Herb layer changes (1954-2000) related to the conversion of coppice-with-standards forest and soil acidiﬁcation

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Abstract

Question: Did the composition of the herb layer of a deciduous forest on loamy soils sensitive to soil acidiﬁca- tion change between 1954 and 2000? How are these change related to the abandonment of traditional cop- pice-with-standards forest management and increased soil acidiﬁcation?

Location: Central Belgium (Europe).

Methods: Twenty semi-permanent phytosociological quadrats from an ancient deciduous forest (Meerdaal forest) were carefully selected out of a total of 70 plots dating from 1954 and were revisited in 2000. Species composition and soil pH H2O were recorded using an analogous methodology. The studied period coincides with a period of forest conversion from coppice-with- standards towards a high forest structure and with an increase in acidifying and eutrophying deposition.

Results: Between 1954 and 2000, species composition of the herb layer changed signiﬁcantly. Redundancy analysis pointed to increased shade resulting from shifts in cover and species composition of the shrub and tree layer as the main driving force. Soil acidity increased and the majority of plots entered the aluminium buffer range, which potentially affected herb layer composition. Obser- vations at the species level, especially a strong decrease in cover of the vernal species *Anemone nemorosa* supported this hypothesis.

Conclusions: Our results show signiﬁcant shifts in the forest herb layer in less than ﬁve decades. These shifts were related to an alteration in the traditional forest management regime and increased soil acidity. Whereas the effect of a changed management regime can be mitigated, soil acidiﬁcation is less reversible. Testing the generality of these patterns on more extensive data sets is certainly needed.

Keywords: Forest conversion; Forest management; High forest; Increased shade; Semi-permanent plots.

Nomenclature: Lambinon et al. (1998):

Introduction

Most plant diversity in forests can be found in the herb layer (Gilliam 2007). Therefore, under- standing complex responses of forest herb layers to climate change, increased airborne pollution and land-use change (e.g. Honnay et al. 2002; Flinn & Vellend 2005; Gilliam 2006) is of primary im- portance to forest diversity and functioning. Comparing historical records and present day spe- cies composition in semi-permanent plots can provide useful information on the long-term impact of these environmental changes. However, only a few studies have described herb layer dynamics over a relatively long time scale by resampling of plots

(e.g. Lameire et al. 2000; Taverna et al. 2005; Van Calster et al. 2008).

One signiﬁcant, though largely overlooked, environmental change in European forests is the large-scale abandonment of coppice or coppice- with-standards management. This traditional man- agement form has been in use in Europe for many centuries (van der Werf 1991; Tack et al. 1993; Kirby & Watkins 1998; Rackham 2003). In a cop- pice-with-standards system, young shoots are cut down in short rotations and new shoots resprout from the cut stumps (coppice). Single-stemmed trees (standards) are retained in a sparse canopy for one or more rotations. During recent decades, coppice- with-standards management has declined in favour of a forest management regime that maintains a tall forest canopy with prolonged rotation periods, i.e. high forest management. The regular cutting of the coppice layer and the attendant cyclic variation in light has gradually declined, and the tree layer has become denser. Because vegetation composition in formerly coppiced forests is partially the result of the environmental conditions created by this man- agement form, these conversions to high forest are likely to have caused signiﬁcant changes in the herb layer (e.g. Barkham 1992b; Decocq et al. 2004; Van Calster et al. 2008).

Other environmental changes may additionally account for long-term vegetation dynamics in semi- permanent plots. Soil acidiﬁcation resulting from increased atmospheric deposition of acidifying pol- lutants is expected to be a second key driver of herb layer changes in European forests (e.g. Falkengren- Grerup 1986; Kuhn et al. 1987; Thimonier et al. 1994; Van Calster et al. 2007). Because the large- scale abandonment of traditional forest management and soil acidiﬁcation occurred simultaneously and interact (Van Calster et al. 2007), it is inherently dif- ﬁcult to disentangle the effect of both processes on the herb layer. Documenting long-term vegetation changes in semi-permanent plots on sites with vary- ing sensitivity to soil acidiﬁcation can provide useful information to explore their importance. Barkham (1992b) and Van Calster et al. (2008) performed such studies on well buffered, calcareous soils, but data on soils sensitive to acidiﬁcation are lacking.

In this study, we analysed vegetation changes in 20 semi-permanent phytosociological plots in Meerdaal forest (central Belgium) between 1954 and 2000. Plots were carefully selected out of a larger data set of 70 plots. The studied period parallels a gradual conversion of the centuries-old coppice- with-standards to a high forest management system. Furthermore, the Meerdaal forest is expected to be

sensitive to soil acidiﬁcation for two reasons. First, the loamy soils on sandy bedrock of the Meerdaal forest have a relatively limited buffer capacity, i.e. ability to resist changes in pH. The cation exchange capacity (a measure of buffer capacity) of the 0.8 m upper soil proﬁle is only 6-8 cmol kg - 1, which is at- tributable to the low clay content ( ± 20%). Second, atmospheric deposition of acidifying pollutants has increased over the past 50 years in Belgium, e.g. ammonium deposition doubled between 1950 and 1980 (Asman et al. 1988). Current levels of atmo- spheric deposition of acidifying pollutants (NHX, NOX, SOY) in forests within the study region are

therefore high (44000 eq · ha - 1 · yr- 1 in 2000, Van

Avermaet et al. 2006). Since Thimonier et al. (1994) showed that compositional changes of the herb layer can be more pronounced on acidic compared to well buffered loamy soils, signiﬁcant shifts in our study sites were expected. Therefore, the aim of this study is (1) to analyse the extent and direction of herb layer changes in the Meerdaal forest, and (2) to ex- plore whether the change in forest management and soil acidiﬁcation can (partially) account for the ob- served patterns.

