying factor to assess statistical significance.

Results

Soil chemistry

Former fields had a mean pH_{KCl} of ca 4.0 at the two uppermost depths (0-15 cm), which was ca 0.3 pH units higher than in the ancient forest soil (Table I). At 0-5 cm, former fields also had a lower carbon concentration in the top soil. These differences disappeared with increasing soil depth. Phosphorus concentrations, however, were consistently higher in former fields throughout the soil profile (0-45 cm, Table I).

Seasonal differences in soil pH were usually <0.1 units between measurements in the same stand, and the mean values confirmed the general differences between land-use categories of 0.3-0.4 pH units (Table II). However, repeated measures analysis revealed a significant effect of sampling season on soil pH at 0-5 and 5-15 cm depth (Table III). Organic matter content differed only at 0-5 cm depth, being about 3 percentage units lower in the former fields than in the ancient forest land. The organic matter content explained part of the soil moisture (R^2=0.400, P<0.001, n=40). At both depths, the soil moisture differed significantly between the seasons, mainly due to low moisture in autumn (Figure 1, Table III). Soil moisture during the early autumn drought spell was only half of that during the previous summer, also resulting in significantly lower soil moisture in the former fields during that season (Figure 1).

The former fields showed higher NO_3^- and lower NH_4^+ mineralization rates than the ancient forest land at 0-5 cm, but rates were similar at 5-15 cm soil depth (Table II). The seasonal variation was substantial with the highest mineralization rates in the spring, second highest in the summer and much lower during the other two seasons (Figure 2, Table III). NH_4^+ mineralization rates were lower in the summer and winter and the NO_3^- mineralization rates were higher in the spring in the former fields than in the ancient forest land at 0-5 (Figure 2, Table III).

Herb layer vegetation

The two-dimensional NMS ordination (Final stress = 16.0) extracted 78.2 % of the variation in species composition – 43.5 % and 34.7 %, respectively, for the two axes. Correlation between axis scores and environmental variates (Table IV) suggested that compositional turnover along the first axis (Figure 3) was mainly due to the combined effect of former land-use and soil pH, clearly separating plots of the two land-use categories. Correlations between soil pH and axis 1 were significant at both soil depths and during all seasons with the highest correlation in spring at 0-5 cm depth and in summer at 5-15 cm, respectively (Table IV). Aspects of nitrogen mineralization were correlated with both NMS-axes. However, NO_3-nitrogen was correlated with floristic variation along the second axis independently of land-use and soil pH (Table IV). Soil moisture was not correlated with the ordination scores.

Indicator species analysis (Table V) showed that five species were indicators of ancient forest stands, *Anemona nemorosa, Deschampsia flexuosa, Lamiastrum galeobdolon, Maianthemum bifolium* and *Sorbus aucuparia.* Plantations on former arable land were indicated by *Adoxa moschatellina, Circaea lutetiana, Festuca gigantea, Fraxinus excelsior, Geranium robertianum, Geum urbanum, Poa nemoralis, Poa trivialis* and *Urtica dioica,* and *Ulmus glabra.*

Discussion

Soil chemistry

The underlying assumption of the present study was that the stands subjected to different former land-use originally had similar soil conditions. The soil characteristics should therefore differ most in the top soil. Our hypothesis was confirmed regarding pH and total C, whereas total P was considerably higher in the former fields than in the ancient forest land throughout the soil profile. Although we logically cannot exclude initial differences in P between land-use categories, the most probable explanation is agricultural P fertilization.

Our results confirm that effects of former arable use persist in the top soil of the studied dystric cambisols at least during the first generation of broadleaved forest (Bossuyt et al., 1999a,b; Compton & Boone, 2000). Differences in soil pH may continue to decrease with time (Bossuyt et al. 1999a,b), whereas the higher P concentrations in former fields probably are more persistent (Dupouey et al., 2002).

The NH_4^+ mineralization rate was higher in the ancient forest land (summer and winter) and the NO_3^- mineralization rates were higher in the former fields (spring). This pattern is partly pH-dependent but may also be caused by lower bioavailability of the organic matter in the ancient forest land, as acid soils have lower faunal activity and the turnover is smaller compared with previously ploughed soils.

