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Restoration of former agricultural fields on acid sandy soils: Conversion to heathland, rangeland or forest?

A.M. Kooijman[a,*], C. Cusell[a,b], J. van Mourik[a], T. Reijman[a]

[a] Institute of Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94248, NL-1090 GE Amsterdam, The Netherlands
[b] Witteveen+Bos, P.O. Box 233, NL-7400 AE Deventer, The Netherlands

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ABSTRACT

Three restoration strategies on agricultural fields with acid sandy soil were evaluated after 18 and 25 years: conversion to heathland, rangeland and forest. Changes in soil microstructure, chemical characteristics, availability of N and P, and vegetation composition were analyzed in agricultural soils, three undisturbed reference sites and five types of restored former agricultural fields.

Agricultural soils were characterized by organic slurry without much soil life. Soil nutrients were especially high for P, mostly in mineral form, and P-desorption rates were high. Partial and complete topsoil removal, aiming at heathland restoration, led to (much) lower soil organic matter and nutrients, but not to recovery of soil life, nor to P-limited soils. Heather was accompanied by many grassland species, even with complete topsoil removal. Conversion to rangeland did not decrease nutrient stocks, but led to improved soil life, although different from reference grasslands due to the higher pH. P-availability remained high, but net N-mineralization and plant N-content were clearly lower after 25 than after 18 years. Plant diversity was relatively high, and cover of eutrophic grasses decreased to 8–39% in intermediate and productive rangelands. Nutrient-poor species remained absent, but the slightly higher pH improved conditions for many grassland herbs. Afforestation did also not lead to nutrient-poor conditions, but soil life clearly increased and nutrients were used for rapid tree growth. Undergrowth species however remained eutrophic.

It was impossible to retrieve the P-limited reference ecosystems within 25 years of restoration, not even with complete topsoil removal. Differences in plant diversity between expensive topsoil removal and much cheaper conversion to rangeland were also relatively small. For restoration on a landscape scale, it may thus be better to focus on conversion to semi-natural grasslands and afforestation. The half-open, nutrient-, mineral-, and species-rich landscape offers opportunities for large grazers, but also for many insects and birds.

1. Introduction

In many countries, forests, heathlands and natural grasslands have been converted to agricultural farmland during the past century, which led to loss of natural habitats and fragmentation of the landscape (e.g., Fischer and Lindenmayer, 2007; Green et al., 2007). In Europe, defragmentation programmes have been an important force behind the reconversion of agricultural fields to more natural ecosystems in the last decades (Natuurbeleidsplan, 1990), and restoration of former agricultural fields has been a major topic (e.g., Gough and Marrs, 1990; Oomes et al., 1996; Pegtel et al., 1996; McCrea et al., 2001; Green et al., 2007; Smolders et al., 2008).

In western Europe, restoration of agricultural land is often constrained by high loads or large pool sizes of N and especially P. It is possible to reduce P-availability by the removal of nutrient-rich topsoils (Oomes et al., 1996; Niemeyer et al., 2006; Smolders et al., 2008). However, topsoil removal is expensive, and not always sufficient to retrieve e.g., the original heathland (Green et al., 2007). Afforestation may be a cheaper method to convert former agricultural land to nature (Son et al., 2003; Kemmers et al., 2005). In this way, young trees may actually profit from high nutrient availability. A method not yet widely used in heavily fertilized agricultural fields is conversion to rangeland, a more or less natural grassland, which can support herds of large grazers (Hendrikx, 1977). Although this is not undisputed, grazing may even lead to reduced nutrient avail-

* Corresponding author.
E-mail address: a.m.kooijman@uva.nl (A.M. Kooijman).

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Table 1
Potential differences between ecosystem types and sampling years for characteristics of the mineral topsoil (0–20 cm). Significant effects are given as probability values; ns = not significant ($p > 0.05$).

	Ecosystem type	Sampling year	Ecosystem type * sampling year
pH	0.0001	0.010	0.007
Soil C-content (%)	0.0001	ns	ns
Soil C-content ($kg\,m^{-2}$)	0.0001	ns	ns
Soil C:N ratio ($g\,g^{-1}$)	0.0001	ns	ns
Soil N-content ($g\,m^{-2}$)	0.0001	ns	ns

Table 2
Soil characteristics of the mineral topsoil (0–20 cm) of different ecosystem types related to agricultural soil, reference vegetation and restored sites on former agricultural soil. Values are means (n = 9–10) and standard deviations of 2007 and 2013 combined. Different letters indicate differences between particular ecosystem types for a particular parameter ($p < 0.01$).

	pH	Soil C (%)	Soil C($kg\,m^{-2}$)	Soil N($g\,m^{-2}$)	C:N soil($g\,g^{-1}$)
Agricultural field (AF)	5.5 (0.3)^{d}	2.2 (0.7)^{cd}	6.3 (1.9)^{cd}	369 (94)^{d}	16.9 (2.0)^{a}
Reference heathland (H0)	4.0 (0.1)^{b}	4.1 (1.0)^{f}	7.4 (1.2)^{d}	259 (48)^{c}	28.7 (2.9)^{c}
Partial topsoil removal (H1)	5.3 (0.5)^{cd}	1.3 (0.4)^{b}	3.3 (0.9)^{b}	160 (43)^{b}	20.6 (2.1)^{b}
Complete topsoil removal (H2)	5.1 (0.5)^{c}	0.6 (0.2)^{a}	1.9 (0.6)^{a}	76 (46)^{a}	28.5 (9.2)^{c}
Reference grassland (G0)	4.1 (0.2)^{b}	3.0 (1.1)^{e}	6.3 (2.2)^{cd}	277 (98)^{c}	23.0 (1.9)^{b}
Productive rangeland (G1)	5.4 (0.4)^{d}	2.7 (0.6)^{de}	6.2 (1.2)^{cd}	358 (41)^{d}	16.7 (2.3)^{a}
Intermediate rangeland (G2)	5.1 (0.3)^{c}	2.2 (0.3)^{cd}	5.4 (1.0)^{c}	281 (55)^{c}	19.5 (2.8)^{ab}
Reference forest (F0)	3.6 (0.1)^{a}	3.1 (0.7)^{e}	7.3 (2.5)^{d}	243 (80)^{c}	31.6 (4.8)^{c}
New forest (F1)	4.3 (0.2)^{b}	2.0 (0.3)^{c}	5.5 (1.1)^{c}	275 (64)^{c}	20.1 (2.5)^{ab}

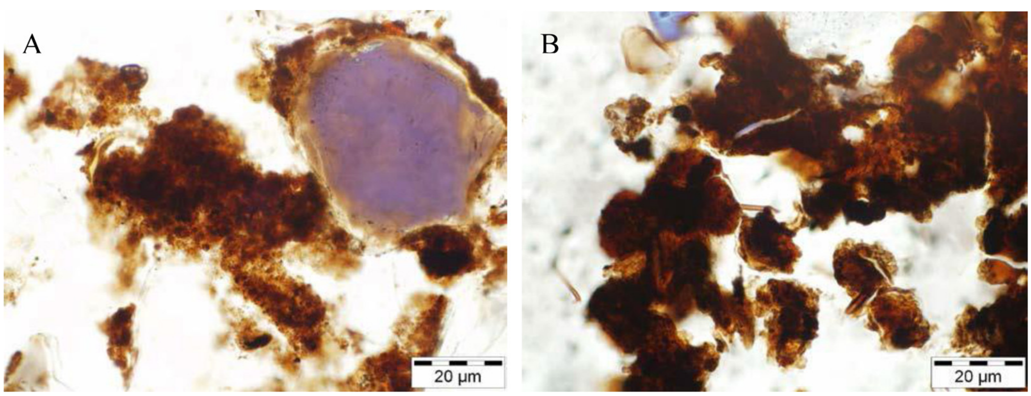

Fig. 1. Comparison of the form of soil organic matter in agricultural soils (A) and reference grasslands (B). In agricultural soil, organic matter is mostly present as intertextic slurry. In reference soil, organic matter mainly consists of aggregates with fungal hyphae.

ability, especially for N (Bullock et al., 1994; McBride, 1994; Smith and Rushton, 1994; Oomes et al., 1996; Pegtel et al., 1996; Janssens et al., 1998; Kemmers et al., 2005).