Materials and Methods

*Study area and management history*

The Meerdaal forest complex is a 1319 ha, mainly ancient forest (i.e. permanent forest cover at least since the map of De Ferraris, 1770-1778) si- tuated in central Belgium. Together with the nearby Heverleebos (635 ha) and some smaller forest pat- ches, it forms the second largest ancient forest complex in Flanders (northern Belgium). It is as- sumed to be a remnant of a vast forest that covered a large part of central Belgium during Roman times (Tack et al. 1993, but see Vanwalleghem et al. 2004). The prevailing sub-Atlantic climate of this region is characterized by a total annual precipitation of ca. 821 mm (uniformly distributed over the year) and minimum and maximum average monthly tempera- tures of 2.51C and 17.21C, respectively. The Meerdaal forest is located on a slightly undulating plateau, with a height above sea level between 55 and 105 m. Predominant soil types in Meerdaal for- est are Luvisols (in the south) and Podzoluvisols (in the north), which developed in Pleistocene aeolian deposits of loamy loess on top of tertiary sandy for- mations (Baeyens et al. 1957). Main vegetation types in Meerdaal forest are *Stellario-Carpinetum* and *Milio-Fagetum* (*sensu* Noirfalise 1984) on Luvisols.

On Podzoluvisols, the predominant vegetation type is *Fago-Quercetum* (*sensu* Noirfalise 1984).

Like most Belgian forests, the Meerdaal forest complex has a long management history. A coppice- with-standards system is indicated on maps of de Ferraris (1770-1778) and is described in detail in documents dating back to the 16th century (Baete´ et al. 2007). The coppice layer was principally made up of hazel (*Corylus avellana* L.), sycamore (*Acer pseudoplatanus* L.) and ash (*Fraxinus excelsior* L.) under a scattered tree layer (‘‘standards’’) domi- nated by oak (*Quercus robur* L.). Since the beginning of the 20th century, there has been a tendency to promote a higher proportion of shoots in the tree layer. Data from 1921 indicate an average basal area

of the standards of 15–20 m2 ha-1, which suggests a

coppice with elevated surface area of standards. This is, however, still far below the present average basal area, ranging from 25 to 40 m2 ha-1. The cop- pice-with-standards forest structure has been abandoned progressively since the second half of the 20th century. Forest conversion was implemented through a combination of cessation of regular cut- ting of the coppice layer and promotion of coppice shoots and uncut shoots to the tree layer (Dethioux 1955; Baete´ et al. 2007). This gradually altered silvi- cultural system resulted in the uneven-age high forest structure of the present-day forest.

*Data collection: 1954 and 2000*

During the early 1950s, a vegetation and soil survey of Belgium was conducted. The study of the Meerdaal forest and its surroundings was carried out during 1954 and 1955 (Dethioux 1955), herein- after indicated as ‘‘1954’’. Seventy vegetation descriptions of the tree (47 m), shrub (1-7 m) and herb layer were made in circular sample plots by es- timating the cover of every species. During vegetation recording, the area of every plot was sys- tematically increased until species saturation (minimum area method). Plots ranged from 125 to 225 m2. At each location, colorimetric soil pH mea- surements were made in the centre of three soil horizons (surface ‘‘A’’, eluviation ‘‘E’’ and illuviation ‘‘B’’ horizon) using a ﬁeld pH meter. Depth below ground level of every measurement was noted. The location of each plot centre was written down as the distance to a reference point (e.g. a road junction) and/or orthogonal distance to a forest track.

The methodology of the 2000 survey was de- signed to maximize reliability of the temporal comparison and consisted of two successive steps:

(1) plot selection and relocation, and (2) a modiﬁed

methodology for vegetation description and mea- surement of soil acidity. Different conversion types have proven to result in different compositional changes of the herb layer (Van Calster et al. 2008) and soil acidity (Van Calster et al. 2007); therefore, we only selected plots within a single conversion type, i.e. 1954 coppice-with-standards plots that currently consist of mixed high forest dominated by oak. Further selection was based on the homo- geneity of vegetation composition within a plot and the availability of cartographic descriptions to ex- isting reference points allowing accurate relocation. This selection process identiﬁed 20 suitable plots. In 1954, plots were not permanently marked so that the exact location of the plot centre was not known. To partially overcome this uncertainty, a new plot de- sign was used. App. 1 gives more detail on the relocation procedure, plot design and methodology of vegetation descriptions. In general, the 2000 plot relocation resulted in a zone with a high probability of comprising the 1954 plot. This zone was further subdivided in 5 mx5 m subplots. Vegetation de- scriptions were made in conformity with the 1954 survey in a subset of these subplots summing up to the area of the 1954 plot.

In each subplot, four soil samples were collected at the corresponding 1954 depths. Soil pH-H2O measurements were performed on a mixture of these four samples for each separate depth with a glass electrode. Thus, measurement methods for de- termining soil pH differed between the two surveys. To account for this difference, a regression between the 1954 and 2000 pH values of the deepest soil horizon (41 m under the surface level) was calcu- lated. Based on the observation that soil acidity at these depths remains relatively constant (e.g. Falk- engren-Grerup 1987; De Schrijver et al. 2006), this regression (slope 5 1.06, intercept 5 - 0.40, coefﬁ- cient of determination 5 0.97) was used to adjust the original 1954 pH values of the topsoil layer (0- 15 cm) to the values obtained with the new measur- ing method.

*Data analysis*

Data analysis was performed in three successive steps: (1) characterization of environmental condi- tions in 1954 and 2000 (canopy-related variables, Ellenberg indicator values); (2) testing the sig- niﬁcance of compositional changes in the herb layer between 1954 and 2000; (3) relating the observed herb layer changes to differences in environmental conditions. Prior to the analyses, all herb species with a frequency of o5% were removed from the

data set. This diminished the effect of the accidental occurrence of herb species caused by the altered plot design. Regeneration of tree and shrub species was also removed because the occurrence of these species is highly dependent on the irregular seed set of the canopy.

