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RESTORATION OF A COPPICE-WITH- STANDARDS MANAGEMENT IN MEERDAAL FOREST (BELGIUM): EFFECTS ON HERB LAYER SPECIES COMPOSITION

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1. Introduction

Coppice-with-standards is an ancient woodland management system that has two main components: the coppice and the standards. The coppice consists of young trees which are cut down on a short-term rotational basis. During each coppice cycle, new shoots develop from their stumps. These shoots are eventually harvested and supply firewood and wood of small size. Between the coppice, a number of single-stemmed trees, the standards, are allowed to grow to a bigger size during multiple coppice cycles, yielding a sparse canopy. The standards are eventually harvested as well to yield construction wood (Stewart, 1980; Van Calster et al., 2007; Vandekerckhove et al., 2016). Along with wood pasture and litter raking, coppicing and coppice-with-standards management have been widespread management systems of European lowland forests for many decades, if not centuries (Peterken, 1993; Tack & Hermy, 1998; Gimmi, Burgi & Stuber, 2008; Szabó, 2010). As a result, many ancient woodlands harbour, besides shade-bearing plants, a large component of “coppicing plants”, not adapted to continuous shade, which have an increase in flowering (e.g. *Primula elatior*) or germinate from buried seeds (e.g. *Euphorbia amygdaloides*) each time the wood is cut down (Rackham, 2006; Van Calster et al., 2008).

Since the beginning of the 19th century, an international tendency to convert coppice and coppice-with-standards to high forest arose. The value of the coppice wood declined together with the demand for firewood as the availability of coal increased. At the same time, the standards were increasingly valued as the demand for industrial round wood and timber strongly increased during the industrial revolution (Poskin, 1934). Moreover, foresters in the 19th and 20th century associated traditional management forms as coppicing with degradation and depletion (Radkau, 2011). As a result, coppicing was almost completely abandoned in central and northwest Europe by the 1940's (Szabó, 2010).

Such a change in forest management and the resulting changes in canopy structure and composition have the potential to significantly alter the herb layer diversity and composition (Roberts, 2007). One of the most obvious effects of coppicing is the strong increase in light reaching the forest floor directly after coppicing and the subsequent decrease thereof during the years thereafter, creating a cyclic light variation at the forest floor (Ash & Barkham, 1976; Mason & MacDonald, 2002). The short phases of high light availability can enable light-demanding herbs to temporarily grow within the forest, while also benefitting shade-tolerant forest herbs through enhanced generative reproduction (Mason & MacDonald, 2002; De Keersmaecker et al., 2011). Abandonment of the coppice-with-standards management results in a long-term reduction of the average light availability for the herb layer, which is expected to increase the dominance of shade-tolerant and vernal forest herb species (Brewer, 1980). The decrease in light availability can also indirectly favour typical forest herbs by suppressing light-demanding species such as *Urtica dioica* (De Keersmaecker et al., 2004).

Large changes in the understory vegetation of ancient, semi-natural deciduous woodlands have indeed taken place. Species composition shifted towards more shade-tolerant and nutrient-demanding species (Baeten et al., 2009; Hedl, Kopecky & Komarek, 2010; Naaf & Wulf, 2011; Verheyen et al., 2012). This eutrophication signal could not be explained only by the increased atmospheric N deposition, but seems

mainly caused by a denser canopy cover resulting in a higher litter input and a higher share of tree species with an easily decomposed litter. The denser canopy as well as the change in tree species composition are both due to the decrease in management intensity following the abandonment of the coppice management (Verheyen et al., 2012).

Reintroduction of coppice management has been suggested in order to reverse this trend (Barkham, 1992a; Kopecky, Hedl & Szabó, 2013; Mairota et al., 2016). Arguments in favor of reintroducing coppice-with-standards management are that the competitive dominance of the ground layer flora is reduced, the interspecific competition is reduced, allowing light-demanding species to reproduce by creating temporary gaps in the canopy and that the species richness is temporarily increased as fast growing herbs and grasses establish soon after coppicing and disappear later on, being outcompeted by shade tolerant herbs as shade increases again (Barkham, 1992b). In Białowieża forest, selective coppicing of hornbeam (*Carpinus betulus*) reversed a trend of declining light-demanding oak-forest species and greatly increased herb layer diversity (Kwiatkowska & Wyszomirski, 1990). Vild et al. (2013) reported a significant increase of light-demanding, oligotrophic species after decades of decline when the historic oak coppice-with-standards management was revived. Coppice management has the ability to maintain both typical forest herbs and herbs with affinity for more open habitats as shade-tolerant species have been shown to be able to sustain the environmental changes caused by this management type (Vild et al., 2013; Van Calster et al., 2008).

One of the biggest challenges to successfully reintroduce coppice-with-standards management for conservation purposes is the increase of ruderal and alien species soon after thinning (Vild et al., 2013; Radtke et al., 2013). Canopy opening increases soil surface temperatures and subsequently also microbial activity (Concilio et al., 2005; Ryu et al., 2009; Rietl & Jackson, 2012). This has been shown to increase the amount of nutrients available to plants (Binkley, 1984; Inagaki et al., 2008). Together with the increase in solar radiation following thinning (Ford & Newbould, 1977), these increased resources potentially amplify the competitive exclusion by, i.a., ruderal herbs (Wilson & Tilman, 1993). The potential release of nitrogen, accumulated over the years as a result of atmospheric deposition, by opening up the canopy has been called a 'nitrogen time bomb' (Verheyen et al., 2012). It is still unclear whether this nitrogen enrichment is permanent or reversible in the long run and what the consequences will be in terms of biodiversity (Baeten et al., 2009; Van Calster et al., 2008). The increased nitrogen availability may only be present immediately after coppicing, but this remains uncertain (Vild et al., 2013). The effect of the nitrogen release on the growth of competitors may also be reduced by the soil phosphorus concentration (Kopecky, Hedl & Szabó, 2013), as it has become the limiting resource in many terrestrial ecosystems (Vitousek et al., 2010; Penuelas et al., 2012).

With this master's thesis, I intend to gain more insight into the value of reviving the historical coppice-with-standards management for conservation purposes. The focus will be on the temporal dynamics of the herb layer composition influenced by the changing biotic and abiotic conditions throughout a coppice cycle. A chronosequence experiment was set up in forest reserve De Heide, part of the Meerdaal Forest, where coppice-with-standards management was experimentally reintroduced in the year 2004 as a small experimental restoration project.

2. Objectives

The goal of this master's thesis is to give an answer to the question whether the reintroduction of coppice-with-standards management in the Meerdaal Forest benefits the conservation value of its herb layer. In this case, a reintroduction after decades of high forest management under high atmospheric nitrogen deposition and implemented with mechanical exploitation. More specifically, I aim to answer the following research questions:

1. Are the typical forest herbs present before the reintroduction of the coppice-with-standards management negatively impacted in terms of number of species and cover? If so, do they recover and how long does it take?
2. Does the reintroduction of the coppice-with-standards management have a positive impact on the so-called "goal species", namely non-competitive, light-demanding herbs?
3. How do ruderal herb species react to the reintroduction of the coppice-with-standards management in terms of number of species and cover?

3. Material and methods

3.1. Study area

3.1.1. General data

Meerdaal Forest is a woodland of approximately 1102 ha situated south of Leuven in central Belgium (Figure 3.1). The Meerdaal Forest is predominantly state owned and managed by the Flemish Nature and Forest Agency as a public forest (ANB, 2007). Meerdaal forest contains seven forest reserves including De Heide, where our study area is located. Forest reserve De Heide covers an area of 32.2 ha and is located centrally within the Meerdaal Forest. De Heide received the status of managed forest reserve in 1999 (Opstaele & Verloove, 2001). In terms of management, De Heide has been subdivided into two main parts: The western part of ca. 20 ha is managed as coppice-with-standards, while the remaining 12 ha in the east are designated to become unmanaged forest after partial transformation of the conifer stands to mixed forest (Opstaele & Verloove, 2001; ANB, 2007). The western part will be referred to as study area from here onwards.

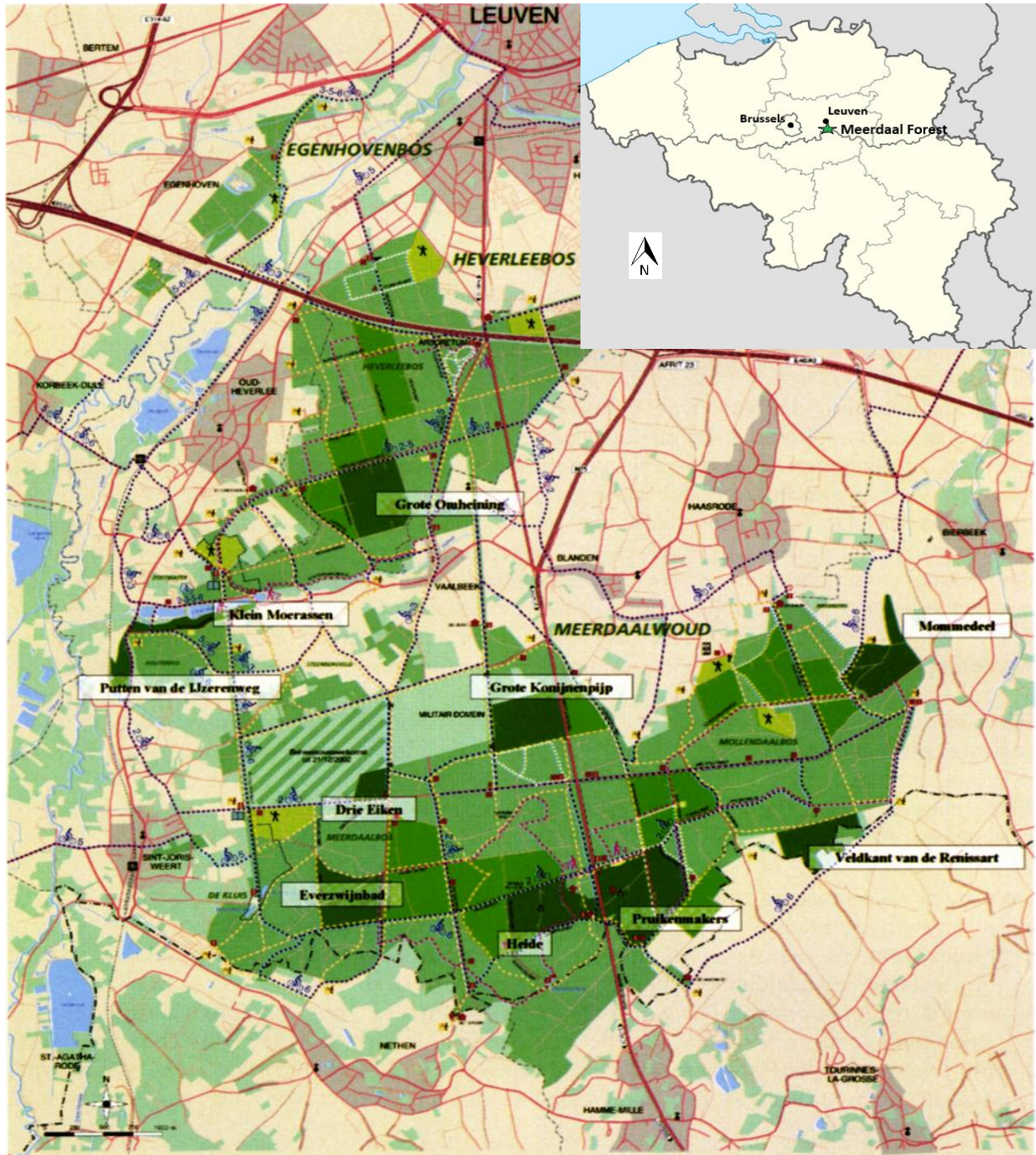


Figure. 3.1: Situation of Meersdal and Heverlee Forest with their forest reserves (Adapted from Nackaerts, Buys & Meuleman, 1999)