Many studies deal with one restoration method in particular. However, on a landscape scale, several methods may be needed at the same time, and integrated studies, comparing several strategies over a time-scale of decades, and dealing with different ecosystem compartments, are needed. Also, conversion of former corn fields to rangelands has not yet been widely applied.

The aim of this study is to evaluate three different strategies for restoration of former agricultural fields on sandy soil after 18 and 25 years in Nature reserve Maashorst, one of the largest nature restoration projects in the Netherlands (Hendrikx, 1977). At the end of the 1980s, large agricultural areas have been converted to an open, partly forested landscape, with free-living herds of moeflon, sheep, highland cattle and horses, and since this year European bison. The restoration strategies used were conversion to heathland by topsoil removal, conversion to rangeland, i.e., more or less natural grassland maintained by large grazers, and afforestation with *Quercus robur* L. The restoration potentials were studied in an integrative approach, in which agricultural fields, reference and restored sites were included, and responses of soil and vegetation analyzed simultaneously.

2. Material and methods

2.1. Study sites

The study was conducted in Maashorst Nature reserve, an area of 4200 ha in the southeastern part of the Netherlands (51°42; 5°37), with sandy, podzolic soils. The climate is humid temperate, with mean annual temperature of 10 °C and 800 mm rainfall, more or less evenly distributed over the year. The natural vegetation consists of deciduous forests, dominated by species such as *Quercus robur* and *Q. petraea* (Matt.) Liebl. (Hendrikx, 1977).

Palynological research showed that conversion of deciduous forest into a more open park landscape started in the Late-palaeolithicum (Van Mourik et al., 2012). In the late middle ages, and especially the 18th century, sand drifting started, mainly due to overexploitation of the until that moment well preserved heath (Vera, 2011). In the 20th century, when artificial fertilizers became widely available, large parts of the heathlands were converted to agricultural fields. Soils were ploughed and fertilized. Agriculture prevailed till the end of the 1980s, after which many agricultural fields were transformed into more natural habitats, such as heathlands, rangelands, i.e., more or less natural grasslands maintained by free-ranging herbivores, and forests. Besides agricultural and fertilization history, restoration may be hampered by high atmospheric N-deposition, which amounted to 50 kg ha^{-1} $year^{-1}$ in the 1990s (GCN, 2009), and decreased to 35–45 kg ha^{-1} $year^{-1}$ in the past decade.

2.2. Experimental set-up

Soil and vegetation samples were collected in nine different ecosystem types: agricultural fields (AF), three reference ecosystems: heathland (H0), grassland (G0) and forest (F0), and five restored ecosystems: heathland with partial topsoil removal (H1), heathland with complete topsoil removal (H2), productive rangeland (G1), intermediate rangeland (G2) and new forest (F1).

Agricultural fields were planted with maize in 2007, and with maize, rye grass or potato in 2013. Natural heathlands and grasslands were located in the northern part of the Nature reserve, where agriculture had been less intensive. Reference forests consisted of one century old *Quercus robur* trees. With partial topsoil removal, only half of the 30 cm thick A_p-horizon was removed 25 years ago, while the organic topsoil was removed completely at sites with complete topsoil removal, which should lead to more nutrient-poor soil conditions (Verhagen et al., 2001). In conversed rangelands, former agricultural fields were sown with *Lolium perenne* L. about 25 years ago, and regularly mown for 2–3 years without fertilization. After this, grazing with free-ranging mouflon, sheep, highland cattle and horses was applied. Productive and intermediate rangelands occurred throughout the area, and differed from each other in aboveground biomass and species richness. The new forests were planted with *Quercus robur* on former agricultural soils some 25 years ago.

For each of the nine situations, five representative and homogeneous sampling sites of 2 × 2 m (for forests 5 × 5 m) were selected in different parts of the 4200 ha Maashorst Nature reserve according to stratified random sampling procedures. GPS-coordinates of the sampling sites were recorded in 2007, and used in 2013 to relocate them. However, due to inaccuracies, it was not possible to sample in exactly the same locations.

2.3. Field survey

In June 2007 and April 2013, two soil samples of the upper 20 cm were collected with a rectangular sampler called 'humushapper' (Wardenaar, 1987) in the centre of each of the five sampling sites for each ecosystem type: one for P-fractionation and other chemical analyses, and the other for the mineralization of N and P. All samples were stored at 4 °C in the dark until further analysis. Organic layers were only present in the forests, and sampled in 25 × 25 cm plots for C-stocks and potential net N-mineralization. To get a better understanding of the soil processes, an intact soil core of the upper 15 cm was collected in Kubiena boxes in one of the plots for each of the nine ecosystem types in 2007. These were used for microscopical analysis of thin sections.

In all reference and restored plots, plant species composition was recorded in quadrants of 2 × 2 m (open vegetation) or 5 × 5 m (forest undergrowth) in summer 2007 and 2013. All species present were listed, and cover values estimated as percentages. Nomenclature of vascular plants was according to Van der Meijden (2011), and for bryophytes according to Van Tooren and Sparrius (2007). Cover of eutrophic species was calculated separately, and included eutrophic grasses such as *Lolium perenne* L., *Dactylis glomerata* L., *Phleum pratense* L., *Poa pratense* L., *Holcus lanatus* L. and herbs such as *Galeopsis tetrahit* L., *Taraxacum officinale* F.H.Wigg. and *Urtica dioica* L.

In July-August, at peak standing crop, vegetation was sampled for aboveground biomass and chemical analysis, in 25 × 25 cm plots except for forests. In the agricultural fields, where plant species composition was not recorded, vegetation was only sampled in 2013, because the fields were already harvested in 2007. In the forests, only undergrowth vegetation was sampled, in plots of 1 × 1 m. Undergrowth vegetation was used for chemical analysis in both 2007 and 2013, but aboveground biomass was only measured in 2013.

2.4. Chemical analysis

Fresh weight and gravimetric moisture content of the mineral topsoil were determined, and dry weight and bulk density calculated. After homogenization, pH-H_2O was measured in water, using a 1:2.5 weight:volume ratio (Allen et al., 1989). One sample in the complete topsoil removal treatment had an unrealistic pH-value above 6.5 in 2013, which normally does not occur in lime-poor soils. This value was discarded. Aboveground vegetation samples were dried for 48 h at 70 °C to determine dry weights. After grinding of soil and vegetation samples, C and N-contents were determined with a CNS analyzer (Westerman, 1990). Plant P-contents were determined on ICPOES after a mixed microwave destruction with 65% HNO_3 and 37% HCl (Bettinelli et al., 1989). Plant K-contents were also measured, but did not show significant differences and were left out of further analyses. Vascular plant N:P ratios, used as indicator whether N or P could be a limiting factor (Koerselman and Meuleman, 1996) were calculated as g g^{-1}.

In 2007, soil extractions were performed to get a better understanding of different P-fractions in the mineral topsoil. Total, inorganic and organic P were analyzed with an H_2SO_4 extractions (Murphy and Riley, 1962). Subsamples of 1 g were heated for 6 h at 500 °C to measure total P, while non-heated subsamples were used to determine inorganic P. Heated and non-heated samples were extracted for 16 h with 50 ml 0.5 M H_2SO_4, centrifuged, filtered over a 0.2 μm filter and measured colorimetrically. Organic P was calculated as the difference between total and inorganic P. In addition to total, organic and inorganic P, the amount of P bound to amorphous sesqui(hydr)oxides and organic Al/Fe complexes was determined by 4 h of extraction in the dark with 0.073 M NH_4-oxalate/0.05 M oxalic acid at pH 3.0 (Schwertmann, 1964). Concentrations of P, Fe and Al were measured on ICPOES. The P-saturation index, calculated as $P_{ox}/(Fe_{ox} + Al_{ox})$, was used as an estimate of P-saturation of the Fe-Al binding sites, which are considered to be saturated around values of 0.30 (Van der Zee and van Riemsdijk, 1988). The amount of Fe and Al present in organic complexes was measured in extractions with 0.1 M Na-pyrophosphate at pH 10 (Dixon and Weed, 1989). However, these values were more or less similar to the total amounts in the oxalate-extractions, indicating that Fe and Al are generally bound to OM-complexes, and were not further used.