Six variables were derived from the shrub and tree layer data to assess canopy-related composi- tional and structural changes at the plot level: (1) species richness in the tree (SRtree) and shrub layer (SRshrub); (2) sum of cover of species in the tree (SCtree) and shrub layer (SCshrub); (3) average litter quality (LQ; Hermy 1985) and average shade-cast- ing ability (SCA; qualitative index based on expert knowledge from Ellenberg 1996). Both average LQ and SCA were calculated as weighted (by cover) averages of litter quality and shade-casting indices of individual canopy species (App. 2). Furthermore, average Ellenberg indicator values (Ellenberg et al. 1992) for light (AIVL), nitrogen (AIVN), soil moist- ure (AIVF) and soil reaction (AIVR) were calculated for every plot to infer environmental conditions reﬂected in the herb layer (Diekmann 2003). Differ- ences between survey years of all variables (canopy- related and AIV values) were tested using Wilcoxon Signed Rank tests for paired samples.

Statistical signiﬁcances of compositional chan- ges in the herb layer were tested using a block multi- response permutation procedure (bMRPP) with the Euclidean distance measure in PC-ORD version

4.41 (McCune & Mefford 1999; cf. Taverna et al. 2005). The bMRPP is the non-parametric, multi- variate equivalent of a paired *t*-test to test the hypothesis of no difference in species composition between survey years (groups). The test accounts for the paired nature of the plots (blocks). The test sta- tistic is based on comparison of the mean dissimilarity within the a priori grouping, in this case survey year, and a random permutation of 999 other possible groupings (Mielke & Berry 2001). Additionally, we tested the difference in the total number of species per plot with a paired *t*-test.

Temporal shifts in herb layer composition were related to changes in canopy layer characteristics (SC tree, SC shrub, LQ and SCA) and soil acidity by means of multivariate redundancy analysis (RDA). The use of a constraint ordination technique, such as RDA, is preferred when relating species composi- tion to a priori selected explanatory variables (Anderson & Willis 2003). A 1954-2000 plotxspecies data matrix (40 plots) was analysed in a single RDA ordination in CANOCO 4.5 for Windows (ter Braak

& Sˇ milauer 2002). Species scores were post-trans-

formed (divided by species standard deviation) so that

the interpretation of the RDA plot follows the bi-plot rule. This means that the perpendicular projection of species positions (or arrow tips of explanatory vari- ables) onto ordination axes or explanatory variables gives an estimate of the correlation between them. Differences in plot scores between years were tested with Wilcoxon Signed Rank tests.

Results

*Changes in canopy layer characteristics and soil acidity*

Soil acidity increased signiﬁcantly, with an average pH H2O drop from 5.0 to 4.3 (Table 1). When an outlier at pH 7.7 (cf. Fig. 1) was deleted, average pH decreased from 4.9 to 4.1. The range of occurring pH values became smaller between 1954 and 2000 because the increase in soil acidity was stronger for plots with high initial pH (Fig. 1).

The dominant role of the shrub layer in the for- est canopy shifted towards the tree layer. Sum of cover doubled in the tree layer, and signiﬁcantly de- creased in the shrub layer (Table 1). A similar trend was observed concerning the number of species in each canopy layer. The signiﬁcant decrease in cover and number of species in the shrub layer was mainly the result of a decrease in species with low shade- casting ability and low shade tolerance. By contrast, the signiﬁcant increase in cover and number of spe- cies in the tree layer was mainly caused by species with high shade-casting ability. In this way, the total (shrub1tree) sum of cover increased from 133% to 150%, and average shade-casting per plot sig- niﬁcantly increased. The average litter quality did not change between survey years.

*Changes in the forest herb layer*

Herb layer composition signiﬁcantly changed between 1954 and 2000 (blocked MRPP *P*o0.001; Fig. 2) and the effect size of this change was rela- tively high (*A* 5 0.103). This effect size should be interpreted as within-group agreement. If *A* 5 1, all plots within a survey year have identical species composition and abundance, while if *A* 5 0, agree- ment in species composition and abundance between plots within one survey year equals that expected by random chance (no ‘‘effect’’ of year). The average total number of species per plot slightly increased from 16.2 to 18.7 (paired *t*-test *t* 5 - 2.2; *P* 5 0.040). Average Ellenberg indicator values for light (AIVL) signiﬁcantly decreased, whereas the

average values for soil moisture (AIVF) signiﬁcantly increased (Table 1).

Results of the RDA analysis are presented in Fig. 2. This ﬁgure is a correlation tri-plot represent- ing correlations between species, plots and explanatory variables. To justify the use of a con- straint ordination, we also performed a principal components analysis (PCA), which is the un- constraint equivalent of RDA. This analysis gave similar results: the Pearson correlation coefﬁcient of plot scores on the ﬁrst PCA and RDA axis was 0.992 (*P*o0.001) and on the second PCA and RDA axis 0.897 (*P*o0.001). Thus, the choice of a constraint instead of an unconstraint technique did not affect our results. The ﬁrst two RDA axes explained 22.6% of the variability in species data. The ﬁrst RDA axis was mainly related to litter quality, shade- casting ability and soil pH. A Wilcoxon Signed Rank test indicated that plot scores on this axis did not differ between years (*Z* 5 - 1.344; *P* 5 0.188).

Table 1. Changes in soil acidity, canopy-related charac- teristics and average Ellenberg indicator values of individual plots between 1954 and 2000. The sum of cover in the tree and shrub layer was subdivided in the sum of cover of species with low (SCA ::: 4) and high (SCA44) shade-casting ability (based on Ellenberg 1996; cf. App.