3.1.2. Environmental factors

3.1.2.1. Relief, hydrology and hydrography and geology

The terrain of De Heide slopes down to the southeast from 80 m to ca. 60 m. No springs or ponds are present (Opstaele & Verloove, 2001).

From top to bottom we can distinguish roughly three Tertiary geological layers:

1. Formation of Sint-Huibrechts-Herne, consisting of sand, layered with green clay-glaucanite, ranging from mica-like clay sand to yellowish sandy clay, dating from the Lower Oligocene (Tertiary).
2. Ledian, consisting of fine yellow sand and white sandstone which is mostly granulated, dating from the Upper Eocene (Tertiary). The layer rests on a gravel layer rich in iron and fossils.
3. Brusselean, consisting of calcareous sand and sandstone, often decalcified and crossed by horizontal layers of white stone. Further downwards, this merges into layers of coarse, grey-brownish and highly permeable sand. This geological layer dates back to the Middle Eocene (Tertiary).

Not all of these layers outcrop throughout the Meerdaal Forest, but they have a distribution related to the relief. In De Heide, only the Brusselean outcrops. The Tertiary layers are covered with a layer of loam of varying thickness. This Quaternary layer of loam consists of aeolian loess depositions created during the last glacial period. The Tertiary outcrops on the hilltops and along the slopes, where this layer of loam has been largely or sometimes entirely eroded. Depressions were filled up with colluvium that had been washed down from the nearby slopes in the Quaternary. This phenomenon is particularly evident in the dry depressions of the areas with loess. In the lower parts of the Meerdaal Forest, including De Heide, the loam mantle can be up to 3m thick (ANB, 2007).

3.1.2.2. Soil

The study area consists of dry loamy soils, having a B horizon with a crumbled texture (Abc and Abp), that merge into gleyic loamy soils (Acp) in the lower zone (Opstaele & Verloove, 2001). Figure 3.2 shows the relative homogeneity of the soil composition throughout the entire study area.



Figure. 3.2: Soil map of De Heide (Esher, 2001: scale: 1/5000)

3.1.2.3. Climate

According to the data of the Royal Meteorological Institute of Belgium, the study area experiences an oceanic climate with an average air temperature of 10.3°C and an average yearly precipitation of 808.9 mm (KMI, 2017).

3.1.3. Phytosociology

Forest reserve De Heide is characterized by the *Stellario-Carpinetum* association -(QCc & QCs) according to Roelandt (2004) (Figure. 3.3).

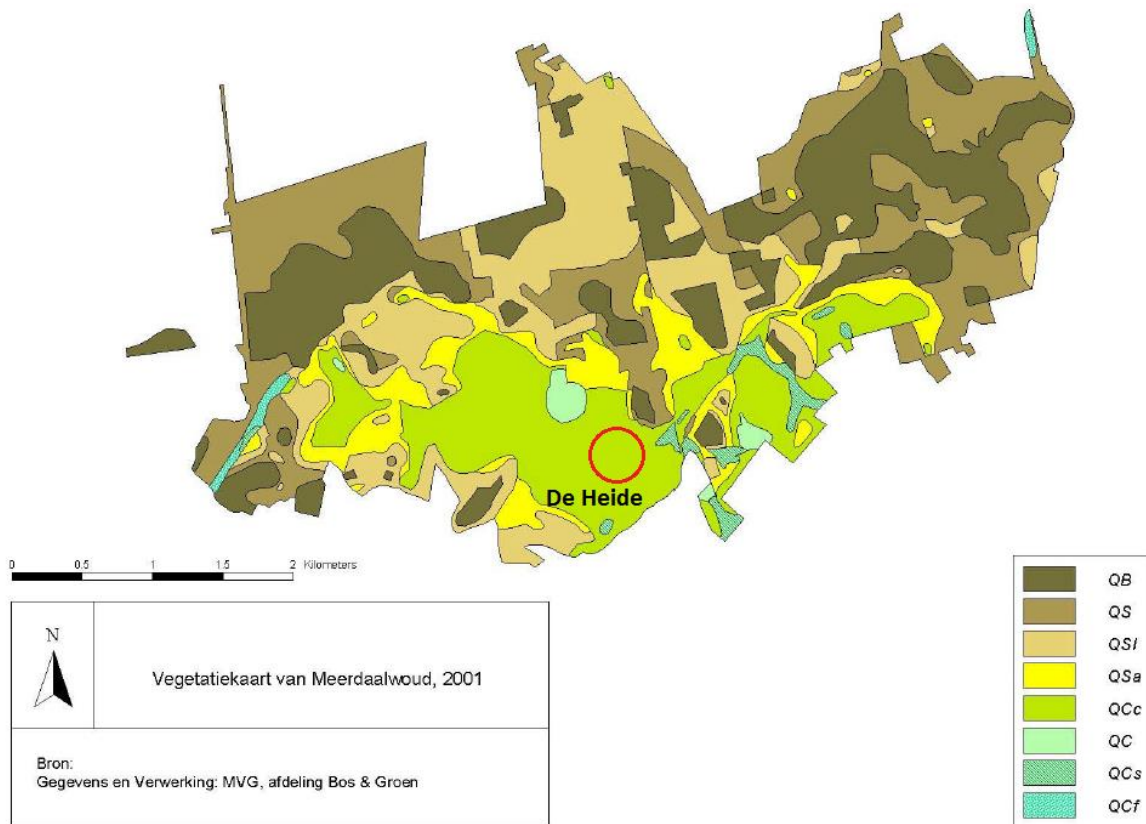


Figure 3.3: Vegetation map (Adapted from Roelandt, 2004)

3.1.4. History and former management

Several historical maps prove that De Heide has always been wooded, from 1771 onwards as it is referred to as forest on the De Ferraris map (1771-1778) and other topographical maps since then. Evidence for the existence of the whole Meerdaal Forest goes further back. Until the early Middle Ages, the Meerdaal Forest was, like the Sonian Forest, part of the so-called 'Coal Forest'. This forest is considered as the most important primary forest area in central Belgium. The fragmentation of the Coal Forest during the Carolingian period (eighth-ninth century), results in a separation between the Sonian Forest and the forests along the Dijle south of Leuven. Like the Sonian forest, the Meerdaal Forest presumably remained spared from large-scale agricultural exploitations through protection as noble domain for hunting and timber production (ANB, 2007).

In 1406, Meerdaal Forest became a so-called "Free Wood" (Vrijwoud). This status allowed the owners, namely the Dukes of de Croÿ and later on the Dukes of Arenberg, to establish their own "Wood Court" (Woudrecht) to speak "higher justice". As a result, it also gave the owners more freedom in terms of management. User rights previously given to the local population were from then onwards solely assigned

to the owner (Vandekerkhove, 2016). The most important of those user rights which characterised the earliest management of the Meerdaal Forest until the 19th Century are the following:

- The so-called “right to soft timber”: The right to fell ‘all tree species of subordinate importance’. Hard types of wood such as oak and beech had to be spared, while ‘secondary tree species’ such as Ash, Alder, Willow, Maple, Lime and Aspen could be felled and therefore disappeared in many forests. Fruit-bearing trees such as “cherry trees” (likely *Prunus avium*), “pear trees” (most likely *Pyrus pyraeaster*) and “apple trees” (probably *Malus sylvestris*), however, are an exception to this rule and had to be spared as well (Vandekerkhove, 2016).
- Pig owners were allowed to let their pigs forage in the forest. Every fall, large herds of pigs were driven through the forest for the ‘mast’, mainly acorns and beechnuts.
- The grazing of cattle was prevented as much as possible by forest owners because the cattle caused damage to the trunks of mature trees as well as to saplings.
- Rights to the gathering of dead wood were issued, while wood was being robbed on a large scale in other places. The result was that – at least until the end of the eighteenth century – almost all of the dead wood was being taken out of the forest systematically.
- Only the owner of the forest, or the ruler was allowed to hunt in the forest (ANB, 2007).

Coppice or coppice-with-standards was, as in most managed deciduous European forests, the most important form of management, at least from the 16th century and possibly earlier until the end of the 19th century. There was no selection within the coppice itself. All stems, young or old were to be cut down. An important exception to this were the valuable, tall oak seedlings. These trees were spared to yield lumber. Documents from the 16th century indeed tell us that a lot of care was taken for the production of large stems that were destined to be used as building material: the so-called standards or “reserve”. To ensure the presence of these standards in the future, young oaks that had the potential to become tall trees were spared. The desired density of those promising trees varied in time. During the 16th century, 16 young oaks per hectare every rotation of 20 years was the norm. From 1597 onwards, this number was increased to 32, while new regulations of the 17th century already mention 40 (Vandekerkhove, 2009; Vandekerkhove, 2016). No direct information has been found concerning the number of trees that had to be spared during the 18th and 19th century. What we do know is that extra young trees were planted on a large scale and that the length of the coppice cycle was reduced: A reduction occurred from 20 years during the 16th and 17th century to 13 years during 1723-1769. Subsequently, there was a slight increase to 14 years during 1835-1860. The coppice cycle was further reduced to 12 years from 1860 until quite some time in the 20th century (Vandekerkhove, 2009; Vandekerkhove, 2016).

