Ecology of Roadside Plant Communities

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Ecology of Roadside Plant Communities

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Proefschrift

ter verkrijging van de graad van doctor
op gezag van de rector magnificus van Wageningen Universiteit
dr. ir. L. Speelman,
in het openbaar te verdedigen
op vrijdag 8 September 2000
des namiddags te half twee in de Aula.

Generalisations about vegetation are urgently required to solve pressing problems created by modern land use, climate change and pollution. If one approaches vegetation with the tools of the watchmaker, there is no limit to the dissection which can be achieved. But if, like Heinz Ellenberg, one raises one's eye to the broader canvas, the generalisations are there to be discovered.

K. Thompson *et al.* (1993). Ellenberg numbers revisited.
Phytocoenologia **23**: 277-289.

Stellingen

1. Vertraging in de afvoer van maaisel is een vorm van kapitaalvernietiging.
   - Dit proefschrift -

2. Het 'Reactionszahl' uit het indicatorwaarden-systeem van Ellenberg dient niet te worden opgevat als zuur- of pH-getal, maar als calcium-getal.
   - Dit proefschrift -

3. De jaarlijkse netto stikstofmineralisatie is sterk gecorreleerd met de hoeveelheid minerale stikstof die op één bepaald moment in de bodem gemeten wordt.
   - Dit proefschrift -

4. Vegetatiebeheer is van groter belang voor de botanische diversiteit dan de biomassaproductie.
   - Dit proefschrift -

5. In natuurlijke systemen geven soortensamenstelling en biomassaproductie een betere indruk van de bodem dan gemeten bodemeigenschappen.

6. De oecologie is bij uitstek de wetenschap die het geheel als uitgangspunt zou moeten nemen. De onderwaardering van beschrijvend en correlatief onderzoek bij toonaangevende oecologische tijdschriften is hiermee in strijd.

7. Herintroductie van soorten is een teken dat natuurbeheer aan 'onthaasting' toe is.

8. Hoewel het uiterst moeilijk is om niet mee te doen aan de consumptiewedloop, wil bijna iedereen óók voldoende groen, voldoende rust, schone lucht en een mooi landschap. Het is daarom de taak van de overheid om deze algemene waarden veilig te stellen, en niet om als economische topmanagers van de B.V. Nederland de consumptiewedloop verder te stimuleren.

9. Als alle kosten die door de landbouw afgewenteld worden op natuur, milieu en landschap doorberekend zouden worden in de prijs van de producten, waren biologische producten plotseling spotgoedkoop.

10. Het krijgen van meer dan twee kinderen dient via eco-tax ontmoedigd te worden.

11. Particulier gebruik van mobiele telefoons zou alleen toegestaan moeten worden in speciaal daartoe te plaatsen, geluiddichte cabines.

12. In natuurlijke plantengemeenschappen is geel met paars één van de meest voorkomende bloemkleur-combinaties.

13. Wegbermen van grote verkeersknooppunten behoren tot de moeilijkst bereikbare plaatsen in Nederland.

14. De snelheid waarmee reorganisaties aan de Universiteit van Wageningen elkaar opvolgen heeft veel weg van een rit met de achtbaan in een gemiddeld pretpark; de meeste mensen komen er misselijk uit.

Stellingen behorend bij het proefschrift 'Ecology of Roadside Plant Communities' van André Schaffers.

Wageningen, 8 september 2000.

to Ab Masselink
who, more than he may have realized,
sowed the seeds of my enthusiasm for vegetation science

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Abstract

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Roadside habitats nowadays contribute considerably to the amount of natural areas in the Netherlands. The ecological role of roadsides is recognized by the Dutch government and road authorities, and the interest in ecological management is growing. The study considers a cross-section of the more valuable plant communities occurring on Dutch road verges and investigates a large number of environmental factors. Aiming to provide an ecological framework that can be used as a reference for ecological management, the study presents an accurate synecological description of the studied syntaxa. An additional field experiment shows that large amounts of nutrients are lost from cuttings, already in the first few weeks after mowing. The effect of various hay removal delay times on the nutrient balance of the different communities is modelled. In most cases, cuttings should be removed within one week (or two at most) if the amounts of nutrients removed are to exceed the inputs through atmospheric deposition. Exploiting the unfertilized, semi-natural character of the sites and the wide range of conditions involved, the data are also used to detect and test general relationships. Investigating soil *versus* biomass relations it is shown that, over a wide environmental gradient, no simple relationship exists between the vegetation tissue concentration and soil availability of a nutrient (with the possible exception of K). Focussing on diversity, unimodal species richness relationships are identified for both maximum standing biomass and productivity, but these only explain a small part of the variation and are apparent only if soil factors are not considered. The 'hump-shape' is more pronounced for standing biomass than for productivity, suggesting that competition for light is the key-factor. Particularly the numbers of rare and endangered species are curtailed strongly by high biomass values. Management affects species richness positively, but also this effect is apparent only if soil factors are not considered. To investigate the nature of Ellenberg indicator values, these are correlated to the measured soil and vegetation parameters. Soil pH is shown not to be adequately indicated by the so-called Ellenberg reaction values, but instead they properly reflect soil total calcium (*i.e.* both exchangeable calcium and calcium in the form of carbonates). Ellenberg nitrogen values best indicate productivity. Over the wide range of unfertilized conditions studied, *in situ* average annual N mineralization can be predicted well from a few directly measured soil parameters. The pool of mineral N just before the growing season is the best correlate. Together with moisture content and pH, this variable can explain 83.5% of the variation in annual N mineralization.

Key-words: *diversity, ecological management, indicator values, infrastructure, nitrogen mineralization, nutrient availability, productivity, standing biomass, vegetation.*

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1

General introduction

General introduction

The ecological importance of road verges

In densely populated countries, the interest in the ecological value of road verges is growing. Numerous studies concerning the flora and fauna in roadside habitats have been performed from various perspectives (*e.g.* Free *et al.* 1975; Way 1977; Ellenberg *et al.* 1981; Ellenberg & Stottele 1984; Braun 1989; Judas 1989; Mederake 1991; Munguira & Thomas 1992; Keizer 1993; Vermeulen 1993). Also the plant communities (syntaxa) occurring along roadsides have recently been described and inventoried in several European countries (*e.g.* Hansen & Jensen 1972; Kopecký 1978; Tanghe 1986; Brandes 1988; Heindl & Ullmann 1991; Heindl 1992; Stottele & Sollmann 1992; Sykora *et al.* 1993; Sayer & Schaefer 1995; Szwed & Sykora 1996; Zwaenenpoel 1998; Godefroid 1998). Although this growing interest can be considered a fortuitous development, it should not be considered a good sign only. As has been stressed before (Sýkora *et al.* 1993) it is mainly due to the enormous reduction in area and quality of our more natural habitats, and this frightful decline makes road verges ever more important. The increasing importance of roadside habitats should therefore be considered in perspective; only in a relative sense are roadsides becoming more and more valuable.

The area of roadside habitats is considerable. In the Netherlands it is estimated to be around 60.000 ha (±10.000 ha), using data for 1992/1993 (CBS 1997a,b) and making some necessary assumptions. This area equals 1.5 to 2.1% of the total land area of the Netherlands; a considerable amount when compared to the 4.2% consisting of natural areas (CBS 1997a). This makes roadside habitats an important constituent of the total reservoir of semi-natural habitats in the Netherlands. In industrialized countries with an intensive agriculture, roadside habitats significantly contribute to the biological diversity of the landscape (Sýkora 1997; Sýkora & De Nijs in prep.). As roadsides are not fertilized, and since they cover large areas, there is a strong potential for the development of aesthetic, species-rich plant communities with a relatively high nature conservation value. Roadside habitats are also thought to provide connections between small and isolated nature reserves (*e.g.* Getz *et al.* 1978; Kaule 1986; Jedicke 1994; Vermeulen 1994; Canters 1997). The total length of roads in the Netherlands outside towns and cities is ca. 70.000 km (CBS 1997b), and the contribution of roadside habitats to an 'ecological infrastructure' (Ministerie LNV, 1990) can therefore be considerable.

The ecological role of roadsides is clearly recognized by the Ministry of Transport, Public Works and Water Management, and by regional and local road authorities. This has led to an increasing interest in ecological management and construction of roadsides, and also other infrastructure such as canals and riverdykes (Van Bohemen *et al.* 1991; Liebrand 1999; Sprangers 1999). The present research project was initiated to generate the specific synecological knowledge required for an adequate management or (re-)construction aiming at the development, maintenance, or restoration of specific plant communities in road verges.

An ecological framework for roadside plant communities

The primary aim of the present project is to provide an ecological framework that can be used as a reference for ecological management and construction directed toward the realization of specific plant communities. For this purpose, accurate ecological descriptions were required for a variety of relatively well-developed and/or relatively species-rich plant communities. In order to make this reference material broadly applicable, a wide selection of community types was made, covering a wide range of edaphic conditions.

A total of 74 sites were selected, with communities belonging to 15 syntaxa (generally 5 sites per syntaxon). After careful description of the vegetation at these sites, a large number of variables was measured over a period of two years to cover at least part of the inter-annual variation. These measurements first of all involved a variety of physical and chemical soil measurements (including groundwater levels and the *in situ* annual N mineralization). Secondly, also biomass characteristics were determined (over the same two-year period) such as standing crop, annual aboveground production, and tissue nutrient composition. Some additional site conditions were recorded as well, such as the presence of overstory trees or shrubs (shading), and management variables such as the frequency of mowing and whether or not cuttings were removed.

The large database generated this way permitted a synecological description (Chapter 2) of a much more detailed nature than the, often scattered, information available from literature on comparable syntaxa. Some of the studied plant communities occur in roadsides only in a fragmentary form (*i.e.* missing a number of character species), and are better developed elsewhere. Other syntaxa appear to be well developed and relatively species-rich in roadside habitats. In the Dutch landscape these communities frequently depend strongly on roadsides, as they are often rare outside these habitats nowadays.

A supplementary study (Chapter 3) considers the effectiveness of hay removal. This topic is relevant to many other semi-natural plant communities as well. Here, the consequences are investigated of different delay times between mowing and the actual removal of the cuttings. This matter is of considerable importance when management aims at soil impoverishment. In such cases the amount of nutrients annually removed with the cuttings should at least exceed the amount annually received by atmospheric deposition, as these two processes constitute the main nutrient in- and outputs in industrialized countries like the Netherlands. Although management guidelines often recognize the need for hay removal, the timespan after which this should be accomplished is not always stated. Roadside cuttings often remain in the field for several weeks to more than one month. The time of removal is frequently determined by practical considerations only. The study uses measurements on cuttings removed after different periods of time to estimate the effectiveness of different removal delay scenarios. The resulting model is subsequently applied to all the studied syntaxa. From these results, management guidelines may be derived.

Toward a wider perspective

The size of the data set (the number of sites and variables available) allows a variety of other ecological problems to be investigated. The semi-natural and unfertilized nature of the plots (usually situated relatively far from the road surface) allows these additional studies to be of general ecological interest.

Because of the wide range of ecological conditions covered, the data are particularly suitable for the detection of general relationships. Also, the general applicability of ecological relationships reported or suggested in other studies (usually covering a much more narrow range of conditions) can be tested.

In Chapter 4, mutual relationships between soil properties and biomass characteristics are investigated. The main issues in this study are: how can biomass productivity of semi-natural vegetation be explained by soil and site properties (including management) when a wide range of edaphic conditions is considered? And also: can nutrient concentrations in vegetation biomass be explained by the availability of nutrients in the soil? These questions may also be reversed: can biomass characteristics (*e.g.* tissue concentrations or productivity) be used to make inferences about soil nutrient availability? Is there a general relationship between tissue nutrient and soil nutrient concentrations?

In a subsequent study (Chapter 5), the relevance of the soil, site and biomass variables is studied with respect to species diversity and the occurrence of rare and endangered species. Here, the questions to be answered are:

- How can species diversity be explained by soil properties, site conditions, and biomass characteristics, when a wide range of plant community types is considered?
- How is species diversity related to aboveground biomass production or standing crop? Can the often reported unimodal relationship between biomass (or productivity) and species richness be confirmed over the wide range of communities studied? If so, how

do the relationships for biomass and productivity differ, and what does this tell us about the cause of unimodal relationships?
- What are the effects of vegetation management?

Chapter 6 utilizes the wide range of ecological conditions included in this study to investigate the nature of the Ellenberg indicator values, specifically those for moisture, nitrogen and soil reaction[1]. These indicator values are widely used in Europe as a practical tool for a rapid assessment of the ecological conditions at a site, as an alternative for actual measurements in scientific studies, as an aid for assessing the probability of occurrence of particular species, and for various other purposes. Some of the problems addressed in Chapter 6 are: do Ellenberg nitrogen and reaction values really indicate the availability of nitrogen and soil acidity, respectively? If not, what precisely do they indicate? How reliable are the indications obtained, and can they be improved? Answers to these questions may provide a sound scientific basis for the continued use and improvement of this important tool.

Chapter 7 focusses on a methodological problem. Here the aim is to answer the question how we can estimate soil N supply without the laborious measurement of net N mineralization through year-round *in situ* incubation of undisturbed soil cores. The availability of both N mineralization data (as measured in the field over two full years), and a large selection of physical and chemical soil measurements, allows the search for one-time soil measurements (preferable simple ones) that may be used to predict the average annual N mineralization in the field. An alternative approach could be to hold on to the incubation technique, but to restrict the period of successive incubations to less than a full year. In that case, the main question is how short this period can be while maintaining a reliable estimate of the relative ordering of the *annual* mineralization rates. The large amount of time (and other resources) involved in year-round field incubation often motivates people to dismiss mineralization assessments altogether, but this study may present effective alternatives.

Finally, in Chapter 8, possible links between the findings of the various chapters will be explored. Here, the variables and relationships repeatedly drawing attention will be discussed from a more general perspective.

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[1] Ellenberg originally used the term '*Bodenreaktion*'. The common translation of this expression is soil reaction, although it is sometimes (but inaccurately) translated as soil acidity.

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2

Synecology of species-rich plant communities on roadside verges in the Netherlands

Schaffers, A.P. & Sýkora, K.V. Synecology of species-rich plant communities on road-side verges in the Netherlands. *Submitted for publication.*

Synecology of species-rich plant communities on roadside verges in the Netherlands

Abstract. Using a large number of physical and chemical soil measurements, biomass measurements, and other site conditions (*e.g.* management, shading, exposition), an accurate synecological description is given of 15 semi-natural, species-rich plant communities occurring on Dutch roadside verges, belonging to 11 alliances, comprising 10 associations and 3 trunk communities: *Urtico-Aegopodietum*, *Alliario-Chaerophylletum*, *Valeriano-Filipenduletum*, *Fritillario-Alopecuretum pratensis*, *Calthion*, *Triglochino-Agrostietum stoloniferae*, *Ranunculo-Alopecuretum geniculati*, *Arrhenatheretum elatioris*, *Mesobromion*, *Phleo-Tortuletum*, *Spergulo-Corynephoretum*, *Genisto-Callunetum*, and *Ericion*. These syntaxa, covering a wide range of (unfertilized) edaphic conditions, represent a cross-section of the more valuable plant communities occurring along roadsides in the Netherlands. The study thus renders a synecological reference framework.

The data were also analysed for 'master factors'; *i.e.* the ecological variables best discriminating between the plant communities. Apart from their ecological importance, measurement of these factors is expected to be sufficient for practical applications such as ecological roadside management and (re-)construction.

Keywords: *associations, ecological management, infrastructure, phytocoenology, syntaxa, vegetation.*

Nomenclature: Van der Meijden (1996) for vascular plants. Margadant & During (1982) for bryophytes. Schaminée *et al.* (1995b, 1996), Stortelder *et al.* (1999), and Sýkora *et al.* (1993) for syntaxa.

Introduction

Due to the ever intensifying land-use in the Netherlands, the relative importance of semi-natural vegetation in roadside habitats is rapidly increasing (Canters 1997). Consequently, concern for the ecological qualities of roadside verges is growing. Sýkora *et al.* (1993) inventoried the syntaxa occurring along roadsides in the Netherlands. A similar survey has been performed in Belgium by Zwaenepoel (1998). Although most of the vegetation in road verges belong to so-called fragmentary or coenologically unsaturated communities (Kopecký & Hejný 1974, 1978; Kopecký 1978; Sýkora *et al.* 1993) they may still be relatively rich in species, and several species-rich syntaxa may even be

Table 1. *The studied plant communities: syntaxon, number of sites, average number of species (bryophytes and terrestrial lichens included), syntaxonomic position, and short characterization. Species with relatively high cover (bold) and some characteristic species (underlined) are indicated. The number/code for the plant communities is used in some of the graphs.*

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0 *Urtico-Aegopodietum*, 5 sites (37 species).
[*Galio-Urticetea, Glechometalia, Galio-Alliarion*]
Woodland/hedge-margins: ***Aegopodium podagraria***, ***Urtica dioica***, ***Anthriscus sylvestris***, ***Glechoma hederacea***, *Rumex obtusifolius*.

1 *Alliario-Chaerophylletum temuli*, 5 sites (31 species).
[*Galio-Urticetea, Glechometalia, Galio-Alliarion*]
Woodland/hedge-margins: ***Chaerophyllum temulum***, ***Bromus sterilis***, *Alliaria petiolata*, *Poa nemoralis*.

2 *Valeriano-Filipenduletum*, 5 sites (46 species).
[*Convolvulo-Filipentuletea, Filipenduletalia, Filipendulion*]
Tall-herb grassland: ***Phragmites australis***, ***Carex acutiformis***, ***Calamagrostis canescens***, ***Lysimachia vulgaris***, ***Calystegia sepium***, *Valeriana officinalis*, *Filipendula ulmaria*, *Eupatorium cannabinum*, *Thalictrum flavum*.

3 Fragmentary *Fritillario-Alopecuretum pratensis*, 2 sites (38 species).
[*Molinio-Arrhenatheretea, Arrhenatheretalia, Alopecurion pratensis*]
Hay-meadow: ***Alopecurus pratensis***, ***Agrostis stolonifera***, ***Elytrigia repens***, *Sanguisorba officinalis*.

4 *Fritillario-Alopecuretum pratensis* (well-developed), 3 sites (52 species).
[*Molinio-Arrhenatheretea, Arrhenatheretalia, Alopecurion pratensis*]
Hay-meadow: ***Alopecurus pratensis***, ***Plantago lanceolata***, ***Anthoxanthum odoratum***, ***Agrostis stolonifera***, *Sanguisorba officinalis*, *Fritillaria meleagris*, *Alchemilla glabra*.

5 *Calthion palustris* trunk community, 5 sites (44 species).
[*Molinio-Arrhenatheretea, Molinietalia, Calthion palustris*]
Hay-meadow: ***Holcus lanatus***, ***Anthoxanthum odoratum***, ***Rumex acetosa***, ***Carex disticha***, ***Calliergonella cuspidatum***, *Lychnis flos-cuculi*, *Lotus pedunculatus*, *Cirsium palustre*, *Angelica sylvestris*.

6 Fragmentary *Triglochino-Agrostietum stoloniferae* (incl. *juncetosum gerardi*), 8 sites (41 species).
[*Plantaginetea majoris, Agrostietalia stoloniferae, Lolio-Potentillion anserinae*]
Grassland: ***Agrostis stolonifera***, ***Calliergonella cuspidatum***, ***Juncus articulatus***, ***Hydrocotyle vulgaris***, ***Potentilla anserina***, *Triglochin palustris*, *Eleocharis uniglumis*.

7 *Ranunculo-Alopecuretum geniculati*, 5 sites (32 species).
[*Plantaginetea majoris, Agrostietalia stoloniferae, Lolio-Potentillion anserinae*]
Grassland: ***Agrostis stolonifera***, ***Ranunculus repens***, ***Holcus lanatus***, ***Carex hirta***, *Alopecurus geniculatus*, *Carex otrubae*, *Potentilla anserina*.

8 *Arrhenatheretum elatioris* (affinity to *typicum*, *medicaginitosum* and/or *luzuletosum*), 5 sites (48 species).
[*Molinio-Arrhenatheretea, Arrhenatheretalia, Arrhenatherion*]
Hay-meadow: ***Arrhenatherum elatius***, ***Festuca rubra***, ***Achillea millefolium***, ***Trisetum flavescens***, *Crepis biennis*, *Knautia arvensis*, *Ranunculus bulbosus*, *Pimpinella saxifraga*, *Plantago media*.