Bio-available P was determined in both 2007 and 2013 with extraction with 0.5 M $NaHCO_3$ at pH 8.5 (Olsen et al., 1954). In 2013, one AF and one H2 sample had unrealistic values, which were not further used.

2.5. Desorption characteristics of soil P

To explore potential differences in P-release between agricultural fields, reference and restored ecosystems, a P-desorption experiment was conducted in 2007. Due to restrictions of the procedure, the amount of samples was limited to one for each of the nine ecosystem types. Dialysis tubes, filled with a hydrous ferric oxide suspension (HFO) of 2.5 mmol Fe l^{-1}, were used as P-sinks in a soil suspension (Freese et al., 1995). The soil suspension consisted of 5 g soil and 80 ml of solution of 2 mM $CaCl_2$ and 0.3 mM KCl. The dialysis tubes were replaced after 19, 58, 120, 278, 437, 1198 and 2535 h of end-over-end shaking. Desorbed P-concentrations were measured colorimetrically after dissolving the HFO-suspension in 1 ml concentrated 97% sulphuric acid (Murphy and Riley, 1962).

Desorbed P-concentrations were used to calculate fast and slow releasing P-pools. Release of P from sesquioxides is mainly a diffusion process (Lookman et al., 1995), with a small pool with fast release kinetics from reactive surfaces, and a large pool with slow release kinetics, bound to the interior sites of sesquioxides (Hingston et al., 1974). Both pools are characterized by a first order reaction, meaning that desorption becomes harder after each moment of previous desorption:

$$P_{des}(t) = P_{poolA}(0) \times (1-\exp^{-kA\times t}) + P_{poolB}(0) \times (1-\exp^{-kB\times t}),$$

in which $P_{poolA}(0)$ and $P_{poolB}(0)$ are the initial P-concentrations of the fast and slow pool respectively, and kA and kB the first order rate constants. The fast and slow releasing P-pools were calculated with the iteratively evaluating Monte Carlo algorithm SCEM-UA, which involved 25,000 evaluations per calculation (Vrucht et al., 2003). Monte Carlo algorithms try to find the distribution of unknown variables in a known formula, that most closely matches the data already known (Metropolis and Ulam, 1949), in this case t and $P_{des}(t)$.

2.6. Laboratory incubation experiment

In 2007 and 2013, potential net N-mineralization was analyzed in a laboratory incubation experiment, which lasted 6–7 weeks. Fresh homogenized mineral samples were placed into petri dishes and stored in the dark at 20 °C. Optimal moisture levels of 50% on weight basis (Tietema, 1992) were checked during the experiment and replenished when necessary. Fresh and incubated samples, an equivalent of 4.5 g dry material, were extracted for 1 h with 50 ml 0.5 M K_2SO_4 (Westerman, 1990). Concentrations of NO_3 and NH_4 were analyzed colorimetrically by a continuous flow auto-analyzer. One AF sample had extreme values for ammonium and nitrate in fresh soil in 2007, possibly due to application of fresh manure, and values were not further used. Net N-mineralization was calculated as the difference in total inorganic N concentrations ($NH_4 + NO_3$) between incubated and fresh samples. One AF and one F1 sample had extremely high values in 2013, and values were discarded. Nitrification was calculated as percentage released NO_3 of the total net N-mineralization.

2.7. Micromorphology

Thin sections of the topsoil were micromorphologically analyzed with an Olympus BH-2 polarizing microscope. Magnification factors of 40 and 100 were used to study distribution patterns of organic matter and minerals, and occurrence of excrements and pedotubules. Magnification factors of 400 and 1000 were used to study fungal hyphae. We selected nine micromorphological characteristics based on earlier research on humus forms, organic matter, soil fauna and ped characteristics (Dijkstra and van Mourik, 1996; Stoops, 2003). These characteristics were scaled semi-quantitatively, on a scale from 0 to 3: 0 = not detected, 1 = low activity or amount, 2 = moderate activity or amount, 3 = high activity or amount (Kooijman et al., 2009).

2.8. Statistics

Differences in soil variables measured in both 2007 and 2013 were tested with a two-way general linear model, with the nine ecosystem types and two sampling years as independent variables (Codey and Smith, 1986). Post-hoc LSmeans tests were used to test differences between individual mean values. Differences in vegetation characteristics measured in both years were tested in the same way, but without the agricultural fields in which vegetation was sampled only in 2013. Differences in P-fractions, Fe and Al, which were only measured in 2007, were tested with one-way general linear models with ecosystem type as independent factor, and LSmeans post-hoc tests for differences between individual mean values. To classify the soil micromorphological characteristics, a Principal Component Analysis (PCA) was performed in Canoco (ter Braak 1986). These results should be seen as indicative only, because calculations were based on only nine topsoil samples. Differences in plant species composition between vegetation types were tested for all sampling sites except the agricultural fields, with Correspondence Analysis (CA) within the same programme. Correlations with environmental parameters were also analyzed; for the missing values for pH and P-Olsen in one H2 sample in 2013, mean values were used for this vegetation type in that year.

3. Results

3.1. General soil characteristics

General soil characteristics did not differ between sampling years, except for pH, which was slightly higher in 2013, especially in sites with topsoil removal (Table 1). This is probably due to slight differences in sampling locations. However, all measured soil variables clearly differed between vegetation types (Table 2). Soil pH was relatively low in the reference heathland, grassland and forest, with values ranging between 3.6 and 4.1. In agricultural fields and all restored sites except new forests, pH was significantly higher, even with topsoil removal, and values ranged between pH 5.1 and 5.5.

Reference soils generally showed higher C-percentage than agricultural fields, although differences per m^2 were not significant. However, N-contents were significantly higher in agricultural fields. As a result, soil C:N ratios were significantly lower in agricultural fields than in reference soils. As expected, topsoil removal resulted in a significant decrease of soil C and especially N compared to agricultural soil, leading to significantly higher C:N ratios. In restored rangelands, soil C and N contents, as well as C:N ratios, were still comparable to agricultural fields. However, intermediate rangelands had significantly lower soil N-content than productive rangelands. In the new forests, soil C did not differ, but N-content was significantly lower than in agricultural fields. Nevertheless, C:N ratio remained much lower than in reference forests.

3.2. Thin sections and soil microstructure

Ploughing and fertilization completely changed the distribution and structure of organic material in the mineral topsoil (Figs. 1 and 2). The position in the PCA-diagram suggested that the three reference soils had well-developed structure and many fecal pellets, microarthropods and fungi. In agricultural fields, however, organic matter had turned into unstructured intertextic slurry, with low microarthropods and fungal activity. In restored sites, intertextic slurry was still present, but microarthropod activity generally increased, except for topsoil removal treatments, where soil life had not improved much, due to the removal of organic matter. In new forests, however, soil life clearly improved. In restored grasslands, even a new type of soil ecoystem developed, with many earthworms and complex peds, probably due to the higher pH.

Table 3
P-fractionation of the mineral topsoil in different ecosystem types related to agricultural soil, reference vegetation and restored sites on former agricultural soil. P_{ox} = oxalate-extractable phosphorus, bound to iron and aluminium; α_{ox} = P-saturation index ($\alpha_{ox} = P_{ox}/(Fe_{ox} + Al_{ox})$). AF = agricultural field; H0 = reference heathland; H1 = partial topsoil removal; H2 = complete topsoil removal; G0 = reference grassland; G1 = productive rangeland; G2 = intermediate rangeland; F0 = reference forest; F1 = new forest. Values are means (n = 9-10) and standard deviations. All parameters showed significant overall differences between ecosystem types; different letters indicate individual differences between particular ecosystem types for a particular parameter ($p < 0.05$).