2). SD 5 standard deviation. test statistic: *Z*-value based on a Wilcoxon Signed Rank test; \*\*\**P* ::: 0.001;

\*\*0.001o*P* ::: 0.01; \*0.01o*P* ::: 0.05; n.s.: not signiﬁcant.

aplot average of litter quality indices of individual woody species (adapted from Hermy 1985) weighted by percen- tage cover. bplot average of shade-casting ability indices of individual woody species (adapted from Ellenberg 1996) weighted by percentage cover.

1954 2000 Test

statistic

Mean SD Mean SD

(a)) pH H2O (0-15 cm) 5.0 0.8 4.3 0.7 - 3.9\*\*\*

1. Canopy-related variables Species richness

Tree layer (SRtree) 1.8 1.1 3.4 1.2 - 3.3\*\*\*

Shrub layer (SRshrub) 6.1 1.9 3.9 1.3 - 3.7\*\*\*

\*\*\*

The second RDA axis was positively related to the sum of cover of the shrub layer and partially to soil pH. Sum of cover of the tree layer was negatively related to this axis. The difference in plot scores be- tween the two survey years was highly signiﬁcant (*Z* 5 - 3.920; *P*o0.001), i.e. this axis strongly dis- criminated between survey years.

Discussion

The most evident result of this study is that community composition of the herb layer in the mixed oak stands of Meerdaal forest signiﬁcantly changed over a period of only 46 years. Moreover, the extent of compositional change – expressed as an effect size – was relatively high compared with other studies focussing on long-term herb layer changes (Taverna et al. 2005, *A* 5 0.002; Van Calster et al. 2008, 0.016 ::: *A* ::: 0.112). Strong vegetation chan- ges over similar time periods have been found elsewhere. Rooney & Dress (1997), for instance, re- ported high species losses in 66 years due to increased deer browsing, and Brewer (1980) re- ported a strong decline in abundant forest herbs resulting from internal forest dynamics. Species richness in the Meerdaal forest slightly increased, but this could be solely the effect of the altered plot design, in which a wider area was sampled. A nat- ural soil gradient, represented by variations in soil pH and litter quality of the occurring species, re- mained the principal source of variation between plots (Fig. 2). This pattern was also found in similar long-term semi-permanent plot studies (e.g. Thi- monier et al. 1994; Lameire et al. 2000; Taverna et al. 2005; Van Calster et al. 2008). The second axis of variation signiﬁcantly discriminated between survey years and was mainly related to soil pH and the sum of cover and shade-casting ability of the tree and shrub layer. We must acknowledge that it remains difﬁcult to disentangle the relative con-

tribution of the explanatory variables because they

Sum cover tree layer (SCtree)

(%)

55 16 103 17 - 3.8

probably affected the herb layer simultaneously.

Low shade-casting ability 47 23 58 23 - 1.3NS

High shade-casting ability 5 14 40 27 - 3.5\*\*\*

Moreover, environmental changes not included in

our analysis could additionally underlie the ob-

Sum cover shrub layer (SCshrub) (%)

78 19 47 32 - 2.9\*\*

served patterns. The changed canopy characteristics

Low shade-casting ability 53 20 34 29 - 2.6\*\*

High shade-casting ability 18 16 11 12 - 1.2NS

Litter quality (LQ)a 2.5 0.5 2.3 0.7 - 1.0NS

Shade-casting ability (SCA)b 3.8 0.3 4.0 0.7 - 2.1\*

1. Average Ellenberg indicator values (AIV*)*

Nitrogen (AIVN) 5.3 0.8 5.4 0.7 - 0.4NS

Soil reaction (AIVR) 5.2 0.9 5.1 0.8 - 0.4NS

Soil moisture (AIVF) 5.4 0.3 5.5 0.3 - 2.4\*

Light (AIVL) 4.3 0.4 4.1 0.4 - 2.3\*

and soil pH are, however, the most likely candidates

to explain the strong shift in species composition of the herb layer. First, the explanatory variables di- rectly relate to the altered management regime in the Meerdaal forest and the increased deposition of acidifying pollutants in the study region during the past 50 years. Second, both factors proved to have an effect on herb layer vegetation in a similar long-