The seasonal variation in N mineralization rates was considerable with two to three times higher rates in the spring than in the summer. Measured over a whole year, the potential net mineralization rate often has a peak during the spring, followed by a declined activity throughout the rest of the year (Ross et al., 2004; Aubert et al., 2005). A high rate of NO_3^- mineralization in spring is usually attributed to the earlier activity of microbes than of plants (Ross et al., 2004). However, the low observed autumn mineralization rates may also be associated with the unusually dry weather conditions in the study year. Negative effects of low moisture levels on N mineralization are known from other studies (Sierra, 1997; Thomsen et al., 1999; Bengtson et al., 2005). Former arable soils lost more water during autumn than the ancient forest soil. This is possibly related to a lower organic matter content in the top soil of the former arable soil.

The difference in soil mineralization between land-use types in our study might not just depend on direct effects of former arable land-use on soil properties, but could also be an indirect effect of vegetation differences. Due to a feedback between vegetation composition and N cycling, herb layer composition may influence net N mineralization and net nitrification (Wedin & Tilman, 1990; van der Krift & Berendse, 2001). Soil conditions on former arable fields with relatively high levels of nitrate and phosphorus promote fast-growing competitive species (Bossuyt & Hermy, 2000; De Keersmaeker et al., 2004), which produce easily decomposable litter. This may in turn lead to a feedback mechanism to mineralization rate.

Herb layer vegetation

Our results show that the effect of soil pH on vegetation patterns is independent of seasonal variability and top soil depth. Effects of N-variables were less robust and appeared during different seasons. *In situ* nitrification did not substantially improve the degree of explained variation in the ordination as compared to initial N concentrations. The former land-use category was the single most important factor explaining NMS axis 1, probably because it integrates the effect on species composition of several environmental variables.

Low soil pH is known to decrease plant diversity in deciduous forests (Bobbink et al., 1998; Falkengren-Grerup & Diekmann, 2003), in particular when the pH approaches levels where aluminium is potentially toxic (pH soil solution <4.2 which corresponds to pH_{KCl} <3.7, Andersson & Brunet, 1993). An increase in top soil pH_{KCl} from 3.7 to 4.0, as observed in our study, may enable establishment and growth of a large number of herbaceous species (Brunet & Neymark, 1992; Falkengren-Grerup & Tyler, 1993).

Soil conditions on former arable fields may promote species that are associated with higher soil pH and fertility levels and that occur ubiquitously in the modern agricultural landscape. Examples in our study are *Geranium robertianum*, *Geum urbanum*, *Poa trivialis* and *Urtica dioica*. Dense stands of *Urtica dioica* may potentially inhibit colonization of other species (De Keersmaeker et al., 2004). However, in the relatively well-drained oak stands of our study, *Urtica* is a frequent, though not dominant, species. Despite frequent occurrence of ruderal species, several typical forest species were found to be more abundant in forest stands on former fields than in ancient woodland stands. These species are known as rather acid-sensitive and nitrophilous (*Adoxa moschatellina*, *Circaea lutetiana*, *Festuca gigantea*, *Fraxinus excelsior*, *Poa nemoralis*, *Ulmus glabra*, Ellenberg et al., 1991), but they are obviously also good dispersers (Bossuyt et al., 1999c; Verheyen & Hermy, 2001; Graae 2002; Brunet, 2007a). Floristic surveys of all oak stands in the study area reveal that also other basiphilous species such as *Brachypodium sylvaticum, Corydalis intermedia, Mercurialis perennis* and *Pulmonaria obscura* are more abundant in the new plantations on former fields than in the original ancient stands containing the source populations (Brunet et al., 2000; Brunet, 2007a). Thus, first generation oak stands contribute significantly to maintenance of the herbaceous flora in forest landscapes, at least when new stands are contiguous with older forest. The results of this study suggest that the higher pH of the new stands is one of the main factors explaining this pattern.

Colonization capacity varies greatly among forest species. *Anemone nemorosa* and *Lamiastrum galeobdolon* are common on base-rich soils but had high indicator values for ancient woodland, which is probably related to a relatively low colonization rate (Bossuyt et al., 1999c; Brunet & von Oheimb, 1998ab; Verheyen & Hermy, 2001). The other three indicators of ancient woodland stands (*Deschampsia flexuosa*, *Maianthemum bifolium*, *Sorbus aucuparia*) are acid-tolerant species, which may suffer from strong competition during recruitment on former fields by tall herbs and grasses.

