SPECIES-ENVIRONMENT RELATIONSHIPS IN THREE WOODLANDS USING CANONICAL CORRESPONDENCE ANALYSIS

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SUMMARY

Relations between plant communities and environment were investigated in an ecological study in three woodlands in the south of Flanders, Belgium. The vegetation was sampled and three environmental variables (light penetration, chemical composition of the soil and species composition of the tree and shrub layer) were measured. By application of canonical correspondence analysis (CCA), relations between the vegetation and the environmental variables could be evaluated. The percentage of Fagus sylvatica in the basal area seemed to be the most decisive environmental variable determining the presence of plant communities. It could be derived as well that CCA can be a very useful technique for the determination of the indicator values of the species for their environment.

INTRODUCTION

In recent years, powerful numerical techniques have been developed to analyse vegetation variation and to describe complex vegetation gradients.
AmonAmong these techniques, several indirect ordination methods, such as principal components analysis and detrended correspondence analysis (DCA) (Hill, 1979), in which the ordination of species and samples is exclusively based on vegetation data, have shown to be very succesful (Swaine & Greig-Smith, 1980; Whittaker, 1986). However the utility of these ordination techniques to relate vegetational patterns to a wide range of environmental factors is rather limited.

Ter Braak (1988) developed a software package CANOCO for a direct ordination technique, canonical correspondence analysis (CCA), which can be applied to relate vegetational composition directly to environmental features (ter Braak, 1987b). Canonical correspondence analysis can be considered as a multidimensional direct gradient analysis into which regression and ordination have been integrated. Canonical or constrained ordination is based on Hutchinson's concept of the niche (Hutchinson, 1944, 1957, 1978; Schoener, 1989), which was first introduced in a footnote to a 1944 paper in Ecology on phytoplankton periodicity:
"the term niche is here defined as the sum of all the environmental factors acting on the organism; the niche thus defined is a region of an n-dimensional hyperspace, comparable to the phasespace of statistical mechanics" (Hutchinson, 1944). Using this concept, Canonical correspondence Analysis is an appropriate method to study ecological complexity and interactions. The general aim of CCA, when used in an

exploratory way, is to turn out an ordination diagram of samples, species and environmental variables which optimally displays how community composition varies with the environment. Biplot scores of environmental variables give the coordinates of the heads of arrows in the ordination diagram. The rules for constructing and interpreting species-environment biplots are the same as those given in ter Braak (1987a) for PCA-biplots : the direction of the arrow indicates the direction in which the amount of the corresponding environmental variable increases most; the length of the arrow equals the rate of change in that direction; the angle between arrows of a pair of variables (environmental, species or samples) provides an approximation of their pairwise correlation. The biplot is constructed most easily by drawing seperate plots of species, samples and environmental variables on transparant paper, each one with its own scaling. However, within each plot the scale units of the axes must have equal physical length. The biplot is obtained by superimposing the plots with the axes aligned and the origins of the coordinate systems coinciding (ter Braak, 1988).

This approach is demonstrated in this paper using vegetational and environmental data of three woodlands in the south of Oost-Vlaanderen, Belgium.

STUDY AREA

The three woodlands - Bos ter Rijst, Koppenbergbos and Kluisbos - are located in the south of the province of Oost-Vlaanderen, Flanders, Belgium (50°45' - 50°48' N; 3°30' - 3°41' W) (fig.1). The area is hilly, with heights in the woodlands up to 130m above sea level.