Historical documents have also provided us with information about the species composition of the coppice layer and the standards. During the whole period of coppice-with-standards management the standard layer consisted mainly of oak (*Quercus robur* and *Q. petraea*). At the end of the 17th century, wild cherry (*Prunus avium*) and crab apple (*Malus sylvestris*) were the main additional species. However, at the beginning of the 19th century these species represented less than 1% of the stem number. Ash (*Fraxinus excelsior*), beech (*Fagus sylvatica*), maple (*Acer pseudoplatanus*) and grey poplar (*Populus canescens*) took their place. The composition of the coppice layer wasn’t documented at the beginning of the 17th century. At the beginning of the 19th century, the coppice layer was dominated (>70%) by hazel (*Corylus avellana*), with additional sweet chestnut (*Castanea sativa*), alder (*Alnus glutinosa*), hornbeam (*Carpinus betulus*) and lime (*Tilia* sp.). The species composition of the herb layer is less well known. Regulations of the 16th

century until the beginning of the 20th century do mention that all brambles (*Rubus* spp.) and broom (*Cytisus scoparius*), had to be removed (Vandekerkhove, 2016).

The greater availability of coal since the beginning of the 19th century reduced the demand for firewood, while the demand for industrial spar and timber strongly increased as a result of the industrial revolution. An international trend of converting coppice or coppice-with-standards to high forest arose. Meerdaal Forest followed and the coppice was replaced by high forest dominated by beech on a fairly large scale (Vandekerkhove, 2009). De Heide, however, can be seen as an exception to this trend. Today, the basis of De Heide consists of an area of old oaks of approximately 250 years of age. Conversion to homogenous beech stands did therefore not take place. We know that De Heide has been managed as high forest dominated by oak since the beginning of the 20th century with a cutting cycle of 6 to 12 years (Opstaele & Verloove, 2001).

From the year 2004, experimental restoration of coppice-with-standards was initiated on an area of 20 ha within this reserve. This area has been divided into eight stands and every second year, one of these stands was scheduled to be coppiced, leaving some large trees as standards. The length of the coppice cycle is therefore equal to 16 years. At this moment, seven of the eight stands have been restored to coppice-with-standards so that now freshly cut open area, re-closing coppice, and uncut area are present. It is in this setting that we conducted a chronosequence experiment in which time is substituted by the different areas of the reserve, as they represent the different successional stages before and after coppicing.

3.2. Data collection and validation

3.2.1. Sampling design

The observations were done in 52 different sampling plots distributed over the 8 stands of the reserve and centred on the intersections of an imaginary North-South oriented grid with a mesh size of 100 m. Some plots were shifted to lie fully within one of the stands or to avoid disturbances (Figure 3.4). The plots situated within stands that had already been coppiced were subdivided into two “substands” per stand to be able to cope with the pseudoreplication present in this space-for-time substitution experiment. The substand to which a plot belongs will be referred to as Substand.

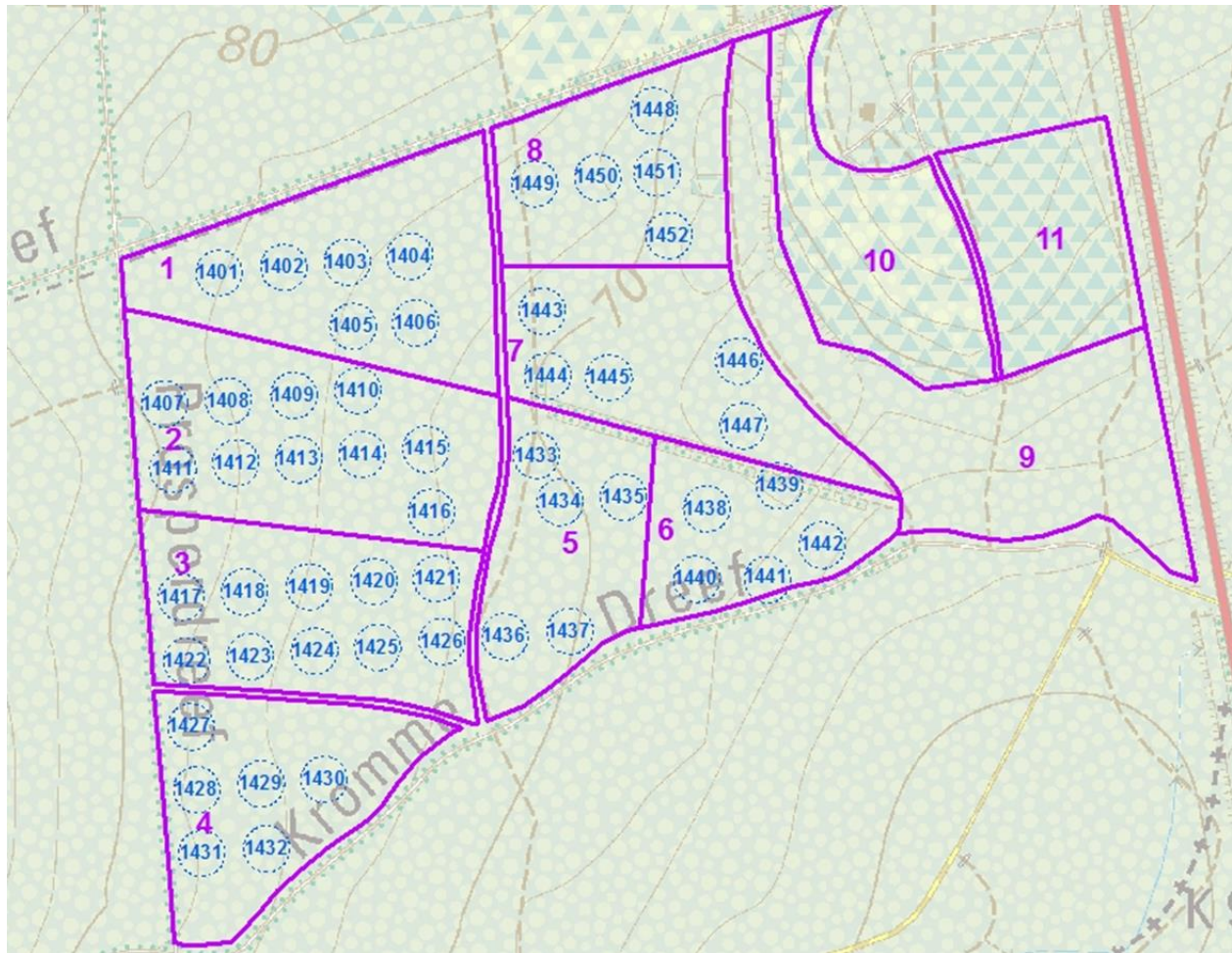


Figure 3.4: Position of the 52 sampling plots within the 8 stands of the study area.

In order to record the vegetation composition of each plot as completely as possible, the understory vegetation was sampled in the spring of 2016 from April 5th until April 11th, as well as in the summer of the same year from July 18th until July 29th. The first sampling session is important to record the full coverage of the vernal herbs, while the second one coincides with the period of maximal aboveground biomass.

Spring and summer survey: Within each of the 52 sampling plots, all vascular plant species present in the understory layer, which comprises the part of the forest vegetation with a height smaller than 2 m, were recorded. The following protocol was used: A square sampling plot of 16 m by 16 m (256 m²) with the grid point of the plot as centre, is delineated using brightly coloured offset rods positioned at 11.3 m from the central grid point in line with the cardinal directions. The percentage cover of the herbs and woody species (< 200 cm) within this plot is then visually estimated using the decimal scale of Londo (1984). In the summer survey, the observations were complemented with a visual estimation of the total cover of the herb layer, the shrub layer and the crown layer. Table 3.1 gives an overview of the different degrees of cover used.

Cover (%)	Notation
< 1	.1
1 - 3	.2
3 - 5	.4
5 - 15	1
15 - 25	2
25 - 35	3
35 - 45	4
45 - 55	5
55 - 65	6
65 - 75	7
75 - 85	8
85 - 95	9
95 - 100	10

Table 3.1: The scale of Londo as applied in the monitoring of forest reserves.

If the cover of a certain plant species is estimated to be less than 1%, the abundance of this plant species is estimated as well by counting the number of above-ground sprouts or rosettes. The abundance classes used are shown in table 3.2.

Abundance	Notation
1 - 3	r
3 - 20	p
20 - 100	a
>100	m

Table 3.2: Species abundance classes, applied for the vegetation monitoring

3.2.2. Dendrometric analysis

Dendrometric data were gathered from all of the plots as follows: Within a circular plot with a radius of 18 m (1018 m²), the position, species, diameter, height and social position according to the IUFRO-classes of all living trees and shoots of coppice stools having a diameter at breast height (DBH) of 40 cm and more were determined. Within 9 m (254 m²) radius, all trees and shoots of at least 5 cm DBH were included.

Within the same sampling plot, the position, species (if possible), diameter, height and stage of decay of all the standing and lying dead trees and coppice shoots having a diameter at breast height or diameter respectively of at least 10 cm and a height or length of 1 m or a diameter at breast height or diameter respectively of at least 20 cm and a height or length of 0.5 m were determined as well. Dead wood with DBH or diameter of at least 5cm and a height or length of 1.3 m were determined within 9m radius.

The amount of natural regeneration of woody species was determined within two additional sampling plots. Within the outer circle with a radius of 4.5 m, all natural regeneration was counted for each woody species in the height classes of 50 - 200 cm and > 200 cm and DBH <5 cm. Within the inner circle with a

radius of 2.25 m, the same procedure was followed, but now in the height classes of 0 - 30 cm and 30 - 50 cm.

3.2.3. Light measurements

Hemispherical photographs of the crown were made on each grid point of the study area. These pictures were used to determine the amount of gaps in the canopy of each plot. The standardized way of making the photographs is as follows: A shelf is placed in a level position on a tripod, 1 m from the ground. Hereupon, the camera (a Nikon Coolpix 990), provided with a fish-eye converter lens (type FC-E8 with a viewing angle of 183° and a focal adjustment of x 0.21) is positioned. The lens is positioned zenithally. The underside of the camera is pointed to the south using a compass. The picture is taken with the aid of a self-timer to avoid movement of the camera. These hemispherical photographs were made in July to ensure concurrence with maximal crown density. It was made sure these pictures were taken 15 minutes before sunrise or 15 minutes after sunset to avoid direct sunlight, which can cause detrimental reflection. Subsequently, the percentage of gap cover of the canopy was calculated using Gap Light Analyzer 2.1 (Frazer, Canham & Lertzman, 1999). The standard value of the pixel threshold was used.