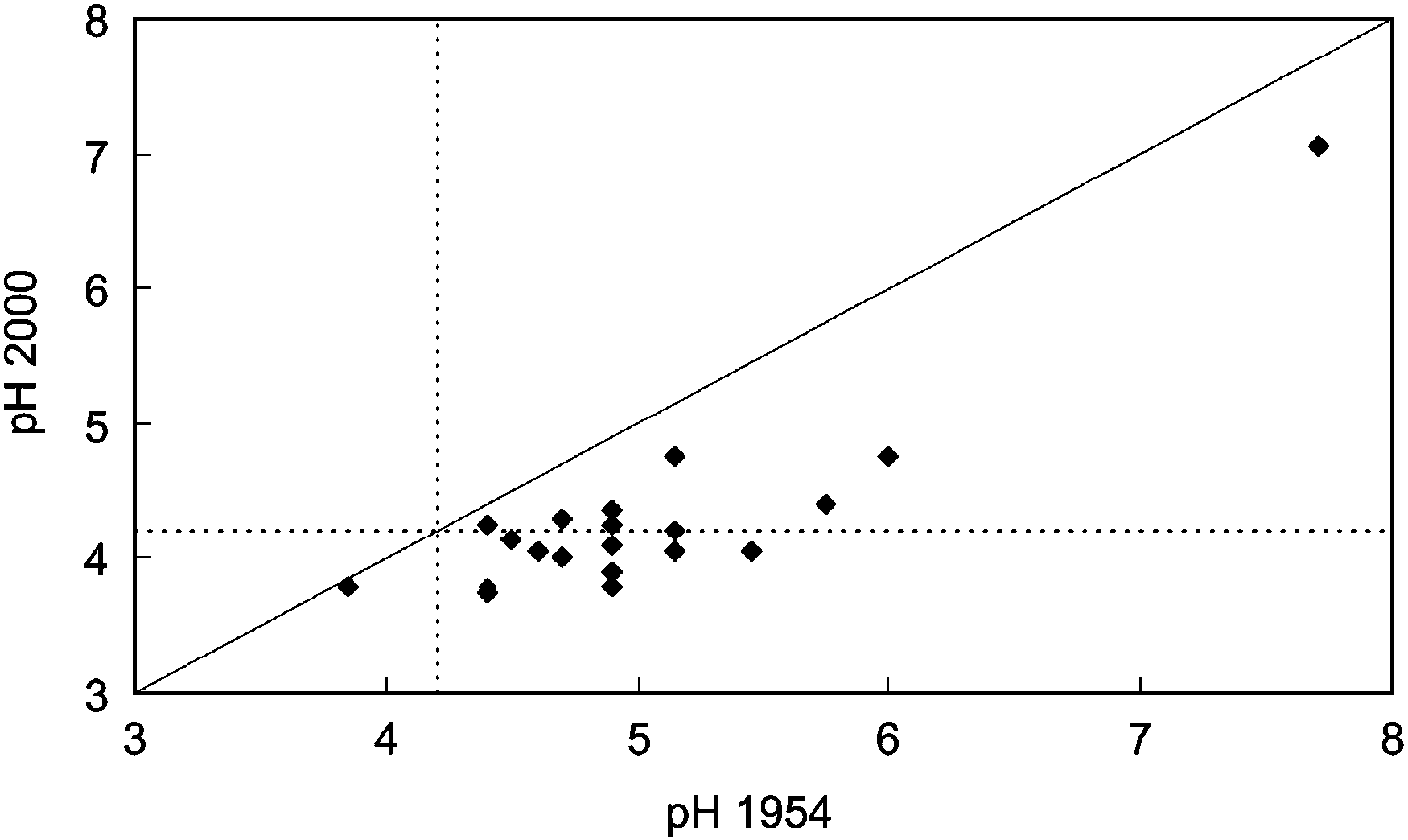


Fig. 1. Soil acidity (pH H2O) of the upper soil horizon of plots in 1954 and in 2000. F, 1:1 line of no change; - - -, theoretical threshold (pH 5 4.2) between the aluminium and cation exchange buffer range (Ulrich 1991).

term study by Van Calster et al. (2007, 2008). Third, unconstrained (PCA) and constrained (RDA) ordi- nation gave very similar results, indicating that the variables included in the RDA were strongly related to the principal axes of species variation between plots and years.

*Vegetation changes related to forest management*

Following the gradual abandonment of coppi- cing practice and the promotion of stems into the tree layer, dominant cover shifted from the shrub to the tree layer (Table 1). Especially high shade- casting woody species such as *Fagus sylvatica* L. and *Acer pseudoplatanus* grew into the tree layer and out-shaded low shade-casting, light-demanding species in the shrub layer. Consistent with this shift in cover, average species richness of the shrub and tree layer decreased and increased, respectively. The net effect was an increase in total canopy cover and intensiﬁcation of shade, which was reﬂected in the plot-level average shade-casting index. Further- more, the change in forest management probably affected the temporal light regime. Coppicing, i.e. the regular cutting of the shrub layer, leads to cyclic light variations at the forest ﬂoor (Ash & Barkham 1976). The cessation of this management practice therefore reduces long-term average light avail- ability, which has an effect on the demography of forest herbs (Barkham & Hance 1982; Jacquemyn et al. 2008).

This year-on-year continuation of low-light availability is expected to increase the dominance of shade-tolerant herb species and vernal species cap- able of phenological escape (e.g. Brewer 1980; de Kroon 1986; Barkham 1992a). At the plot level, this was expressed as a signiﬁcant decrease in the average Ellenberg indicator value for light between the sur-

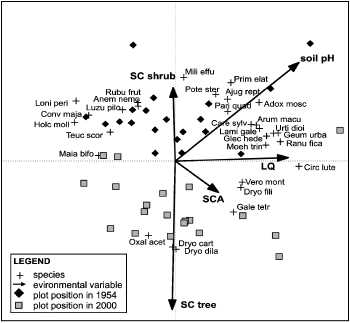


Fig. 2. Redundancy analysis tri-plots of species, 1954 and 2000 plots and environmental variables. Only species with a ﬁt 415% are shown. SCtree/shrub, sum of cover of species in the tree/shrub layer; LQ, average litter quality of cano- py species; SCA, average shade-casting ability of canopy species; soil pH, soil acidity (pH H2O, 0–15 cm).

vey years. At the species level, we found that light- demanding species such as *Lonicera periclymenum* L.*, Rubus fruticosus* agg. and *Ajuga reptans* L. were more conﬁned to the 1954 plot positions (Fig. 2). Some shade-tolerant herbs and ferns (e.g. *Oxalis acetosella* L.*, Dryopteris dilatata* (Hoffm.) A.Gray, *Dryopteris carthusiana* (Vill.) H.P.Fuchs) were more indicative of 2000 plot positions.

*Vegetation changes related to soil acidiﬁcation*

A number of studies have shown that soil acid- iﬁcation can be a main contributor to long-term vegetation change in European forests (Falkengren- Grerup 1986; Kuhn et al. 1987; Thimonier et al. 1994; Van Calster et al. 2007). Since average soil pH signiﬁcantly decreased during the last 46 years (Table 1; Fig. 1), this may also apply to vegetation changes in the Meerdaal forest. The pH of soils with low initial 1954 soil acidity (high pH H2O) decreased markedly. Soil acidiﬁcation results from internal processes such as soil forming and forest growth, but the increased acidiﬁcation rates in European forests over the past 50 years are generally attrib- uted to a high deposition of acidifying pollutants (e.g. Falkengren-Grerup 1987; Miller et al. 2001; De Schrijver et al. 2006). Therefore, the observed de- crease in soil pH in the Meerdaal forest is not surprising given the limited buffer capacity of the prevailing soils and high loads of acidifying deposi-

tion in northern Belgium, which is still among the highest in Europe (UNECE-EC 2003).