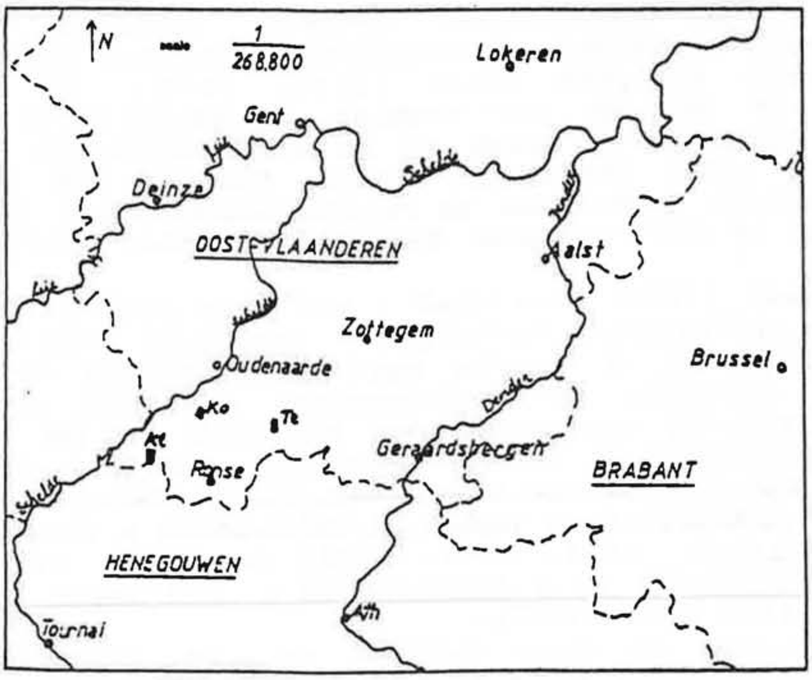

Fig 1 : Map of Oost-Vlaanderen and neighbouring provinces, with Te : Bos ter Rijst, Ko : Koopenbergbos and Kl : Kluisbos.

The subsoil consists of a series of layers slightly sloping to the north-northeast, dating from the tertiary period. These consecutive layers of sand and clay were deposited by the withdrawal and upcoming of tertiary seas. This succession of impervious and pervious layers provokes wells that determine the characteristic vegetation in the woodlands of this region (fig. 2).

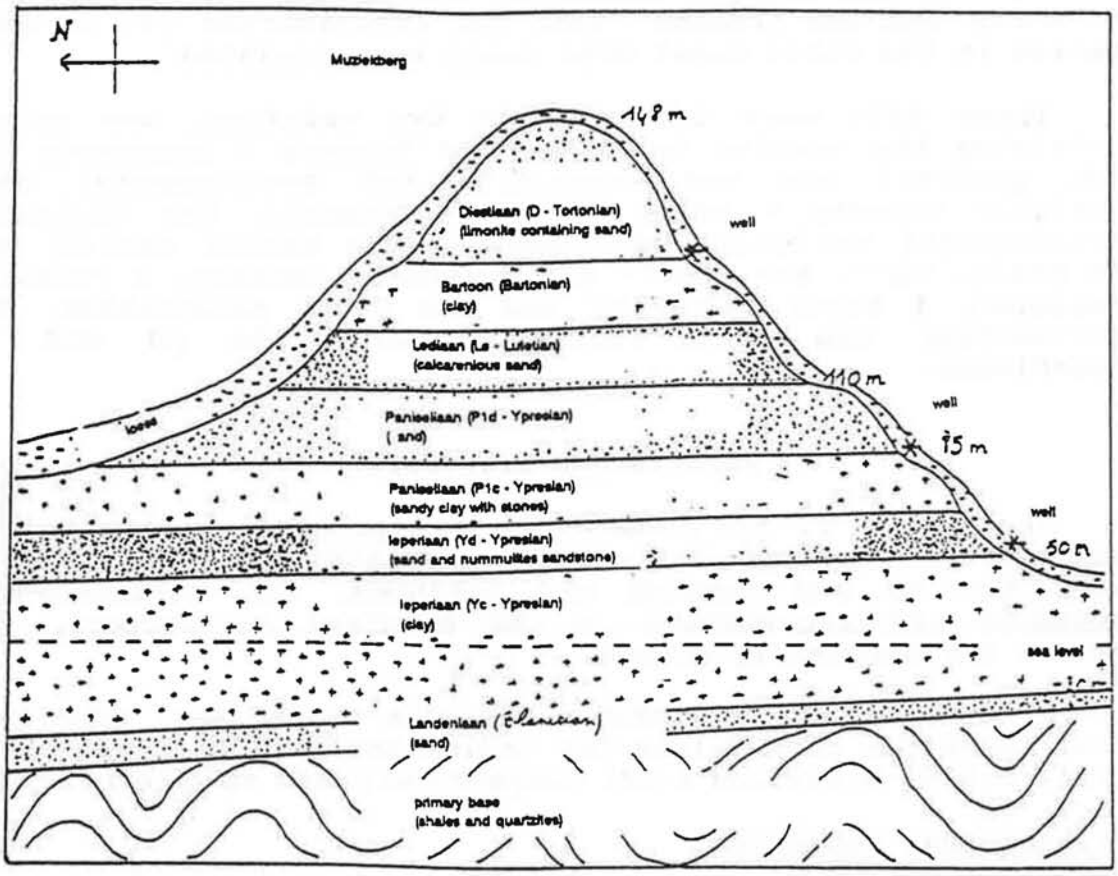

Fig 2 : Sequence of geological layers in Muziekberg hill (Ronse)