The percentage gap cover ranged from 1.86 to 29.95% and will be used in further analyses as it is expected to be one of the main abiotic variables influenced by the coppice management.

3.2.4. Soil analysis

The data collection is concluded with a survey of the soil. At each centre of the previously described sampling plots, the mineral topsoil (0 - 10 cm) is collected. In case of a discontinuity in the soil profile, the depth of this discontinuity is noted and both soil horizons are collected separately. Next, the soil samples are dried, sifted and the following characteristics are determined: texture, carbon content, current moisture content, Kjeldahl nitrogen, cation exchange capacity (Ca, K, Na, Mg, Al, H), pH (CaCl₂) and plant available phosphorus.

The soil of the 52 plots was composed of 8-26% clay, 62-76% silt and 3-21% sand. The overall variance in soil texture was low. All plots had a high silt fraction combined with low clay and sand fractions (Figure 3.5). The sand fraction was used for further analyses because of its relatively high amplitude and the negative correlation with the clay fraction.

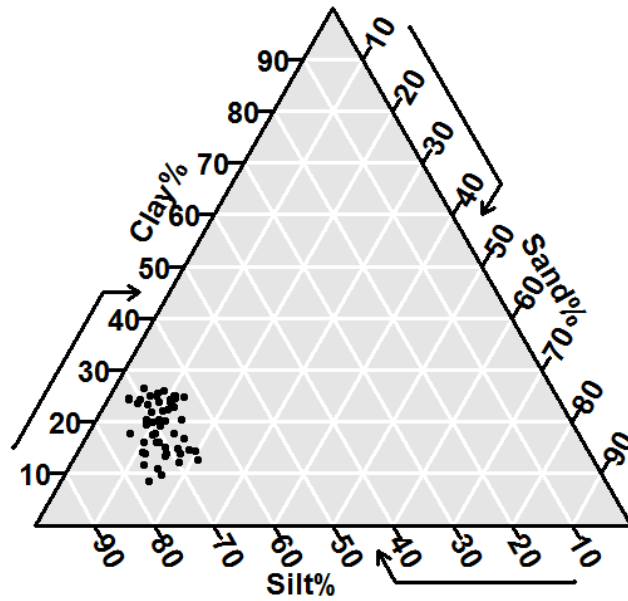


Figure 3.5: Soil texture of the study plots.

Kjeldahl nitrogen and pH will also be used in further analyses because of their apparent variance in space within the study area and possibly important influence on the vegetation composition. Kjeldahl nitrogen ranged from 1.6 to 4.8 g/kg and the pH ranged from 3.21 to 4.94.

The plant available phosphorus data contained too many missing values and was therefore not used in further analyses.

3.3. Data analysis

3.3.1. Data compilation

The data of the vegetation surveys, including coppice age, as well as the dendrometric, light and soil data were brought together within a database using Microsoft Access 2016. The whole of these data, except the cover data of the herb layer species will be referred to as environmental data. The vegetation cover data, saved as values of the Londo scale, were transformed to the corresponding percentage cover.

3.3.1.1. Beta diversity

The mean Sørensen index of dissimilarity of each plot relative to all other plots was calculated as a measure of the beta diversity. The calculation was performed using the package “vegan” in R (Oksanen et al., 2015).

3.3.1.2. Ellenberg indicator values

Mean plant indicator values for light (L), moisture (F), acidity (R) and fertility (N) were calculated for each plot, weighted by individual plant cover. Ellenberg indicator values of a plant species are the optima of that species, based on its realised ecological niche. The mean of the values for central Europe, as given by Ellenberg et al. (1992) and the UK, as calculated by Hill et al. (1999) were used, given the intermediary geographic position of our study area. These mean values will be referred to as Ellenberg indicator values.

3.3.1.3. C-S-R signatures

The C-S-R theory of J.P. Grime says there are three main life strategies for plants to deal with the trade-offs of resource allocation to growth, reproduction and maintenance. Plants can be categorised as competitors (C), stress tolerators (S) and ruderals (R) (Grime, 2001). The C, S and R values, ranging from zero to one, are a numerical representation of how strongly the life strategy of a plant species corresponds to the respective strategy. The values of Hunt et al. (2004) were used in this study. The mean C-S-R value of each plot was calculated, weighted by individual plant cover.

3.3.2. Exploratory analysis

Exploratory analysis was conducted prior to the actual testing of the hypotheses to get a broad insight into the changes of the herb layer composition and the related variables throughout the coppice cycle. It is intended that any clear trends in this exploratory analysis will be tested for significance in the data analysis dealing with the testing of the hypotheses afterwards. All analyses were performed in R, version 3.0.2 (R Core Team, 2013).

3.3.2.1. C-S-R plot

The weighted mean C-S-R values were used as coordinates to position each plot within a C-S-R triangle, where the three axes represent the C, S and R values, using the package “soiltexture” in R (Moeys & Shangguan, 2014).

3.3.2.2. Ordination of species composition and plots

Ordination is a method used in multivariate data analysis which orders objects in such a way that objects with similar characteristics are close to each other, while objects with dissimilar characteristics are farther away from each other (Leps & Smilauer, 2003). Ordination was used as a means to visualise changes in herb layer species composition and to relate those changes to the varying environmental conditions throughout the coppice cycle. Ordination was done on the data matrices containing the percentage cover of all plant species per plot and the environmental data per plot.

First, Detrended Correspondence Analysis (DCA) was performed to determine the type of ordination method. The longest gradient length along the first ordination axis was determined. If this length is shorter than 3 standard deviations, a linear method is recommended. If this value is greater than 4, a unimodal method should be used. Within the range between 3 and 4, both types of methods can be used (Leps & Smilauer, 2003).

Thereafter, Redundancy Analysis (RDA) was performed on the fourth root of the vegetation cover data. A fourth root transformation of the data was chosen to reduce the large asymmetry of the species distributions (Legendre & Legendre, 2012). A Permutational Multivariate Analysis of Variance (PERMANOVA) was used to select the environmental variables that significantly explain the variability in the dissimilarity matrix based on Jaccard distance (Anderson, 2001). The best model was selected using a backwards selection procedure. The variables retained were selected based on the highest residual R^2 and a significance level of 5%.

All ordinations were performed with the R package “vegan” (Oksanen et al., 2015).

3.3.3. Model construction

Selection of the explanatory variables is based on the outcome of the PERMANOVA model. The variables selected are: stand age, meaning the number of years after coppicing (Age), whether or not the stand has been coppiced (C), soil pH-CaCl₂ (pH) and the percentage sand fraction of the soil (Sand).

The percentage of gaps in the canopy (gap), the Kjeldahl nitrogen (KjN) as a measure of the organic nitrogen in the mineral topsoil, the pH of the mineral topsoil (pH) and the Sørensen index of dissimilarity (Beta), were selected as response variables of the exploratory analysis. The goal of this analysis is to

determine the response of these variables to the coppice-with-standards management so they can be used to explain the observed changes of the vegetation composition.

For each research question formulated in section 2, several vegetation characteristics describing those characteristics under analysis were selected as response variables.

The first research question focuses on typical forest herbs. A distinction was made between Ancient Forest Species (AFS) and “other” forest species (FS). The selection of AFS was based on the list of AFS in Flanders by De Keersmaeker et al. (2011), while FS were defined as non-AFS and having an Ellenberg indicator value for light (L) smaller than or equal to 5. The response variables for the first research question are: (1) number (#AFS) and (2) total percentage cover of AFS (coverAFS), (3) number (#FS) and (4) total percentage cover of FS (coverFS), the percentage cover of some individual AFS: (5) *Anemone nemorosa* L. (*A. nemorosa*), (6) *Oxalis acetosella* L. (*O. acetosella*), (7) *Lamium galeobdolon* (L.) L. (*L. galeobdolon*) and (8) the percentage cover of FS *Dryopteris filix-mas* (L.) Schott (*D filix-mas*). These species were selected on the basis of sufficient cover, presence in more than a few plots and being representative for the species category, in this case typical forest herbs.

The second research question is about the “goal species” of the coppice-with-standards reintroduction. Endangered species were not modelled as only one rare species, *Hypericum hirsutum* L., was observed. Other goal species are the light-demanding species that aren't strong competitors (LS) (Ellenberg indicator value for light $5 < L \leq 7$ and $C < 50\%$ (Hunt et al., 2004)). The response variables for the second research question are: (1) number (#LS) and (2) total percentage cover of LS (coverLS) and (3) the percentage cover of *Holcus lanatus* L. (*H. lanatus*).

The third research question is about the impact of the coppice-with-standards management on ruderal herbs. Ruderal herbs were defined as having an intermediate light requirement combined with a high competitive ability (Ellenberg indicator value for light $5 < L \leq 7$ and $C > 50\%$ (Hunt et al., 2004)). The response variables for the third research question are: (1) mean C-value weighted by individual plant cover (C signature), (2) number (#Rud) and (3) total percentage cover of ruderal herbs (coverRud) and the percentage cover of (4) *Rubus fruticosus* L. (*R. fruticosus*) and (5) *Urtica dioica* L. (*U. dioica*).

Linear Mixed-Effects Models (LMM) and Generalized Linear Mixed-Effects Models (GLMM) were made using backwards selection based on a significance level of 5% to select the best model. Age was transformed logarithmically to better approximate a linear response. Substand was added as a random effect to account for the variation in abiotic conditions. The structure of the models is as follows:

Variable ~ C + log(Age + 1) + pH + Sand + (1|Substand)

The models were made using the packages lme4 (Bates et al., 2014) and nlme (Pinheiro et al., 2015)

4. Results

4.1. Exploratory analyses

4.1.1. C-S-R signatures

In general, the herb layer of the coppiced plots has a lower S-coordinate than the herb layer of the uncut plots: only 19% of the coppiced plots has a dominant (> 50%) stress-tolerant vegetation, relative to 73% of the uncut plots. Recently coppiced plots show the lowest S-coordinates, while the S-coordinates of the older plots are only marginally lower than those of the Uncut plots. Coppicing seems to increase the importance of the C-coordinate, especially during the first years after the cut. However, the average C-coordinate decreases again to a value similar to that of the uncut plots as the coppice matures ,after 9 to 12 years, indicating that this signature only benefits from the coppice-with-standards management during the first years of the coppice cycle. Furthermore, recently coppiced plots also show a higher variance in C-coordinate compared to the older and uncut plots (Figure 4.1).