9 *Arrhenatheretum elatioris festucetosum arundinaceae*, 5 sites (39 species).
[*Molinio-Arrhenatheretea, Arrhenatheretalia, Arrhenatherion*]
Hay-meadow; many species in common with previous community: ***Arrhenatherum elatius***, ***Brachypodium pinnatum***, *Helictotrichon pubescens*, *Origanum vulgare*, *Agrimonia eupatoria*, *Picris hieracioides*.

M *Mesobromion erecti* trunk community, 5 sites (47 species).
[*Festuco-Brometea, Brometalia erecti, Mesobromion erecti*]
Chalk grassland: ***Brachypodium pinnatum***, ***Centaurea scabiosa***, *Briza media*, *Scabiosa columbaria*, *Galium pumilum*, *Cirsium acaule*, *Thymus pulegioides*, *Fissidens cristatus*, *Campylium chrysophyllum*.

P Fragmentary *Phleo-Tortuletum ruraliformis*, 5 sites (43 species).
[*Koelerio-Corynephoretea, Cladonio-Koelerietalia, Tortulo-Koelerion*]
Pioneer vegetation: ***Tortula ruralis*** **var.** ***ruraliformis***, ***Brachythecium albicans***, ***Carex arenaria***, ***Hypnum cupressiforme*** **var.** ***lacunosum***, *Phleum arenarium*, *Erodium cicutarium* ssp. *dunense*, *Sedum acre*, *Saxifraga tridactylites*.

S *Spergulo-Corynephoretum*, 5 sites (32 species).
[*Koelerio-Corynephoretea, Corynephoretalia canescentis, Corynephorion canescentis*]
Pioneer vegetation: ***Corynephorus canescens***, ***Polytrichum piliferum***, various ***Cladonia*** spp., *Agrostis vinealis*, *Spergula morisonii*.

G *Genisto anglicae-Callunetum*, 5 sites (29 species).
[*Calluno-Ulicetea, Calluno-Ulicetalia, Calluno-Genistion pilosae*]
Heath vegetation: ***Calluna vulgaris***, ***Hypnum jutlandicum***, ***Empetrum nigrum***, ***Deschampsia flexuosa***, ***Festuca ovina***, ***Dicranum scoparium***, *Genista anglica*, *Genista pilosa*, *Lycopodium clavatum*, *Diphasiastrum tristachyum*.

E *Ericion tetralicis* (trunk community and *Lycopodio-Rhynchosporetum*), 6 sites (34 species).
[*Oxycocco-Sphagnetea, Ericetalia tetralicis, Ericion tetralicis*]
Heath or grass-heath vegetation: ***Erica tetralix***, ***Molinia caerulea***, ***Agrostis capillaris***, *Lycopodiella inundatum*, *Drosera intermedia*, *Rhynchospora fusca*.

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considered best developed along roadsides nowadays and rarely occur at other locations in the Netherlands (*e.g. Thero-Airion* and *Arrhenatheretum elatioris*).

Because of the actual and potential ecological importance of road verges in the agricultural, industrial, and urbane landscape, the interest for the maintenance, development, and restoration of species-rich communities in road verges is strongly increasing (Van Bohemen *et al.* 1991). However, ecological engineering can only be successful if accurate ecological knowledge is available on physical and chemical soil properties, groundwater depth, light regime, etc. Unfortunately, such information is scarce. Specific ecological information concerning individual syntaxa is urgently required.

Very few studies have considered the ecology of roadside vegetation on the basis of a full set of abiotic site measurements (but see Mederake 1991; Szwed & Sýkora 1996; Godefroid 1998). Plant communities in road verges generally occur on more or less artificial substrates and under relatively high disturbance frequencies. Their ecology may therefore differ from the ecology of comparable communities under less artificial conditions, for which more extensive synecological data may sometimes be available. In addition, synecological information is very often expressed in general terms only, also for syntaxa in less artificial situations (*e.g.* Schaminée *et al.* 1995b, 1996; Stortelder *et al.* 1999).

Our main objective was to create an ecological framework that can be used as a reference during ecological construction and management directed toward the realization of specific target communities. To guarantee wide applicability, a broad range of relatively well-developed syntaxa occurring in roadverges was studied. We characterized the synecology by measuring a large variety of environmental variables, many of which were followed during a full two-year period.

The collected data were also statistically screened for 'master factors'. In this study, we defined master factors as the environmental parameters best discriminating between the communities. They may be considered to represent the most important ecological factors within the data, as far as the variation in studied plant communities is concerned. Although data on the other variables will also be presented, the master factors may serve as a subset that can be used for practical applications. Field measurements of these factors only should still enable users to obtain a reasonable estimate of the syntaxa to be expected.

Sites and measurements

Investigated sites

A total of 74 roadside plots were studied, scattered over the Netherlands and belonging to 15 different semi-natural unfertilized plant communities (11 alliances, comprising 10 associations and 3 trunk communities: Table 1), and reflecting a wide range of environmental conditions. The variation includes: open pioneer vegetation on extremely dry and poor sandy substrates (both at low and high soil pH), grasslands on dry and poor, lime-rich soils, on loamy soils, and on wet or poorly drained clay or peat, tall-herb grassland communities on soils with permanently high groundwater levels (often peaty), partly shaded tall-herb communities on clay or sand, and dry and wet heath and grass-heath vegetation on poor, acid sand or loam. Both motorways (40%), regional roads (20%) and municipal roads (40%) were involved.

Each plant community was typically represented by five sites; occasionally six or eight sites were studied. Only the two investigated forms of the *Fritillario-Alopecuretum* were represented by fewer plots (3 well-developed plots, 2 fragmentary plots). These two forms were initially considered to represent a single community. However, it appeared that not only the species composition, but also the ecology of the two forms differed clearly. For this reason they are regarded as different communities during this study.

Species composition

Each site was described by a single plot of 25 m^2. Relevés were made in summer 1992 using a nine-point modified Braun-Blanquet scale (Table 2), which combines cover and abundance. In the remainder of this study the term 'abundance' is used to denote values on this combined scale. Both vascular plants and bryophytes were recorded. The species composition of the tree and shrub layers at the two partly shaded plant communities were not considered, as these had been planted.

Table 2. *Ordinal cover/abundance scale after Van der Maarel (1979). The abundance values presented denote the values applied in the present study (plot-size 25 m^2).*

Value	Cover %	Abundance
1	< 5	1
2	< 5	2-50
3	< 5	50-250
4	< 5	> 250
5	5 - 12.5	any
6	12.5 - 25	any
7	25 - 50	any
8	50 - 75	any
9	75 - 100	any

Site conditions

The absence or presence of an overstory tree- or shrub-layer was considered an important site condition, and a variable (values: 0/1) was created reflecting this condition. A related variable was also introduced, characterizing the intensity of shading in three classes. Value 0 indicated unshaded, 1 indicated shading from one roadside only, 2 indicated shading from both roadsides.

Soil measurements

From January 1993 to January 1995 various soil parameters were measured. All soil measurements refer to the top 10 cm of the soil. Bulked samples consisting of five subsamples per plot were used in all cases. Samples were kept cool during transport to the laboratory, stored at 1 - 4 °C (for 2.5 days at most), dried at 40 °C, and sieved using a 1-mm sieve. The material remaining on the sieve was weighed so that the results could be adjusted to the complete sample size. Bulk density was measured by taking 5 random samples of exactly 0.2 L undisturbed soil using a specially designed 10 cm long auger. Chemical results were expressed on a volume of soil basis (amount ha^{-1} to 10 cm depth), as this was considered most informative ecologically, and different soils with very different soil densities were to be compared.

Net annual N mineralization rates were assessed during two full years. Assessment took place by *in situ* incubation during 16 consecutive incubation periods (eight per year). Incubation was achieved using polyvinyl chloride tubes with sharpened lower rims (length 15 cm, inside diameter 2.5 cm) allowing undisturbed soil cores to be obtained (*cf.* Raison *et al.* 1987; Adams *et al.* 1989). During each incubation period five pairs of soil cores were used per plot, distributed in a regular pattern. One sample of each pair served as initial sample, the other remained in the field. The five initial samples were bulked, and the same was done with the five incubated samples after retrieval.

Dried samples were extracted using 0.01 *M* $CaCl_2$ which is a weak extraction solution approaching the average ion strength of many soil solutions (Houba *et al.* 1994, 1996). Extraction was performed using 3 g soil in 30 ml of extraction solution by shaking during two hours. After centrifuging for 10 minutes at 3000 g, the centrifugate was used for spectrophotometric determination of NO_3-N and NH_4-N by a Segmented Flow Analyzer (Skalar, Breda, the Netherlands). N mineralization rate per incubation interval was defined as the amount of mineral N (NO_3-N + NH_4-N) in the incubated sample minus the amount of mineral N in the reference sample. Annual mineralization rates were calculated for both years and averaged.

Available amounts of NO_3, NH_4, PO_4 and K were determined at regular intervals (8 times per year, 17 sampling dates in total). $CaCl_2$ extraction was used as described above. Mineral N was taken to be the sum of NO_3-N and NH_4-N, and average amounts were calculated. The nitrification degree was defined as the fraction of mineral N occurring as NO_3.

Total amounts of N and P were determined once, after digestion with H_2O_2 at 100 °C, followed by digestion with concentrated sulphuric acid at 300 °C under the influence of selenium as a catalyst (Houba *et al.* 1995). Salicylic acid was added to prevent the loss of nitrate. N and P were measured spectrophotometrically using a Segmented Flow Analyzer.

Carbon contents were determined once, according to Kurmies (Houba *et al.* 1995) by oxidizing the organic matter with $K_2Cr_2O_7$ in very strong sulphuric acid for 1.5 h at 100 °C. The concentration of Cr^{3+} formed was measured spectrophotometrically. C:N ratios were subsequently calculated.

Soil pH was measured twice, once in winter (early January) and once in summer (August). Measurement took place in the settling suspension of the $CaCl_2$ extracts, before centrifuging (Houba *et al.* 1994; Schofield & Taylor 1955). The resulting pH-$CaCl_2$ usually takes values approximately halfway between pH-H_20 and pH-KCl (Gupta & Rorison 1975).

The amounts of carbonates were determined once by adding HCl and measuring the volume of CO_2 produced. This volume was compared to the volume that developed from pure $CaCO_3$ (the Scheibler method; see Houba *et al.* 1995).

Cation exchange capacities (CEC) were determined once, at the actual soil pH and at a low ionic strength using unbuffered $BaCl_2$ (Houba *et al.* 1995). Samples were equilibrated with a 0.01 M $BaCl_2$ solution after saturation with Ba^{2+} by three extractions with 0.1 M $BaCl_2$. Subsequently, a known excess of 0.02 M $MgSO_4$ was added, causing all Ba^{2+} to precipitate as $BaSO_4$ and causing all sites with exchangeable ions to be occupied by Mg^{2+}. The excess of Mg was measured by flame atomic absorption spectrometry. Exchangeable amounts of the individual bases Ca, Mg, K and Na were analysed in the 0.1 M $BaCl_2$ extracts. Ca and Mg were determined by flame atomic absorption spectrometry, K and Na by flame emission spectrometry.

Both individual and total base saturation levels were defined as the ratio of exchangeable positive charges of the bases (Ca, Mg, K and Na; in kmol+ ha^{-1}) relative to the total CEC (kmol+ ha^{-1}).

The absolute amounts of the individual exchangeable bases (Ca, Mg, K and Na) as well as their combined amount (kmol ha^{-1}; ions, not charge), were also used as soil parameters. For Ca, the total amounts present were calculated also, including Ca in the exchangeable form as well as in the form of carbonates. These data were available for all sites except one.

Groundwater levels were determined at regular intervals (8 times per year, 17 sampling dates in total), up to 1.5 m below surface. Average levels, average spring levels (March and April), average highest levels (winter) and average lowest levels (summer) were calculated. At several sites groundwater level was permanently below 1.5 m. To circumvent missing values the average depths were transformed to 8 groundwater level classes as shown in Table 3.

***Table 3.** Transformation of groundwater depth to groundwater level as applied in this study.*

Level	Groundwater depth (cm)
0	Inundation
-1	+1 to -2
-2	-3 to -30
-3	-31 to -60
-4	-61 to -90
-5	-91 to -120
-6	-121 to -150
-7	-151 or below

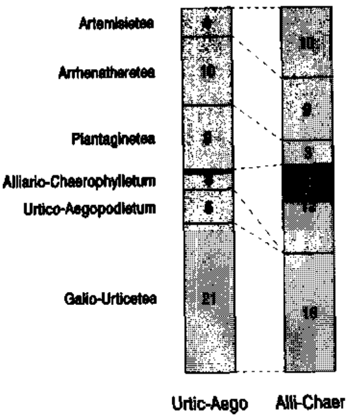
Soil moisture contents were also determined at all 17 sampling dates. These were expressed on a volumetric basis. We calculated the annual average, the average highest (winter) and the average lowest (summer) soil moisture contents.

Soil texture was determined once, using a method based on differences in sedimentation velocity (Houba *et al.* 1995). Organic matter contents were determined by weight-loss on ignition at 550 °C and were corrected for the loss of water bound to clay minerals using the soil clay content (Houba *et al.* 1995).

Using moisture content, granular composition and organic matter content, soil pF values at all sampling dates were calculated on the basis of matric potential characteristics obtained from literature (Wösten *et al.* 1994). Annual averages, average lowest (winter) and average highest (summer) values were calculated.

Vegetation measurements

Aboveground annual biomass production was determined in both years by clipping the vegetation just before it was mown by the road authorities. Most sites were mown twice per year (early summer and autumn) or only once (autumn). Any late autumn regrowth (if present) was also determined. In unmanaged sites biomass production was estimated by clipping the peak standing crop in late summer. Trees were not included in the biomass samples. Per plot, five subplots (0.5x0.5 m) were cut at ground level, bulked, dried at 70 °C for 48 hours, and weighed. Tissue concentrations of N, P and K were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Urtico-Aegopodietum
Galio-Urticetea
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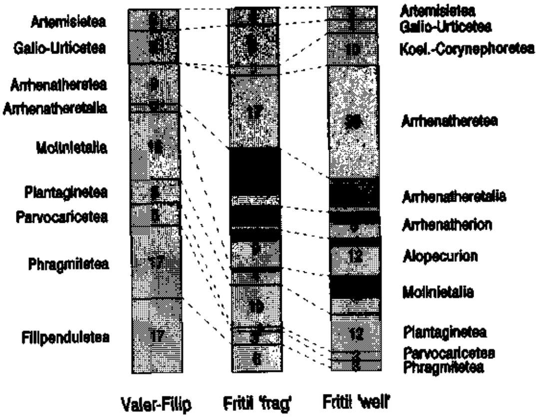
Urtic-Aego
Alli-Chaer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Filipenduletea
Artemisietea
Galio-Urticetea
Koel.-Corynephoretea
Arrhenatheretea
Arrhenatheretalia
Arrhenatherion
Alopecurion
Molinietalia
Plantaginetea
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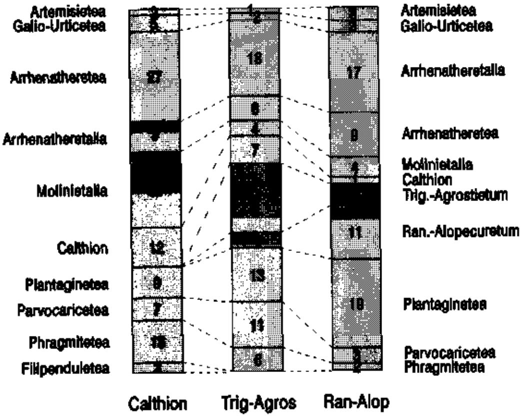
Fritil 'well'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Filipenduletea
Artemisietea
Galio-Urticetea
Arrhenatheretalia
Arrhenatheretea
Molinietalia
Calthion
Trig.-Agrostietum
Ran.-Alopecuretum
Plantaginetea
Parvocaricetea
Phragmitetea
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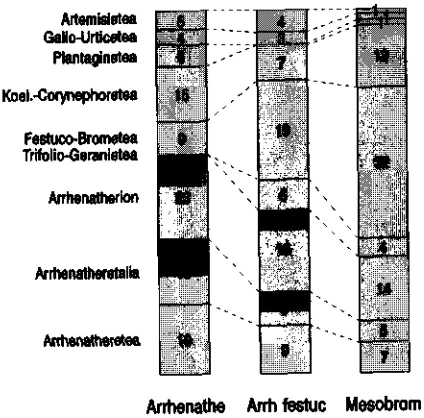
Calthion
Trig-Agros
Ran-Alop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Trifolio-Geranietea
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Arrhenatheretalia
Arrhenatheretea
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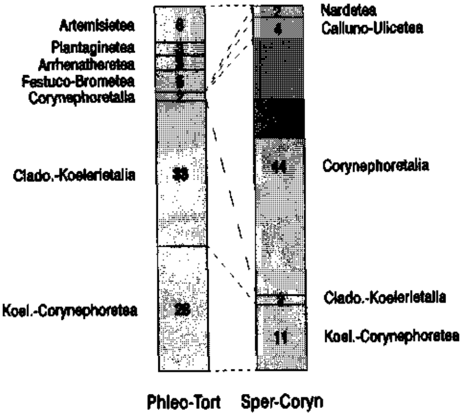
Arrhenathe
Arrh festuc
Mesobrom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Clado.-Koelerietalia
Koel.-Corynephoretea
Nardetea
Calluno-Ulicetea
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Clado.-Koelerietalia
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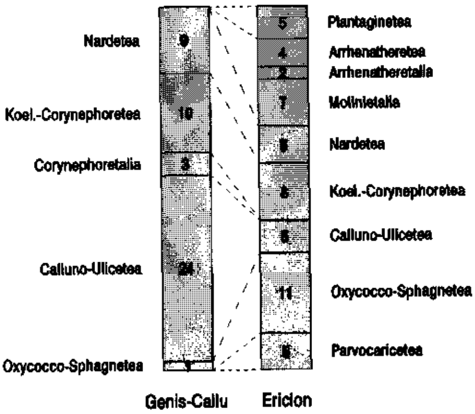
Phleo-Tort
Sper-Coryn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Plantaginetea
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Arrhenatheretalia
Molinietalia
Nardetea
Koel.-Corynephoretea
Calluno-Ulicetea
Oxycocco-Sphagnetea
Parvocaricetea
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Genis-Callu
Ericion

determined as described for total soil N, P and K (Walinga *et al.* 1995). Weighted average tissue nutrient concentrations were calculated, using the dry weight of each clipping as the weighting factor. We also calculated the annual aboveground accumulation of nutrients.