MATERIALS AND METHODS

As the application of CCA requires species data as well as environmental data, vegetation sampling and measurement of environmental features were carried out in twenty quadrats of 20 x 20 m, pegged out in the three woodlands.

The abundance of each higher plant species was recorded in a square of 10 x 10 m in the middle of each quadrat, using Londo's scale (Londo, 1984).

Site descriptions were recorded by measuring three environmental variables. Light penetration was calculated from hemispherical photographs of the canopy, taken with a fish eye objective (Lemeur, Leong & Schalck,

1983). By means of a digital conversion of the photograph, the contribution (%) of the light spots in the total surface of the picture could be calculated.
Soil samples of the upper 15 cm of each quadrat were analysed on pH, C/N ratio, plant available Na+-, K+-, Mg++-, Ca++- and phosphate content, using methods described in Cottenie et al. (1982).
The composition of the tree and shrub layer in each quadrat was considered as the third environmental variable. Therefor, an inventory was made by measuring the basal area of each tree and shrub species present. Then the contribution (%) of each species in the total basal area could be calculated.

These data were collected in two matrices, one matrix containing the species data (species numbers + abundance for each quadrat) and one containing the environmental data (variable numbers + value for each quadrat). The following environmental variables were used in the second matrix: pH, C/N ratio, Na+-, K+-, Mg++- and phosphate content, % *Fraxinus excelsior*, % *Fagus sylvatica*[1] and the light penetration. The Ca++-content was well correlated with the pH and so superfluous.

RESULTS AND DISCUSSION

The result of the canonical correspondence analysis is a twodimensional representation of the multidimensional space in which species and samples are arranged. The environmental variables are represented in the diagrams by vectors, the species and samples by points.

A canonical correspondence analysis of the data described above, provides eigenvalues for ordination axis one to four of 0.554, 0.322, 0.262 and 0.221 respectively are obtained.

Environmental variables

As can be seen in fig. 3, the environmental variable %Fagus is strongly related to the first ordination axis (r=0.957); there is a small angle between vector and axis. The pH of the soil is well correlated with the second CCA axis (r=0.828). These two variables have the longest vectors in the multidimensional space, and thus can be considered to be the most important environmental features explaining the vegetational patterns.
No enviromental variable is well correlated with axis three and four, so no obvious explanation can be found for these axes. When the species ordination is carefully examined, rare species are found to occupy the extremes of axis three and four. These axes can thus be considered as some sort of "noise" axes, as was found by Whittaker (1987).

The order of importance of the environmental variables is: %Fagus, pH, %Fraxinus, C/N ratio, Mg++, Na+ and phosphate, K+, light penetration.

%Fagus is well correlated with the C/N ratio of the soil (r=0.689) : the higher the basal area of Fagus sylvatica in the total area, the higher is the C/N ratio. %Fraxinus is strongly correlated with the Mg++ content of the soil. This

[1]Nomenclature follows that of De Langhe et al. (1983).

confirms that the tree species have an important influence on the chemical composition of the soil and through this also on the vegetational patterns.
Apparently, the influence of the chemical composition of the soil on the composition of the herb layer is expressed best by the contribution of Fagus sylvatica in the basal area of the quadrats.