Our results show that soil pH, P and *in situ* nitrification potential were considerably higher still after 70 years of forest growth on former fields, as compared to reference stands on ancient forest land. We conclude that new woodlands on former fields can offer new habitats for acid-sensitive and nutrient-demanding woodland species which have suffered from reduction in habitat area during historic periods of deforestation and cultivation. However, the dystric cambisols of the study area are prone to natural leaching and acidification which may be further accelerated by tree species with a slowly decomposing, acid litter, such as oak and beech. Promotion of mixed stands including species producing base-rich litter, e.g. ash, elm, hazel, lime and maple (Nordén, 1994; Hagen-Thorn et al., 2004) might counteract acidification and increase the persistence of conditions favourable for woodland herbs.

Acknowledgements

The authors would like to thank Ursula Falkengren-Grerup for help and advice. The study was financed by grants from Lund University (to KV and HHB) and the research programme 'Sustainable Management of Broadleaved Forests' at the Swedish University of Agricultural Sciences (to JB).

References

Alriksson, A. & Olsson, M. T. (1995). Soil changes in different age classes of Norway spruce (*Picea abies* (L.) Karst.) on afforested farmland. *Plant and Soil*, *168/169*, 103–110.

Andersson, M. & Brunet, J. (1993). Sensitivity to H- and Al ions limiting growth and distribution of the woodland grass *Bromus benekenii*. *Plant and Soil*, *153*, 243-254.

Aubert, M., Bureau, F. & Vinceslas-Akpa, M. (2005). Sources of spatial and temporal variability of inorganic nitrogen in pure and mixed deciduous temperate forests. *Soil Biology and Biochemistry*, *37*, 67-79.

Bengtson, P., Falkengren-Grerup, U. & Bengtsson, G. (2005). Relieving substrate limitation-soil moisture and temperature determine gross N transformation rates. *Oikos*, *111*, 81-90.

Bobbink, R., Hornung, M. & Roelofs, J. G. M. (1998). The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology*, *86*, 717-738.

Bossuyt, B. & Hermy, M. (2000). Restoration of the understorey layer of recent forest bordering ancient forest. *Applied Vegetation Science*, *3*, 43-50.

Bossuyt, B., Deckers, J. & Hermy, M. (1999a). A field methodology for assessing man-made disturbance in forest soils developed in loess. *Soil Use and Management*, *15*, 14-20.

Bossuyt, B., Diels, J. & Deckers, J. (1999b). Changes following cultivation and reforestation of loess soils in central Belgium: consequences for future land use. *The Land*, *3*, 151-166.

Bossuyt, B., Hermy, M. & Deckers, J. (1999c). Migration of herbaceous plant species across ancient - recent forest ecotones in central Belgium. *Journal of Ecology*, *87*, 628-638.

Brunet, J. (2007a). Plant colonization in heterogeneous landscapes - An 80-year perspective on restauration of broadleaved forest vegetation. *Journal of Applied Ecology*, *44*, 563-572.

Brunet, J. (2007b). *Från ollonskog till pelarsal – Förändringar i skogsareal och skogsstruktur efter införandet av modernt skogsbruk på Skabersjö gods 1838. (Changes in forest area and forest structure after introduction of modern forest management at the Skabersjö estate, S-Sweden, in 1838).* Arbetsrapport nr 35. Inst. f. sydsvensk skogsvetenskap, SLU Alnarp.

Brunet, J. & Neymark, M. (1992). Importance of soil acidity to the distribution of rare forest grasses in south Sweden. *Flora*, *187*, 317-326.

Brunet, J. & Oheimb, G. v. (1998a). Migration of vascular plants to secondary woodlands in southern Sweden. *Journal of Ecology*, *86*, 429-438.

Brunet, J. & Oheimb, G. v. (1998b). Colonization of secondary woodlands by Anemone nemorosa. *Nordic Journal of Botany*, *18*, 369-377.

Brunet, J., Diekmann, M. & Oheimb, G. v. (2000). Factors influencing vegetation gradients across ancient – recent woodland borderlines in southern Sweden. *Journal of Vegetation Science*, *11*, 515-524.