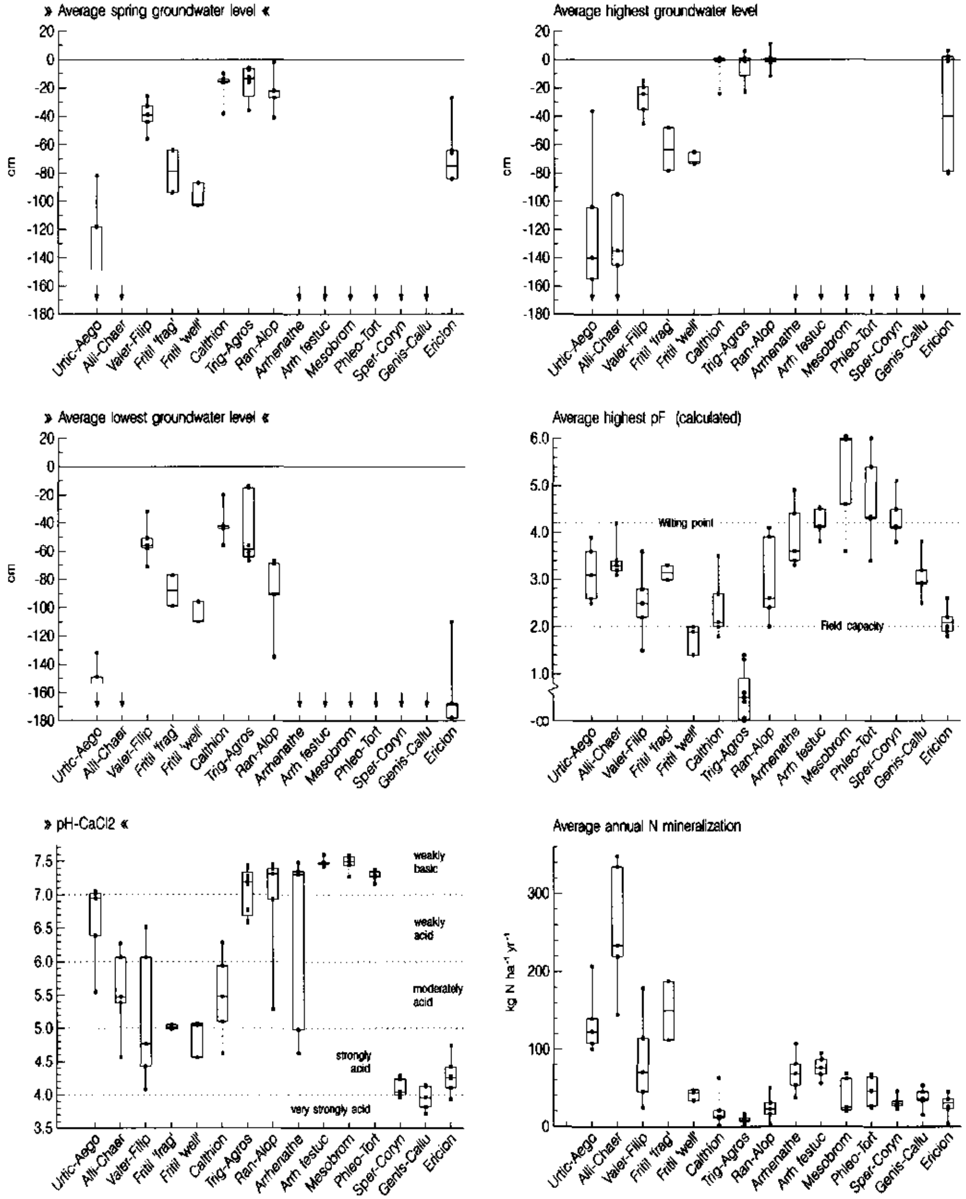
For two sites, biomass measurements failed in both years as vegetation management at these sites appeared unpredictable. Tissue nutrient concentrations were therefore only available for 72 sites. At some sites, the annual biomass production and accumulation of nutrients could not be measured. These included some of the heath sites dominated by ericaceous dwarf shrubs. Since these sites were mown only once every few years, standing crop measurements would reflect the production of several years, not of one. Measurements of the increase in standing crop at these sites appeared unreliable due to a very large variability, including negative results. Thus, biomass production and nutrient accumulation figures were available for 66 sites only.

Data analysis

Syntaxonomic description

The fidelity of each species to one or more syntaxa (at any hierarchical level) was derived from Schaminée *et al.* (1995b, 1996) and Stortelder *et al.* (1999). The resulting groups of species characteristic of a particular syntaxon are referred to as syntaxonomic elements. We aggregated these elements to the highest possible syntaxonomic level without losing information relevant for the various syntaxa actually studied. For this purpose, species characteristic of a particular syntaxon (at any hierarchical level) were also considered characteristic at the higher level. For instance, species characteristic of a particular association were regarded to be characteristic also at the alliance level, species

***Figure 1** (opposite). Syntaxonomic species composition of the studied plant communities. Values inside the bar-segments represent the average sum of abundance of the syntaxonomic element (the group of species characteristic for a specific syntaxon). Differential species are indicated with darker shading. These should only be considered when comparing syntaxa belonging to the same next-higher syntaxonomic level. For instance, differential species for the* Molinietalia *can be used when comparing the* Fritillario-Alopecuretum *and the* Calthion *(since both belong to the* Molinio-Arrhenatheretea*), but not when comparing these two with the* Valeriano-Filipenduletum *(which belongs to the* Convolvulo-Filipenduletea*). Aggregation of syntaxonomic elements was sometimes carried on to higher levels than described in the section 'data analysis', when lower levels were of little relevance for the syntaxon depicted.*



» Average spring groundwater level «

Average highest groundwater level

» Average lowest groundwater level «

Average highest pF (calculated)

» pH-CaCl2 «

Average annual N mineralization

Figure 2. *Boxplots presenting the values for environmental variables as measured at the studied plant communities. Boxes represent values between the 25% and 75% percentile; the median is indicated by a horizontal division. Values outside the interquartile range are connected to the box by a line (a dotted line is used for plots that were considered atypical specimens of the community concerned). Master factors indicated in the plot heading by: » factor «. Communities appear in*

characteristic of an alliance were regarded to be characteristic also at the order level, etc. Preferably, aggregation continued up to the class level. However, if more than one of the studied syntaxa belonged to the same class, aggregation of syntaxonomic elements ended at the highest syntaxonomic level still discriminating the studied syntaxa. From there on, species characteristic of higher level syntaxa constituted a new (higher level) syntaxonomic element, and aggregation was performed anew, either up to the class level, or again up to the highest level still making discrimination possible with other studied syntaxa.

For instance, since the *Valeriano-Filipenduletum* was the only studied *Convolvulo-Filipenduletea* community, species characteristic of any syntaxon belonging to the *Convolvulo-Filipenduletea* (including *Valeriano-Filipenduletum* species) were considered to belong to the *Convolvulo-Filipenduletea* element. Since we studied two *Lolio-Potentillion* associations (*Triglochino-Agrostietum* and *Ranunculo-Alopecuretum*), the *Triglochino-Agrostietum* element and the *Ranunculo-Alopecuretum* element were not aggregated into a *Lolio-Potentillion* element. Only species characteristic of other *Lolio-Potentillion* associations were. These, and other *Lolio-Potentillion* species, were subsequently aggregated with species characteristic of other *Plantaginetea* syntaxa (at any hierarchical level) into a *Plantaginetea* element.

Species differentiating between subassociations were not used. Differential species at other syntaxonomic levels were used (as if they were characteristic species) only if *both* the syntaxa between which the species differentiated were actually present in this study, and only at the sites actually representing one of these two syntaxa.

At each site, we calculated the sum of the cover/abundance values for the species of each syntaxonomic element. Subsequently, the average sum of abundances per syntaxonomic element was calculated for each of the 15 plant communities studied. To visualize the syntaxonomic species composition of the investigated communities, we presented these data in a stacked bar graph (Fig. 1). A fixed total bar size was used for each of the communities, and irrelevant syntaxonomic elements (low presence) were left out of the graphs.

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the same order as in Table 1. Class limits for soil pH from Scheffer et al. *(1989). In the groundwater graphs, down-arrows (↓) indicate levels well below -150 to -160 cm.*

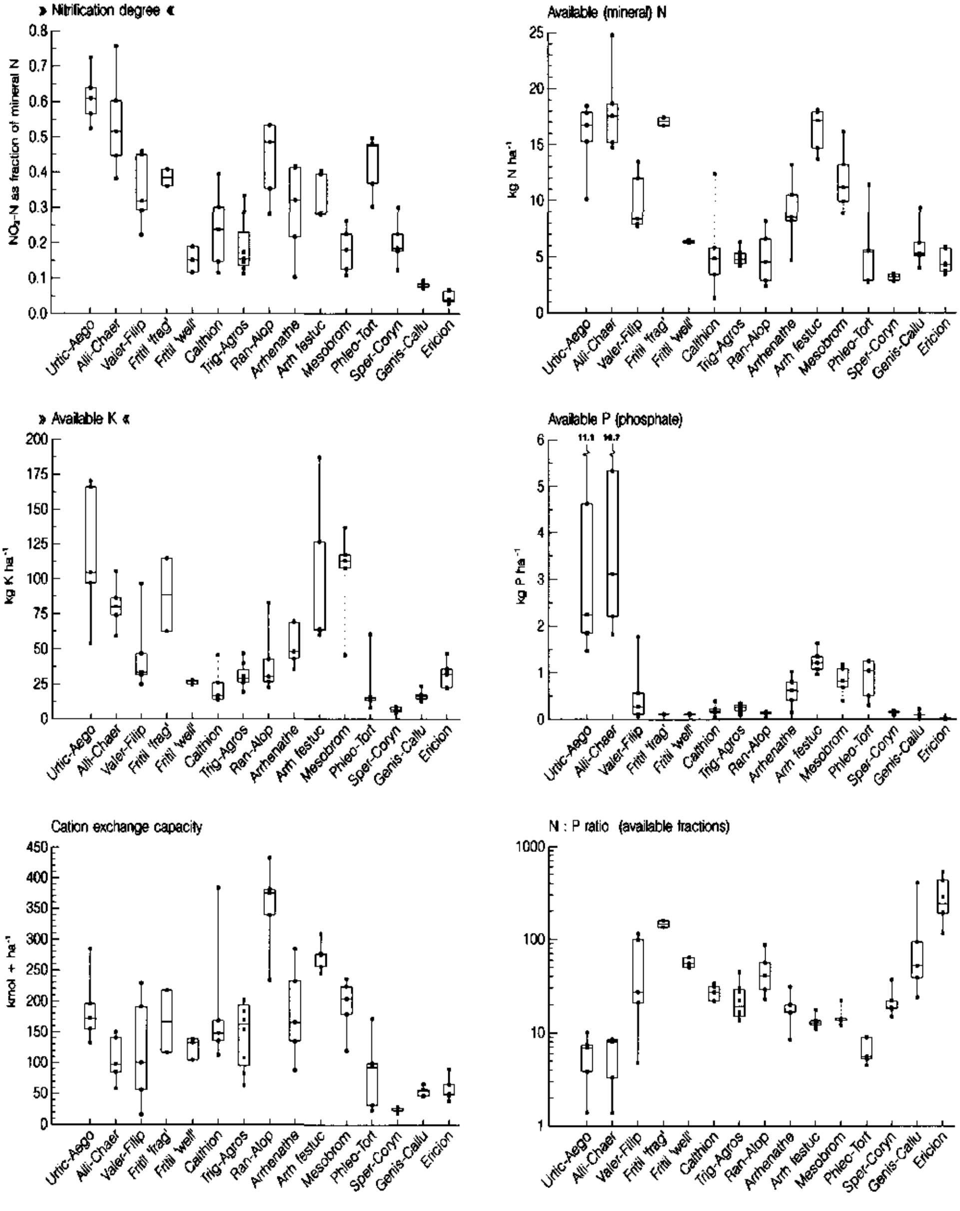

Figure 3. *Boxplots presenting the values for environmental variables as measured at the studied plant communities. Boxes represent values between the 25% and 75% percentile; the median is indicated by a horizontal division. Values outside the interquartile range are connected to the box by a line (a dotted line is used for plots that were considered atypical specimens of the community concerned). Master factors indicated in the plot heading by: » factor «. Communities appear in the same order as in Table 1. Soil N:P ratio (available fractions) on a logarithmic scale.*

Ecological master factors

To obtain a relatively small subset of variables capable of discriminating between the plant communities as much as possible, we used the stepwise variable selection procedure associated with a linear discriminant analysis (Norusis 1986). Discriminant analysis constructs linear combinations (discriminant functions) of the selected independent variables (predictor variables) that serve as the basis for separating the communities. Each of the selected variables was required to contribute significantly to the final discrimination.

An important restriction applies to discriminant analysis. The coefficients of the discriminant functions may not be stable if the number of cases per group (in our case sites per community) is less than three times the number of selected predictor variables (Williams & Titus 1988). In such cases the resulting discriminant functions may not be reliable for predictions. Since our data may be subject to this constraint, it should be stressed that we did not use analysis for the purpose of prediction. Our intention was to determine a subset of predictor variables performing well in discriminating between the communities in the current study. Users may characterize their sites by measuring these 'master factors', and compare the measurements with the values presented in this study to obtain an impression of the plant community to be expected. We will *not* present the classification function coefficients from the discriminant analysis for this purpose.

Nevertheless, classification coefficients were used implicitly during the analysis when assessing the misclassification rate for a particular set of predictor variables. We used a jackknife method to alleviate the problems connected with this. When judging how a site would be classified, we always omitted that particular site during the calculation of the discriminant functions. Thus, in order to obtain this improved misclassification rate for a particular set of variables, the analysis was performed 74 times. This technique also reduced the problem of unstable coefficients, since the analysis was now performed many times, each time with a slightly different set of sites.

Because of the relatively low sample sizes involved, extra attention was also paid to the significance levels. We set the maximum tolerable probability of mistakenly accepting one or more variables at 0.01. The required level of significance for each individual variable included may then be calculated as $1 - 0.99^{1/n}$, with n representing the number of selected variables. Based on this formula we set this level at 0.001 (0.1%), a value which would satisfy our over-all level of 0.01 for up to 10 selected variables.

To further validate the merit of the master factors obtained by the stepwise selection in discriminant analysis, we also investigated how these variables performed when explaining the variation in syntaxonomic composition. For this we applied

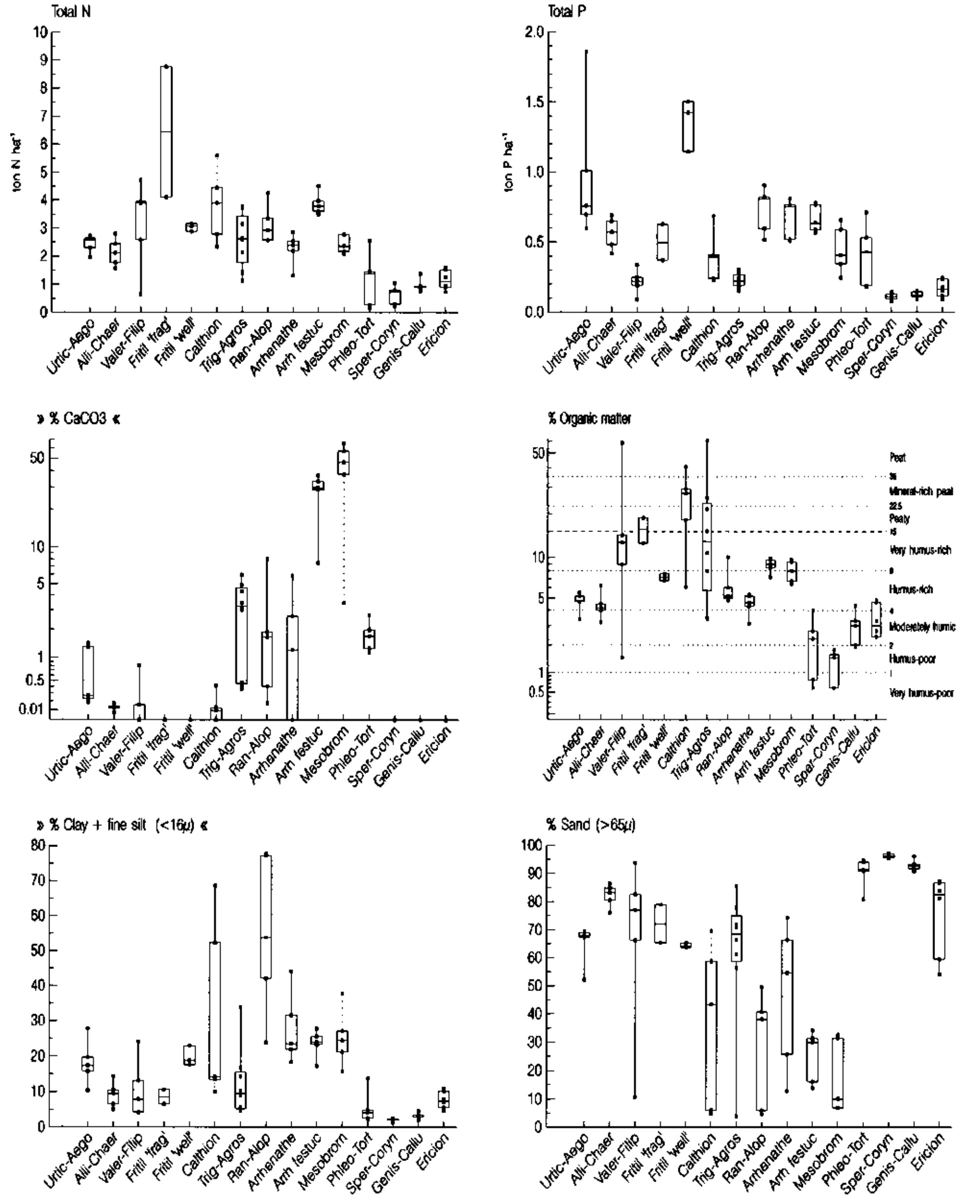

Figure 4. Boxplots presenting the values for environmental variables as measured at the studied communities. Master factors indicated in the plot heading by: » factor «. Communities appear in the same order as in Table 1. For the plots concerning the percentages of the individual soil separates, 100% includes the mineral components as well as $CaCO_3$ and organic matter. $CaCO_3$ and organic matter on logarithmic scale. Organic matter class limits from Scheffer et al. *(1989).*

canonical correspondence analysis (CCA) as provided by the computer program CANOCO (Ter Braak 1987-1992; Ter Braak 1988), using as 'species data' not the original species but the syntaxonomic elements described in the previous section. In order to give equal potentials to each of the syntaxonomic elements, the actual magnitude of an element in a site was divided by the total number of species belonging to that element (considering our entire species data). Monte Carlo permutation was used to obtain the significance of the contribution of each individual master factors, by supplying the other master factors as covariables.

Only site and soil variables were considered as possible master factors, not vegetation derived parameters. The latter were used only to obtain indirect (additional) synecological information. Most variables were log-transformed and some were arcsine-transformed to better suit statistical requirements.

Presentation

BOXPLOTS

We intended to present the synecological data for each variable in a way that would facilitate the perception 'at a glance' of both the typical value, and the amplitude, for each plant community. For this, we used a graphic representation (Figs 2 to 4, and 7) resembling 'box and whisker plots' (Sokal & Rohlf 1995). In such plots, the 25% and 75% percentile values are represented by the top and bottom of a box, the height of which represents the so-called inter-quartile range. Within the box, the median is indicated by a horizontal line. Values outside the inter-quartile range are indicated through lines attached to the upper and lower sides of the box (the whiskers). An advantage of these plots lies in the implicit use of percentiles, instead of the mean and standard deviation. The latter depend much on the transformation used, and may lead to unrealistic interpretations if the distribution of values for a community is skewed. The median is little influenced by transformations, and using the box and whisker plots skewed distributions can immediately be recognized.

We deviated from the general rules for box and whisker plots in several respects. First of all, the actual data points were always indicated as well. Secondly, extreme observations (more than 1.5 interquartile ranges from the top or bottom of the box) are also connected to the box by the whisker, instead of being plotted as a disconnected point. Due to the relatively low number of sites per community, the occurrence of such 'extreme' observations was rather common in our data. Moreover, we intended to visualize the full range of ecological values at which each plant community occurred, and this range would be obscured if the extremes were not connected to the box. Two sites, however, appeared to be rather atypical synecologically (discriminant analysis), and on reflection they also appeared atypical from the syntaxonomic viewpoint. If, at these two sites, the value for a particular variable was anywhere outside the interquartile range, this value was connected to the box by a dotted instead of a solid line. From here on we will refer to the graphs simply as 'boxplots'.

In our data, the number of sites per plant community was generally 5. In these cases the median simply equalled the third value, and the quartiles equalled the second and fourth value. When the number of sites was even, we always used untransformed data to determine the percentiles. We usually applied a linear scale for the boxplots (except in extreme cases), even if during other analyses the data had been transformed.