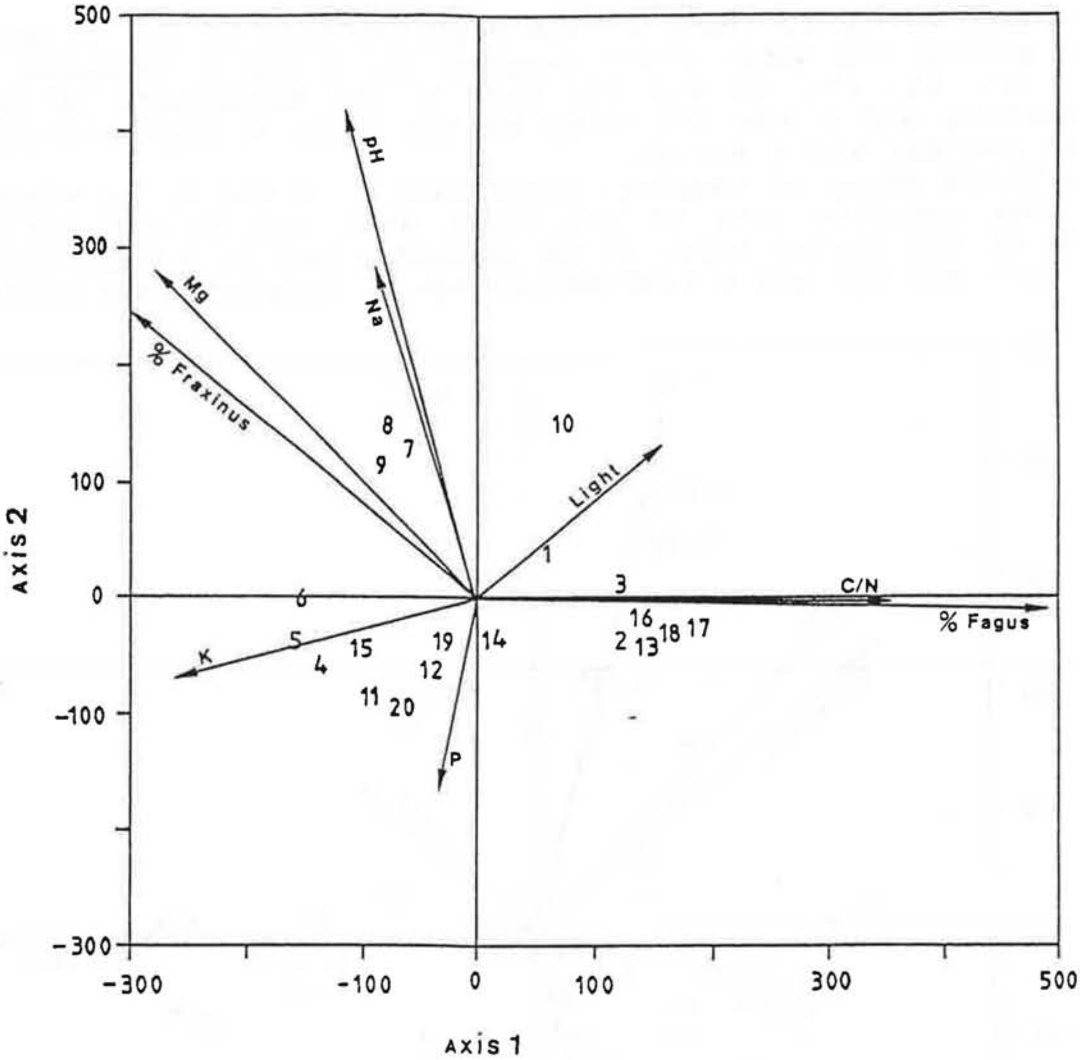

Fig 3 : Biplot of environmental variables and samples.

Surprisingly, the light penetration is the least important environmental factor. Moreover, there is no correlation between %Fagus and the light penetration. This can be explained by the fact that some sampling was done in coppice stands with a very dense shrub layer and in Fraxinus excelsior stands with a thin canopy but with a strongly developed shrub layer, transmitting little light. So the intensity of the penetrated light reaching the herb layer is very low and the difference in light penetra- tion between these samples and the Fagus sylvatica samples is very small.