Compton, J. E. & Boone, R. D. (2000). Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. *Ecology*, *81*, 2314-2330.

De Keersmaeker, L., Martens, L., Verheyen, K., Hermy, M., De Schrijver, A. & Lust, N. (2004). Impact of soil fertility and insolation on diversity of herbaceous woodland species colonizing afforestations in Muizen forest (Belgium). *Forest Ecology and Management*, *188*, 291-304.

Dufrêne, M. & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs*, *67*, 345-366.

Dupouey, J. L., Dambrine, E., Laffite, J. D. & Moares, C. (2002). Irreversible impact of past land-use on forest soils and biodiversity. *Ecology*, *83*, 2978-2984.

Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W. and Paulißen, D. 1991. *Zeigerwerte von Pflanzen in Mitteleuropa*. Scripta Geobotanica 18. Verlag E. Goltze KG.

Ewald, J. (2003). The calcareous riddle: why are there so many calciphilous species in the Central European flora? *Folia Geobotanica, 38*, 357-366.

Falkengren-Grerup, U. (1995). Long-term changes of flora and vegetation in deciduous forests of southern Sweden. *Ecological Bulletins, 44*, 215-226.

Falkengren-Grerup, U. & Diekmann, M. (2003). Use of a gradient of N-deposition to calculate effect-related soil and vegetation measures in deciduous forests. *Forest Ecology and Management*, *180*, 113-124.

Falkengren-Grerup, U., ten Brink, D.-J. & Brunet, J. (2006). Land-use effects on soil N, P, C and pH persist over 40-80 years of forest growth on agricultural soils. *Forest Ecology and Management*, *225*, 74-81.

Falkengren-Grerup, U. & Tyler, G. (1993). Experimental evidence for the relative sensitivity of deciduous forest plants to high soil acidity. *Forest Ecology and Management*, *60,* 311-326.

Flinn, K. M. & Vellend, M. (2005). Recovery of forest plant communities in post-agricultural landscapes. *Frontiers in Ecology and Environment*, *3*, 243-250.

Garz, J., Schliephake, W. & Merbach, W. (2000). Changes in the subsoil of long-term trials in Halle (Saale), Germany, caused by mineral fertililzation. *Journal of Plant Nutrition and Soil Science, 163*, 663-668.

Graae, B. J. (2002). The role of epizoochorous seed dispersal of forest plant species in a fragmented landscape. *Seed Science Research, 12*, 113-121.

Hagen-Thorn, A., Callesen, I., Armolaitis, K., Nihlgård, B., 2004. The impact of six European tree species on the chemistry of mineral topsoil in forest plantations on former agricultural land. *Forest Ecology and Management 195*, 373-384.

Hermy, M. & Verheyen, K. (2007). Legacies of the past in the present-day forest biodiversity, a review of past land-use effects on forest plant species composition and diversity. *Ecological Research*, *22*, 361-371.

Honnay, O., Hermy, M. & Coppin, P. (1999). Impact of habitat quality on forest plant species colonization. *Forest Ecology and Management*, *115*, 157-170.

Koerner, W., Dupouey, J. L., Dambrine, E. & Benoit, M. (1997). Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. *Journal of Ecology*, *85,* 351-358.

Marschner, H. (1991). Mechanisms of adaptation of plants to acid soils. *Plant and Soil, 134,* 1-20.

McCune, B. & Mefford, M. J. (1997). *PC-Ord, Multivariate Analysis of Ecological Data, version 3.0*. Gleneden Beach: MjM Software Design.

Noble, A. D. & Hurney, A. P. (2000). Long-term effects of lime additions on sugarcane yield and soil chemical properties in north Queensland. *Experimental Agriculture, 36*, 397-413.

Nordén, U. 1994. The influence of broad-leaved tree species on pH and organic matter content of forest topsoils in Scania, South Sweden. Scandinavian Journal of Forest Research, *9*, 1–8.

R Development Core Team, 2008, *A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. Wien, Austria.

Rabbinge, R. & van Diepen, C. A. (2000). Changes in agriculture and land use in Europe. *European Journal of Agronomy, 13,* 85–100.

Ritter, E., Vesterdal, L. & Gundersen, P. (2003). Changes in soil properties after afforestation of formerly intensively managed soils with oak and Norway spruce. *Plant and Soil*, *249*, 319-330.