In some cases, differences between communities are reported as statistically significant. Such statements are based on *a posteriori* comparisons (LSD tests) following a one-way analysis of variance using all plots and using the plant community as the

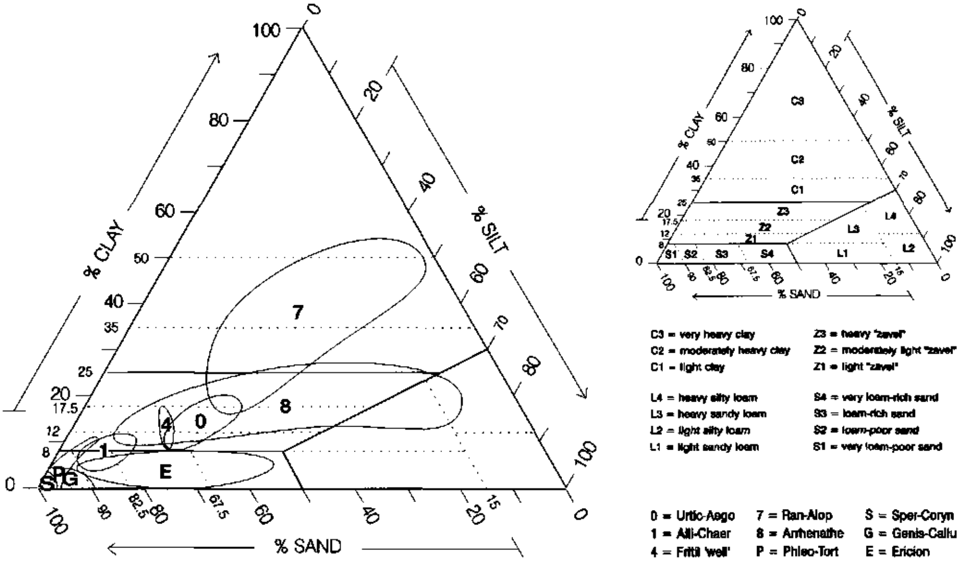

Figure 5. *Soil texture diagram for the soil separates: sand (>65μ), silt (2-65μ) and clay (<2μ); the sum of these is 100%. Indicated are the ranges observed for the plant communities on mineral soils. Communities where the top 10 cm of the soil generally contained more than 10% organic matter or more than 10%* $CaCO_3$ *were omitted since the large amounts of these constituents were considered to outweigh the relevance of the size-distribution for the remaining particles. Texture classification as used in the Netherlands (RGD 1977 in Locher & De Bakker 1990) indicated on the right. Numbers/codes of plant communities explained at the bottom right (see also Table 1).*

'treatment'. Before analysis, most variables were log-transformed or arcsine-transformed to conform to statistical requirements (even though the boxplots usually present the data on a linear scale). Unless stated differently, significant differences refer to $p<0.05$.

SOIL TEXTURE

Soil texture is presented not only in boxplots (Fig. 4), but also using the conventional triangular texture diagram (Fig. 5). These two approaches take different viewpoints. In the boxplots, the percentage of each soil separate refers to all solid soil components (including $CaCO_3$ and organic matter). In the triangular diagram, the sum of the sand, silt, and clay components is set to 100% (omitting $CaCO_3$ and organic matter). For this reason, the triangular diagram only includes the plant communities at which the soils generally contained less than 10% organic matter and less than 10% $CaCO_3$ in the upper 10 cm of the soil. Sites containing more than 10% organic matter (up to 61% in our data; Fig. 4) usually are peaty or true peat soils, and the size-distribution of the mineral components is of little relevance in these cases. Sites containing more than 10% $CaCO_3$ in the top 10 cm (up to 65% in our data; Fig. 4) comprise the shallow soils on limestone; here the abundance of lime and the shallowness of the soil are of more importance than the size-distribution of the remaining particles.

RELATIVE TISSUE N:P:K COMPOSITION

Indirect information on possible nutrient shortage may be derived from the tissue nutrient ratios. However, we regard focussing on separate nutrient ratios of restricted value since each ratio disregards at least a third macronutrient. When, for instance, K is the actual nutrient that limits growth, inspecting the N:P ratio only may erroneously suggest N or P limitation, or co-limitation by both. When K is abundant, inspecting the N:P ratio is equally uninformative as it may again suggest either N or P limitation whereas the most important fact is that both are now limiting growth (the fact that one may be more limiting than the other is only of secondary importance). Interpreting three separate nutrient ratios is often difficult and sometimes leads to inconclusive results. We therefore constructed a graphical presentation of the relative tissue N, P, and K composition, using a triangular diagram similar to the one commonly used for soil texture. For this, the amounts of tissue N, P, and K were expressed as relative percentages and subsequently plotted as a single point in the triangular diagram (Fig. 6). Since the amount of P is always low in tissues compared with N and K, the data points all lie in a relatively small part of the triangle. Only this part of the graph is presented, after inflation of the scale in the (vertical) P direction.

Recently, authors have tried to establish critical nutrient ratios indicating limitation of plant growth by a specific nutrient (*e.g.* Wassen *et al.* 1995; Pegtel *et al.* 1996; Koerselman & Meuleman 1996; Boeye *et al.* 1997). The review by Koerselman & Meuleman (1996) has received considerable attention, indicating threshold values at N:P = 14 to 16. Below 14, sites were usually N limited, whereas above 16 the sites were typically P limited. However, their study (as well as many other studies on this subject) was directed mainly toward wet communities (fens, marshes, wet grasslands, wet heaths and dune slacks). In the present study more than half of the sites classify as other, drier community types, and it is unclear to which extent the reported threshold values can be used here. Under dry conditions the critical N:P ratios may well be considerably lower. For instance, for agricultural crops (cereals) in the Sahel region in West Africa, Van Duivenbooden (1992) adopted an N:P ratio as low as 6.67 as the optimum ratio; higher

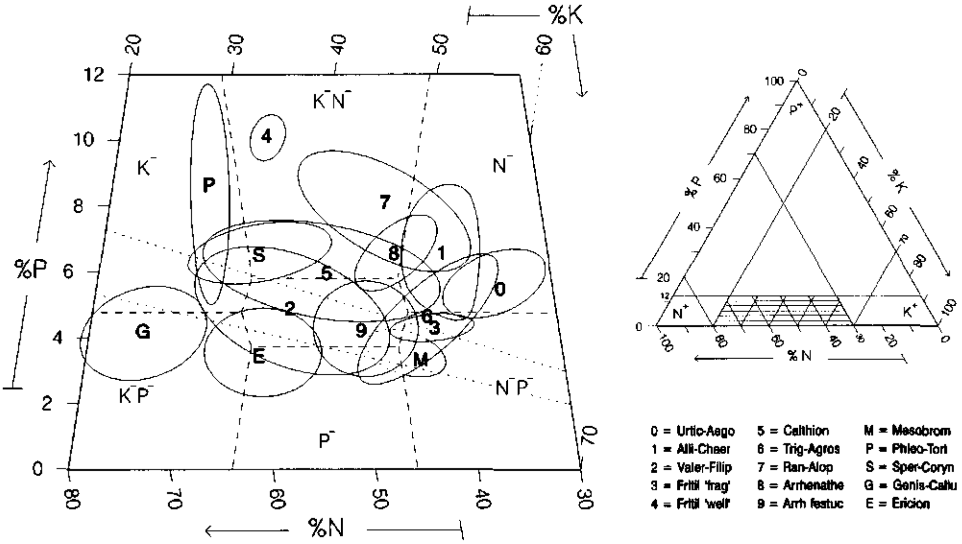

Figure 6. *Relative tissue nutrient composition. Indicated are the relative percentages of N, P and K (sum = 100%). A triangular graph comparable to that used for soil texture is utilized, but only part of this full triangle is presented (see bottom of explanatory graph on the right) and the scale for tissue P is strongly inflated (vertical). Dashed lines delineate areas with relative shortage of nutrients. For example, K^- or K^-N^- indicate relative shortage of K or both K and N (respectively). Presented are the full ranges observed for each community studied. Numbers/codes for the communities plotted near the centre of their range (except* Mesobromion: *plotted near the centre when the atypical site is omitted). The dotted straight lines are added for comparison with a single ratio and represent N:P ratios of 10 (upper line) and 14 (lower line).*

values indicating a relative P shortage, and lower values N shortage. Many other N:P threshold ratios have also been used. Aerts *et al.* (1992) adopted N:P ratios ≤10 or ≥14 as critical values. Shaver & Chapin (1995) used N:P thresholds at ≤8 and ≥10.

Although the existence of a relation between tissue nutrient ratios and relative nutrient shortage is rarely questioned, it is unlikely that a single 'universal' threshold value exists. Shaver & Chapin (1995) concluded the tissue N:P ratio to be "a useful, but rough, indicator of the relative importance of N- *versus* P-limitation". In this light, it may be worthwhile to pay attention to the *average* nutrient ratios in plants. The amount of P in plants is known to be generally about 1/10th of the amount of N, when considering a broad range of plant species and habitats (Allen 1989; Aber & Melillo 1991; Pegtel *et al.* 1996). In our data, covering a wide range of ecological conditions as well, the average N:P ratio was similar (10.4). This implies that N:P ratios around 10 could be considered typical values, suggesting that higher or lower ratios generally reflect a relative P or N shortage. Given this consideration and the various reported critical ratios, we feel that sites with N:P values below 14 should not indisputably be considered N limited. Only for N:P ratios below 10 is N most likely to be the limiting nutrient (see also Fig. 7), provided K is not limiting. We assume that values as high as 14(-16) or above are likely to be P limited. An N:P ratio between 10 and 14 may be considered an inconclusive indication, in agreement with Aerts *et al.* (1992). As far as tissue N:K ratios are concerned, no consensus has (yet) been reached on critical values either. The average value for plants was calculated to be around 1.2 (Pegtel *et al.* 1996). In our data the average again is similar (1.22). These values agree with a critical N:K ratio between 1.0 and 1.5, as reported by Roem & Berendse (1999).

We may conclude that it is not known exactly at which relative N:P:K compositions some nutrients can be considered to limit plant growth more than others. However, since our average nutrient ratios are similar to the average nutrient ratios reported in the literature for a wide range of conditions, the centroid of our data may be considered to reflect a 'typical' relative nutrient composition. Thus, the edges of our diagram (Fig. 6) likely correspond to situations with a relative shortage of one or two nutrients. Areas with different relative nutrient shortages have roughly been demarcated in the graph: *e.g.* relative tissue P low (below), relatively tissue K low (upper left), relative tissue N low (upper right). The location of a site in relation to these areas may be used as a possible indication (but not prove!) of the nutrients limiting vegetation growth. In general we may assume that near the centroid none of the three nutrients is more limiting than the others (indicating co-limitation by all three), whereas near the edges one or two nutrients are likely to be limiting more than the other(s).

Results

Master factors

Discriminant analysis with stepwise variable selection showed that eight variables contributed independently to the ecological discrimination of the plant communities, with significance levels ≤ 0.001 (Table 4). Seven of these eight variables were even significant at $p<0.0001$. The overall probability that one (or more) of the variables were selected mistakenly is smaller than 0.0007, more than ten times smaller than the level we initially set. One site was always omitted during the analysis phase of the discriminant analysis since on closer inspection it appeared to be transitional between a *Mesobromion* and an *Arrhenatherion*, and its exclusion much improved the results.

The most important discriminating variables were the intensity of shading and the average spring groundwater level. The next important factor appeared to be the average lowest groundwater level. Together, the spring level and the lowest level represent the annual fluctuation in (ground-) water levels.

The percentage of $CaCO_3$ and the soil pH appear to be important factors. The magnitude of their individual contributions may not seem particularly large (as judged

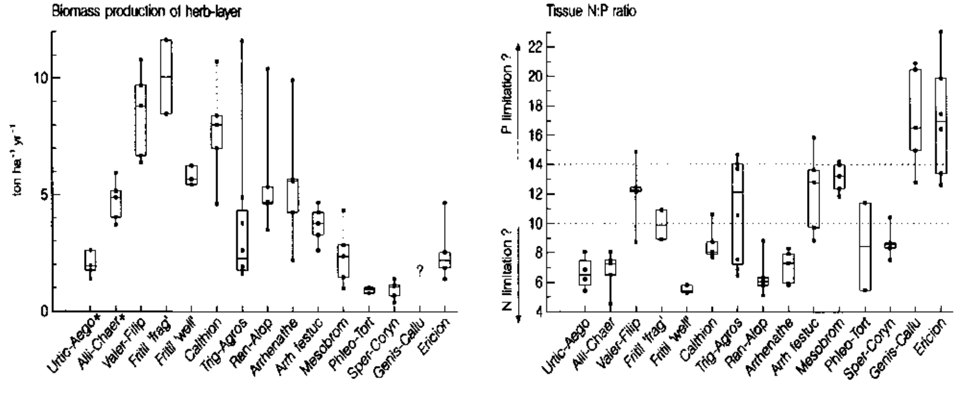

Figure 7. *Boxplots for vegetation-derived parameters. Average annual aboveground biomass production may be considered a measure indicating general soil fertility. Since only the herb-layer was considered this does not hold for the two syntaxa with a tree/shrub layer (indicated by '*' after the community name). No measurements on biomass production were available for the* Genisto-Callunetum, *but the assumed average value is indicated by '?'. The average tissue N:P ratio may provide an indication on possible nutrient limitation; we used 10 and 14 as the threshold ratios (see data analysis).*

Table 4. *Master factors. Variables selected (stepwise) during linear discriminant analysis. Indicated are the* F*-ratio and significance of each variable (relating to the change in Wilks' lambda when the variable would be removed), and the sequence ('S') in which the variables were selected. Units and applied transformations are presented; units for soil parameters refer to a depth of 0-10 cm. One site was always omitted from the analysis-phase (see text), but included in the classification-phase.*

S	Predictor variable	Unit	Trans.	*F*-ratio	Sign.	Additional statistics
1	Shading intensity	roadsides	0/1/2	44.5	0.0000	73 sites, 15 plant communities.
2	Spring groundwater level	classes	Table 3	19.7	0.0000	Wilks' lambda: 6.33 x 10^{-7}; p=0.0000.
4	Lowest groundwater level	classes	Table 3	16.2	0.0000	Significance of all canonical discriminant functions < 0.002.
5	Particles <16μ	% (w/w)	Log	10.1	0.0000	
3	$CaCO_3$ content	% (w/w)	Log	7.8	0.0000	Probability that one or more variables were included unjustified < 0.0007.
6	Nitrification degree	-	Arcsine	7.6	0.0000	
7	Available K	kg K ha^{-1}	Log	6.8	0.0000	Correct classification rate (jackknifed): 64 sites out of 74 = 86.5%.
8	pH	-	-	3.7	0.0003	

from their F values), but this is due to their correlated nature. During variable selection, $CaCO_3$ content was the third variable selected, immediately following shading intensity and spring groundwater level. If $CaCO_3$ was temporarily removed from the analysis, soil pH was the third variable selected. At high and relatively constant soil pH, there is still much variation in the percentages of $CaCO_3$ which apparently further discriminates between communities. At low (or zero) $CaCO_3$ contents there is still much variation in pH, and again this apparently is a additional discriminating factor. Thus, despite their correlation, pH and $CaCO_3$ content both contribute significantly.

Three other factors appeared to be important. First this concerns soil texture. The texture variable with best discriminating properties appeared to be the fraction of fine particles (particles <16μ), including both the clay and the fine silt fraction. The other two discriminating factors were chemical soil factors. Of these, only the amount of available K was directly related to soil nutrient availability. The other one concerned the degree of nitrification (the fraction of mineral N occurring as NO_3).

Other variables remained that still provided additional explanation, most notable soil N:P ratio (available amounts), N mineralization, and soil total P. However, their significance levels were higher, and the misclassification rate (when based on the jackknife procedure) did not change when these variables were included. Besides, canonical correspondence analysis (CCA) based on the syntaxonomic composition could not significantly (p=0.01) confirm their additional importance, although it may be argued that such an analysis involves a slightly different perspective. The CCA did confirm the importance of the eight selected master factors. These variables were all highly significant (Monte Carlo permutation tests; $n=9999$) and the overall probability of one or more variables mistakenly being accepted as an explanatory variable was again shown to be less than 0.01. The CCA explained approx. 62% of the variation in the syntaxonomic composition (74 sites; 24 syntaxonomic elements).

Using the eight master factors (Table 4), the classification phase of the discriminant analysis correctly classified 64 of the 74 sites (86.5%; using the jackknife procedure). This may be considered a satisfactory result, especially considering that several of the misclassified sites contained a relatively large number of species characteristic of the syntaxon it was (mis-)classified as. For instance, a *Valeriano-Filipenduletum* site which was classified by the discriminant analysis as *Calthion* (exclusively based on the environmental variables), indeed appeared to contain a relatively weak *Convolvulo-Filipenduletea* element and relatively strong *Calthion* and *Molinietalia* elements (compared to the other *Valeriano-Filipenduletum* sites). An *Urtico-Aegopodietum* site classified as *Alliario-Chaerophylletum* by the discriminant analysis (based on the environmental measurements), appeared to contain a clear *Alliario-Chaerophylletum* element.

Only three of the misclassified sites were classified as an entirely unrelated syntaxon based on the eight master factors. This concerned a *Phleo-Tortuletum* site (the most fragmentary one) with an exceptionally large amount of particles $<16\mu$ which was classified as *Arrhenatheretum*, an *Arrhenatheretum* site (with tendency toward the *luzuletosum*) with very low soil pH and nitrification degree which was classified as *Genisto-Callunetum*, and an *Ericion* site with a relatively large amount of particles $<16\mu$ and a high nitrification degree which was classified as *Fritillario-Alopecuretum*. If however, instead of following the jackknife procedure, these sites were themselves included during the analysis-phase, they were subsequently classified correctly.

The analyses showed that two sites needed special attention. Both sites were never classified as the original syntaxon, even if additional environmental variables were used as well and if jackknifing was omitted. First, this concerned a *Calthion* site which was invariably classified as *Valeriano-Filipenduletum*. This site appeared to contain a relatively small amount of *Calthion*-species and a relatively large amount of species characteristic of tall-herb communities (*Filipendulion* and *Galio-Urticetea*). The site can be considered a relatively ruderalized specimen and not a typical *Calthion*. The other site was the '*Mesobromion*' site mentioned at the beginning of this section which was omitted from the analysis phase. This site was invariably classified as *Arrhenatheretum*. Syntaxonomically, this site appeared to contain an unproportional amount of *Molinio-*

Arrhenatheretea species and a relatively strong *Arrhenatherion* element. The site clearly constituted a transition between the *Mesobromion* and the *Arrhenatherion*. Since both sites were considered to be atypical examples of the plant community they were supposed to represent, they are treated with special consideration in the diagrams and syntaxonomic discussion, especially if these sites showed a variable value which was higher or lower than those for the other sites of the community.

Synecology

URTICO-AEGOPODIETUM AND *ALLIARIO-CHAEROPHYLLETUM TEMULI*

These associations (both belonging to the *Galio-Alliarion*) may be characterized as occurring in semi-shaded locations along woodland or hedge margins (all other syntaxa studied were unshaded). The *Urtico-Aegopodietum* plots (all belonging to the *alliarietosum* subassociation) generally occurred under moister conditions than the *Alliario-Chaerophylletum* plots (most resembling the *geetosum* subassociation).

Moister conditions in the *Urtico-Aegopodietum* are reflected by various different aspects. First of all, shading is generally more intense. The *Urtico-Aegopodietum* plots were shaded from both roadsides (except one which was only shaded from the east). The *Alliario-Chaerophylletum* were all lightly shaded from one side only, generally from the north (3 plots) or east (1 plot). In one case shading was from the west but here shading was relatively light as it was caused only by a hedgerow.

Secondly, moister conditions at the *Urtico-Aegopodietum* stands were indicated by their occurrence on significantly heavier soils than the *Alliario-Chaerophylletum*. This can be seen in the boxplots for the percentage fine particles (clay plus fine silt) and for the percentage sand (Fig. 4), but it may be illustrated best by the soil texture diagram (Fig. 5: communities 0 and 1). The *Urtico-Aegopodietum* (community 0) occurred on light to heavy "zavel" whereas the *Alliario-Chaerophylletum* (community 1) occurred on sand, or also on light "zavel" but always with higher percentages of sand than for the *Urtico-Aegopodietum* plots. According to Weeda *et al.* (1999) the *Urtico-Aegopodietum* can also be found under unshaded conditions, but only on heavy soils. We only studied shaded conditions.