	Total P($mg\,kg^{-1}$)	Inorganic(% total P)	Organic(% total P)	P_{ox}($mg\,kg^{-1}$)	P_{ox}(% total P)	Al-Fe($mmol\,kg^{-1}$)	α_{ox} ($m\,m^{-1}$)
AF	615 (57)^{c}	73 (3)^{c}	27 (3)^{a}	541 (30)^{c}	88 (4)^{b}	61 (6)^{ab}	0.29 (0.02)^{c}
H0	136 (18)^{ab}	14 (5)^{a}	86 (5)^{c}	72 (19)^{a}	58 (10)^{a}	97 (40)^{b}	0.03 (0.02)^{a}
H1	272 (124)^{b}	63 (11)^{c}	37 (11)^{a}	238 (111)^{b}	87 (4)^{b}	58 (14)^{ab}	0.13 (0.04)^{b}
H2	132 (92)^{ab}	49 (21)^{b}	51 (21)^{b}	114 (91)^{ab}	82 (9)^{b}	48 (6)^{a}	0.07 (0.05)^{a}
G0	138 (23)^{ab}	13 (1)^{a}	87 (1)^{c}	78 (23)^{a}	52 (7)^{a}	84 (45)^{b}	0.03 (0.01^{a}
G1	776 (168)^{c}	66 (5)^{c}	34 (5)^{a}	673 (164)^{c}	86 (4)^{b}	80 (22)^{b}	0.28 (0.05)^{c}
G2	714 (127)^{c}	70 (6)^{c}	30 (6)^{a}	630 (102)^{c}	89 (3)^{b}	98 (17)^{b}	0.22 (0.04)^{c}
F0	93 (31)^{a}	26 (7)^{a}	74 (7)^{c}	55 (28)^{a}	57 (11)^{a}	41 (29) ^{a}	0.06 (0.03^{a}
F1	542 (169)^{c}	70 (4)^{c}	30 (4)^{a}	478 (159)^{c}	88 (3)^{b}	69 (16)^{ab}	0.22 (0.07)^{c}

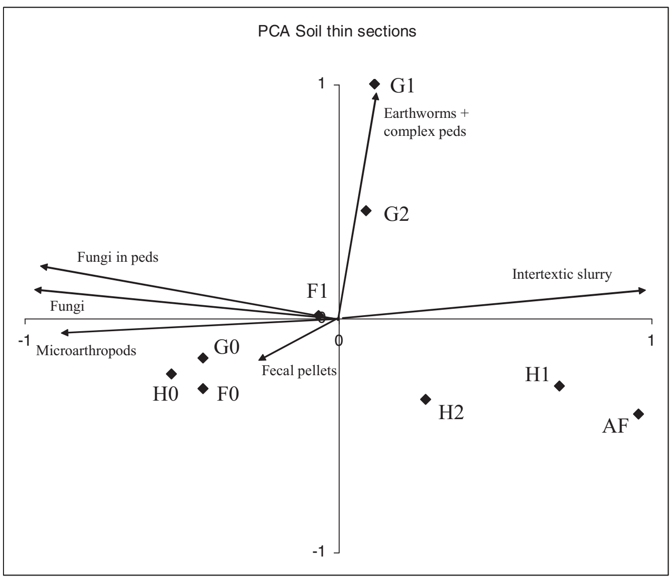

Fig. 2. Principal Component Analysis of micromorphological thin sections of the mineral topsoils of different ecosystem types related to agricultural soil, reference vegetation and restored sites on former agricultural soil. AF = agricultural field; H0 = reference heathland; H1 = partial topsoil removal; H2 = complete topsoil removal; G0 = reference grassland; G1 = productive rangeland; G2 = intermediate rangeland; F0 = reference forest; F1 = new forest.

3.3. Availability of P

In the P-fractionation, P could be divided in total P, organic P, inorganic P and P bound to amorphous Fe and Al (Table 3). Total P strongly increased from reference to agricultural soils. In reference soils, total P ranged between 93 and 138 $mg\,kg\,ds^{-1}$, and consisted for 74–87% of organic P. With only 3–6% of the binding places occupied with P, P-saturation (α_{ox}) was also very low. In agricultural soils, total P was approximately five times higher than in reference soils, and mainly consisted of inorganic P. Also, P-saturation increased to more or less maximum values of 0.29 $mol\,mol^{-1}$. In restored sites, total P only decreased in plots where the topsoil was removed. When the topsoil was removed completely, total P and P-saturation even decreased to values found in reference heathlands. However, even with complete topsoil removal, total P still consisted for a large part of inorganic P. In restored rangelands and new forests, total P was as high as in agricultural fields, and still mainly consisted of inorganic P. P-saturation values also remained high.

Differences in P-fractions between reference, agricultural and restored soils were supported by P-desorption experiments, even if only one replicate could be used (Fig. 3, Table 4). For almost all soils, the slow releasing P-pool accounted for 71–86% of total P, except for reference forests, in which the fast P-pool seemed more important. Reference heathland, grassland and forest soils desorbed only small amounts of P, and only at the start of the experiment. In contrast, agricultural soil released large amounts of P during the entire experiment, although desorption slowed down with time. The fast releasing P-pool was relatively small and the slow pool was very large. In topsoil removal treatments, fast and slow releasing P-pools decreased, especially with complete topsoil removal. In productive rangelands, fast and slow pools were slightly higher than in the agricultural soil, but in intermediate rangelands slightly lower. Similar concentrations were found for new forests.

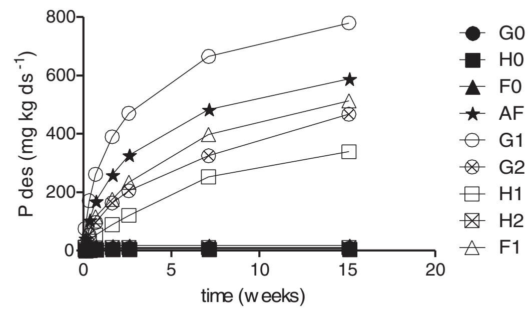

Fig. 3. Cumulative desorption of phosphorus over a 15 week period in the mineral topsoil (0–20 cm) in different ecosystem types related to agricultural soil, reference vegetation and restored sites on former agricultural soil. For each of the reference, agricultural and restored sites, one soil sample was used, so that results should be seen as indicative only. G0 = reference grassland; H0 = reference heathland; F0 = reference forest; AF = agricultural field; G1 = productive rangeland; G2 = intermediate rangeland; H1 = partial topsoil removal; H2 = complete topsoil removal; F1 = new forest;.

The above patterns in P-availability were supported by the concentration of bio-available P-Olsen in the soils (Table 5, Fig. 4). Differences between sampling years were not significant, which suggested that P-availability has not changed in the past seven years. In both years, P-Olsen was very low in reference heathland, grassland and forest. Concentrations strongly increased in agricultural fields and remained high in conversed rangelands and new forests. Bio-available P only decreased with topsoil removal, especially when the topsoil was removed completely.

3.4. Availability of N

Differences in N-availability between ecosystem types were less clear than for P (Table 5 and 6, ; Fig. 4). In fresh samples, NO_3 concentrations did not differ between sampling years, but NH_4 concentrations and NH_4:NO_3 ratios were slightly higher in 2013 than

Table 4
Values of the fast and slow P-pools in different ecosystem types related to agricultural soil, reference vegetation and restored sites on former agricultural soil.

	Fast P-pool (mg kg^{-1})	Slow P-pool (mg kg^{-1})	Slow P-pool (%)
Agricultural field (AF)	142	478	77
Reference heathland (H0)	2	5	71
Partial topsoil removal (H1)	68	273	80
Complete topsoil removal (H2)	2	8	80
Reference grassland (G0)	2	9	82
Productive rangeland (G1)	196	593	75
Intermediate rangeland (G2)	69	396	85
Reference forest (F0)	15	3	17
New forest (F1)	71	434	86

Table 5
Potential differences between ecosystem types and sampling years for soil nutrient characteristics. Significant effects are given as probability values; ns = not significant ($p > 0.05$).