Ross, D. S., Lawrence, G. B. & Fredriksen, G. (2004). Mineralization and nitrication patterns at eight northeastern USA forested research sites. *Forest Ecology and Management*, *188*, 317-335.

Sierra, J. (1997). Temperature and soil moisture dependence of N mineralization in intact soil cores. *Soil Biology and Biochemistry*, *29*, 1557-1563.

Stanturf, J. A. & Madsen, P. (2002). Restoration concepts for temperate and boreal forest of North America and Western Europe. *Plant Biosystems*, *136*, 143-158.

Thomsen, I. K., Schönning, P., Jensen, B., Kristensen, K. & Christensen, B. T. (1999). Turnover of organic matter in differently textured soils. II. Microbial activity as influenced by soil water regimes. *Geoderma*, *89*, 199-218.

van der Krift, T. A. J. & Berendse, F. (2001). The effect of plant species on soil nitrogen mineralization. *Journal of Ecology*, *89*, 555-561.

Verheyen, K., Bossuyt, B., Hermy, M. & Tack, G. (1999). The land-use history (1278-1990) of a mixed hardwood forest in western Belgium and its relationship with chemical soil characteristics. *Journal of Biogeography*, *26*, 1115-1128.

Verheyen, K. & Hermy, M. (2001). The relative importance of dispersal limitation of vascular plants in secondary forest succession in Muizen Forest, Belgium. *Journal of Ecology*, *89*, 829-840.

Weber, N. (2005). Afforestation in Europe: lessons learned, challenges remaining. In J. A. Stanturf & P. Madsen (Eds.), Restoration of boreal and temperate forests (pp. 121-135). London, UK: CRC Press.

Wedin, D. A. & Tilman, D. (1990). Species effects on nitrogen cycling, a test with perennial grasses. *Oecologia*, *84*, 433-441.

Table I. Soil ph, total C, N, P (mol m^{-2} depth^{-1}), and C:N ratio at four soil depths. Mean values are given for ancient forest land and former fields. Differences due to former land-use were tested within soil depths using Student's t-test (n=20). *** P<0.001, ** P<0.01, * P<0.05, (*) P<0.10, ns P>0.10.

Depth	Land-use	pH_{KCl}		Total C		Total N		C:N ratio		Total P	
0-5 cm	Ancient	3.74	***	143.7	*	9.28	(*)	16.1	ns	0.39	*
	Fields	4.05		109.8		7.13		15.5		0.70	
5-15 cm	Ancient	3.72	***	189.0	ns	13.9	ns	15.5	ns	0.72	**
	Fields	3.97		179.7		16.5		13.8		1.61	
15-30 cm	Ancient	3.87	(*)	203.9	ns	13.6	ns	16.7	(*)	1.09	**
	Fields	3.97		203.0		14.5		14.1		2.05	
30-45 cm	Ancient	4.01	ns	130.5	ns	11.4	ns	16.1	ns	1.00	**
	Fields	4.01		135.0		10.6		13.0		1.98	

Table II. Soil pH, organic matter content, moisture, *in situ* net potential mineralization rates of NO_3^-, NH_4^+ and N (mmol d^{-1} m^{-2} $depth^{-1}$) at two soil depths. Mean values (SE) for ancient forest land and former fields sampled over one year (four sampling occasions). Differences due to land-use were tested at each soil depth using repeated measures analysis (n=80). *** P<0.001, * P<0.05, (*) P<0.10, ns P>0.10.

Depth (cm)	Land-use	pH_{KCl}		Organic matter content, %		Moisture %		NO_3^-		NH_4^+		N	
0-5	Ancient forest	3.64 (0.03)	***	10.7 (<0.1)	*	25.9 (0.9)	ns	0.82 (0.15)	*	0.40 (0.09)	*	1.22 (0.19)	ns
	Former fields	4.03 (0.03)		8.0 (<0.1)		22.8 (0.9)		1.27 (0.28)		0.13 (0.07)		1.40 (0.28)	
5-15	Ancient forest	3.72 (0.02)	***	5.3 (<0.1)	ns	19.2 (0.6)	ns	0.98 (0.18)	ns	0.07 (0.05)	ns	1.06 (0.19)	ns
	Former fields	3.98 (0.02)		5.1 (<0.1)		17.9 (0.6)		1.07 (0.17)		0.01 (0.05)		1.08 (0.16)	

Table III. Significance levels (P-value) of the factors land-use and season, and of their interaction according to repeated measures analysis of variance for soil pH, organic matter content, moisture, *in situ* net potential mineralization rates of NO_3^-, NH_4^+ and N (mmol d^{-1} m^{-2} $depth^{-1}$) at two soil depths; ns P>0.05.