Thirdly, moister conditions in the *Urtico-Aegopodietum* are indicated by the higher groundwater-levels encountered (Fig. 2). Two of the plots showed average spring levels of -120 cm or higher and average lowest levels of -150 cm or higher. From the water level in a nearby ditch it could be inferred that groundwater levels in a third plot could not have been deeper than -200 cm throughout the year. This probably indicates that stands of this association are not always entirely groundwater-independent, as Weeda *et al.* (1999) suggested to be the case for the *Galio-Urticetea* syntaxa. In the *Alliario-Chaerophylletum* plots, spring groundwater levels were well below -200 cm in all cases, and this syntaxon may thus be characterized as groundwater-independent. However, the average highest groundwater is unexpectedly high for some of the *Alliario-Chaerophylletum* plots. This is due to the occurrence of two subsequent winters with exceptionally high levels of the rivers near which the plots were located. The plots involved are even known to have been inundated on these occasions (although this was no longer the case at the fixed dates of measurement). Winter inundations are well endured by both associations, but by no means required.

As a result of the differences discussed above, soil moisture contents were significantly higher in the *Urtico-Aegopodietum* than in the *Alliario-Chaerophylletum* plots (average contents as well as highest or lowest contents; not in Figs). Also the annual fluctuations in moisture content were significantly weaker in the *Urtico-Aegopodietum* plots than in the *Alliario-Chaerophylletum.* When soil moisture conditions are expressed as pF values, the same patterns were present, but differences were relatively small. Partly, this may be due to the fact that pF values were not actually measured, but calculated using average formulas for a few relatively wide soil types (Wösten *et al.* 1994). This procedure may have affected some differences. Nevertheless, although the *Alliario-Chaerophylletum* clearly occurs under dryer conditions than the *Urtico-Aegopodietum,* it is also clear that plots of both associations seldom or never reached the wilting point at pF = 4.2 (Fig. 2; average *highest* pF). In general, the *Urtico-Aegopodietum* soils may be described as moist but not wet. In contrast to Weeda *et al.* (1999), we tend to characterize the *Alliario-Chaerophylletum* soils as moderately dry, and not as moist.

The plots of the two syntaxa differed significantly with respect to soil pH (Fig. 2). While the *Urtico-Aegopodietum* soils were generally neutral to weakly acid (pH-$CaCl_2$: 6.4 - 7.0), and moderately acid in one case only (5.5), the *Alliario-Chaerophylletum* soils were generally moderately acid (ranging from strongly to weakly acid; pH 4.5 - 6.3). This does not agree with the ecology described by Weeda *et al.* (1999) who reported that the *Alliario-Chaerophylletum* occurs on weakly acid to weakly basic soils, a range they also ascribed to the whole *Galio-Urticetea.* The difference in acidity between the two associations is also reflected by a significant difference in soil $CaCO_3$ content (Fig. 4). While this content ranged from 0.18 to 1.5% for the *Urtico-Aegopodietum,* the *Alliario-Chaerophylletum* plots contained only very little $CaCO_3$ (0.07 to 0.13%).

Soil organic matter content in both syntaxa may be described as humus-rich (sometimes only moderately humic) ranging from 3 to 7% (Fig. 4). In comparison to the other syntaxa studied and considering the large amounts of leaf litter from overstory trees, these amounts are not particularly high. The high rates of N mineralization (see below) may be held responsible.

Both associations may be described as nitrophyllic. The degree of nitrification (the fraction of the mineral N pool occurring as NO_3) is high; generally higher than for any of the other communities studied, ranging from 0.38 to 0.76 (Fig. 3). For the *Urtico-Aegopodietum* the degree of nitrification is significantly higher ($p<0.01$) than that in any other community studied (except the *Alliario-Chaerophylletum*). Also N mineralization rates were high, especially for the *Alliario-Chaerophylletum* where mineralization rates may be considered very high. For the *Urtico-Aegopodietum* mineralization rates varied from 100 to 200 kg N ha^{-1} yr^{-1}, for the *Alliario-Chaerophylletum* from 150 up to 350 kg ha^{-1} yr^{-1} (Fig. 2). The high mineralization rates as well as the difference between the two syntaxa confirms the results of Ellenberg (1977). Most probably, the high mineralization rates are partially caused by leaf litter from overstory trees and shrubs. As the two syntaxa are only partly shaded, sunlight reaches the soil and this further stimulates decomposition. In addition, decomposition may be stimulated by the relatively light soils involved (Weeda *et al.* 1999). For P and K the availability is also relatively high. For available P, both associations display some exceptionally high levels, ranging from 1.5 up to more than 11 kg P ha^{-1} (Fig. 3). This again is significantly higher than the amounts encountered in any other community. The amounts of available P were unproportionally high also in comparison with the amounts of mineral N, resulting in some exceptionally low soil available N:P ratios (Fig. 3). The amount of available K and the cation exchange capacity (CEC) generally appeared to be higher in the *Urtico-Aegopodietum* than in the *Alliario-Chaerophylletum*. These differences are likely to be partly associated with the larger amounts of fine soil particles in the *Urtico-Aegopodietum* plots.

In agreement with the high availabilities of N, P and K, the tissue concentrations of these elements were also high in the two syntaxa (not presented in Figs). For the *Urtico-Aegopodietum* plots, tissue concentrations were generally higher than those in any of the other communities studied, especially for tissue K (significant at $p<0.05$). Surprisingly, the relative composition of tissue nutrients (Figs 6, 7) suggests both associations to be limited by N. This corresponds with the very low soil available N:P ratio. Apparently, despite the very high N mineralization rates N probably still limits herb-layer growth. K most likely does not, as it appeared to be very abundant in the tissues compared to other nutrients, especially in the *Urtico-Aegopodietum* (Fig. 6:

community 0). Possibly the herb-layer profits from canopy leaching of K from the overstory trees, as K particularly is known to be leached from both living and dead material and may cycle rapidly through the vegetation (Tukey 1970; see also Chapter 3: Schaffers *et al.* 1998). The fact that soil available K levels were especially high in the *Urtico-Aegopodietum*, which is the syntaxon shaded most heavily, may support this.

In both associations, plots were present with a slight floristic affinity to the other association. When using multiple regression to explain a gradual arrangement of the plots from typical *Urtico-Aegopodietum* to border situations to typical *Alliario-Chaerophylletum* (based on the syntaxonomic elements), it appeared that the combination of shading intensity and soil pH, or alternatively the combination of soil texture and groundwater level, both explained 85 to 90% of the variation (the individual variables contributing significantly at $p<0.05$). This result indicates that within the *Galio-Alliarion* especially these 4 (interrelated) factors are important synecological determinants (master factors).

Biomass production of the herb layer was relatively low to intermediate in the two syntaxa (Fig. 7), since much of the site productivity is realized by the trees and shrubs. Herb-layer productivity was low in the heavier shaded *Urtico-Aegopodietum* plots (1.4 to 2.6 ton ha^{-1} yr^{-1}). In the *Alliario-Chaerophylletum*, which is less shaded, herb-layer productivity was 3.7 to 5.9 ton ha^{-1} yr^{-1}.

The encountered management for the *Urtico-Aegopodietum* was generally cutting of the herb layer (with or without removal) once or twice per year. Management was absent in one case only. The *Alliario-Chaerophylletum* plots were either unmanaged, or cut once per year (with or without removal as well). These observations did not confirm the assertion of Weeda *et al.* (1999) that mowing an *Urtico-Aegopodietum* may lead to an *Alliario-Chaerophylletum*. For a long-term persistence, both associations will need at least irregular management to prevent tree/shrub establishment.

VALERIANO-FILIPENDULETUM

This tall-herb community (of which four of the five plots bear closest resemblance to the *calamagrostietosum* subassociation) was found under moist to wet conditions, with groundwater remaining available to the vegetation throughout the year (Fig. 2). The average spring groundwater level varied from -25 to -55 cm, the average lowest level from -30 to -70 cm. The plots were not inundated in winter and the average highest groundwater level was below -15 cm. The soils hardly ever dry out, the average highest pF values in summer (Fig. 2) generally ranged between 2 and 3 (inter-quartile range).

The types of soil involved varied widely, indicating that groundwater and moisture conditions are much more important for the occurrence of this association than the actual soil type. This is clear from the broad range in sand percentage, and also the amount of organic matter varied widely (Fig. 4). The *Valeriano-Filipenduletum* may occur on peat or peaty soils but also on humus-poor sand, as long as groundwater conditions (and of course the nutrient status) are suitable.

Soil pH varied from strongly to weakly acid (pH-$CaCl_2$ 4.0 to 6.5; Fig. 2), which is fairly in line with the range of 4.5 to 8.0 (solution unknown) reported by Van 't Veer *et al.* (1999), although they mistakenly label the lower range as 'weakly acid'. $CaCO_3$ was absent or virtually absent (but 0.8% in one case).

Nutrient conditions in the *Valeriano-Filipenduletum* may be described as eutrophic. The N mineralization rate was usually moderately high (45 to 115 kg N ha^{-1} yr^{-1}) but may be as high as 180 and as low as 25 kg ha^{-1} yr^{-1}. The median soil C:N ratio was higher than in any other community if the heathland and pioneer syntaxa are excluded (not in Figs). The amounts of available K were generally low, and the amounts of available P low to very low. Low levels for P were found in all unshaded, groundwater-dependent syntaxa studied. However, in these communities nutrients are likely not only supplied by mineralization or by the amounts available in the top layers of the soil, but also by nutrient-rich groundwater or surface water in reach of the roots, especially in the *Valeriano-Filipenduletum*. Consequently, biomass production in this association can be high to very high, ranging from 6.4 to 10.8 ton ha^{-1} yr^{-1} (Fig. 7).

The relative tissue nutrient composition (Fig. 6: community 2) indicates no clear limitation by one particular nutrient. In most cases the three macronutrients are probably co-limiting, although some plots demonstrated relatively small amounts of tissue K and/or P and could be slightly limited by these elements. In Fig. 3 it may be observed that the amounts of soil available K and P were also relatively low for many of the *Valeriano-Filipenduletum* plots.

The plots were either mown once per year (with or without removal), or not managed. During the study, the unmanaged plots were noted to attain a more ruderalized character and to lose characteristic species. Also Van 't Veer *et al.* (1999) reported that, although the association may endure for quite some time, it generally needs management to prevent the often rapid succession toward woodland or scrub. The best developed *Valeriano-Filipenduletum* plots in our study were those where cuttings were removed.

FRAGMENTARY AND WELL-DEVELOPED *FRITILLARIO-ALOPECURETUM PRATENSIS*

Fritillario-Alopecuretum grasslands were found in moist locations with groundwater most likely remaining in reach of the vegetation throughout the year, although clearly remaining at deeper levels than in any of the other unshaded groundwater-dependent grassland and tall-herb communities studied (Fig. 2). For the spring levels this was significantly so. Average spring levels at the *Fritillario-Alopecuretum* sites varied from -65 to -105 cm. The average lowest levels were only slightly lower (-75 to -110 cm). The plots were not inundated in winter and average highest groundwater level ranged from -50 to -75 cm. According to Zuidhoff *et al.* (1996) *Alopecurion* soils may dry out superficially during summer, but the average *highest* pF values at our sites were nevertheless calculated to be 3.3 or lower (Fig. 2). The well-developed form of this association (resembling the *typicum* subassociation most and showing least resemblance with the *calthetosum*) occurred on moister soils than the fragmentary form, both in terms of actual moisture contents (difference small; not presented) as well as in terms of the calculated pF values (difference significant; Fig. 2). No clear differences between the two existed in groundwater levels.

The well-developed form occurred on humus-rich (*c.* 7%), light to moderately light "zavel" soils (Figs 4 and 5), whereas the fragmentary form occurred on very humus-rich (but loam-poor) sand or on peaty sand. Organic matter contents in the latter were 12.5 and 18.7% (Fig. 4).

Soil acidity did not differ between the two forms of this association and can be described as strongly to moderately acid (pH-$CaCl_2$ ranging from 4.5 to 5.1; Fig. 2). No $CaCO_3$ was present in any of the plots.

A significant difference existed in the N mineralization rates for the two forms (Fig. 2). Whereas N mineralization was relatively low for the well-developed form (ranging from 33 to 48 kg N ha^{-1} yr^{-1}), high values (110 and 190 kg ha^{-1} yr^{-1}) were obtained for the fragmentary form. The spring increase in mineralization rate seemed to start slightly later in the well-developed form than in the fragmentary form. This may affirm the assertion by Corporaal *et al.* (1993) and Zuidhoff *et al.* (1996) that a low soil temperature in spring (caused for instance by high groundwater levels and/or inundations) is important for proper development of this syntaxon, as the resulting low soil temperature restrains early development of grasses and gives *Fritillaria meleagris* an advantage.

Differences between the two forms of the association also exist for the pools of mineral N and available K ($p<0.01$; Fig. 3). For K, the amounts available at the fragmentary sites were even significantly higher than those in any other unshaded, groundwater-dependent community. For N, the same trend existed ($p=0.0602$), causing the N:P ratio of the soil available fractions at the fragmentary sites to be higher than in any other grassland or tall-herb community (Fig. 3). Consequently, absolute tissue K and N concentrations in the fragmentary sites were significantly higher than those in any other unshaded, groundwater-dependent community ($p<0.01$ for K, $p<0.05$ for N; not in Figs). Also the degree of nitrification differed significantly between the two *Fritillario-Alopecuretum* forms ($p<0.01$); whereas in the well-developed form only 11 to 19% of the available N was present as NO_3, this ranged from 36 to 41% in the fragmentary form of the association.

Biomass production of the two forms differed in line with the differences in nutrient availability. In the well-developed form production was intermediate to moderately high (5.4 to 6.3 ton ha^{-1} yr^{-1}), whereas it was high to very high in the fragmentary form (8.4 and 11.7 ton). The latter values are among the highest encountered in our study, and are likely responsible for the fragmentary development at these sites.

The well-developed form of the *Fritillario-Alopecuretum* contained large amounts of P in its tissues, not only when expressed as concentrations, but also when judged relative to the other nutrients (Fig. 6: community 4). From this it may be deduced that the well-developed form of this syntaxon is probably strongly K and N limited. In the fragmentary form, K is not likely to be limiting at all. In this case, some N and P co-limitation may be indicated (Fig. 6: community 3).

The soil P status of the well-developed form is puzzling. The total amounts of soil P were exceptionally high (Fig. 4). Soil C:P ratios were exceptionally low (20-30; not in Figs), which could indicate high potential mineralization rates for P; an assumption supported by the high levels of tissue P for the well-developed form. However, the pool of soil available P was found to be very low throughout the association (0.100 to 0.125 kg P ha^{-1}), also in the well-developed form. Of course, pool sizes need not be correlated with mineralization rates exactly, but they may be expected to correlate at least to some extent, as reported for N in Chapter 7 (Schaffers 2000). Soil P is notorious for the many processes affecting its availability. P is not very mobile, its mineralization is not easily measured, and many insoluble salts may be formed depending on soil pH. It was noted that the soils at the well-developed sites had a distinct orange hue, and the water in nearby ditches was orange-brown coloured. This may indicate the presence of large quantities of iron, which is known to form insoluble phosphorus salts at relatively low pH levels (Scheffer *et al.* 1989). This would account for the measured low levels of soil available P. However, it contradicts the very high tissue P levels, unless the vegetation has means to either make iron salts available to them, or to use mineralized P before insoluble salts are formed. Mycorrhiza possibly play an important role here, since P nutrition is known to be enhanced by this form of symbiosis (Schachtman *et al.* 1998).

All the plots were cut twice per year. The cuttings were generally removed, but in one of the fragmentary plots this was not the case. Hay removal is likely to be crucial for the persistence of a well-developed *Fritillario-Alopecuretum*. Zuidhoff *et al.* (1996) reported that the association does not endure fertilization well, and hay removal may also be needed to compensate for atmospheric nutrient inputs (see also Chapter 3: Schaffers *et al.* 1998).

CALTHION PALUSTRIS TRUNK COMMUNITY

This hay-making community was found in wet and soggy situations, with groundwater levels higher than at the previous groundwater-dependent syntaxa, especially in winter and spring (Fig. 2). Although the *Calthion* plots could not be assigned at the association level, they some affinity with the *Lychnido-Hypericetum* (subassociation *orchietosum morionis*) and/or with the *Ranunculo-Senecionetum*. One of the *Calthion* plots needs special attention. Discriminant analysis (based on environmental variables only) consistently classified this plot as *Valeriano-Filipenduletum* and additional syntaxonomic evaluation revealed that this plot was (indeed) not a typical *Calthion* but a relatively ruderalized form. In the boxplots, environmental values for this plot laying outside the interquartile range are therefore connected to the box by a dotted line, to indicate that these values may not be representative for the ecology of a true *Calthion*.

It is clear that groundwater in a true *Calthion* community is at the surface in winter (Fig. 2; dotted lines omitted), and is still very high in spring (-10 to -20 cm). In summer, the groundwater levels fell to between -20 and -60 (interquartile range -40 to -45 cm). Such summer levels are still relatively high (the *Calthion* showed the highest median of all communities studied), but deep enough to allow the upper soil layers to become aerated during the growing season which is required for the development and persistence of a *Calthion* (Zuidhoff *et al.* 1996). Nonetheless, the *Calthion* soils remained relatively moist in summer and the average *highest* pF values were calculated to be 2.7 or less for most plots (but 3.5 in one case; Fig. 2). With moisture contents expressed on a volume-wise basis, the *Calthion* demonstrated the highest medians of all communities studied. Average, as well as highest and lowest contents, were significantly higher than in any other community studied, except the *Triglochino-Agrostietum*. Seasonal differences in moisture content were among the lowest in our entire data (not in Figs).

The soils involved were generally peaty or peats, with organic matter contents ranging from 18% for the atypical plot up to 41% (Fig. 4). The soils classify as peaty sand (the atypical plot), peaty clay, clayey peat and peat. In one case, however, the soil was a humus-rich, moderately heavy clay (almost heavy clay as 49% of the mineral components were smaller than 2μ).

Soil acidity was generally moderately acid (pH-$CaCl_2$ between 5 and 6; Fig. 2), in one case only weakly acid (6.3). The pH of the atypical ruderalized plot was strongly acid (pH 4.6). The pH range is in general agreement with the ranges presented by Zuidhoff *et al.* (1996) for the *Lychnido-Hypericetum* and the *Ranunculo-Senecionetum*. The $CaCO_3$ contents are low, or $CaCO_3$ is absent (Fig. 4).

The average annual N mineralization was very low, ranging from 1.8 to 21 kg N ha^{-1} yr^{-1}. Only the atypical plot showed a moderately high mineralization rate (63 kg ha^{-1} yr^{-1}). The very low values are in accordance with the very low values reported by Ellenberg (1977) for non-fertilized meadows on wet soils, although the actual syntaxa involved do not exactly correspond to the *Calthion*. The values are, however, much lower then the values measured in an undrained *Calthion* by Grootjans *et al.* (1985) for which the three-year average was 60 kg N ha^{-1} yr^{-1}. Also the pools of available N, P and K were relatively low to very low. Compared to other grasslands (heath and pioneer syntaxa excluded), especially the amount of available K is low. Average annual aboveground production, however, was intermediate to high (4.6 to 8.4 ton ha^{-1} yr^{-1}; Fig. 7). The atypical (ruderalized) plot had a high to very high productivity (10.7 ton ha^{-1} yr^{-1}), in accordance with its higher N mineralization. These production levels suggest a better nutrient availability than indicated by the soil measurements. Probably a large part of the nutrients in the *Calthion* is provided by the groundwater (rheotrophy). Also Zuidhoff *et al.* (1996) describe *Calthion* communities as often depending on mineral-rich (and base-rich) groundwater. The CEC was the only studied soil nutrient availability variable of which the values measured in the *Calthion* may be described as intermediate instead of low (Fig. 3). The CEC in the clay plot was very high.

The relative tissue nutrient composition (Fig. 6: community 5) indicates that in some plots no particular macronutrient is likely to be limiting growth (co-limitation by all three), and that others may experience a slight limitation by N and/or K. Of all the syntaxa studied, the *Calthion* is most similar to the communities involved in the review of tissue N:P ratios by Koerselman & Meuleman (1996). If the critical N:P ratios suggested in their study are applied (≤ 14 *vs.* ≥ 16), N limitation would be indicated for all *Calthion* plots.