	Ecosystem type	Sampling year	Ecosystem type * sampling year
P-Olsen (mg kg^{-1})	0.0001	ns	ns
Net P-mineralization (mg kg^{-1} day^{-1})	0.019	ns	ns
Fresh NH_4-content (mg kg^{-1})	ns	0.0001	0.032
Fresh NO_3-content (mg kg^{-1})	0.0001	ns	ns
Ratio NH_4-NO_3 (% NH_4)	0.0001	0.0001	0.0001
Net N-mineralization (mg kg^{-1} day^{-1})	0.0001	0.0001	0.016
Nitrification (%)	0.0001	ns	ns

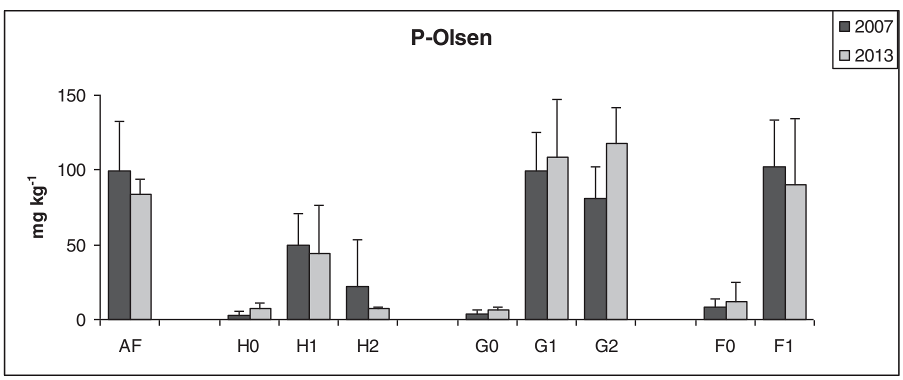

Fig. 4. Nutrient availability in the mineral soil (0–20 cm) of different ecosystem types related to agricultural soil, reference vegetation and restored sites on former agricultural soil, and different sampling years. AF = agricultural field; H0 = reference heathland; H1 = partial topsoil removal; H2 = complete topsoil removal; G0 = reference grassland; G1 = productive rangeland; G2 = intermediate rangeland; F0 = reference forest; F1 = new forest. Mean values (n = 9-10) and standard deviations are given.

Table 6
Inorganic nitrogen in fresh samples of the mineral topsoil (0–20 cm) and net P-mineralization in a 6-7 week laboratory incubation experiment in different ecosystem types related to agricultural soil, reference vegetation and restored sites on former agricultural soil. Values are means (n = 9-10) and standard deviations. Different letters indicate differences between particular ecosystem types for a particular parameter ($p < 0.01$).

	Net P-mineralization(μg kg^{-1} day^{-1})	N-NH_4(mg kg^{-1})	N-NO_3(mg kg^{-1})	NH_4-NO_3 ratio (% NH_4)	Nitrification (%)
Agricultural field (AF)	3 (7)^{a}	5.1 (6.2)^{ab}	8.9 (7.0)^{d}	0.37 (0.29)^{a}	100 (1)^{c}
Reference heathland (H0)	−1 (2)^{a}	3.9 (3.1)^{ab}	0.3 (0.3)^{a}	0.88 (0.11)^{d}	21 (36)^{a}
Partial topsoil removal (H1)	4 (5)^{a}	5.3 (5.9)^{ab}	0.4 (0.6)^{a}	0.88 (0.11)^{d}	100 (1)^{c}
Complete topsoil removal (H2)	1 (4)^{a}	3.1 (2.1)^{a}	0.1 (0.2)^{a}	0.90 (0.11)^{d}	87 (28)^{bc}
Reference grassland (G0)	0 (1)^{a}	3.6 (4.3)^{a}	1.1 (1.5)^{ab}	0.71 (0.26)^{c}	72 (39)^{b}
Productive rangeland (G1)	58 (58)^{b}	3.8 (2.5)^{ab}	5.2 (2.9)^{c}	0.41 (0.23)^{a}	100 (0)^{c}
Intermediate rangeland (G2)	15 (8)^{a}	3.3 (2.4)^{a}	1.4 (0.9)^{ab}	0.65 (0.23)^{bc}	100 (0)^{c}
Reference forest (F0)	17 (28)^{a}	4.3 (3.2)^{ab}	2.5 (1.2)^{bc}	0.56 (0.22)^{b}	98 (5)^{c}
New forest (F1)	1 (94)^{a}	7.0 (9.4)^{b}	3.9 (2.1)^{b}	0.47 (0.29)^{ab}	99 (2)^{c}

in 2007. In fresh samples, NH_4 concentrations showed no overall differences between ecosystem types, but NO_3 concentrations were much higher in agricultural fields than in reference heathland, grassland and forest. In treatments with topsoil removal, NO_3 concentrations decreased again and showed concentrations similar to the reference heathland. As a result, ratios of NH_4:NO_3 were very high in reference heathland and in both topsoil removal sites, and ranged from 88 to 90% NH_4. In agricultural soil, this ratio was reduced to only 37%. In productive rangelands and new forests, NO_3 concentrations remained relatively high, but in intermediate rangelands, values decreased compared to agricultural soil. Ratios of NH_4:NO_3 remained low in all three ecosystem types.

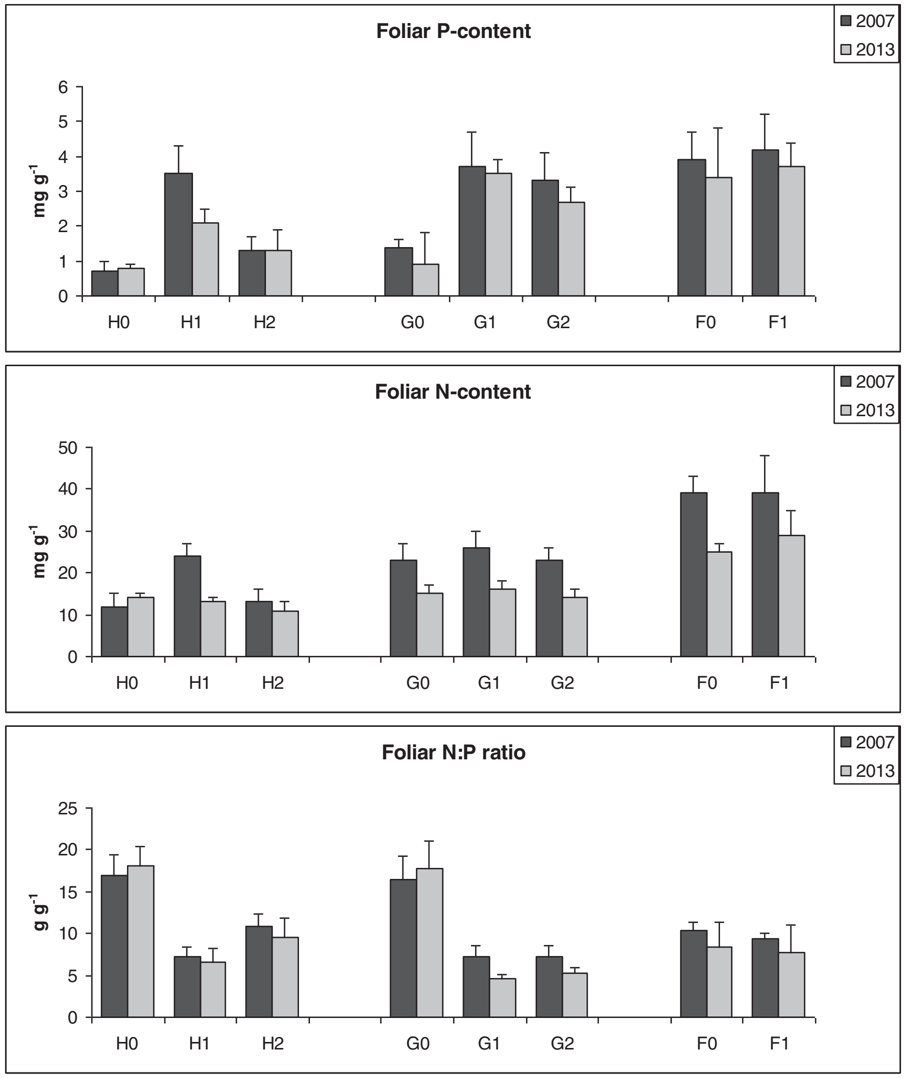

Fig. 5. Plant nutrient characteristics in different ecosystem types related to reference vegetation and restored sites on former agricultural soil, and different sampling years. H0 = reference heathland; H1 = partial topsoil removal; H2 = complete topsoil removal; G0 = reference grassland; G1 = productive rangeland; G2 = intermediate rangeland; F0 = reference forest; F1 = new forest. Mean values (n = 9-10) and standard deviations are given.