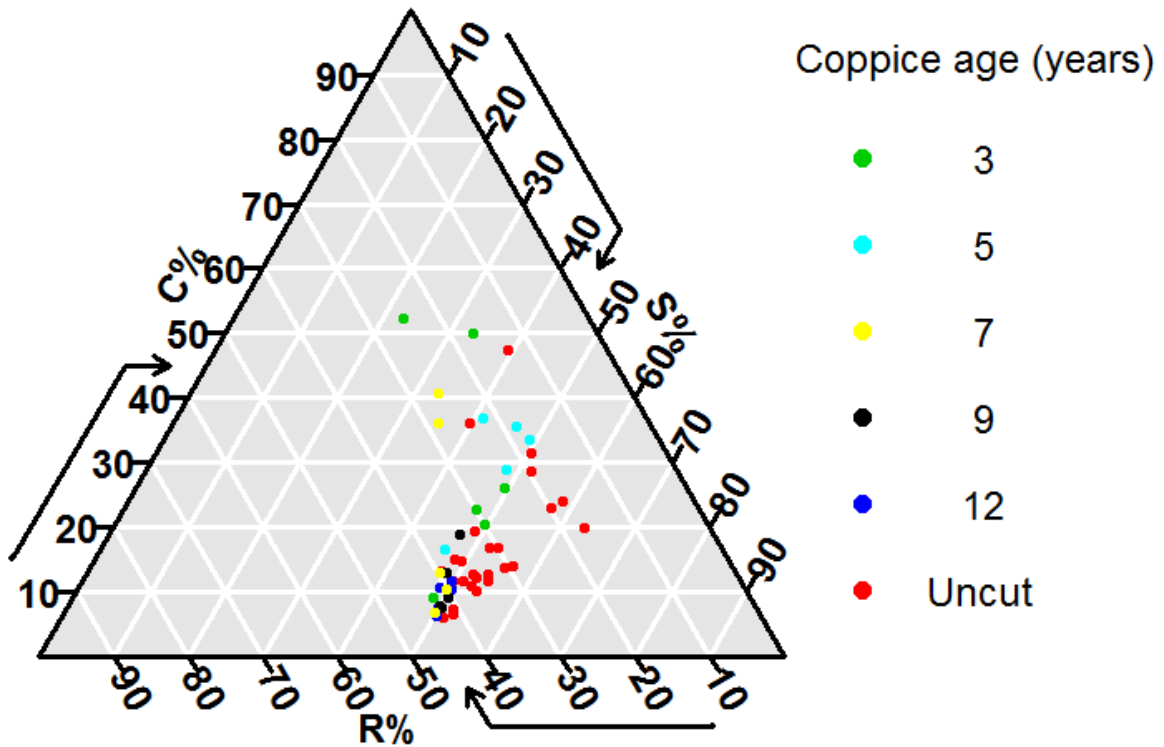


Figure 4.1: C-S-R signature of all plots; Colours indicate the age of the coppice.

4.1.2. Ordination of plots

PERMANOVA analysis retained coppice age (Age), soil pH (pH) and soil sand fraction (Sand) as explanatory variables of the herb layer composition. Figure 4.2 shows that the greatest variation in herb layer composition is observed along the coppice age gradient. With increasing coppice age, the vegetation shifts from a relatively light-demanding composition with *Rubus idaeus* L., *Galeopsis* sp, *Holcus lanatus* L., *Rubus fruticosus* L., *Milium effusum* L. and others to a vegetation characterised by *Dryopteris dilatata* (Hoffmann) A. Gray, *Lamium galeobdolon* (L.) L., *Hedera helix* L. and seedlings of *Fagus sylvatica* L. and *Acer pseudoplatanus* L. The most recently coppiced plots are widely scattered along the Sand and pH gradients, indicating that their herb layer composition is determined more by the soil sand fraction and pH than the other plots, although a large variance is apparent. Characteristic plants of these plots are, among others, *Urtica dioica* L., *Adoxa moschatellina* L., *Stachys sylvatica* L., *Rubus fruticosus* L. and *Glechoma hederacea* L.

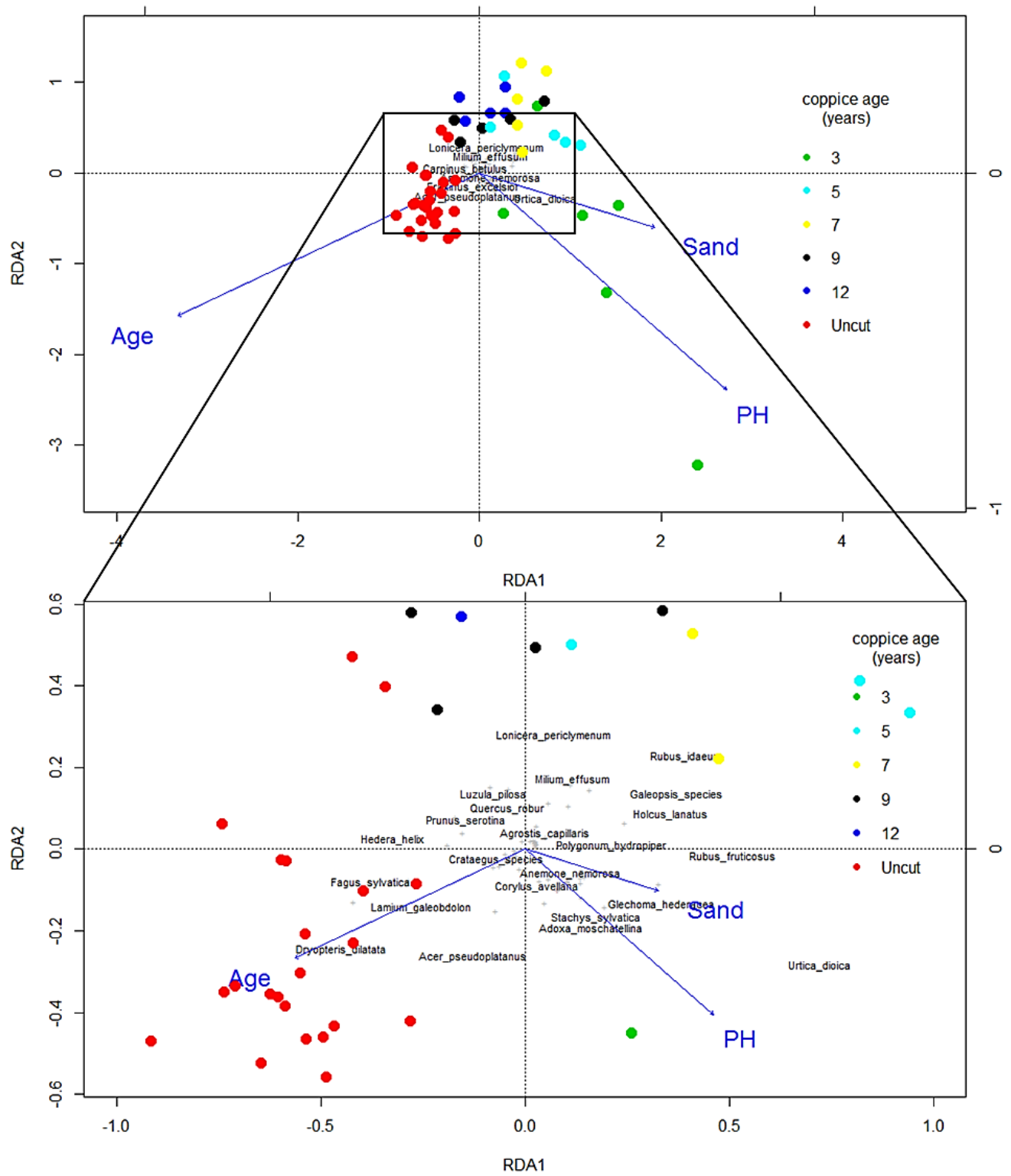


Figure 4.2: Triplot based on the PERMANOVA model of the herb layer with coppice age, soil pH and sand fraction as explanatory variables; Circles represent vegetation plots; Species are represented either by + or by their species names.

4.2. Model outcome

The results of the LMM and GLMM are presented in Table 4.1 and in Figure 4.3.

The percentage of gaps in the canopy seems unaffected by the coppice-with-standards management. The amount of organic nitrogen in the mineral topsoil was significantly lower in coppiced plots compared to uncut plots and increased as the coppice matured. The soil pH, on the other hand, was significantly higher in coppiced plots compared to uncut plots, but decreased with increasing coppice age. None of the explanatory variables were able to explain the Sørensen index of dissimilarity.

AFS, on average, seem to be unaffected by the coppice-with-standards management. Neither their number, nor their total cover differed significantly between coppiced and uncut plots. Number and cover of AFS remained stable over time as well. The response of the individual ancient forest species varied. *Anemone nemorosa* L. was unaffected, while the cover of *Oxalis acetosella* L. did not significantly differ between treatments, but did decline over time. The cover of *Lamium galeobdolon* (L.) L. decreased after coppicing, but was unaffected by coppice age. Coppicing increased the number of FS by about two on average, but this number gradually declines again as the coppice ages. FS were, on average, unaffected by the coppice-with-standards management in terms of cover. This is reflected in the cover of *Dryopteris filix-mas* (L.) Schott, which was unaffected as well.

Coppicing increased the number of LS. The total percentage cover of LS, however, was not influenced by the coppice-with-standards management, but was strongly determined by soil pH. High pH values were associated with high total percentage cover of LS. The cover of individual LS *Holcus lanatus* L. was unaffected by the coppice-with-standards management and coppice age.

The C signature was unaffected by the coppice-with-standards management and the coppice age, but was significantly positively influenced by soil pH. The total number as well as the cover of ruderal herbs and the cover of *Rubus fruticosus* L. were higher in the coppiced plots and declined with increasing coppice age. A different result was obtained for the cover of *Urtica dioica* L., as it was modelled to be lower after coppicing and strongly positively affected by an increasing soil pH.