Furthermore, 17 out of 20 plots approached or entered the aluminium buffer range (pH H2Oo4.2 *sensu* Ulrich 1991). This pH threshold is regarded as a critical point for the successful establishment and growth of forest herbs in deciduous forests (Falk- engren-Grerup & Tyler 1993). Soil acidiﬁcation is therefore not unlikely to have caused, at least par- tially, signiﬁcant shifts in vegetation composition. Observations at the species level further support this suggestion. Frequency of occurrence or cover of some demanding species with high indicator values for soil reaction such as *Primula elatior* (L.) Hill*, Paris quadrifolia* L.*, Ajuga reptans* and *Potentilla sterilis* (L.) Garcke clearly decreased (App. 3; Fig. 2). Nevertheless, the average Ellenberg indicator value for soil reaction did not decrease. Analogous to Thimonier et al. (1992), this could be due to the fact that acidiﬁcation is obscured by light limitation; some acidophilic species (e.g. *Lonicera periclyme- num*, *Teucrium scorodonia* L.) were also light demanding and declined.

The change in cover of the vernal species *Ane- mone nemorosa* L. forms an interesting case to demonstrate the effect of acidiﬁcation. Barkham (1992a) suggested that its shade-avoiding strategy gives this vernal herb a competitive advantage in highly shaded environments. This would account for the strong increase of *A. nemorosa* in abandoned coppice woods over the past 100 years in British woodlands. More recently, Van Calster et al. (2008) showed that the increase in cover of *A. nemorosa* over four decades was correlated with increased ca- nopy shade. In the Meerdaal forest, however, average cover of *A. nemorosa* signiﬁcantly (Wilcox- on Signed Rank test *P* 5 0.019) decreased from 46% to 28%, indicating environmental constraints on the growth of this herb. Given the observation that the majority of plots entered the aluminium buffer range, we hypothesize that aluminium toxicity and reduced availability of mineral nutrients such as magnesium and calcium (Marschner 1995) might have caused growth limitation of this vernal species. This result suggests that acidiﬁcation might also have contributed to the decline of other herb species in Meerdaal forest.

Acidiﬁcation is often observed in combination with eutrophication (Thimonier et al. 1994) because both are partially the result of increased atmo- spheric nitrogen deposition. In this study, however, no increase in average Ellenberg nitrogen values was found. Pulse releases of nutrients following regular cutting of the coppice layer ceased (Barkham 1992a)

and total woody biomass accumulated. Therefore, it is expected that nutrients such as nitrogen, phos- phorus and potassium are being locked up in humus and biomass. Additionally, some competitive spe- cies that would normally beneﬁt from an increased nitrogen availability (e.g. *Rubus fruticosus* agg., *Scrophularia nodosa* L.) were probably simulta- neously limited by the low-light availability.

Conclusions

In less then ﬁve decades, herb layer composition in the Meerdaal forest changed signiﬁcantly. More- over, the decline of some forest herbs (e.g. *Primula elatior, Paris quadrifolia, Anemone nemorosa*) is of considerable concern for the conservation of herb layer diversity because the recovery of these herbs is limited by a slow colonization capacity (Hermy et al. 1999). Several authors have proposed reinstating the traditional coppice (with-standards) management system in some ancient woodlands to maintain for- est herb diversity (Peterken 1981; Barkham 1992a; Hermy et al. 1999; Harmer & Howe 2003). We sug- gest that in the Meerdaal forest this change back to coppice management would be insufﬁcient to main- tain and restore diversity of the herb layer. Soil acidiﬁcation is largely irreversible and is expected to additionally place restrictions on the growth of cer- tain target species for restoration. One mitigating measure would be the promotion of woody species with base-rich litter to beneﬁt demanding forest herbs (van Oijen et al. 2005). Furthermore, reinstat- ing coppicing might create a one-shot pulse of nutrients stored in the litter layer and biomass. This would potentially result in increased dominance of competitive herbs.

Vegetation changes in this study were strong compared to similar studies by Barkham (1992b) and Van Calster et al. (2008). We suggest that this difference partially results from differences in soil conditions (cf. Thimonier et al. 1994). For instance, in Meerdaal forest, soil acidiﬁcation pushed the majority of the plot into the aluminium buffer range. This negatively affected *A. nemorosa* and presumably many other demanding species. Further testing of this hypothesis on a larger data set com- prising other, contrasting soil conditions is needed.

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App. 1: Methodology of Plot Relocation, Plot Design and Vegetation Description Used in the 2000 Vegetation Survey

The original 1954 plots were not permanently marked but were accurately described in the original survey notes and maps. Therefore, an adapted plot design was used during the 2000 survey to maximize temporal comparability. Fig. A1 represents the plot relocation procedure. Based on the available de- scriptions and cartographic data, we determined a likely location of the 1954 plots (point ‘‘A’’). Then, we estimated the relocation error of this point as (1)

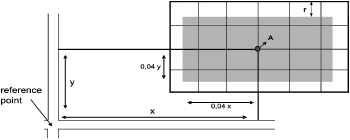


Fig. A1. Example of a plot relocation and design for the 2000 survey. Point A represents a likely location of the 1954 plot centre based on ﬁeld descriptions and carto- graphic data. The grey area represents the relocation error of this point based on an error estimation of 4 m per 100 m distance from the reference point indicated in the ﬁeld de- scriptions. The bold rectangle, divided in 5 mx5m subplots, encloses the most likely location of the initial 1954 circular plot with radius ‘‘*r*’’.