<u>Samples</u>

In the sample-environment diagrams (fig. 4), three groups of samples can be distinguished.
One group, containing samples 2, 3, 13, 16, 17 and 18, is arranged at the positive end of the first CCA axis. It is characterized by a high percentage of Fagus sylvatica and by a high C/N ratio of the soil. The pH and the content of Mg++, Na+ and K+ are low.
A second group is found at the negative side of the first and the second CCA axis. These samples (4, 5 and 6 (coppice) and 11, 12, 14, 15, 19 and 20) have a low percentage of Fagus sylvatica and a low C/N ratio of the soil, a high content of Mg++ and Na+ and a low pH.
The third group of samples, containing 7, 8 and 9, is situated at the negative side of the first axis and at the positive side of the second axis. It is characterized by a high content of Mg++ and Na+ and a high percentage of Fraxinus excelsior.

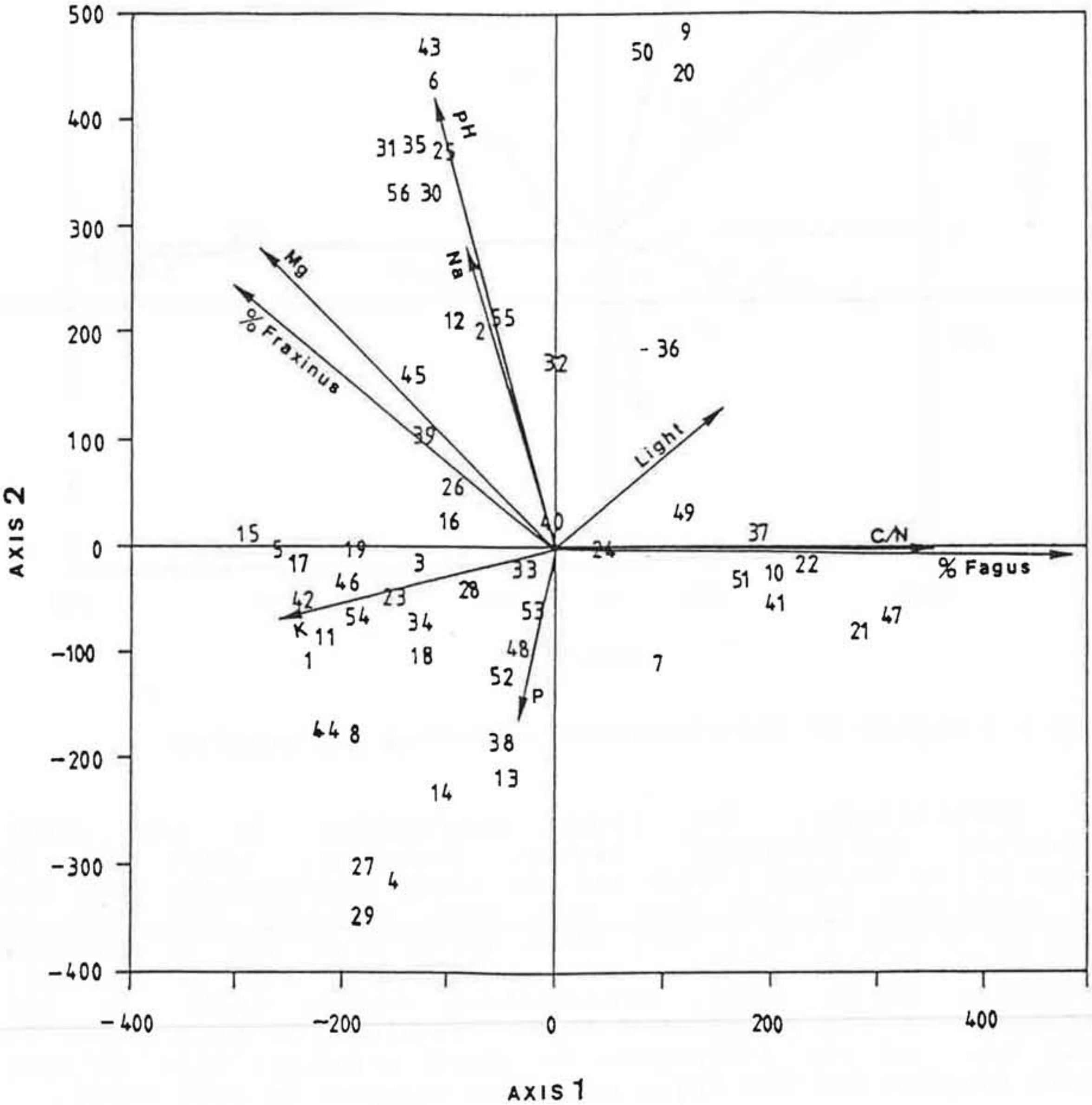

Fig 4 : Biplot of environmental variables and species.