Table 4.1 Parameter estimates of LMM and GLMM for (a) exploratory variables and (b, c, d) response variables of research questions one, two and three respectively with baseline set as C = TRUE (coppiced)

	df	Intercept	C	Log(Age + 1)	pH	Sand
(a)						
gap	39	8.263289 ***	-	-	/	/
KjN	39, 10, 10	2.8967373 ***	-1.978030 **	0.9670904 **	/	/
pH	39, 10, 10	3.388077 ***	1.158965 ***	-0.475724 **	/	/
Beta	39	0.3852964 ***	-	-	/	/
(b)						
#AFS	-	2.16465 ***	-	-	-	-
coverAFS	39	48.16897 ***	-	-	-	-
#FS	-	0.3254 NS	2.0192 **	-1.0439 **	-	-
coverFS	39	1.30114 *	-	-	-	-
A. nemorosa	39	37.36337 ***	-	-	-	-
O. acetosella	39, 11	3.862166 ***	-	-1.659877 **	-	-
L. galeobdolon	39, 11	5.428086 ***	-4.688183 **	-	-	-
D. filix-mas	39	0.8513455 NS	-	-	-	-
(c)						
#LS	-	0.4055 *	0.5108 *	-	-	-
coverLS	38, 38	-28.045676 ***	-	-	8.599302 ***	-
H. lanatus	39	0.7721093 NS	-	-	-	-
(d)						
C signature	38, 38	-0.5032199 **	-	-	0.1954917 ***	-
#Rud	-	1.1846 ***	1.7438 ***	-0.5732 **	-	-
coverRud	37, 10, 10, 37, 37	-79.43029 ***	46.81013 *	-19.46232 *	27.47712 ***	-1.06647 *
R. fruticosus	39, 10, 10	0.766339 NS	28.922747 **	-12.085196 **	-	-
U. dioica	38, 11, 38	-87.52369 ***	-1.81806 *	-	25.83853 ***	-

df: degrees of freedom; C: coppiced TRUE/FALSE; Age: number of years since last coppiced; pH: pH-CaCl₂; Sand: soil sand fraction; #AFS, coverAFS: number and percentage cover of ancient forest species; #FS, coverFS: number and percentage cover of "other" forest species; #LS, coverLS: number and percentage cover of non-competitive light-demanding species; C signature: mean C-value (Hunt et al., 2004) weighted by individual plant cover; #Rud, coverRud: number and percentage cover of ruderal species; /: variable not included; -: variable excluded by model selection; NS: not significant; *: p < 0.05; **: p < 0.01 and ***: p < 0.001

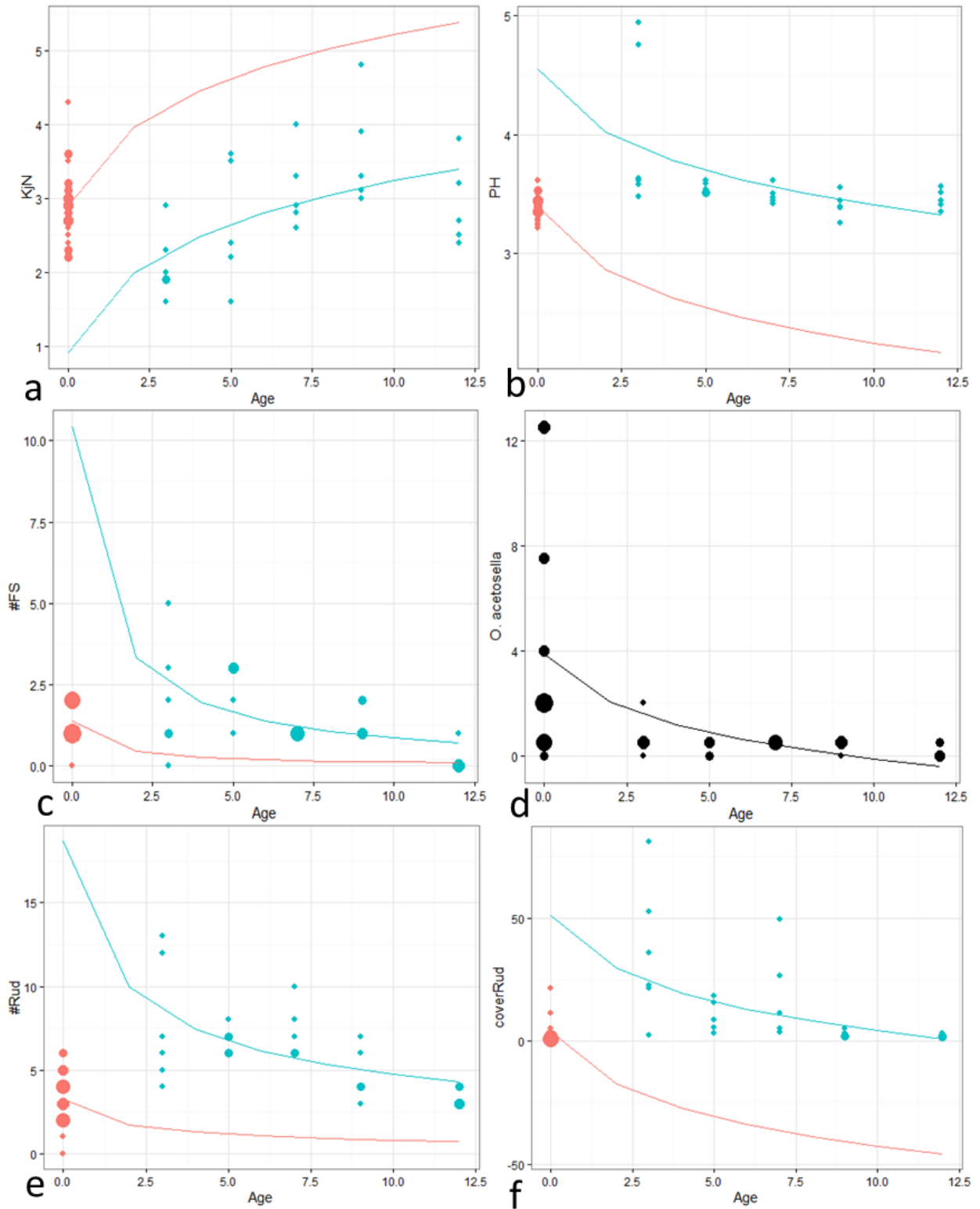


Figure 4.3

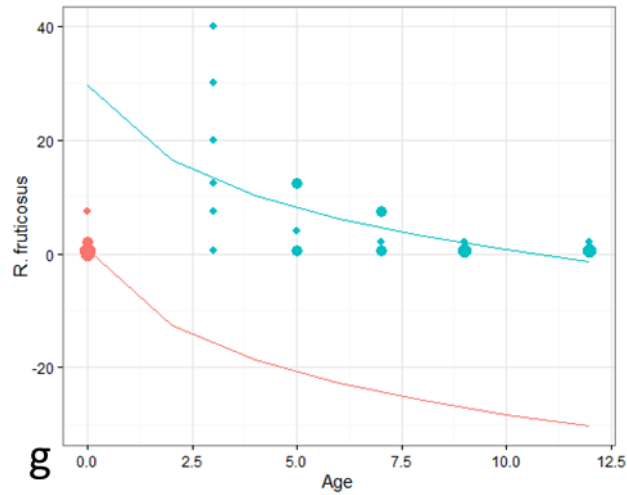


Figure 4.3 (continued): Graphs with linear mixed-effects models and generalized linear mixed-effects models for environmental and vegetation characteristics (a: Kjeldahl nitrogen; b: pH of the mineral topsoil; c: number of “other” forest species; d: percentage cover of *Oxalis acetosella* L.; e: number of ruderal herb species; f: total percentage cover of ruderal herbs; g: percentage cover of *Rubus fruticosus* L.). Red circles: uncut plots; blue circles: coppiced plots; black circles: all plots; red line: model prediction for uncut plots; blue line: model prediction for coppiced plots; black line: model prediction for all plots; Size of the circles is directly proportional to the number of observations.

5. Discussion

This study was initiated to assess the effects of the reintroduction of coppice-with-standards management in De Heide on the herb layer. It was unclear how typical forest species would react to this change in management, because the disturbance caused by the mechanical exploitation and the fact that the coppice had been abandoned for a long time constituted factors with unknown effects. The results show that the AFS were unaffected or reacted slightly positively. Also, the expected positive response of the goal species was indeed observed. Yet, it was limited, as the cover did not increase. The long abandonment of the coppice raised the question whether the coppice stools would still regrow vigorously enough to cast shade on ruderal species early on, so that they would not be able to competitively exclude other species. Ruderal species do seem to benefit directly after coppicing, however, a lasting ruderalisation of the herb layer is not observed.

AFS do not seem to have been negatively affected by the coppice-with-standards management in terms of total cover and number of species. This is in accordance with previous studies indicating the ability of coppice-with-standards to maintain the shade tolerant flora (Ash & Barkham, 1976; Decocq et al., 2004; Decocq et al., 2005; Vild et al., 2013), taking into account that AFS are often more shade tolerant than other forest plant species (Hermy et al., 1999). The stability of the AFS is probably largely due to the overall highly abundant *Anemone nemorosa* L., constituting almost 60% of the total herb cover, being unaffected by the coppice-with-standards management. The central position of this species in the ordination triplot (figure 4.2) corresponds to the outcome of the LMM in terms of being unaffected by the coppice-with-standards management as well as the age of the coppice. Confirmation of *Anemone nemorosa* L. performing well under coppice management is given by Mason and MacDonald (2002). Besides a fourfold increase in flowering, they found that the abundance of *Anemone nemorosa* L. did not change throughout the coppice cycle. Barkham (1992) reports a significant increase in cover of this species following coppicing. Being a shade evader, this species leafs and flowers in early spring before the canopy trees leaf. Therefore, I hypothesise that coppicing does not significantly change the amount of light *Anemone nemorosa* L. can use during its growing period. Moreover, in this study, no significant change was found in the percentage gaps in the canopy cover, used as a measure of the amount of light available to the herb layer. Besides being counter-intuitive, this also seems to contradict previous studies reporting increased light on the forest floor following coppicing (Ash & Barkham, 1976; Mason & MacDonald, 2002; Vild et al., 2013). The reason of this apparent contradiction can be found in the rapid decrease in light availability during the first years after coppicing (Ash & Barkham, 1976; Mason & MacDonald, 2002) combined with the fact that the youngest stand in this study had already been coppiced three years before the measurements were carried out. I conclude there is no reason to assume that the coppice-with-standards management did not increase the light availability of the herb layer. This study was possibly carried out too late to capture the peak light availability directly after coppicing.

The responses of the individual AFS, however, are not univocally positive. *Oxalis acetosella* L. and *Lamium galeobdolon* (L.) L. respectively show a significant decrease in cover with increasing coppice age and between coppiced and uncut localities. It could be that the stable cover of *Anemone nemorosa* L. masks the decline of other AFS. A possible explanation for the decline in cover of these two species could be that

they suffer more than *Anemone nemorosa* L. from the shade cast by competitive herbs in summer as they are summer green.