All plots were cut once or twice per year, typically with removal of the cuttings. Only at the ruderalized plot the cuttings were not removed. Light machinery was generally needed as ordinary machinery would damage the sward. Probably for much the same reason, the *Calthion* is sensitive to grazing and develops best under a management purely consisting of hay-making (Zuidhoff *et al.* 1996).

The ecology of the atypical, slightly ruderalized plot suggests that too low a groundwater level may be associated with enhanced N mineralization and increased productivity (Grootjans *et al.* 1985). This most likely causes the decline of the typical *Calthion* character and will induce ruderalization and/or succession toward another syntaxon, a process accelerated further if cuttings are not removed.

FRAGMENTARY *TRIGLOCHINO-AGROSTIETUM STOLONIFERAE*, AND *RANUNCULO-ALOPECURETUM GENICULATI*

Like the previous grasslands, the studied *Lolio-Potentillion* grasslands are groundwater-dependent (Fig. 2). In winter, groundwater was at the surface, or the sites were inundated for long periods. Groundwater levels were still very high in spring (-6 to -41 cm). These winter and spring levels are rather similar to those encountered in the *Calthion*. The two *Lolio-Potentillion* associations differed strongly as far as the summer groundwater level is concerned (Fig. 2). In the *Triglochino-Agrostietum*, the average lowest groundwater levels remain between -14 and -67 cm which is still fairly similar to the situation in the *Calthion* (though in the *Calthion* the median is 15 to 20 cm higher). In the *Ranunculo-Alopecuretum*, however, annual groundwater fluctuations were significantly larger than in any other grassland community studied (up to 136 cm) and the average lowest groundwater levels ranged from -67 to -135 cm. Consequently, *Ranunculo-Alopecuretum* soils may dry out considerably during summer and the calculated average *highest* pF values approached the wilting point in some cases. *Triglochino-Agrostietum* soils on the other hand, were permanently wet (see average highest pF: Fig. 2). Soil moisture contents in the *Triglochino-Agrostietum* were among the highest in our data (together with the *Calthion* and the *Valeriano-Filipenduletum* plots). Seasonal differences in moisture content (not in Figs) were among the lowest.

The soil types involved also differed between the two associations. In the *Triglochino-Agrostietum*, soils differed from moderately to very humic sands (or very light "zavel" soils), to peaty clay and clayey peat, to peat. It should be noted that the organic matter contents presented in Fig. 4 concern an average over the upper 10 cm of the soil. One *Triglochino-Agrostietum* plot was situated on a deep peat, but the other plots of this association only exhibited a peaty top-layer of varying depth. In some cases this peaty top layer was less than 10 cm thick, thus leading to the somewhat misleading (averaged) characterization 'moderately to very humic' for the entire upper 10 cm. For the *Ranunculo-Alopecuretum*, all soils were classified as heavy "zavel" to moderately heavy clay (Fig. 5: community 7). At two plots the soils very nearly classified as heavy clay. *Ranunculo-Alopecuretum* soils were significantly heavier than the soil at any other groundwater-dependent community studied. They were generally humus-rich (4.8 to 6.0% organic matter; Fig. 4). One plot was very humic (10%); this concerned the one *Ranunculo-Alopecuretum* site where cuttings were not removed (due to the use of a flail mower).

Soil acidity and $CaCO_3$ content in both associations were significantly higher than in any other unshaded, groundwater-dependent community studied ($p<0.01$; Figs 2 & 4). The pH in the two associations was comparable (pH-$CaCl_2$ generally 6.5 to 7.5), and may be described as weakly acid to weakly basic, or neutral. However, Sýkora *et al.* (1996) reported the *Triglochino-Agrostietum* to occur under moderately acid conditions. This was not the case for any of our plots. Apparently, the mesotrophic nature of the soil (see below) is of more importance for this syntaxon than soil acidity. Only for a *Ranunculo-Alopecuretum* plot (the very humic plot where cuttings are not removed) the soil was moderately acid (pH-$CaCl_2$ 5.3). Similar to the situation for soil pH, $CaCO_3$ contents were comparable in both associations (ranging from 0.17 to 8.1%).

The species composition of some *Triglochino-Agrostietum* sites indicate slightly brackish conditions. Two plots clearly belong to the *juncetosum gerardi* subassociation, characterized by the salt-marsh plants *Juncus gerardi* and *Carex distans*. Several others occurred in regions where the nearby surface water and groundwater are known to be slightly brackish. At all *Ranunculo-Alopecuretum* sites studied water conditions were most probably fresh, since these were situated far away from known brackish situations.

In both associations, N mineralization rates were generally low, as was also the case for the *Calthion* (Fig. 2). Median mineralization rates in these three syntaxa were lower than in any other community studied. If the heathland and pioneer syntaxa are omitted, this also holds for the soil available N pool. Mineralization rates were significantly lower in the *Triglochino-Agrostietum* (1.4 to 16 kg N ha^{-1} yr^{-1}; median 9.3) than in the *Ranunculo-Alopecuretum* (3.3 to 50 kg ha^{-1} yr^{-1}; median 23). This difference is also reflected by the C:N ratios, which were significantly lower in the *Ranunculo-Alopecuretum* (9.4 to 12.8) than in the *Triglochino-Agrostietum* (generally between 14 and 19, but 10.3 for one plot). A similar difference was present for the C:P ratios, ranging from 33 to 63 for the *Ranunculo-Alopecuretum* and from 124 to 220 for the *Triglochino-Agrostietum*, suggesting lower mineralization rates also for P in the *Triglochino-Agrostietum*. These differences are probably related to the differences in moisture conditions. Moisture differences are most likely also responsible for the significant difference in nitrification degree ($p<0.01$; Fig. 3). Whereas generally only a small fraction of the mineral N pool was available as NO_3 in the *Triglochino-Agrostietum* (0.11 to 0.33; median 0.16), these fractions ranged from 0.28 to 0.54 (median 0.49) in the *Ranunculo-Alopecuretum.* The median value in the *Ranunculo-Alopecuretum* is higher than that in any other unshaded community. A further significant difference between the two associations was present for the CEC ($p<0.01$; Fig. 3). Whereas the CEC for the *Triglochino-Agrostietum* was relatively low to intermediate (63 to 202 kmol + ha^{-1}), it was high to very high for the *Ranunculo-Alopecuretum* (generally more than 335 kmol + ha^{-1}). The CEC values measured for the *Ranunculo-Alopecuretum* were among the highest in our entire data. Like the high value at one of the *Calthion* plots, these high CEC values are most likely associated with the heavy soils involved at the *Ranunculo-Alopecuretum* sites (Figs 4 and 5). The amounts of available P were very low in both associations (less than 0.34 kg P ha^{-1}; Fig. 3). Amounts of available K were also low in both syntaxa (19 to 47 kg K ha^{-1} in general, but up to 83 kg ha^{-1} for one *Ranunculo-Alopecuretum* plot).

In line with the differences in mineralization, nitrification degree, and CEC, the aboveground productivity was significantly lower in the *Triglochino-Agrostietum* (interquartile range 1.7 to 4.4 ton ha^{-1} yr^{-1}) than in the *Ranunculo-Alopecuretum* (interquartile range 4.6 to 5.4 ton ha^{-1} yr^{-1}). Aboveground production in the *Triglochino-Agrostietum* was even significantly lower than that in any other unshaded, groundwater-dependent grassland community studied. Yet, both *Lolio-Potentillion* associations exhibited a large range in productivities (Fig. 7) and in both syntaxa a site was present with very high productivity (> 10 ton ha^{-1} yr^{-1}). Such productivity levels are higher than would be expected from the relatively low N mineralization rates and the low amounts of soil available P and K. As was assumed for *Calthion* and *Valeriano-Filipenduletum* plots, a large part of the nutrients is probably provided by groundwater or by surface water.

Tissue nutrient concentrations revealed another clear difference between the two associations. The absolute concentrations for N and P were significantly lower in the *Triglochino-Agrostietum* than in the *Ranunculo-Alopecuretum* ($p<0.01$). The relative tissue nutrient composition shows a similar difference; whereas *Triglochino-Agrostietum* biomass appeared to be relatively low in N and/or P (Fig. 6: community 6), *Ranunculo-Alopecuretum* biomass (community 7) appeared low in N or low in N and K (but relatively high in P). This suggests that the two associations tend to be limited by different nutrients: the *Triglochino-Agrostietum* by P, N+P, or N with a tendency toward P co-limitation; the *Ranunculo-Alopecuretum* by N+K, or N with a tendency toward K co-limitation (but definitely not by P).

Both syntaxa were mown once or twice per year. The *Ranunculo-Alopecuretum* was generally cut twice and the cuttings were removed except in one case where the cuttings were left in the field (leading to a very high productivity but a low number of species). The *Triglochino-Agrostietum* was generally cut once if productivity was low, twice if productivity was high. The cuttings were generally removed as well, although sometimes they were left in the field in an effort to avoid extra damage to the sward. For *Triglochino-Agrostietum* management, the use of light machinery should be preferred instead of choosing to leave the cuttings unremoved.

The synecology of the *Triglochino-Agrostietum* may be noted to resemble that of the *Calthion* considerably. The two syntaxa attract attention because of their remarkably low mineralization rates (median values around 10 kg N ha^{-1} yr^{-1}), their high summer groundwater levels, their highly organic (peaty) soils, and the very high moisture contents with relatively little variation between summer and winter. Within our soil data, only pH and the $CaCO_3$ content differed significantly between the two, with higher values occurring in the *Triglochino-Agrostietum*. Aboveground production was significantly lower in the *Triglochino-Agrostietum*, although the range of production figures was large and some very productive *Triglochino-Agrostietum* sites were present. Some indication exists that the two syntaxa may also differ with respect to the growth-limiting nutrients. Whereas the *Calthion* is probably subject to some N and/or K limitation, the *Triglochino-Agrostietum* appears to be N and/or P limited, and is not likely to be limited by K (Fig. 6). Also the tissue N and P concentrations were significantly lower in the *Triglochino-Agrostietum* than in the *Calthion* ($p<0.01$).

Sýkora *et al.* (1996) reported that the *Triglochino-Agrostietum* is not a hay-making association, and generally exists under low-intensity grazing. Hay-making instead of grazing may cause the *Triglochino-Agrostietum* to develop toward a *Calthion*. Since all our *Triglochino-Agrostietum* plots were mown and not grazed, this may constitute an additional reason why (syntaxonomically) the borderline between *Triglochino-Agrostietum* and *Calthion* is not always very clear in our material. Two of the *Triglochino-Agrostietum* plots and one *Calthion* plot may perhaps be considered borderline cases.

ARRHENATHERETUM ELATIORIS (AFFINITY TO *TYPICUM*, *MEDICAGINITOSUM* AND/OR *LUZULETOSUM*)

This community concerns *Arrhenatheretum* stands which - although they do not clearly represent a particular subassociation - bear some resemblance or affinity to the *typicum*, the *medicaginitosum* and/or the *luzuletosum* subassociation. We will refer to this community simply as *Arrhenatheretum*. Its 5 plots show little influence of the *Trifolio-*

Geranietea, contrary to 5 other plots belonging to a specific form of the *Arrhenatheretum elatioris festucetosum arundinaceae* subassociation which is therefore treated as a separate community (see below). In cases where the plots of both communities are considered together we will explicitly refer to: *Arrhentheretum sensu lato*.

Hay-communities belonging to the *Arrhenatheretum* can exist entirely independent of the groundwater. Groundwater levels were well below -200 cm during the entire year (Fig. 2). The association is known to be sensitive to flooding during the growing season, and characteristic species may already disappear when the site is flooded for more than 10 to 20 days in the growing season (Sýkora 1983, 1984; Sýkora *et al.* 1988; Zuidhoff *et al.* 1996). The soils were relatively dry; the average highest pF in summer ranged from 3.3 to 4.9. These values were significantly higher than at the *Ranunculo-Alopecuretum* where the upper soil layers also dried out considerably during summer. The two *Arrhenatheretum* sites with the highest pF values (above the wilting point) were those showing most affiliation with the *luzuletosum* subassociation. Also Zuidhoff *et al.* (1996) reported that this subassociation is confined to drier locations than the *typicum* (although this may also hold for the *medicaginitosum*).

The soil types involved were among the heaviest encountered in this study, and concerned light to heavy "zavel" soils, to light clays or heavy loams (Fig. 5). The heaviest example (44% particles $<16\mu$) was the plot showing the strongest resemblance to the *typicum* subassociation, which was described by Zuidhoff *et al.* (1996) as occurring on relatively heavy soils. However, one of the two plots resembling the *luzuletosum* was also situated on a relatively heavy soil (32% particles $<16\mu$; 17% $<2\mu$), whereas Zuidhoff *et al.* (1996) mentioned this subassociation as occurring at a low clay contents compared to the others.

The encountered soils were generally humus-rich (4.3 to 5.3% organic matter; Fig. 4), one was only moderately humic (3.1%). Particularly the heavier examples of these soils have the potential to hold moisture relatively well, suggesting that during large parts of the year the vegetation will not suffer moisture shortage. The average *lowest* pF values (not in Figs) were found to be around field capacity or even lower. It is the capacity to withstand much drier conditions during lengthy warm and dry periods which is characteristic for the studied *Arrhenatheretum* sites.

Soil acidity and calcium content differed remarkably within the community. A clear division appeared to be present between the plots most resembling the *luzuletosum* (pH-$CaCl_2$ 4.6 and 5.0; no $CaCO_3$) and the other plots, occurring on weakly basic, calcium containing soils (pH-$CaCl_2$ 7.3 to 7.5; $CaCO_3$ 1.2 to 5.8%). Zuidhoff *et al.* (1996) also maintained that the *luzuletosum* generally occurs on less basic soils than the other subassociations, but whereas they labelled the soils involved as weakly acid to neutral, the *luzuletosum* soils in our study classify as strongly acid (bordering moderately acid in one case).

The average annual N-mineralization was generally moderate (interquartile range: 53 to 80 kg N ha^{-1} yr^{-1}), but in one case it was as low as 37 and in another as high as 107 kg ha^{-1} yr^{-1} (Fig. 2). These values are significantly higher than those in the *Calthion*, the *Triglochino-Agrostietum*, and the *Ranunculo-Alopecuretum* ($p = 0.01$). The amounts of available N, P and K (Fig. 3) were not particularly high or low, and little differentiation between subassociations could be discerned. The CEC (Fig. 3), however, was highest for the plot most resembling the *typicum* subassociation which is thought to be associated to slightly more nutrient-rich situations than the others (Zuidhoff *et al.* 1996). The CEC was lowest for the plots most resembling the *luzuletosum* which is thought to be associated with relatively nutrient poor situations. Probably due to the low soil pH, also the nitrification degree was relatively low at the two *luzuletosum* plots (Fig. 3). The C:N ratio was highest for these two plots.

The productivity of the *Arrhenatheretum* plots varied considerably, from low (2.2) to high (9.9 ton ha^{-1} yr^{-1}; Fig. 7). The encountered range is much wider than the approximate range of 4 to 6 ton suggested by Zuidhoff *et al.* (1996). Nevertheless, the interquartile range of the present data was indeed situated between 4 and 6 ton ha^{-1} yr^{-1}. The median (5.6 ton) was higher than that in any other unshaded, groundwater-independent community studied. The lowest aboveground productivities coincide with the two *luzuletosum* plots (2.2 and 4.3 ton ha^{-1} yr^{-1}).

The relative tissue nutrient compositions indicate that the *Arrhenatheretum* sites are possibly limited by N alone or by N in combination with K (Fig. 6: community 8). However, it may be assumed that also moisture plays a limiting role.

With regard to the ecology of individual subassociations, our data only allow (cautious) statements regarding the *luzuletosum*. We surmise that the most important ecological characteristics of this subassociation are a relatively low soil pH and the absence of $CaCO_3$. Also moisture content in summer is relatively low, CEC is low, nitrification degree is low, C:N ratio is high, and productivity low. A lower fraction of fine soil particles as mentioned by Zuidhoff *et al.* (1996) appears not to be imperative.

The *Arrhenatheretum* is a typical hay-making community. The plots were usually mown twice per year, or (when productivity was low) only once in August. Cuttings were always removed.

ARRHENATHERETUM ELATIORIS FESTUCETOSUM ARUNDINACEAE, AND *MESOBROMION ERECTI* TRUNK COMMUNITY

The sites belonging to these grassland syntaxa were all located in the south of the country, in calcareous (marl) regions. Partly because of this, the plots belonging to these two communities show a considerable syntaxonomic resemblance (Fig. 1). Both contain a substantial *Festuco-Brometea* element and a notable *Trifolio-Geranietea* influence (mostly *Rubo-Origanetum* species). The studied *Arrhenatheretum festucetosum* sites are more or less related to the *Rubo-Origanetum typicum.* They were of a slightly ruderalized nature, not only compared to the *Mesobromion* but also when compared to other *Arrhenatheretum* sites (previous community)

One of the *Mesobromion* plots needs special attention. This concerns the site omitted during discriminant analysis since it appeared to be transitional between a *Mesobromion* and an *Arrhenatherion* (due to relatively large *Molinio-Arrhenatheretea* and *Arrhenatherion* elements, and a relatively small *Trifolio-Geranietea* element). This is most probably due to the $CaCO_3$ content at the site, which was exceptionally low compared to the 'typical' *Mesobromion* plots. As was done for one of the *Calthion* sites, environmental values for this *Mesobromion* plot which lie outside the interquartile range were connected to the box by a dotted line in the boxplots. It may be questioned whether these values are representative of the ecology of a true *Mesobromion.*

As already mentioned, both the *Arrhenatheretum festucetosum* and the *Mesobromion* plots typically occurred on very calcareous soils. The amount of $CaCO_3$ in the upper 10 cm soil was 7.5 to 37% for the *Arrhenatheretum festucetosum* plots, and 37 to 65% for the true *Mesobromion* plots (Fig. 4; dotted lines omitted). This is significantly higher than in any other community studied (p=0.01). The high $CaCO_3$ values are partly caused by the shallowness of the soils involved. The exact soil depth is often arbitrary and depends on where one draws the border between 'soil with large chunks of marl' and 'marl bedrock', but soil depth could frequently be considered less than 10 cm, especially at the *Mesobromion* sites. The high amounts of calcium naturally cause high pH levels of the soils. pH-$CaCl_2$ in both syntaxa was 7.4 or above (except in the borderline *Mesobromion* plot where it was 7.3).

When the blocks of marl within the upper 10 cm of the soil are disregarded, the remaining soil can often be classified as (aeolic) clay. To avoid confusion, however, these soils have not been plotted in Fig. 5. In such a diagram the $CaCO_3$ would need to be omitted, whereas the large amounts of $CaCO_3$ (and the implied shallowness of soils) should be considered the prime characteristic of the two syntaxa with major ecological consequences. The amounts presented in Fig. 4 for the two syntaxa should be interpreted taking the $CaCO_3$ amounts into account. For instance, the soils classify as humus-rich to very humus rich (average of the upper 10 cm), even though a large part of the upper 10 cm consists of $CaCO_3$. Nonetheless, these organic matter contents were higher than in any other unshaded, groundwater-independent community. Even the individual organic matter contents were all higher than those in the previous community (*Arrhenatheretum* stands with no affinity to the *festucetosum* subassociation), although this difference was not significant in an analysis of variance including all the studied communities.

The *Mesobromion* and the *Arrhenatheretum festucetosum* are entirely groundwater-independent (Fig. 2). The average highest pF values (in summer) were particularly high at the true *Mesobromion* sites; all values were above the wilting point (Fig. 2). The median value in the *Mesobromion* is higher than that in any other community studied, and values are significantly higher than in any other community except the *Phleo-Tortuletum*. For the *Arrhenatheretum festucetosum* the average highest pF values are significantly lower, but still very high. They lie around the wilting point, comparable to the values reached for the *Arrhenatheretum* sites resembling the *luzuletosum*.