Species

Evidently, the tree species Fagus sylvatica and Fraxinus excelsior are arranged in the diagrams very close to the %Fagus and %Fraxinus axis respectively.

Herb species typical for samples with a high % Fagus contribution are Rubus fruticosus, Athyrium filix-femina, Luzula pilosa, Pteridium acquifolium and Lonicera periclymenum. The species Ranunculus ficaria, Anemone nemorosa, Polygonatum multiflorum, Vinca minor, Lamium galeobdolon and some others are situated at high %Fraxinus values.
Hyacinthoides non-scripta is found very close to the origin, which means that this species has no specific preference for certain environmental conditions and thus can be called indifferent, which corresponds to the fact that Hyacinthoides non-scripta was a constant species in the samples.

When the preferential value of the species for each environmental variable (obtained by the perpendicular projection on each environmental axis) are compared to Ellenberg's indicator values for Central-Europe (Ellenberg, 1977), some differences can be noticed.
According to Ellenberg, Hyacinthoides non-scripta is a half shadow plant, found on fresh, more or less neutral and moderate nitrogen rich soil. From the ordination diagram, this species is rather indifferent.
Vinca minor was found at the higher pH values measured. In Ellenberg's classification, this species was pH indifferent.
In the ordination diagram Lamium galeobdolon is projected near the origin of the pH axis, which means that the species was found on acid soil, since the pH values measured varied from 3.8 to 6. Yet, according to Ellenberg, Lamium galeobdolon prefers a neutral pH.
From these facts can be concluded that the indicator values of Ellenberg for Central-Europe should be critically approached when used for vegetational data of regions like the studied area. Canonical correspondence analysis can be a decent help when these indicator values are adapted to other regions.

CONCLUSION

Using correspondence analysis (CCA), relations between the vegetation in three woodlands and some environmental variables could be directly detected. Apparently, the contribution of Fagus sylvatica in the basal area was the most important environmental variable determining the vegetational patterns. CCA can also be a useful technique for the determination of the indicator values of the herbaceous species for their environment.

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Appendix

List of species

1 Acer pseudoplatanus (boom)
2 Acer pseudoplatanus (struik)
3 Acer pseudoplatanus (kruid)
4 Adoxa moschatellina
5 Alnus glutinosa
6 Angelica sylvestris
7 Athyrium filix-femina
8 Betula pendula
9 Carex pendula
10 Carex sylvatica
11 Carpinus betulus (boom)
12 Carpinus betulus (struik)
13 Castanea sativa (boom)
14 Castanea sativa (struik)
15 Chrysoplenium alternifolium
16 Circaea lutetiana
17 Corylus avellana (boom)
18 Corylus avellana (struik)
19 Crataegus monogyna
20 Deschampsia cespitosa
21 Digitalis purpurea
22 Fagus sylvatica (boom)
23 Fagus sylvatica (struik)
24 Fagus sylvatica (kruid)
25 Filipendula ulmaria
26 Fraxinus excelsior (boom)
27 Fraxinus excelsior (struik)
28 Fraxinus excelsior (kruid)
29 Galium aparine
30 Geranium robertianum
31 Glecoma hederacea
32 Hedera helix
33 Hyacinthoides non-scripta
34 Lamium galeobdolon
35 Listera ovata
36 Lonicera periclymenum
37 Luzula pilosa
38 Oxalis acetosella
39 Polygonatum multiflorum
40 Populus alba (boom)
41 Populus alba (struik)
42 Populus x euramericana
43 Primula elatior
44 Prunus avium (boom)
45 Prunus avium (struik)
46 Prunus spinosa
47 Pteridium aquilinum
48 Quercus robur (boom)
49 Quercus robur (kruid)
50 Rosa canina
51 Rubus fruticosus
52 Sambucus nigra
53 Sorbus aucuparia
54 Stellaria holostea
55 Vinca minor
56 Viola reichenbachiana

List of samples

1 to 10 samples in Bos ter Rijst
11 to 15 samples in Koppenbergbos
16 to 20 samples in Kluisbos