Coppicing significantly increased the number of FS. This number decreases, however, with increasing coppice age. Assuming an increase in light availability to the herb layer did take place just after the coppicing, this increase in resources could have supported the increase in number of FS, as the species-energy theory predicts (Wright, 1983). Moreover, the creation of gaps in the canopy has been shown to decrease the competitive intensity for species adapted to disturbed sites as well as for typical shade-tolerant species, possibly altering the competitive rankings of those species (Suding, 2001). Therefore, I conclude that the gaps created in some of the plots just after coppicing possibly allowed more FS to coexist.

Coppice-with-standards management has already proven to be beneficial for light-demanding species before (e.g. Ash & Barkham, 1976; Ford & Newbould, 1977; Vild et al., 2013). Although not observed in the current study, it is generally accepted that coppice-with-standards management induces a cyclic light variation at the forest floor (Ash & Barkham, 1976; Mason & MacDonald, 2002), enabling light-demanding herbs to temporarily grow within the forest. The small increase of the number of LS together with the stability of the AFS and increase of number of FS in the current study could therefore be explained as the result of temporal resource heterogeneity (light in this case) which enables the coexistence of these plant species with contrasting plant strategies (Grime, 2001; Craine, 2002).

The total cover of LS increases with increasing pH of the mineral topsoil. Although the total cover of LS seems to be unaffected by the coppice-with-standards management, coppicing did increase the pH. Hölsher, Schade & Leuschner (2001) confirm this finding. They reported a higher pH value of the mineral soil in German coppice woods compared to high forest. Ash deposition after biomass burning is given as a possible explanation for the elevated pH. Biomass burning did, however, not take place in the current study area. It is unclear which aspects of the coppice-with-standards management caused the increase in pH and the subsequent decrease with increasing coppice age in this study. The soil disturbance caused by the mechanical exploitation possibly plays a role. After all, the compacted soil from wheel tracks left by heavy logging machinery has been shown to have a higher pH than the adjacent uncompacted soil (Schnurr-Putz et al., 2006). The increase in pH after reintroduction of coppice-with-standards management may be beneficial, considering that the soil of the Meerdaal Forest has been acidifying during the last decades, mainly due to acidifying pollutants (Baeten et al., 2009). Continued measurement of the pH in the study area during the following coppice cycles is important to verify the effect of coppice-with-standards management on the pH, as Baeten et al. (2009) state that soil acidification is largely irreversible, rendering the reintroduction of the coppice management insufficient to maintain and restore herb layer diversity.

The C-signature is determined by the pH of the mineral topsoil. High C-values correspond to the plots with a high pH. This result is reflected in the C-S-R-plot (figure 4.1) and the ordination triplot (figure 4.2): The highest C-values are found in the plots having the youngest coppice and these plots also show the highest spread along the pH gradient, which indicates that their vegetation is strongly determined by the pH. As mentioned in the previous paragraph, the high pH values may be a result of the soil disturbance caused by the mechanical exploitation. The soil disturbance may have also influenced the C-signature directly by creating favourable conditions for competitive species, such as *Rubus fruticosus* L. to thrive (Deconchat &

Balent, 2001). As expected, the number as well as the total cover of ruderal species increased as a result of the coppice management. This increase has been reported by previous studies of coppice management (e.g. Decocq et al., 2004; Vild et al., 2013). The number, as well as the total cover of ruderal species do decline again as the coppice ages. The ruderalisation, as feared by Vild et al. (2013), is only temporary, at least in this study. *Rubus fruticosus* L. follows this pattern with an increase in cover after the coppicing, followed by a gradual decrease over time. The cover of *Urtica dioica* L. depended on the pH, being high in plots with high pH, possibly due to the link with soil disturbance by mechanical exploitation. Baeten et al. (2009) stated that reinstating coppice management might cause a sudden increase in nutrients, possibly resulting in increased dominance of competitive herbs (called ruderal herbs in this study). Taking the KjN as measure, this sudden increase in nutrients was not observed. On the contrary, the KjN decreased following coppicing and gradually increased with increasing coppice age. I hypothesise that an increase in available nutrients has been masked due to the rapid uptake by the abundant growth of the herbs soon after coppicing.

6. Conclusion

In general, the typical forest herbs present before the reintroduction of the coppice-with-standards management were not negatively impacted. The typical forest herbs as a whole were either unaffected or reacted slightly positively. The cover of some individual forest species did decrease, however, without any signs of recovery.

The reintroduction of the coppice-with-standards management had a small, yet positive impact on the goal species in terms of number of species. The cover of the goal species did not increase, however, leading to the conclusion that the overall positive effect of the coppice-with-standards management is limited.

Ruderal herb species reacted to the coppice-with-standards management with an increase in the number of species and cover. However, this reaction is only temporary. The number of ruderal species as well as their cover gradually declined throughout the coppice cycle, eventually attaining values similar to those of before the coppicing.

The general conclusion of this study is that the reintroduction of coppice-with-standards management in the Meerdaal Forest has had a moderately positive effect on the conservation value of the herb layer. However, it is important to take into account that these are the results of the first coppice cycle since decades of abandonment. Large volumes of wood had to be taken out, involving a relatively large amount of disturbance. I expect the total amount of disturbance to be smaller and the coppice to grow back more quickly in the following coppice cycles. As a result, ruderal plants may have more difficulty to attain dominance, which can prove to be beneficial for the goal species as well as the typical forest plants as they have to compete less intensely with them. Therefore, I would advocate the continuation of the coppice-with-standards management. However, a thorough follow up will be vital to determine whether individual forest species will be able to remain present.

7. Summary

7.1. English version

Coppice-with-standards is an ancient woodland management system that has two main components: the coppice and the standards. The coppice consists of young trees which are cut down on a short-term rotational basis. During each coppice cycle, new shoots develop from their stumps. These shoots are eventually harvested and supply firewood and wood of small size. Between the coppice, a number of single-stemmed trees, the standards, are allowed to grow to a bigger size during multiple coppice cycles, yielding a sparse canopy. The standards are eventually harvested as well to yield construction wood.

Coppice-with standards has been a widespread management system of European lowland forests for many decades, if not centuries. As a result, many ancient woodlands harbour a large component of typical “coppicing plants”, adapted to this management system. However, due to several socio-economic reasons, coppicing was almost completely abandoned in central and northwest Europe by the 1940’s. The characteristic cyclic light variation at the forest floor disappeared, the forest canopies became denser, resulting in a higher litter input and the share of tree species with an easily decomposed litter increased. This caused the species composition of the herb layer to shift towards more shade-tolerant and nutrient-demanding species.

Reintroduction of coppice management has been suggested to reverse this trend. Several reintroduction experiments have already yielded promising results: Light-demanding herbs can benefit while the shade-tolerant species are able to sustain the changed management. However, the resulting increase in light availability and nutrients potentially leads to amplified competitive exclusion of forest species by ruderal herbs. This, in turn is detrimental to the conservation value of the forest.

The goal of this master’s thesis is to give an answer to the question whether the reintroduction of coppice-with-standards management in the Meerdaal Forest (Belgium) benefits the conservation value of its herb layer. More specifically: What is the effect on the typical forest herbs, the “goal-species”, namely non-competitive, light demanding herbs and finally also the ruderal herbs?

A chronosequence experiment was set up in forest reserve De Heide, part of the Meerdaal Forest, where coppice-with-standards management was reintroduced on an area of 20 ha within this reserve in the year 2004 as a small experimental restoration project. This area has been divided into eight stands and every second year, one of these stands was scheduled to be coppiced, leaving some large trees as standards. At this moment, seven of the eight stands have been restored to coppice-with-standards so that now freshly cut open area, re-closing coppice, and uncut area are present.

Coppice-with-standards management has been the main form of management in the Meerdaal Forest, at least from the 16th century and possibly earlier, until the end of the 19th century. The basis of De Heide now consists of an area of oaks, approximately 250 years of age. The vegetation of De Heide is

characterized by the *Stellario-Carpinetum* association and the soil composition, being dry and gleyic loamy soils, is homogeneous throughout the reserve.

Within the 52 different sampling plots distributed over the eight stands of the reserve, the understory vegetation was sampled, dendrometric data were gathered, light measurements were carried out and the soil was analysed.

Next, these data were compiled and several derivative variables were calculated: Beta diversity, the Ellenberg indicator values and the C-S-R signatures. Thereafter, exploratory analyses were conducted: The C-S-R signatures were visualised and an ordination of the species and plots was conducted using Redundancy Analysis (RDA). A Permutational Multivariate Analysis of Variance (PERMANOVA) was used to select the significant environmental variables. Finally, Linear Mixed-Effects Models (LMM) and Generalized Linear Mixed-Effects Models (GLMM) were made using backwards selection based on a significance level of 5% to explain the environmental variables and the vegetation characteristics representative for the typical forest herbs, the goal species or the ruderal herbs.

Ancient forest species (AFS) do not seem to have been negatively affected by the coppice-with-standards management in terms of total cover and number of species. This is in accordance with previous studies indicating the ability of coppice-with-standards to maintain the shade tolerant flora. The stability of the AFS is probably largely due to the overall highly abundant *Anemone nemorosa* L., constituting almost 60% of the total herb cover, being unaffected by the coppice-with-standards management. This can be due to the fact that *A. nemorosa* is a shade evader that leafs and flowers before the canopy trees leaf. Therefore, it is possible that coppicing does not significantly change the amount of light *A. nemorosa* can use during the growing period. Important to mention is that no significant change was found in the amount of light reaching the herb layer in this study. As light availability quickly decreases after coppicing, it may be that this study was carried out too late to capture the peak light availability directly after coppicing.

The responses of the individual AFS, however, are not univocally positive. *Oxalis acetosella* L. and *Lamium galeobdolon* (L.) L. respectively show a significant decrease in cover with increasing coppice age and between coppiced and uncut localities. It could be that the stable cover of *Anemone nemorosa* L. masks the decline of other AFS. A possible explanation for the decline in cover of these two species could be that they suffer more than *Anemone nemorosa* L. from the shade cast by competitive herbs in summer as they are summer green.

Coppicing significantly increased the number of other forest species (FS). This number decreases, however, with increasing coppice age. The creation of gaps in the canopy may have decreased the competitive intensity among the herb species, allowing more FS to coexist.