Mineralization in the *Arrhenatheretum festucetosum* was moderate (55 to 95 kg N ha^{-1} yr^{-1}); generally slightly higher than in the previous *Arrhenatheretum* community (median 75 *versus* 68 kg N). For the *Arrhenatheretum sensu lato* (communities 8 and 9 together), N mineralization was higher than in any other groundwater-independent community studied. In the *Mesobromion*, N mineralization was significantly lower (even with the borderline plot included). Values ranged from 19 to 62 kg N ha^{-1} yr^{-1} (borderline plot excluded), with 25 as the median value. This median is within the range of mineralization values reported by Ellenberg (1977; different method) for dry grasslands on calcareous soils.

Both the *Arrhenatheretum festucetosum* and the *Mesobromion* tended to have higher amounts of available N, P and K, and higher CEC values than the *Arrhenatheretum* community discussed before (Fig. 3). This especially holds for the *Arrhenatheretum festucetosum*, in agreement with its slightly ruderalized nature. Here, the amounts of available N, P and K were significantly higher than those in the previous *Arrhenatheretum* community (lacking resemblance to the *festucetosum*); for available P the median was even higher than that in any other unshaded community studied (1.22 kg P ha^{-1}).

The *Arrhenatheretum festucetosum* and the *Mesobromion* differed significantly in nitrification degree (p=0.01; Fig. 3). Whereas this degree was moderate in the *Arrhenatheretum festucetosum* (0.28 to 0.41), it was remarkably low in the *Mesobromion* (0.11 to 0.26). Such low levels are in conflict with the general notion that ammonium is rapidly transformed into nitrate on basic soils (*e.g.* Runge 1983; Kinzel 1983). They are possibly caused by the low availability of water, hampering the nitrification process (Runge 1983). Whatever the reason, low nitrification degrees in the *Mesobromion* are in conflict with the general belief that many species characteristic of limestone prefer nitrate instead of ammonium (see Schaminée & Willems 1996).

Productivity was generally lower than that in the previously discussed *Arrhenatheretum* (Fig. 7). For the *Mesobromion* this difference is significant ($p=0.01$) with production levels ranging from 1.0 to 2.9 ton ha^{-1} yr^{-1} (borderline plot 4.3). Productivity in the *Arrhenatheretum festucetosum* was between 2.6 and 4.7 ton ha^{-1} yr^{-1}. Also the tissue concentrations of N, P and K in the two communities were significantly lower ($p=0.01$; not in Figs) than those in the previous *Arrhenatheretum* community.

The relative tissue nutrient composition indicates that the two syntaxa tend toward a slight P limitation (Fig. 6: communities 9 and M), in contrast to the *Arrhenatheretum* (community 8). The true *Mesobromion* (community M) is likely to experience a slight co-limitation by N as well. Limitation by P is not unexpected in communities on calcareous soils, as the availability of phosphate is reduced due to the formation of insoluble calcium-phosphates (Scheffer *et al.* 1989; Tyler 1992). However, the amounts of 'available' P were relatively high in both syntaxa. Possibly the P measured as being 'available' cannot be used by the vegetation completely at high soil pH. Measured available P comprises different forms (H_xPO_4 with x = 0 to 3). Schachtman *et al.* (1998) suggest that P is taken up only in the monovalent form ($H_2PO_4^-$), based on many studies showing that P uptake rate is highest between pH 5.0 and 6.0 where the monovalent form dominates. However, moisture shortage may be a more important limiting factor than shortage of nutrients. If we consider the very high summer pF values, the shallowness of the soils involved, and the fact that the plots of the two syntaxa were frequently situated on south or west facing slopes (increasing the intensity of solar radiation), it may be assumed that nutrients only play a secondary role in limiting vegetation growth.

Management at both syntaxa consisted of mowing once per year in late summer or autumn. In the *Mesobromion* the cuttings were removed, in one *Arrhenatheretum festucetosum* plot this was not the case.

FRAGMENTARY *PHLEO-TORTULETUM RURALIFORMIS*

All plots belonging to this pioneer association were situated in sand-dune areas near the west coast, where the sand is relatively calcium-rich compared to the sand-dunes in the north-west and northern part of the country. The soils were generally classified as very humus-poor to moderately humic, very loam-poor sands (Figs 4 & 5), and hardly any soil development was present. At one plot the soil could be considered a light "zavel", due to contamination with heavy soil used during road construction. This plot was the most fragmentary developed plot from a syntaxonomical point of view, and also the discriminant analysis (ecological point of view) generally misclassified this plot unless the jackknife procedure was omitted. We can thus consider the relatively high amount of fine particles in this plot (Figs 4 & 5) to be atypical for the *Phleo-Tortuletum*.

The association exists entirely independent of the groundwater (Fig. 2). The average highest pF values in summer were generally above the wilting point, comparable to those in the *Mesobromion*. However, when absolute amounts of moisture are considered (not in Figs), the average lowest amounts (summer) appear to be significantly lower than in the *Mesobromion* ($p=0.01$), ranging from 1.1 to 2.8% only (volume based; atypical plot omitted). The median is lower than that of any other community studied. Also the average highest moisture contents (winter) were among the lowest in this study (10.4 to 18.2%). The very low moisture values in combination with the very sandy and humus-poor nature of the soils, suggest that moisture content fluctuates heavily and within relatively short periods. The *Phleo-Tortuletum* also is the syntaxon where the plots showed the largest relative difference between the average highest and the average lowest moisture content. Microclimate was not studied, but the combination of low moisture contents, sandy soils, and low standing crop, creates a condition susceptible to the regular occurrence of very high surface temperatures (as reported by Boerboom 1964; see also Weeda *et al.* 1996).

The soils were moderately calcium-rich, with $CaCO_3$ contents ranging from 1.1 to 2.7% (Fig. 4). Soil pH is correspondingly high; pH-$CaCl_2$ ranged from 7.1 to 7.3 (Fig. 2).

N mineralization was low to moderate (Fig. 2) and ranged from 24 to 68 kg N ha^{-1} yr^{-1}. The higher values are perhaps unexpected, given the low productivity of this community. Apparently, considerable N mineralization can take place during the (often short) periods when moisture content does not limit this process. Rapid warming of the soil, due to the open vegetation and the sandy and relatively dry nature of the soil, may play a role as well. In addition, the *Phleo-Tortuletum* sites were grazed by rabbits and it is conceivable that the supply of faeces and the slight disturbances caused by these animals may enhance the mineralization to levels higher than expected (see also Weeda *et al.* 1996). The nitrification degree was moderately high (0.30 to 0.50; Fig. 3); the median was higher than in any other unshaded, groundwater-independent community. These moderately high values might have been expected considering the high soil pH, but they are in contrast to the low levels in the *Mesobromion* plots with correspondingly high soil pH and pF values. Omitting the atypical *Phleo-Tortuletum* plot, amounts of available K were among the lowest encountered in this study, and also the CEC was low (Fig. 3). In both cases this may be due to the very low amounts of fine particles in these sandy soils. The available amounts of N and P were low to intermediate (Fig. 3). Whereas for N these amounts are significantly lower than those at the *Arrhenatheretum* (*sensu lato*) and *Mesobromion* sites, for P these amounts are similar. This is reflected in the remarkably low available N:P ratio (Fig. 3; lower than in any other unshaded community), indicating a relative abundance of P. A comparable situation may be discerned for the soil total N and P amounts (Fig. 4). Whereas total N was low, the amounts of total P were higher than would be expected given the low organic matter contents.

The productivity of the plots was among the lowest encountered in this study (0.8 to 1.1 ton ha^{-1} yr^{-1}, measured as peak standing crop in exclosures; Fig. 7). The annual aboveground accumulation of N was two to three times smaller than the annual N mineralization. This suggests that N availability is not the limiting factor, and that part of the N mineralized is leached from the soil. Although productivity was low, the tissue concentrations for N and P were moderately high (not in Figs). Tissue K was relatively low, however, in agreement with the low amounts of soil available K. From the relative tissue nutrient composition (Fig. 6: community P) it is clear that K is most likely to be the limiting nutrient and that in some cases this limitation may be strong. Apparently, the low amounts of soil available K outweigh the implications of the low soil available N:P ratio. However, we should again be aware that moisture shortage may play an equally important role as nutrient limitation in this association.

Road construction activities in coastal sand-dune areas often create conditions suitable for the development of the *Phleo-Tortuletum,* as long as the sand is moderately calcium-rich, no other soil materials are used in the verges, and no sowing or fertilization is applied. Typical *Phleo-Tortuletum* sites were not managed, but rabbits were present and may serve to maintain the pioneer character of the vegetation through their activities (*e.g.* grazing and digging). In addition, irregular anthropogenic disturbance is often needed to prevent succession towards another syntaxon. Weeda *et al.* (1996) maintained that the light wind erosion induced by slight disturbances ensure a continued supply of relatively calcium-rich material. This prevents acidification and also impedes litter accumulation through stimulated decomposition.

SPERGULO-CORYNEPHORETUM

The *Spergulo-Corynephoretum* sites were situated in pleistocene sand regions with (remnants of) a dry heathland landscape, on locations where the soils had been heavily disturbed during the construction of the road. The pioneer association may be considered the acid counterpart of the *Phleo-Tortuletum*. The soils were again classified as humus-poor to very humus-poor, very loam-poor sands (Figs 4 & 5), and again hardly any soil development was present. Organic matter content was lower than in any other community (only the difference with the *Phleo-Tortuletum* was not significant). Also the amount of fine particles was generally lower than in any other syntaxon, and the amount of sand higher.

As in the *Phleo-Tortuletum*, the plots were entirely independent of the groundwater level (Fig. 2) and the average highest pF values in summer were generally around the wilting point. The average lowest amounts of moisture (not in Figs) were only slightly higher than in the previous association, ranging from 2.1 to 4.3% (volume based). Concerning the average highest moisture contents (winter), the lowest value encountered in the present study occurred in this association (range: 9.9 to 14.2%). This causes the average lowest pF (winter) to show the highest median encountered; the obtained values (2.6 to 2.9) were significantly higher than those in any other community except the *Phleo-Tortuletum*. As in the *Phleo-Tortuletum*, we may assume soil moisture contents to fluctuate strongly within relatively short intervals. Also, the temperature of the soil surface fluctuates strongly and very high temperatures occur frequently (Stoutjesdijk 1959). The capacity of the *Spergulo-Corynephoretum* soils to hold moisture may be limited further due to a minute coating of soil particles by algae or organic material (Weeda *et al.* 1996; but see Pluis 1994).

In sharp contrast to the *Phleo-Tortuletum*, the soils were strongly acid to very strongly acid, and pH was among the lowest encountered in this study (pH-$CaCl_2$ ranging from 3.9 to 4.3; Fig. 2). $CaCO_3$ was always entirely absent (Fig. 4).

N mineralization was low (23 to 46 kg N ha^{-1} yr^{-1}; Fig. 2), with the median near 30, which is lower than in the *Phleo-Tortuletum* (though not significantly). Ellenberg (1977) reported similar low values (albeit slightly lower, probably due to methodological differences). The *Spergulo-Corynephoretum* is generally considered to be confined to nutrient-poor conditions (Weeda *et al.* 1996) which is confirmed by the low mineralization rate encountered and the fact that (contrary to some of the groundwater-dependent syntaxa) no additional N can be obtained from surface-water or groundwater. The nitrification degree is also low (0.12 to 0.30; Fig. 3), but not as low as might have been expected considering the very low soil pH. The values are still significantly higher than those in the two other acid heathland syntaxa discussed below, probably due to the relatively low moisture contents involved. The pools of available N, P and K were very small and the CEC was very low (Fig. 3), in accordance with the nutrient-poor nature expected. Available N and K, and the CEC were especially low, lower than in any other studied community. For K and CEC, the difference with all other communities is significant at $p=0.01$, possibly due partly to the low amounts of fine particles and low organic matter contents. The ratio between available N and P was not exceptionally high or low (Fig. 3). In accordance with the low organic matter content, soil total N and P were also extremely low (Fig. 4)

As in the previous association, biomass production was very low (0.4 to 1.4 ton ha^{-1} yr^{-1}; Fig. 7). Also the tissue nutrient concentrations were relatively low (not in Figs), causing the average annual aboveground accumulations of N, P and K in the *Spergulo-Corynephoretum* to be lower than in any other community studied (not all differences significant). Especially tissue N and (most notably) K concentrations were low. The relative tissue nutrient composition (Fig. 6: community S) suggests K limitation, with or without co-limitation by N. This corresponds with the very small pools of soil available N and (especially) K, mentioned above.

Road construction activities in nutrient-poor pleistocene sand areas often create conditions suitable for the development of this pioneer association, as long as no other soil materials are used in the road verges, and no sowing or fertilization is applied. Typical *Spergulo-Corynephoretum* sites do not need mowing or hay removal since productivity is far to low for this. However, in the absence of irregular disturbances stimulating a light wind erosion (sand-blow) or erosion by rainwater, natural succession may lead to other syntaxa (*Thero-Airion* or *Calluno-Genistion pilosae*).

GENISTO ANGLICAE-CALLUNETUM

This association embodies dry heathland vegetation, occurring independent of the groundwater. The average highest pF values (summer) ranged from 2.5 to 3.8, but most were around 3.0 (Fig. 2). Compared with the other unshaded, groundwater-independent communities these values are low, but the average lowest pF values in winter (not presented) are higher than in most other communities. Only the two pioneer syntaxa on loose sand discussed above showed higher values for the average lowest (winter) pF. The soils involved were very loam-poor sands (Figs 4 & 5), like in the previous pioneer syntaxa. However, they were generally moderately humic (Fig. 4), which partly explains the somewhat larger moisture contents in summer. Also, there was more soil development. The plots were usually situated on re-developing podzolic soil profiles, showing accumulation of organic matter (and possibly also iron and/or aluminium) in the B-horizont. The original soil profiles were often disturbed during road construction, but in one case the podzolic profile was undisturbed. Usually, the upper few cm of the soil was strongly humic (A1 horizont).

As in the previous association, the soils were strongly acid to very strongly acid. Soil pH was lower than that in any other community studied (pH-$CaCl_2$ 3.7 to 4.2; Fig. 2). Only with the other studied heathland syntaxon (*Ericion*) and the above pioneer association (*Spergulo-Corynephoretum*) was the difference not significant; with the other communities it was significant at $p=0.01$. $CaCO_3$ was entirely absent (Fig. 4).

N mineralization rates were low; 14 to 53 kg N ha^{-1} yr^{-1} with the median at 36 (Fig. 2). These values roughly correspond with the values reported by Ellenberg (1977). Surprisingly, mineralization rates are rather similar to those in the *Spergulo-Corynephoretum* (previous association), the pioneer syntaxon from which the *Genisto-Callunetum* usually develops. Both the average value and the median are only negligibly higher. Possibly the positive effects of the slightly higher organic matter content and moisture content are countered by the slightly lower pH levels, and perhaps by the slightly higher C:N ratios as well (17 to 33 instead of 11 to 30). These factors probably cause the rate of decomposition expressed as the percentage of soil total N annually mineralized to be lower for the *Genisto-Callunetum* (1.6 to 5.9%) than for the *Spergulo-Corynephoretum* (2.1 to 13.7%). Apparently, decomposition is slower in the *Genisto-Callunetum*. Stortelder *et al.* (1996) also reported decomposition in the *Genisto-Callunetum* to be slow. However, it should be noted that the rate of decomposition (when expressed as the percentage of soil total N annually mineralized) is more rapid in the *Genisto-Callunetum* than in all other communities except the two pioneer syntaxa and the two syntaxa of woodland- and hedge-margins. Nevertheless, the C:N ratio is highest of all the syntaxa studied, significantly higher than that in any other community except the *Ericion* and the *Spergulo-Corynephoretum* (not in Figs).

The pool of available (mineral) N was not particularly small (Fig. 3), but contrary to the mineralization of N it was significantly larger than in the previous pioneer association. On the other hand, the levels of soil available P and K were among the lowest encountered in this study, as was the CEC (Fig. 3). The resulting soil available N:P ratio was significantly higher than in any other groundwater-independent community (Fig. 3; $p=0.01$). Nitrification degree was very low, as might be expected given the very low soil pH. Less than 10% of the mineral N was present in the form of NO_3 (7.2 to 9.4%). Only the wet heathland syntaxon (*Ericion*) showed lower values. Also the amounts of soil total N and P were low to very low (Fig. 4). *Genisto-*

Callunetum soils are indeed nutrient poor and acid, as traditionally reported (Stortelder *et al.* 1996).

Annual biomass production and nutrient accumulation could not be measured in the *Genisto-Callunetum* (see sites and measurements section), but on average a value between 1.5 and 2.0 (possibly up to 2.5) ton ha^{-1} yr^{-1} may be assumed. Standing crop mainly depends on the age, and varied between 1.2 and 13.3 ton ha^{-1} (8-10 on average). Tissue nutrient concentrations were very low (not in Figs). Tissue N concentrations were lower only in the *Spergulo-Corynephoretum.* Tissue P and K concentrations were lower than in any other community studied. For tissue K this difference was significant ($p=0.01$), for tissue P too except with the *Ericion.* To some extent, the low tissue concentrations may be due to the relatively large amount of woody material included in the biomass. The tissue N:P ratios suggest the plots to be generally limited by P (Fig. 7). If also the role of K is considered, using the relative tissue nutrient composition (Fig. 6: community G), the plots would appear to be strongly co-limited by K (or perhaps sometimes limited by K only). This is in agreement with the small pools of soil available P and K. It has sometimes been maintained that nutrient limitation shifts during primary succession from N limitation in early successional stages towards P limitation in later stages (*e.g.* Verhoeven *et al.* 1996). As far as only N and P are concerned, this corresponds with the results of the present study when considering the *Spergulo-Corynephoretum* (pioneer vegetation) and the *Genisto-Callunetum* (usually developing from the previous association). Whereas no P limitation is indicated in the *Spergulo-Corynephoretum* (K or N+K limited), a clear P limitation is suggested for the *Genisto-Callunetum* (P or P+K limited). Atmospheric N deposition is often assumed to cause an additional shift towards P limitation in these otherwise nutrient-poor environments (Roem & Berendse 1999; see also Chapter 5). Still, a similar shift could be suspected toward K limitation. This would be in line with the present data, as the *Spergulo-Corynephoretum* and the *Genisto-Callunetum* (both in nutrient-poor environments) both tend toward K (co-)limitation.

Management usually consisted of mowing with removal of the cuttings once every 5 to 10 years. Some sites were not managed. Such sites are expected to turn into forest or woodland communities after some time, unless regular removal of juvenile trees and shrubs is performed to prevent this succession.

ERICION TETRALICIS (TRUNK COMMUNITY AND *LYCOPODIO-RHYNCHOSPORETUM*)

This syntaxon embodies wet heathland and wet grass-heath vegetation. The syntaxon depends on groundwater, but this often concerns 'perched groundwater levels', caused by the stagnation of water on relatively impermeable soil layers. In winter, the apparent groundwater was just above or below the surface in most cases, but the variation included inundated plots to levels around -80 cm (Fig. 2). Actual inundation was confined to the two *Lycopodio-Rhynchosporetum* plots. Soils were generally saturated with moisture in winter, and the lowest pF values (not in Figs) were well below field capacity for all plots. The average apparent groundwater levels in spring varied between -84 and -24 cm, with the median at -75 cm (Fig. 2). In summer, these levels dropped considerably. Perched groundwater usually disappeared entirely, leaving only the (often deep) true groundwater. In most plots the average lowest levels in summer (Fig. 2) were well below -150 cm, in one case (true groundwater) it remained as high as -110 cm. Still, even in summer perched groundwater levels sometimes occurred temporarily after heavy rain. The *Ericion* was nevertheless the syntaxon with the largest difference between the lowest summer and highest winter levels. Despite the low values for the lowest groundwater levels in summer, the average highest pF values in summer ranged from 1.8 top 2.6 only (Fig. 2). This would suggest that even after warm and dry periods in summer, moisture content generally remains near field capacity in the *Ericion*.

The upper soil layers consisted of sand, but whereas these classify as loam-poor at the *Ericion* trunk community sites, the sand was very loam-rich at the *Lycopodio-Rhynchosporetum* plots (Fig. 4; Fig. 5: community E). More or less developed podzolic profiles could sometimes be discerned. The upper 10 cm of the soils were moderately humic to humus-rich (Fig. 4). Deeper, an often compact loamy or clayey layer or a layer of boulder-clay was present in all the plots, starting at a depth varying between 34 and 145 cm. When true groundwater levels are deep, the existence of such layers (in undisturbed form) can be considered crucial for the existence of the *Ericion*.