Potential net N-mineralization in the mineral soil clearly differed between sampling years and ecosystem types. In 2013, net N-mineralization was generally lower than in 2007. In reference heathlands, net N-mineralization was lower than in agricultural soils, but in reference grasslands and forests, rates were more or less the same. For reference forests, total net N-mineralization would be higher, as net N-mineralization in the organic layer was approximately as high as in the mineral topsoil (data not shown). Topsoil removal clearly led to decreased net N-mineralization compared to agricultural soils. In converted rangelands, however, net N-mineralization was as high or even higher than in agricultural soils. In new forests, net N-mineralization was high in 2007, but low in 2013. Moreover, the contribution of the organic layer to net N-mineralization was still negligible (data not shown).

Nitrification in the mineral topsoil only differed between ecosystem types. In reference soils, nitrification was relatively low for heathland and grassland. In reference forests, nitrification was also relatively low in the organic layer, with 50% of the net N-mineralization (data not shown), but values were higher in the mineral topsoil. In agricultural soil, nitrification increased up to 100% of net N-mineralization, and remained high in restored ecosystems, even in topsoil removal treatments.

3.5. *Response of the vegetation*

The gradient in P-availability in the soil was more or less reflected in plant tissue P-concentrations (Table 7, Fig. 5). Plant P-concentrations were low in reference heathland and grassland, and in sites with complete topsoil removal. Plant P-concentrations were however very high in converted rangelands and in sites with partial topsoil removal. In these ecosystems, values were more or less comparable to the plant P-concentration in agricultural fields in 2013 of $3.9 \pm 1.0\,mg\,g^{-1}$. In old and new forests, plant P-concentrations were also high, although P-fractions in the mineral soil had been low in the reference vegetation.

In general, plant P-concentrations were slightly, but significantly lower in 2013 than in 2007. The decrease in plant N-concentrations between 2007 and 2013 was, however, much higher. In 2007, in reference grassland, partial topsoil removal sites and converted rangelands, plant N-concentrations ranged around $23–26\,mg\,g^{-1}$. These concentrations were more or less similar to the $27 \pm 13\,mg\,g^{-1}$ measured in plants on agricultural soil in 2013. However, in 2013, plant N-concentrations in reference grasslands, partial topsoil removal sites and converted rangelands had decreased to $13–16\,mg\,g^{-1}$. Such concentrations were

Table 7
Potential differences between ecosystem types and sampling years for vegetation characteristics. The statistical analyses were conducted only for reference vegetation and restored sites in former agricultural fields, as aboveground biomass in agricultural fields was only sampled in 2013, and vegetation descriptions were not made at all. Significant effects are given as probability values; ns = not significant ($p > 0.05$).

	Ecosystem type	Sampling year	Ecosystem type * sampling year
Plant P-content ($mg\,g^{-1}$)	0.0001	0.007	ns
Plant N-content ($mg\,g^{-1}$)	0.0001	0.0001	0.0001
Plant N:P ratio ($g\,g^{-1}$)	0.0001	0.022	ns
Peak aboveground biomass ($g\,m^{-2}$)	0.0001	ns	0.007
Total P in vegetation ($g\,m^{-2}$)	0.0001	ns	0.010
Total N in vegetation ($g\,m^{-2}$)	0.0001	ns	0.002
Total number of species	0.0001	ns	ns
Number of vascular plant species	0.0001	ns	ns
Number of moss and lichen species	0.011	ns	ns
Herb cover (%)	0.0001	0.023	ns
Moss and lichen cover (%)	0.0001	ns	0.015
Cover of eutrophic species (%)	0.0001	ns	ns

found in reference heathland and complete topsoil removal sites in 2007. The clear decrease in plant N-concentrations also occurred in old and new forests, although values remained relatively high compared to other ecosystem types. Since the decrease in plant N-concentrations was stronger than the decrease in P, the N:P ratios also decreased significantly between 2007 and 2013, except for reference heathland and grassland in which they remained high. In these two ecosystems, N:P ratios were higher than 15, which indicates P-poor conditions. On agricultural soil, where plants were only analyzed in 2013, foliar N:P ratios ranged around 6.9, which points to excess P. All restored ecosystems also had very low N:P ratios, with values around 10 or lower. This was even the case in the two topsoil removal treatments.

Aboveground biomass did not differ between sampling years, although the interaction between sampling year and ecosystem type was significant, due to reference heathlands in which heather shrubs had grown substantially between 2007 and 2013. In other vegetation types, changes in biomass between 2007 and 2013 were not significant. Reference heathland had very high aboveground biomass values, because of the perennual nature of the heather shrubs (Table 8). However, agricultural maize and potatofields, only measured in 2013, also showed $971 \pm 142\,g\,m^{-2}$. In all other ecosystem types, aboveground biomass (in the undergrowth) was clearly lower. Even in productive rangelands, mean standing crop was only $356\,g\,m^{-2}$, and values in intermediate rangelands were almost two times lower. In productive rangelands, cover of eutrophic species was higher than in any other site, but was still only 39%, and mostly consisted of *Holcus lanatus*. For cover of eutrophic species, differences between sampling years were not significant, although productive rangelands showed a decrease between 2007 and 2013 from 45 to 30%, mainly due to a shift from *H. lanatus* to *A. capillaris*.

Total species number and species composition only differed between ecosytem types. Total species number was relatively low in reference heathland, grassland and forests, probably due to the low pH. Species richness increased considerably in restored sites, especially with topsoil removal and in intermediate rangelands. In sites with topsoil removal, *Calluna vulgaris* L. (Hull) was an important species, which established in most plots (Table 9). In the CA-diagram, the two topsoil removal treatments were also relatively close to their reference heathland, especially with complete topsoil removal (Fig. 6). However, sites with topsoil removal contained additional species which were not present in reference heathland. Part of these were species such as *Ornithopus perpusillus* L., *Jasione montana* L., *Filago minima* (Sm.) Pers. and *Teesdalia nudicaulis* (L.) R.Br., which belong to pioneer stages of nutrient-poor grasslands with slightly elevated pH. In addition, more eutrophic grassland species had established, such as *Cerastium fontanum* Baumg. and *Plantago lanceolata* L., even with complete topsoil

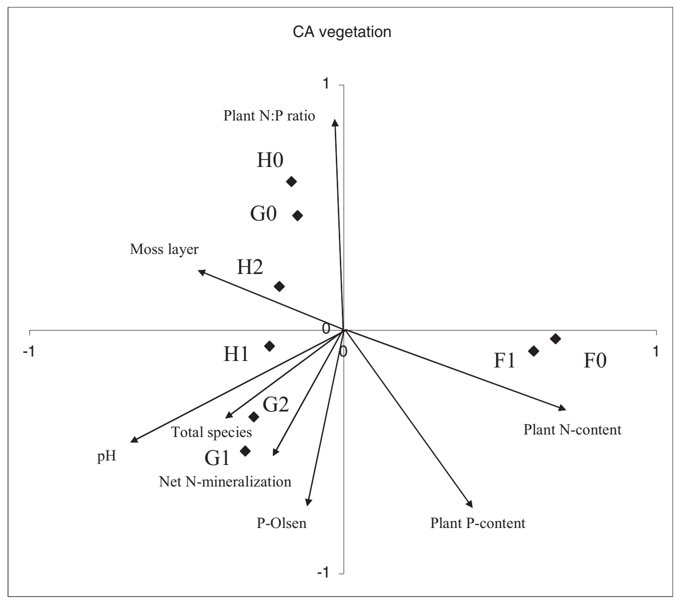

Fig. 6. Correspondence analysis of plant species composition and environmental variables in different ecosystem types related to reference vegetation and restoration sites on former agricultural soil. H0 = reference heathland; H1 = partial topsoil removal; H2 = complete topsoil removal; G0 = reference grassland; G1 = productive rangeland; G2 = intermediate rangeland; F0 = reference forest; F1 = new forest. The eigenvalues of axis 1 and 2 are 0.937 and 0.801 respectively.