Depth 0-5 cm	Land-use	Season	Interaction
pH KCl	<0.001	0.002	ns
Organic matter content	0.038	ns	ns
Moisture	ns	<0.001	ns
NO_3^-	0.048	<0.001	0.004
NH_4^+	0.046	0.027	ns
N	ns	<0.001	ns
Depth 5-15 cm			
pH KCl	<0.001	<0.001	ns
Organic matter content	ns	<0.001	ns
Moisture	ns	<0.001	ns
NO_3^-	ns	<0.001	ns
NH_4^+	ns	ns	ns
N	ns	<0.001	ns

Table IV. Correlation coefficients between stand position on the two NMS axes (Non-metric Multidimensional Scaling, two-dimensional) and site characteristics. Only statistically significant coefficients are shown. For pH, only the season with the highest correlation coefficient is included. Conc. = initial concentration, min. = mineralization rate.

Variables	Correlation coefficient	P-value 1st axis	Correlation coefficient	P-value 2nd axis
Former land-use	0.65	0.001		
pH 0-5 cm spring	0.53	0.001		
pH 5-15 cm summer	0.53	0.001		
N conc. 5-15 cm spring	0.34	0.040		
NH4 conc. 0-5 cm autumn	-0.44	0.006		
NO3 conc. 0-5 cm winter	0.40	0.014		
NO3 conc. 0-5 cm autumn			-0.35	0.034
NO3 min. 0-5 cm summer			-0.39	0.016

Table V. Indicator values for herb layer species in oak plantations with different former land-use. The observed indicator value is given for the group for which the species had its maximum indication. P-values are based on 999 permutations of the classification variable. Woody plant saplings were included as pseudo-species in two height classes (<0.5 m and 0.5 – 2 m). Only species with significant indicator values are shown.

Plant species	Former land-use	Observed indicator value	P-value
Anemone nemorosa	Forest	88	0.001
Deschampsia flexuosa	Forest	70	0.008
Lamiastrum galeobdolon	Forest	63	0.018
Maianthemum bifolium	Forest	76	0.001
Sorbus aucuparia <50 cm	Forest	50	0.028
Adoxa moschatellina	Arable	50	0.027
Circaea lutetiana	Arable	90	0.001
Festuca gigantea	Arable	60	0.009
Fraxinus excelsior <50 cm	Arable	62	0.045
Geranium robertianum	Arable	59	0.038
Geum urbanum	Arable	70	0.001
Poa nemoralis	Arable	65	0.026
Poa trivialis	Arable	50	0.037
Ulmus glabra <50 cm	Arable	49	0.028
Urtica dioica	Arable	77	0.023

Figure 1. Soil moisture (%, mean ± SE) at two depths and four seasons in ancient forest land (empty bars) and former fields (shaded bars). Student's t-test was used to test for differences between stands with different former land-use. Differences were found for autumn and 0-5 cm (P=0.026) and 5-15 cm (P=0.055). N=10 for each land-use.