0.04-times the distance to a reference point indicated in the 1954 descriptions, or (2) a deviation of 51 from the orthogonal angle when the location was de- scribed as a distance perpendicular to a forest track. This relocation error was empirically determined by the team who performed the 1954 inventory. This procedure results in a grey rectangle with a high probability of comprising the ‘‘real’’ 1954 plot cen- tre. Extending this surface by the radius of the 1954 circular plot marked the zone within which the ori- ginal plot must have been located. To obtain equal 1954 and 2000 plot areas (range: 125-225 m2), the rectangular zone was divided into 5 mx5 m subplots and only a random subset summing up to the 1954 plot area was resampled.

A vegetation survey of all 20 locations was car- ried out in spring (April 2000). Plots were resampled earlier in 2000 compared to 1954, with a maximum

App. 2 Indices of Shade-Casting Ability (SCA) and Litter Quality (LQ) for Woody Species in the Tree or Shrub Layer. 1Species shade-casting ability index increases from 1 (low) to 6 (high shade-casting, adapted from Ellenberg 1996). 2Species litter quality index increases from 1 (low) to 5 (high litter quality, adapted from Hermy 1985).

difference of 21 days. In a similar semi-permanent plot study in southern Belgium, Van Calster et al. (2008) already showed that the growing season in 1967 lagged on average 16 days behind the season of 2000. This indicates that our resampling period matches the original period reasonably well. Lon- do’s (1976) decimal scale was used to estimate the cover of every species in the tree (47 m), shrub (1- 7 m) and herb layer. Cover of species in the herb layer was estimated in the set of 5 mx5 m subplots. Cover of each species in shrub and tree layers was estimated at the whole plot level because a 5 mx5m plot is too small to obtain a representative cover value for these layers. In addition, all plots were visited again in July 2000 to verify determination of some late-ﬂowering species and to complete cover data of species that show high expansion in late spring and early summer.

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App. 3 Species list and frequency *f* (%) of all species in the

20 plots in 1954 and 2000. The change in frequency between years (2000-1954) is given as D*f* (%).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Species name | Species ID | *f* (1954) | *f* (2000) | D*f* |
| *Acer platanoides* | Acer plat | 0 | 5 | 5 |
| *Acer pseudoplatanus* | Acer pseu | 30 | 100 | 70 |
| *Adoxa moschatellina* | Adox mosc | 45 | 45 | 0 |
| *Aesculus hippocastanum* | Aesc hipp | 0 | 10 | 10 |
| *Ajuga reptans* | Ajug rept | 45 | 35 | -10 |
| *Alliaria petiolata* | Alli peti | 0 | 5 | 5 |
| *Anemone nemorosa* | Anem nemo | 90 | 95 | 5 |
| *Anthoxanthum odoratum* | Anth odor | 5 | 0 | -5 |
| *Arum maculatum* | Arum macu | 20 | 25 | 5 |
| *Athyrium ﬁlix-femina* | Athy ﬁli | 75 | 95 | 20 |
| *Betula pendula* | Betu pend | 0 | 5 | 5 |
| *Brachypodium sylvaticum* | Brac sylv | 5 | 0 | -5 |
| *Cardamine pratensis* | Card prat | 15 | 20 | 5 |
| *Carex hirta* | Care hirt | 5 | 0 | -5 |
| *Carex pilulifera* | Care pilu | 15 | 10 | -5 |
| *Carex remota* | Care remo | 0 | 45 | 45 |
| *Carex sylvatica* | Care sylv | 50 | 45 | -5 |
| *Carpinus betulus* | Carp betu | 5 | 25 | 20 |
| *Castanea sativa* | Cast sati | 0 | 10 | 10 |
| *Chrysosplenium oppositifolium* | Chry oppo | 0 | 5 | 5 |
| *Circaea lutetiana* | Circ lute | 20 | 35 | 15 |
| *Convallaria majalis* | Conv maja | 45 | 30 | -15 |
| *Corylus avellana* | Cory avel | 10 | 80 | 70 |
| *Crataegus monogyna* | Crat mono | 0 | 5 | 5 |
| *Deschampsia cespitosa* | Desc cesp | 20 | 25 | 5 |
| *Deschampsia ﬂexuosa* | Desc ﬂex | 5 | 5 | 0 |
| *Dryopteris carthusiana* | Dryo cart | 10 | 90 | 80 |
| *Dryopteris dilatata* | Dryo dila | 0 | 65 | 65 |
| *Dryopteris ﬁlix-mas* | Dryo ﬁli | 5 | 20 | 15 |
| *Epilobium angustifolium* | Epil angu | 10 | 0 | -10 |
| *Fagus sylvatica* | Fagu sylv | 5 | 75 | 70 |
| *Filipendula ulmaria* | Fili ulma | 5 | 0 | -5 |
| *Fraxinus excelsior* | Frax exce | 0 | 50 | 50 |
| *Galeopsis tetrahit* | Gale tetr | 15 | 45 | 30 |
| *Galium aparine* | Gali apar | 5 | 15 | 10 |

Species name SCA1 LQ2 Frequency shrub layer

Frequency tree layer

1954 2000 1954 2000

0 0 0 1

|  |  |  |
| --- | --- | --- |
| *Abies alba*  *Acer campestre* | 4 | 4 |
| *Acer platanoides* | 5 | 3 |
| *Acer pseudoplatanus* | 5 | 3 |
| *Aesculus hippocastanum* |  |  |
| *Alnus glutinosa* | 4 | 4 |
| *Alnus incana* | 5 | 3 |
| *Betula pendula* | 2 | 2 |
| *Carpinus betulus* | 6 | 3 |
| *Cornus sanguinea* | 3 | 5 |
| *Corylus avellana* | 4 | 3 |
| *Crataegus monogyna*  *Fagus sylvatica* | 6 | 1 |
| *Frangula alnus* |  | 5 |
| *Fraxinus excelsior* | 4 | 5 |
| *Ilex aquifolium*  *Mespilus germanica* |  |  |
| *Picea sitchensis* |  |  |
| *Pinus sylvestris* | 2 | 3 |
| *Populus alba* | 3 | 4 |
| *Populus canescens* | 3 | 4 |
| *Prunus avium* | 4 | 4 |
| *Prunus serotina* |  |  |
| *Prunus spinosa*  *Quercus petraea* | 3 | 1 |
| *Quercus robur* | 3 | 1 |
| *Quercus rubra* | 4 | 1 |
| *Robinia pseudoacacia* | 4 | 4 |
| *Salix caprea* |  | 3 |
| *Sambucus nigra* |  | 5 |
| *Sorbus aucuparia* | 3 | 3 |
| *Tilia cordata* | 5 | 4 |