removal. Productive and intermediate rangelands hardly looked like reference grasslands at all. Many species from more eutrophic grassland habitats had established, such as *Jacobaea vulgaris* Gaertn. and *Crepis capillaris* (L.) Wallr. In intermediate rangelands also some nutrient-poor grassland species were found, such as *Hypericum perforatum* L. and *Veronica officinalis* L. Red-list species were rare, but *Dianthus deltoides* L. had established, if only once in each rangeland type. In new forests, some reference forest species established in the undergowth, such as *Ceratocapnos claviculatum* (L.) Lidén and *Dryopteris dilatata* (Hoffm.) A.Gray. However, eutrophic species such as *Galeopsis tetrahit* and *Urtica dioica* still remained after 25 years, and the total cover of undergrowth species was still low.

4. Discussion

4.1. Conversion of reference ecosystems to agricultural fields

Agricultural use drastically changed the reference soil ecosystem, with destruction of the soil microstructure and decrease of C-content and soil life. Ploughing generally leads to decreased car-

Table 8
Vegetation characteristics in different ecosystem types related to reference vegetation and restored sites on former agricultural soil. Mean values (n = 9-10) and standard deviations are given. Different letters indicate individual differences between particular vegetation types for a particular parameter ($p < 0.05$).

	Biomass($g\ m^{-2}$)	Herb cover (%)	Mosses and lichens (%)	Eutrophic species (%)	Total species number
Reference heathland (H0)	1285 (1614)^{b}	77 (12)^{d}	20 (25)^{b}	0 (0)^{a}	7 (3)^{a}
Partial topsoil removal (H1)	123 (51)^{a}	68 (18)^{cd}	28 (20)^{bc}	6 (8)^{a}	21 (3)^{d}
Complete topsoil removal (H2)	73 (87)^{a}	45 (22)^{bc}	43 (35)^{c}	1 (1)^{a}	19 (3)^{cd}
Reference grassland (G0)	165 (74)^{a}	56 (14)^{c}	29 (23)^{bc}	0 (0)^{a}	9 (2)^{ab}
Productive rangeland (G1)	356 (112)^{a}	98 (8)^{e}	7 (11)^{ab}	39 (25)^{b}	13 (4)^{b}
Intermediate rangeland (G2)	187 (76)^{a}	83 (17)^{de}	31 (25)^{bc}	8 (4)^{a}	17 (3)^{c}
Reference forest (F0)	18 (15)^{a}	36 (20)^{b}	2 (3)^{a}	1 (2)^{a}	9 (3)^{ab}
New forest (F1)	7 (7)^{a}	15 (10)^{a}	1 (1)^{a}	5 (3)^{a}	12 (5)^{b}

bon contents, due to increased exposure to the air and increased mineralization (Dick, 1992; Nieder and Benbi, 2008). Decrease of soil microarthropods in agricultural fields has also been shown by Abbas and Parwez (2012). Also, the more than fourfold increase in total P is not uncommon at all (e.g., Gough and Marrs, 1990; Barberis et al., 1996; Janssens et al., 1998; McCrea et al., 2001). Considering the differences between reference and agricultural soils in P-Olsen and P-desorption, the increase in available P was probably even higher.

4.2. Conversion of agricultural fields to forest

Afforestation is a relatively cheap restoration method, which can make good use of the excess nutrients in the soil (Son et al., 2003; Kemmers et al., 2005). The appearance of more complex peds, due to higher activity of fungi and microarthropods, showed that soil life and soil microstructure gradually improved. However, afforestation does not lead to P-poor conditions. Actually, plant P-concentrations in the understorey were already high in the old forests, and low plant N:P ratios pointed to high P-availability even here (Koerselman and Meuleman, 1996). In old forests, understorey plants may profit from high P-mineralization in the organic layer, which is generally larger than in mineral soil, due to lack of chemical sorption. Availability of N may have decreased to some extent, as indicated by the decrease in plant N-concentrations and net N-mineralization between 2007 and 2013. However, in both old and new forests, high plant N-concentrations and high nitrification may point to higher N-availability than in other ecosystems.

It is not expected that the new oak forests will soon be important to undergrowth diversity, although some forest species had already established. It may take centuries or more before forests are fully restored, due to dispersal limitations (Dupouey et al., 2002; Honnay et al., 2002). Also, on former agricultural soils, with elevated nutrient levels, ruderal species may be favoured to forest species for a long time.

4.3. Conversion of agricultural fields to heathlands

The general establishment of *C. vulgaris* showed that partial and complete topsoil removal led to heathland development at least to some extent. Nutrient stocks clearly decreased, especially with complete topsoil removal, in accord with other studies (Oomes et al., 1996; Verhagen et al., 2001; Niemeyer et al., 2006; Smolders et al., 2008). Like in other topsoil removal studies (Frouz et al., 2009), soil life did not really recover after 25 years of restoration, probably due to the absence of organic matter. Also, although P-stocks and P-desorption had clearly decreased, topsoil removal did not lead to P-limited ecosystem characteristics. In reference heathland, P was a limiting factor, although this may partly be due to high atmospheric N-deposition. In the topsoil removal treatments, low plant N:P ratios point to N as a limiting factor (Koerselman and Meuleman, 1996), despite high N-deposition. Low N-availability may reflect the lack of soil organic matter and N in young successional stages (Sparrius et al., 2013). However, low N:P ratios could also point to high P-availability. In our study, in the treatment with complete topsoil removal, available P was two times higher than in Frouz et al. (2009). Relatively high P-availability is supported by the presence of eutrophic grassland species, such as *Cerastium fontanum*, *Plantago lanceolata* and *Holcus lanatus*. This suggests that, even though organic topsoil material was removed completely, it is difficult to remove all P.

The presence of grassland rather than heathland species may reflect dispersal limitation of the latter, but is probably also due to the slightly higher pH. Heathland restoration may be stimulated by artificial acidification with sulphate, as reported by Green et al. (2007). However, high pH may also have advantages, such as establishment of red-list pioneer species, such as *Ornithopus perpusillus*, *Jasione montana, Filago minima* and *Teesdalia nudicaulis* (Weeda et al., 1999).

On longer term, it is not clear whether heathland really develops. After 25 years of restoration, mean heath cover was 11 and 18% with partial and complete topsoil removal respectively, while grassland species already covered 57 and 27%. In the Maashorst area, heathland development may be restricted by the high pH or relatively high P-availabilty even after complete topsoil removal, but also by high atmospheric N-deposition. Since vegetation differences with converted rangelands, other than *C. vulgaris*, are relatively small, and topsoil removal such an expensive method, it should perhaps not be used on a large scale. Topsoil removal could, however, from time to time be applied on a small scale, to ensure suitable conditions for establishment of red-list pioneer species, also in the future. In that case it is best to remove the topsoil completely.

4.4. Conversion of agricultural fields to rangelands

In depopulated areas, conversion of former agricultural fields to rangelands is a more or less natural process after land abandonment (Lesschen et al., 2008). In heavily fertilized areas such as western Europe, conversion to rangelands has less often been applied. Because soil nutrients are left in place, this is a relatively cheap and easy restoration method. The method also led to clearly improved soil life, although the presence of earthworms differed from reference grassland, due to the higher pH. These animals contribute to restoration of the soil structure by increasing aggregation (Blanchart, 1992).