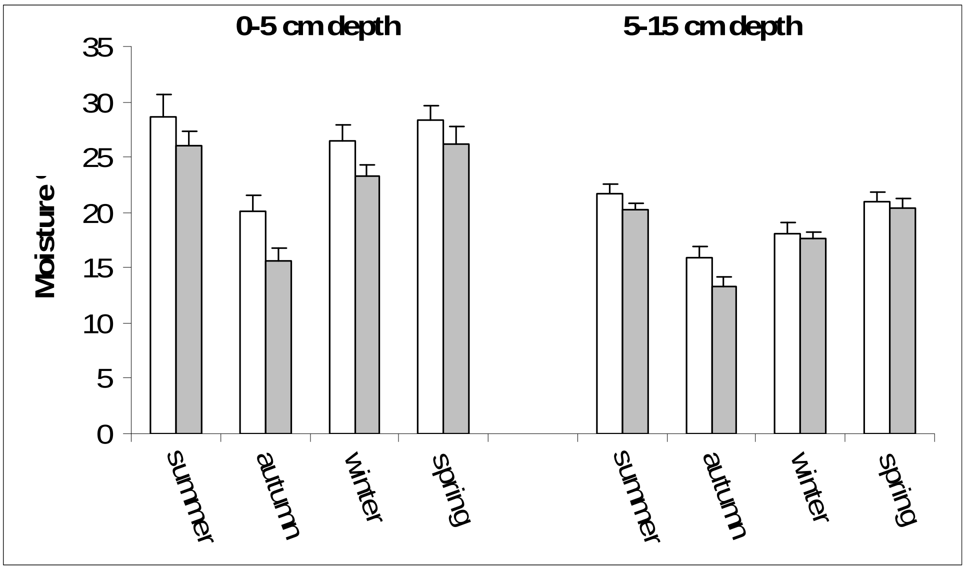

Figure 2. Net potential mineralization rates of NH_4^+ and NO_3^- (mmol m^{-2} $depth^{-1}$ day^{-1}, mean + SE) at two soil depths and four seasons in ancient forest land (first column) and former fields (second column). Differences (Student's t-test, P<0.05) between land-use categories are shown by different lower case (for NH_4^+) or upper case letters (for NO_3^-). N=10 for each land-use.

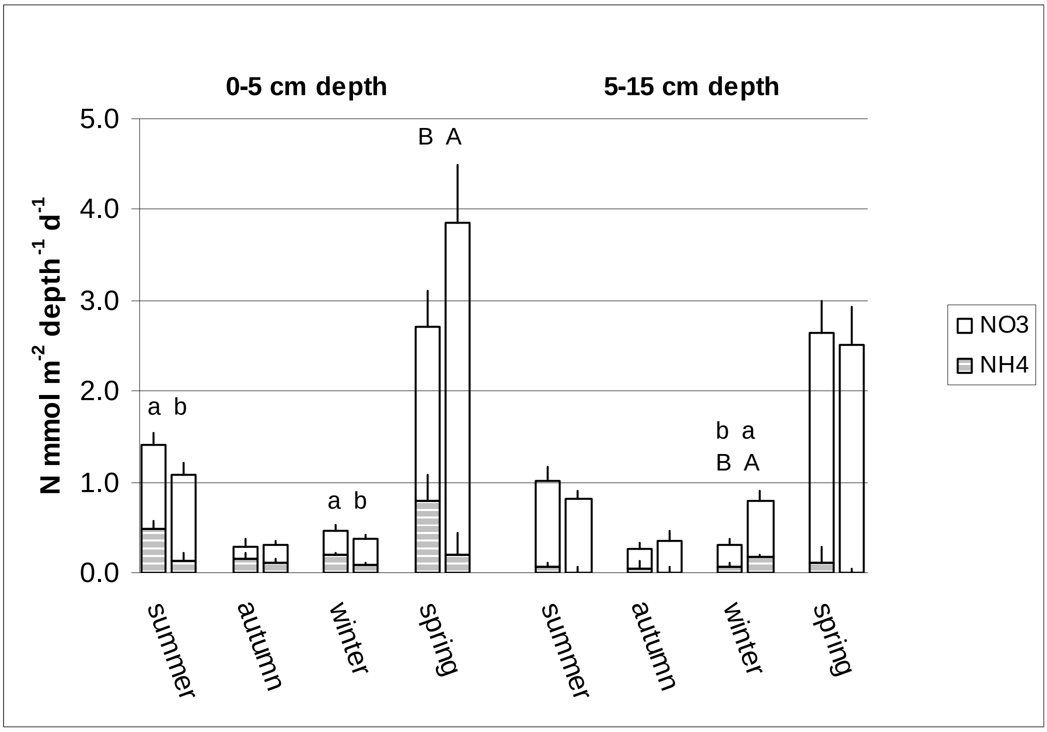

Figure 3. Ordination (NMS in 2 dimensions) of vegetation in stands with different former land-use. Filled square = former fields, open square = ancient forest stands. Mean values of stands with different land use differ along the first axis (t-test, P<0.001), but not along the second axis.