1 0 0 0

1 1 0 0

19 19 2 17

1 0 1 1

10 1 0 1

3 1 0 0

7 0 0 2

5 5 0 4

2 1 0 0

20 19 0 0

1 1 0 0

4 8 3 8

1 0 0 0

7 0 3 9

2 0 0 0

0 1 0 0

0 0 0 1

0 0 2 0

4 0 3 0

0 0 0 1

1 0 0 0

2 4 0 0

3 0 0 0

0 0 3 3

10 5 18 17

1 1 1 1

1 0 0 0

5 0 0 0

2 4 0 0

7 6 0 1

2 1 0 1

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| App. 3. *(Continued).* |  | | | |
| Species name | Species ID | *f* (1954) | *f* (2000) | D*f* |
| *Geranium robertianum* | Gera robe | 0 | 10 | 10 |
| *Geum urbanum* | Geum urba | 25 | 35 | 10 |
| *Glechoma hederacea* | Glec hede | 45 | 50 | 5 |
| *Hedera helix* | Hede heli | 25 | 35 | 10 |
| *Heracleum sphondylium* | Hera spho | 15 | 10 | -5 |
| *Holcus mollis* | Holc moll | 60 | 65 | 5 |
| *Hypericum pulchrum* | Hype pulc | 10 | 0 | -10 |
| *Ilex aquifolium* | Ilex aqui | 5 | 20 | 15 |
| *Juncus effusus* | Junc effu | 20 | 10 | -10 |
| *Lamium galeobdolon* | Lami gale | 80 | 90 | 10 |
| *Lonicera periclymenum* | Loni peri | 75 | 50 | -25 |
| *Luzula pilosa* | Luzu pilo | 65 | 40 | -25 |
| *Lysimachia nemorum* | Lysi nemo | 0 | 5 | 5 |
| *Maianthemum bifolium* | Maia bifo | 15 | 20 | 5 |
| *Melica uniﬂora* | Meli unif | 5 | 35 | 30 |
| *Milium effusum* | Mili effu | 90 | 100 | 10 |
| *Moehringia trinervia* | Moeh trin | 15 | 20 | 5 |
| *Oxalis acetosella* | Oxal acet | 35 | 95 | 60 |
| *Paris quadrifolia* | Pari quad | 30 | 10 | -20 |
| *Poa nemoralis* | Poan nemo | 40 | 15 | -25 |
| *Poa trivialis* | Poat triv | 0 | 20 | 20 |
| *Polygonatum multiﬂorum* | Poly mult | 45 | 45 | 0 |
| *Polygonum bistorta* | Poly bist | 5 | 5 | 0 |
| *Populus alba* | Popu alba | 0 | 5 | 5 |
| *Potentilla sterilis* | Pote ster | 35 | 5 | -30 |
| *Primula elatior* | Prim elat | 45 | 10 | -35 |
| *Prunus avium* | Prun aviu | 0 | 5 | 5 |
| *Prunus serotina* | Prun sero | 0 | 20 | 20 |
| *Pteridium aquilinum* | Pter aqui | 10 | 25 | 15 |
| *Quercus petraea* | Quer petr | 0 | 10 | 10 |
| *Quercus robur* | Quer robu | 0 | 85 | 85 |
| *Quercus rubra* | Quer rubr | 5 | 10 | 5 |
| *Ranunculus ﬁcaria* | Ranu ﬁca | 40 | 45 | 5 |
| *Ribes rubrum* | Ribe rubr | 5 | 0 | -5 |
| *Rubus fruticosus* | Rubu frut | 85 | 90 | 5 |
| *Rubus idaeus* | Rubu idae | 20 | 15 | -5 |
| *Rumex acetosella* | Rume acet | 5 | 0 | -5 |
| *Sambucus nigra* | Samb nigr | 0 | 30 | 30 |
| *Scrophularia nodosa* | Scro nodo | 30 | 5 | -25 |
| *Sedum telephium* | Sedu tele | 5 | 0 | -5 |
| *Senecio ovatus* | Sene ovat | 10 | 0 | -10 |
| *Sorbus aucuparia* | Sorb aucu | 15 | 45 | 30 |
| *Stachys sylvatica* | Stac sylv | 0 | 5 | 5 |
| *Stellaria holostea* | Stel holo | 35 | 50 | 15 |
| *Teucrium scorodonia* | Teuc scor | 20 | 10 | -10 |
| *Urtica dioica* | Urti dioi | 40 | 30 | -10 |
| *Vaccinium myrtillus* | Vacc myrt | 10 | 5 | -5 |
| *Valeriana repens* | Vale repe | 15 | 0 | -15 |
| *Veronica chamaedrys* | Vero cham | 20 | 0 | -20 |
| *Veronica hederifolia* | Vero hede | 0 | 20 | 20 |
| *Veronica montana* | Vero mont | 15 | 35 | 20 |
| *Vinca minor* | Vinc mino | 15 | 10 | -5 |
| *Viola reichenbachiana* | Viol reic | 5 | 5 | 0 |
| *Viola riviniana* | Viol rivi | 20 | 0 | -20 |