Coppicing increased the number of light-demanding herbs (LS). The cyclic light variation at the forest floor caused by coppicing, an example of temporal resource heterogeneity, may have enabled this increase together with the stability of the AFS and increase of, as it makes the coexistence of plant species with contrasting plant strategies possible. The total cover of LS, however increased with increasing pH of the mineral topsoil. Although the total cover of LS seems to be unaffected by the coppice-with-standards

management, coppicing did increase the pH. This increase in pH may be due to soil disturbance caused by the mechanical exploitation.

The number of ruderal herbs as well as their cover increased as a result of the coppice management. However, both numbers decline again as the coppice ages. Therefore, “ruderalisation” seems to be only temporary. *Rubus fruticosus* L. follows this pattern with an increase in cover after the coppicing, followed by a gradual decrease over time. The cover of *Urtica dioica* L. depended on the pH, being high in plots with high pH, possibly due to the link with soil disturbance by mechanical exploitation. The C-signature of the plots was determined by the pH as well.

The general conclusion of this study is that the reintroduction of coppice-with-standards management in the Meerdaal Forest has had a moderately positive effect on the conservation value of the herb layer. As I expect the results of following coppice cycles to be better, I advocate a continuation of the coppice-with-standards management. However, follow up has to ensure that individual species aren't lost.

7.2. Samenvatting

Middelhoutbeheer is een aloude vorm van bosbeheer die bestaat uit twee elementen: het hakhout en de overstaanders. Het hakhout bestaat uit jonge bomen die op korte termijn herhaaldelijk worden omgehakt. Tijdens elke hakhoutcyclus ontwikkelen de overgebleven stronken nieuwe scheuten. Deze scheuten worden uiteindelijk geoogst om brand- en geriefhout te leveren. Een aantal enkelstammige bomen, de overstaanders, krijgen de kans om verder te groeien tussen het hakhout gedurende verschillende hakhoutcycli, zodat een ijle boomlaag wordt gevormd. Ook de overstaanders worden uiteindelijk gekapt om hout te leveren voor de bouw.

Gedurende vele decennia of zelfs eeuwen is middelhoutbeheer een wijd verspreide vorm van bosbeheer geweest voor bossen van het Europese laagland. Het gevolg hiervan is dat vele oude bossen vandaag de dag een groot aandeel van zogenaamde “hakhoutplanten” herbergen die goed aangepast zijn aan deze beheervorm. Echter, omwille van verschillende socio-economische redenen werd het middelhoutbeheer bijna volledig verlaten in centraal en noordwest Europa rond de jaren 1940. Hierdoor verdween de kenmerkende cyclische variatie van licht op de bosbodem, werden de boomlagen dichter wat dan weer resulteerde in een hogere strooiselproductie en verhoogde het aandeel van boomsoorten met een goed verteerbaar strooisel. Dit heeft er voor gezorgd dat de soortensamenstelling van de kruidlaag veranderd in de richting van meer schaduwtolerante en nutriëntenbehoevende soorten.

Om deze trend te keren is herinvoering van het middelhoutbeheer reeds voorgesteld. Verschillende herinvoeringsexperimenten hebben al veelbelovende resultaten voortgebracht: Lichtminnende planten kunnen voordeel halen uit de wijziging in het beheer terwijl schaduwtolerante planten in staat zijn om het te doorstaan. De resulterende toename in beschikbaarheid van licht en nutriënten leidt echter mogelijk tot een versterkte competitieve uitsluiting van typische bosplanten door ruderaal planten. Dit is dan weer nadelig voor de instandhoudingswaarde van het bos.

Het doel van deze thesis is om een antwoord te bieden op de vraag of herinvoering van middelhoutbeheer in het Meerdaalwoud een positief effect heeft op de instandhoudingswaarde van zijn kruidlaag. Concreet: Wat is het effect op de typische bosplanten, op de doelsoorten, namelijk niet-competitieve, lichtminnende planten en op ruderaal planten?

Om hier een antwoord op te geven werd een experiment gebaseerd op een chronosequentie opgezet in bosreservaat De Heide, onderdeel van het Meerdaalwoud. In 2004 werd in het kader van een klein experiment middelhoutbeheer opnieuw ingevoerd op 20 hectare van De Heide. Deze oppervlakte werd verdeeld in acht bestanden. Om de twee jaar werd in één van deze bestanden hakhout afgezet waarbij enkele grote bomen bewaard bleven om dienst te doen als overstaanders. Op dit moment is het middelhoutbeheer hersteld in zeven van de acht bestanden zodat er nu recent gekapte open delen, zich sluitend hakhout en ongekapt hooghout aanwezig zijn.

Middelhoutbeheer was de belangrijkste beheervorm in het Meerdaalwoud, ten minste vanaf de 16^e eeuw en mogelijks eerder, tot het eind van de 19^e eeuw. Bosreservaat De Heide bestaat vandaag de dag uit een bestand van eiken van rond de 250 jaar oud. De vegetatie van De Heide wordt gekenmerkt door de associatie van het eiken-haagbeukenbos (*Stellario carpinetum*). De bodemsamenstelling van de Heide, namelijk droge en gleyige leembodems, is homogeen over de ganse oppervlakte van het reservaat.

In elk van de 52 verschillende plots, verdeeld over de acht bestanden van het reservaat, werd de vegetatie opgenomen, werden dendrometrische gegevens verzameld, lichtmetingen uitgevoerd en werd een bodemanalyse uitgevoerd.

Vervolgens werden deze gegevens samengebracht en werden verschillende afgeleide variabelen berekend, namelijk: Beta-diversiteit, de Ellenberg indicatorwaarden en de C-S-R-signaturen. Daarna werden de volgende verkennende analyses uitgevoerd: De C-S-R-signaturen werden gevisualiseerd en er werd ordinarie toegepast op de soorten en plots door middel van redundantie-analyse (RDA). Selectie van de significante omgevingsvariabelen gebeurde met behulp van Permutationele Multivariate Variantie-analyse (PERMANOVA). Tot slot werden Linear Mixed-Effects Modellen (LMM) en Generalized Linear Mixed-Effects Modellen (GLMM) opgesteld, gebruik makend van “achterwaartse” selectie gebaseerd op een significantieniveau van 5%. Deze modellen dienen om de omgevingsvariabelen en de eigenschappen van de vegetatie die representatief zijn voor de typische bosplanten, de doelsoorten of de ruderaal planten te verklaren.

Oud-bosplanten lijken geen nadeel te hebben ondervonden van het middelhoutbeheer wat aantal soorten en totale bedekking betreft. Dit stemt overeen met de bevindingen van vorige studies die aangeven dat middelhoutbeheer in staat is om de schaduwtolerante flora te behouden. De stabiliteit van de oud-bosplanten is waarschijnlijk grotendeels te wijten aan de reactie van bosanemoon (*Anemone nemorosa* L.). Bosanemoon, die bijna 60% uitmaakt van de totale bedekking van de kruidlaag, blijkt onaangestast te zijn door het middelhoutbeheer. Dit kan te wijten zijn aan het feit dat bosanemoon een plant is die schaduw ontwijkt door in blad te komen en te bloeien vooraleer de bomen in blad komen. Het is daarom mogelijk dat het middelhoutbeheer de hoeveelheid licht die de plant kan gebruiken tijdens het groeiseizoen niet significant verandert. Belangrijk om te vermelden is dat er geen significant verschil gevonden is in de hoeveelheid licht die de kruidlaag bereikt in deze studie. Aangezien de

lichtbeschikbaarheid snel daalt na het afzetten van het hakhout kan het zijn dat deze studie te laat is uitgevoerd om de piek in lichtbeschikbaarheid waar te nemen.

De responsen van de individuele oud-bosplanten zijn echter niet eenduidig positief. Witte klaverzuring (*Oxalis acetosella*) L. en gele dovenetel (*Lamium galeobdolon* (L.) L.) vertonen respectievelijk een significante daling in bedekking en tussen gekapte en niet-gekapte plots. Het kan zijn dat de stabiele bedekking van bosanemoon de achteruitgang van andere oud-bosplanten maskeert. Een mogelijke verklaring voor deze achteruitgang is dat deze soorten meer lijden onder de schaduw van competitieve planten gedurende de zomer dan bosanemoon aangezien ze zomergroen zijn.

Het middelhoutbeheer verhoogde het aantal andere typische bosplantensoorten significant. Dit aantal daalt weliswaar opnieuw naarmate het hakhout ouder wordt. De creatie van gaten in de boomlaag heeft mogelijks de competitie tussen de plantensoorten verlaagd, waardoor meer typische bosplanten naast elkaar konden bestaan.

Het middelhoutbeheer verhoogde ook het aantal lichtminnende bosplantensoorten (Dit zijn doelsoorten.). De cyclische variatie in lichtbeschikbaarheid voor de kruidlaag veroorzaakt door het middelhoutbeheer, een voorbeeld van temporele heterogeniteit van hulpbronnen, kan deze verhoging mogelijk gemaakt hebben terwijl de oud-bosplanten stabiel bleven. Dit is mogelijk aangezien deze heterogeniteit de co-existentie van planten met contrasterende strategieën mogelijk kan maken. De totale bedekking van lichtminnende bosplanten steeg echter met een stijgende pH van de minerale bodem. Hoewel de totale bedekking van lichtminnende bosplanten niet beïnvloed bleek door het middelhoutbeheer, verhoogde het middelhoutbeheer echter wel de pH. Deze verhoging kan te wijten zijn aan de bodemverstoring door mechanische exploitatie.

Het aantal en de bedekking van ruderaal plantensoorten stegen ten gevolge van het middelhoutbeheer. Beiden dalen echter opnieuw naarmate het hakhout ouder wordt. Ruderalisatie lijkt daarom slechts tijdelijk op te treden. Gewone braam (*Rubus fruticosus* L.) volgt dit patroon met een toename in bedekking net na het afzetten van het hakhout, gevolgd door een geleidelijke afname daarna. De bedekking van grote brandnetel (*Urtica dioica* L.) hing af van de pH. De bedekking van grote brandnetel was hoog in plots met een hoge pH, mogelijks omwille van de link met bodemverstoring door mechanische exploitatie. Ook de C-signatuur was verklaard door de pH.

De algemene conclusie van dit onderzoek is dat de herinvoering van middelhoutbeheer in het Meerdaalwoud een matig positief effect heeft gehad op de instandhoudingswaarde van de kruidlaag. Aangezien ik verwacht dat de resultaten van de volgende hakhoutcycli beter zullen zijn, pleit ik voor een voortzetting van het middelhoutbeheer. Een goede opvolging zal wel nodig zijn om na te gaan of er geen individuele bosplantensoorten verdwijnen.

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