As expected, conversion to rangeland did not change nutrient stocks in the soil. Even after 25 years, P-availability in the new grasslands was not substantially reduced. However, N-availability probably decreased between 2007 and 2013, as predicted by other grassland studies (McBride, 1994; Oomes et al., 1996; Janssens et al., 1998). Net N-mineralization rates were lower in 2013 than in 2007, although this may to some extent be due to sampling earlier in the season when microbial populations and activity may have been lower due to lower soil temperatures (Frey et al., 2013).

However, plant N-concentrations were also lower in 2013. As these samples were collected in the same period, this points to a real decrease in N-concentrations. On the other hand, apart from conversed rangelands, the decrease in N-availability was also found in reference grasslands and new forests. This may point to a generally lower use of fertilizer in the surrounding area, in which agricultural fields have been converted to more natural ecosystems on a large scale. Also, atmospheric N-deposition has decreased in the study period. Maashorst Nature reserve is located in a region with N-deposition values of more than 50 kg ha^{-1} $year^{-1}$ in the 1990s (GCN, 2009), but values have substantially decreased to 35–45 kg ha^{-1} $year^{-1}$ in the past decade.

Despite high P-availability, plant diversity in conversed rangelands was relatively high. The slightly higher pH improved conditions for many grassland herbs. Real nutrient-poor species were absent, but the cover of eutrophic grasses had decreased to 39% even in productive rangelands. Plant species composition was even more or less similar to lime-poor coastal dune grasslands dominated by *Agrostis capillaris* (Van Til and Mourik, 1999). Species diversity may be relatively high, because competition for light decreases under a grazing regime (Olff and Ritchie, 1998; Oomes, 1992; Mittelbach et al., 2001). Also, higher-productive grasslands require fertilization each year. In Oomes (1992), species diversity clearly decreased when standing crop was above the limit value of 600–670 g m^{-2}. In our study, even in the productive rangelands, mean aboveground biomass was only 356 g m^{-2}. In the intermediate rangelands, aboveground biomass was even almost two times lower, and species-richness higher. This corresponds to some degree with the slightly lower soil N-content, lower net mineralization of N and lower P-desorption for intermediate than for productive rangelands. Lower nutrient availability may be due to differences in fertilization history rather than present-day developments. However, if N-availability continues to decrease, even the productive rangelands may look like the intermediate ones in the future.

On a landscape scale, conversed rangelands may be important for more than plant diversity alone. In the study area, rangelands are part of the open landscape with forest patches, and free-living herds of moeflon, sheep, highland cattle, horses and European bison. Roe deer are also present. The relatively species- and nutrient-rich vegetation may be a good food source for the larger herbivores, but also for smaller herbivores and pollinating insects (e.g., Forup and Memmott, 2005; Dumont et al., 2009). The nutrient- and mineral-rich soil also favours soil animals, such as earthworms and insect larvae. Together they form a reliable food source for breeding birds, such as the Red backed shrike, which has returned to the study area after an absence of many years (Sovon, 2013).

4.4.1. Concluding remarks

The results suggest that, on a time scale of decades, it is not possible to reduce P-loads without complete removal of the topsoil. However, even with topsoil removal, the originally P-limited ecosystems from before the conversion to agricultural land were not retrieved. Also, in terms of plant diversity, differences between expensive topsoil removal and much cheaper conversion to rangeland were relatively small. For restoration of former agricultural fields on a landscape scale, it may thus be better to focus on afforestation and conversion to semi-natural grasslands. The half-open, nutrient- and mineral-rich landscape offers many opportunities for large grazers, and overwintering and breeding birds.

Conflict of interest

The authors declare that they have no conflict of interests.

Table 9
Vascular plant species composition (of the undergrowth) of different ecosystem types related to reference vegetation and restoration sites on former agricultural soil. H0 = reference heathland; H1 = partial topsoil removal; H2 = complete topsoil removal; G0 = reference grassland; G1 = productive rangeland; G2 = intermediate rangeland; F0 = reference forest; F1 = new forest. Frequency is based on n = 9-10, and given as I (1-20% of releves), II (20-40%), III (40-60%), IV (60-80%) and V (80-100%).

	H0	H1	H2	G0	G1	G2	F0	F1
Heathland species								
Calluna vulgaris	V	IV	V	IV	–	II	–	–
Festuca ovina	II	I	IV	–	I	–	–	–
Erica tetralix	II	–	II	–	–	–	–	–
Aira praecox	–	V	IV	III	–	II	–	–
Veronica officinalis	–	IV	V	–	I	II	–	–
Ornithopus perpusillus	–	IV	V	–	–	IV	–	–
Erigeron canadense	–	III	I	–	–	–	–	–
Jasione montana	–	III	II	–	–	II	–	–
Hypericum perforatum	–	III	V	–	–	III	I	I
Trifolium arvense	–	III	–	–	–	–	–	–
Trifolium dubium	–	III	–	–	–	II	–	–
Filago minima	–	–	V	–	–	–	–	–
Teesdalia nudicaulis	–	–	II	–	–	–	–	–
Grassland species	H0	H1	H2	G0	G1	G2	F0	F1
Danthonia decumbens	–	–	–	II	–	–	–	–
Galium saxatile	–	–	–	I	–	–	–	–
Juncus squarrosus	I	–	II	II	–	–	–	–
Potentilla erecta	–	–	II	II	–	–	–	–
Carex pilulifera	IV	–	II	V	–	–	–	–
Molinia caerulea	IV	–	–	V	–	–	II	–
Tragopogon pratense	–	–	–	–	II	–	–	–
Hieracium pilosella	–	–	I	–	I	–	–	–
Ranunculus acris	–	I	–	–	III	–	–	I
Lolium perenne	–	I	–	–	III	II	–	–
Dactylus glomerata	–	–	–	–	III	I	–	–
Linaria vulgaris	–	I	–	–	II	II	–	–
Geranium molle	–	I	–	–	II	II	–	–
Vicia sativa	–	–	–	–	I	II	–	II
Dianthus deltoides	–	–	–	–	I	I	–	–
Senecio sylvaticus	–	I	–	–	I	I	–	I
Vulpia myuros	–	–	–	–	–	IV	–	–
Agrostis capillaris	II	V	V	V	V	V	–	–
Rumex acetosella	–	V	V	III	III	V	I	–
Luzula campestris	III	IV	V	III	I	III	–	–
Jacobaea vulgare	–	V	II	–	V	V	–	–
Cerastium fontanum	II	IV	IV	–	V	V	–	–
Plantago lanceolata	–	V	IV	–	IV	II	–	I
Holcus lanatus	–	V	IV	–	V	V	II	III
Poa pratense	I	III	II	–	IV	IV	II	IV
Crepis capillaris	–	V	II	–	III	V	–	–
Bromus hordeaceus	–	III	I	–	III	IV	–	–
Veronica arvense	I	IV	I	–	III	IV	–	–
Trifolium repens	–	IV	III	–	III	IV	–	–
Achillea millefolium	–	III	III	–	III	II	–	–
Hypochaeris radicata	I	V	V	–	I	V	–	I
Forest species	H0	H1	H2	G0	G1	G2	F0	F1
Deschampsia flexuosa	III	III	III	IV	–	–	V	–
Sorbus aucuparia	–	–	II	I	–	–	V	V
Rubus fruticosus	–	–	–	IV	–	–	V	IV
Ceratocapnos claviculatum	–	–	–	–	–	–	V	II
Prunus serotina	–	–	I	I	–	I	IV	V
Dryopteris dilatata	–	–	–	–	–	–	IV	I
Urtica dioica	–	–	–	I	–	–	–	IV
Galeopsis tetrahit	–	–	–	–	–	–	–	III
Taraxacum officinale	–	II	–	–	II	–	–	III
Rumex obtusifolius	–	–	–	–	–	–	–	III
Lonicera peryclymenum	–	–	–	–	–	–	–	I
Hieracium murorum	–	–	–	–	–	–	–	I

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