The soils were strongly to very strongly acid (Fig. 2). pH-$CaCl_2$ was usually below 4.5, in one grass-heath plot of relatively atypical nature (large cover of *Juncus acutiflorus* and *Erica tetralix* absent) it was 4.7. The pH in the *Ericion* plots appeared to be negatively correlated with the cover of ericaceous dwarf-shrubs ($r = -0.91$; $p < 0.05$; $n = 6$). This is probably due to the production of litter containing large amounts of humic-acids by the dwarf-shrubs (Stortelder *et al.* 1996).

N mineralization was low to very low; 3.7 to 45 kg N ha^{-1} yr^{-1} with the median at 31 (Fig. 2). Ellenberg (1977; using a different method) reported similar values, ranging from 21 to 30. The low to very low rates encountered in the present study are in accordance with the relatively high soil C:N ratios (18 to 26; not in Figs). Within the *Ericion*, a positive correlation was present between the cover of ericaceous dwarf-shrubs and the soil C:N ratio ($r=0.78$; $p=0.062$; $n=6$), possibly due to a relatively high C:N ratio of ericaceous litter and the negative effects of this litter on soil pH.

The pool of available mineral N was low to intermediate (Fig. 3), with lowest values occurring in the *Lycopodio-Rhynchosporetum*. However, the degree of nitrification was very low to extremely low; only 2.9 to 6.9% of the available N was present in the form of NO_3 (Fig. 3). This was lower than in any other syntaxon; only the difference with the dry heath (*Genisto-Callunetum*) was not significant ($p=0.01$). These very low levels are most probably caused by the combination of a very low soil pH and the prevailing anaerobic conditions during part of the year. The amounts of available P were extremely low as well, only 0.008 to 0.032 kg P ha^{-1} (Fig. 3). This was significantly lower than the values in any other community, dry heath included ($p=0.01$). The result is a very high ratio between soil available N and P. This ratio ranged from 116 to 538 (Fig. 3). This is higher than in any other community; only with the fragmentary *Fritillario-Alopecuretum* was the difference not significant. Contrary to P, the available K levels were significantly higher than in the dry heath, and CEC values were similar (Fig. 3). Nevertheless, also *Ericion* soils can be concluded to be nutrient poor and acid, as usually reported for this syntaxon (Schaminée *et al.* 1995a).

Annual biomass production and nutrient accumulation could not be measured in two of the *Ericion* since these sites were dominated by ericaceous dwarf shrubs and were not managed annually (see also the section: sites and measurements). Standing crop at these sites (depending on the number of years since the last cut) was 6.3 and 6.8 ton ha^{-1}. At the remaining sites (grass-heath and *Lycopodio-Rhynchosporetum*) the average annual production was measured successfully. Values were generally low and varied between 1.4 and 2.6 ton ha^{-1} yr^{-1} (Fig. 7). Similar values (1.0 to 3.0) may be expected for the other *Ericion* sites, although for the slightly atypical plot 4.7 ton was measured. Tissue nutrient concentrations (not in Figs) were relatively low, especially for P where levels were only slightly higher than those in the *Genisto-Callunetum*, but significantly lower than those in the other communities. Tissue N:P ratios suggest the plots to be usually limited by P (Fig. 7). The relative tissue nutrient composition (Fig. 6: community E) suggest the *Ericion* to be limited mostly by P, or by P and K together. Limitation by P is what might be expected given the very low levels of soil available P. As was the case for the *Genisto-Callunetum*, P limitation may be enhanced by atmospheric N deposition in these otherwise poor environments.

Management usually consisted of mowing with removal of the cuttings once every year, or once every 4 to 8 years. The *Lycopodio-Rhynchosporetum* sites were mown annually. This is probably crucial since, together with the winter inundations, this serves to keep the vegetation open enough for the characteristic species. Outside roadside habitats the *Lycopodio-Rhynchosporetum* is generally reported from paths, tracks and other open areas in wet heath (Schaminée *et al.* 1995a). One of the *Ericion* sites was not managed. This site already showed signs of turning into woodland. Regular removal of juvenile trees and shrubs may prevent (or at least slow down) this succession in unmown sites.

HEATH- AND PIONEER SYNTAXA

The two heathland syntaxa together (*Ericion* and *Genisto-Callunetum*) are characterized by their very low nitrification degrees (<10%; Fig. 3). Soil C:N ratios in these syntaxa were higher than in the other syntaxa (not in Figs). P appeared an important element in these syntaxa. Both tissue P concentrations and soil available P tended to be lower than in any of the other syntaxa; tissue P significantly so, soil available P significantly so for the *Ericion* only. In both heathland syntaxa growth would appear to be limited by P (Figs 6 & 7).

The last three syntaxa discussed (*Ericion*, *Genisto-Callunetum*, and *Spergulo-Corynephoretum*) are all part of heathland succession series typical for heathland landscapes, and may also be considered as a group. Their foremost ecological characteristic is the low soil pH compared to the other communities (Fig. 2; only with the *Fritillario-Alopecuretum* communities the difference is not significant). A very low base saturation level is another characteristic of the three syntaxa. Whereas saturation levels were relatively high in the other studied communities and showed only limited differentiation between them, levels were conspicuously lower ($p<0.001$) in the three heath landscape syntaxa. The same is true for the Ca saturation. The absolute amount of exchangeable bases and the absolute amount of exchangeable Ca were also significantly lower than in other communities ($p<0.001$). The same is true for the total calcium amount (consisting of both exchangeable Ca^{2+} and Ca in the form of $CaCO_3$). In addition, soil C:N ratios were higher (not in Figs), CEC was lower (Fig. 3), total amounts of soil P were lower (Fig. 4), and tissue K concentrations were lower (not presented). However, not all the possible differences are significant in these cases.

The last four syntaxa discussed, encompass the studied heath- and pioneer syntaxa (the *Ericion*, *Genisto-Callunetum*, *Spergulo-Corynephoretum*, and *Phleo-Tortuletum*). For these syntaxa, soil total N was lower than in any other community (Fig. 4), and consequently C:N ratios were higher (not in Figs). Organic matter content was generally lower, the amount of fine particles was lower, and consequently the CEC

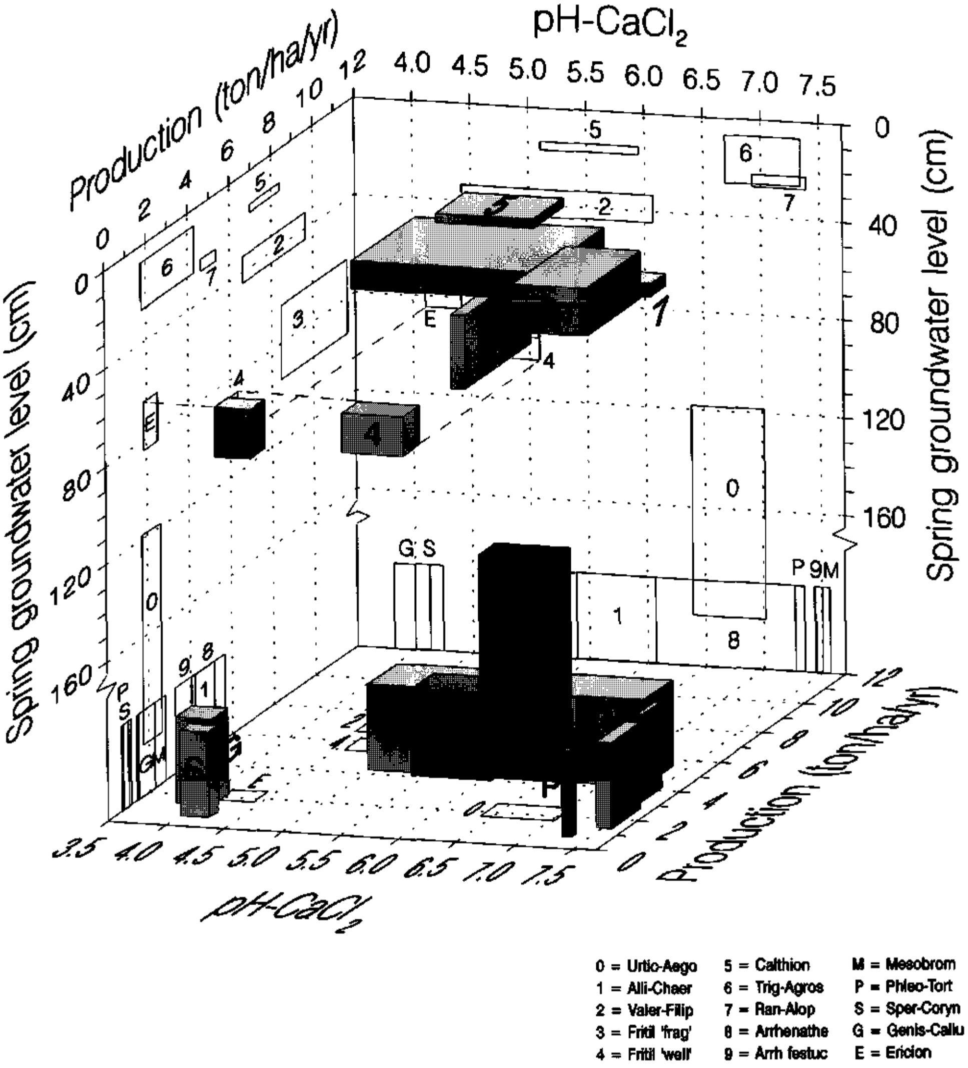

Figure 8. *Eco-diagram. Three dimensional representation of the ecological position of the studied plant communities with respect to: moisture (average spring groundwater level; vertical axis), soil acidity (pH-CaCl$_2$; horizontal axis), and productivity (average annual aboveground production; 'depth'-axis). Plotted are the interquartile ranges of these measured variables. For entirely groundwater-independent communities, low but equal arbitrary groundwater levels are plotted. On each of the side surfaces of the diagram, projections are drawn to facilitate locating the communities. Light condition (a fourth principal ecological factor) is indicated by grey tone: the semi-shaded communities (0 and 1) are presented in a darker shade of grey.*

levels were lower (Figs 3 & 4). Tissue K concentrations were lower than in the other syntaxa. Consequently, biomass production often is likely to be K, K+N or K+P limited, although some may be limited by P only (Fig. 6: communities P, S, G & E). The syntaxa would seem not to be limited by N or N+P.

If we only consider the two pioneer associations (*Spergulo-Corynephoretum* and *Phleo-Tortuletum*), it appears that these may be characterized by lower organic matter contents and lower soil total N amounts than the other syntaxa (Fig. 4). Moisture contents of the loom-poor and humus-poor soils were lower than in any other community. Although the *Mesobromion* showed higher values for the average highest pF in summer (Fig. 2), the pioneer associations showed higher values than any other community for the average lowest pF in winter (not in Figs). Aboveground productivity was lower than in other syntaxa, and growth would seem to be limited by K, or by K and N (Fig. 6: communities S & P).

Synecological overview

For a general ecological understanding, the 8 master factors (measured variables) may be categorized into 4 groups, each representing a fundamental ecological principle. The variable shading intensity stands by itself, as a representation of the fundamental ecological factor 'light'. The groundwater level variables may be considered representations of the factor 'moisture'. Soil pH and the percentage of $CaCO_3$ both represent the soil 'acidity'. The master factors available K, degree of nitrification, and percentage of fine soil particles, are representations of 'nutrient availability'. This, of course, is only a general categorization. For instance, the percentage of $CaCO_3$ (especially when very high) and the percentage of fine particles, are to some extent related to soil moisture and soil nutrient conditions as well.

If we now choose one measured parameter to represent each of the groups, and temporarily disregard the factor light (since most communities were unshaded), we may construct a three dimensional 'eco-diagram' to obtain a general ecological overview of the studied communities. For this purpose, we chose the average groundwater level in spring, the soil pH, and the average annual aboveground biomass production, respectively. Annual aboveground production does not represent nutrient availability only, as it is determined by other ecological factors as well. However, no single measured parameter was considered to better serve its purpose.

The resulting eco-diagram (Fig. 8) summarizes the ecology of the studied communities along the three main axes. For each community, only the interquartile ranges are plotted (*i.e.* the 'boxes' from the boxplots). For entirely groundwater-independent communities (spring groundwater levels always below -150 cm), low but equal, arbitrary levels are plotted. The *Urtico-Aegopodietum* takes an intermediate position. In some of its plots the average spring level was higher than -150 cm whereas in others it was lower (but almost certainly not as low as in most of the entirely groundwater-independent communities).

The inter-quartile ranges of the studied communities appear to be well separated in the eco-diagram. Only the *Alliario-Chaerophylletum* (community 1) is not entirely separated from the others, but this is because the factor light is disregarded. This community (as well as the *Urtico-Aegopodietum*: community 0) occurs under semi-shaded conditions. To incorporate the factor light, the two semi-shaded communities were given a darker shade of grey in Fig. 8. If the factor light could be considered along a fourth axis, full separation would be obtained.

It may be concluded that measured environmental parameters can provide adequate ecological descriptions of plant communities. Even with the eight master factors in this study reduced to a subset of four principal ecological factors, good results were obtained. Using our approach, the ecology of the respective communities can clearly be distinguished.

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3

Effects of delayed hay removal on the nutrient balance of roadside plant communities

Schaffers, A.P., Vesseur, M.C., & Sýkora, K.V. (1998). Effects of delayed hay removal on the nutrient balance of roadside plant communities. *Journal of Applied Ecology* **35**: 349-364.

Effects of delayed hay removal on the nutrient balance of roadside plant communities

Abstract. Mass losses and nutrient losses from fresh roadside cuttings were studied in the field during a 6-week period. Large amounts (up to more than 50%) appear to be lost from the cuttings. The losses were positively related to initial nutrient concentrations during this short-term study. Mass and nitrogen losses were best explained by the initial C:N ratio, phosphorus and potassium losses by the initial phosphorus concentration.

For potassium the losses were particularly large (up to 90%). For this element only, the observed relation between loss rate and initial chemical composition could not be established significantly. It is concluded that potassium is mainly lost by leaching whereas the major nitrogen, phosphorus and mass losses are most probably caused by rapid microbial decomposition of readily-soluble substances.

Using existing data on chemical composition of other roadside cuttings, nutrient losses after different hay removal delay times were modelled for different plant communities. All or most of the losses were assumed to return to the soil system. When soil impoverishment is aimed for, cuttings should be removed within 1 or 2 weeks in most plant communities. If removal is delayed longer, the amounts of nutrients removed will often fall below the annual atmospheric input. In plant communities where annual above-ground production of nitrogen and phosphorus are lower than the annual atmospheric deposition already, rapid removal of the cuttings may be the only way to maintain at least potassium at a limiting level.

The main effect of hay-making on the soil nutrient status most likely consists of a reduction of the potassium availability, at least on sandy soils with a low cation exchange capacity and provided there is little delay in hay removal.

Key-words: *decomposition, mineralization, mowing of grassland, soil impoverishment, vegetation management.*

Introduction

Cutting and hay removal is a common form of management in road verges, as it is in many other grassland ecosystems. Apart from traffic safety aspects and the occasional need for the hay as conserved fodder, the objective usually is to either conserve a particular plant community (Bobbink *et al.* 1987) or to develop more diverse communities (Oomes 1990). The effects of cutting and hay removal are many, e.g. increased carbon allocation to shoots, a change in light regime, creation of gaps and disturbance of the soil. Another important effect is the removal of nutrients (Bakker 1989). As the constant input of nutrients through atmospheric deposition may lead to accumulation in the soil, the removal of nutrients has inevitably become an important tool in counteracting or reversing changes in plant species composition of the vegetation. Removal of cuttings and atmospheric deposition are quantitatively the most important components of the nitrogen balance in unfertilized Dutch grasslands under a management of hay-making (Berendse *et al.* 1994). This is probably also true for other macronutrients such as phosphorus and potassium, at least in industrialized countries with an intensive agriculture where nutrient inputs through atmospheric deposition are high. Soil impoverishment thus can only be achieved when removal of nutrients exceeds atmospheric input.

In agricultural practice cutting aims at producing hay of good quality. As the hay itself is important in these cases, hay-making often takes place during a dry period, and the hay is usually removed within 1 week of cutting. In road verges however (and in many other situations where hay production is not the primary objective), an important concern is often nutrient removal. The vegetation is usually cut during a previously designated period regardless of the weather, and the cuttings are often only removed after a considerable period (sometimes 3 to 4 weeks or even more). Removed cuttings are dumped as waste in many cases.

Although nutrient removal usually is the main concern in nature conservation and roadside management, little attention has been paid to the losses of potentially removable nutrients during the period between cutting and the removal of the sward. Some of the nutrients may well return to the soil by leaching and other decomposition processes prior to hay removal. The extent to which nutrients are lost from fresh cuttings within the first few weeks is largely unknown.

Much experimental work has been done on the decomposition of litter. A large part of this work is on tree or shrub litter (*e.g.* Attiwill 1968; Gosz *et al.* 1973; Staaf 1980; Berg & Ekbohm 1983; Melillo *et al.* 1989; Berg *et al.* 1992) and on litter from heathland communities (Van Vuuren & Van der Eerden 1992; Van Vuuren *et al.* 1993). Few studies have been concerned with the litter of grasses (Bloemhof & Berendse 1995) or herbs (Taylor *et al.* 1989; Rawat & Singh 1995).

Nutrient losses from cut material may be different to losses from litter, especially during the first stage of decomposition. Most of the material is still alive when it is cut and no nutrients have been withdrawn. In plant parts that have died off naturally, some of the nutrients will have been reallocated before abscission, as has often been reported (Goodman & Perkins 1959; Ernst 1975; Morton 1977; Berendse *et al.* 1987b). Dickinson (1984), however, reports no nutrient withdrawal in grassland vegetation. Only a few studies deal with the decomposition of cut material instead of litter (Floate 1970; Tian *et al.* 1992; Bloemhof & Berendse 1995).

Most of the studies mentioned above concern either long-term decomposition (1 year or longer) or decomposition under laboratory conditions (Floate 1970; Taylor *et al.* 1989). Moreover, in all the studies encountered the material was dried and sometimes even ground before the experiment. To our knowledge no work has been done with fresh cut materials in short-term field experiments that would realistically simulate nutrient losses from grassland cuttings waiting to be removed. It has been noted frequently that long-term mass loss curves show a rapid initial decline (Floate 1970; Howard & Howard 1974; Swift *et al.* 1979). This rapid initial mass loss is often ascribed to leaching of substances during the first stages of decomposition.

The objective of the present study is to obtain insight into the amounts of macronutrients lost from *fresh* grassland *cuttings* in the *field* during a relatively *short* period (up to 6 weeks). We determined the factors related to the nutrient losses during this period and quantified the relationships. Using the experimental results we attempt to predict the amounts of nutrients removed in various roadside plant communities for different removal regimes. The calculated removals (outputs) are compared with the inputs through atmospheric deposition. This comparison enables us to predict the changes in the amounts of nutrients in the various ecosystems, as affected by different management regimes.

Methods

Field experiment

The field experiment was carried out at roadside locations situated in the middle and eastern parts of the Netherlands. Seven locations were selected, involving two grassland plant communities: the *Ranunculo-Alopecuretum geniculati* Tüxen 1937 and the *Arrhenatheretum elatioris* Braun 1915. An eighth contrasting location was also selected, involving a grass-heath community belonging to the *Ericion tetralicis* (fragmentary *Lycopodio-Rhynchosporetum albo-fuscae* Paul *ex* Allorge *et* Gaume 1925). On each location, a plot of 1.50 by 0.75 m was established. An overview of the plots, including the plant community to which they belong is given in Table 1. A short characterisation of the plant communities is given in Table 2.

The experiment took place between 24 May and 6 July 1993. At different locations, the starting and ending dates were different. For the seven grassland plots the duration of the experiment was five to six weeks, but that on the grass-heath plot (*Ericion*) lasted only four weeks because its low productivity led to less biomass being available.

Table 1. *Overview of the experimental plots with plot name, plant community name, above-ground biomass (ton dry wt ha^{-1}) at time of cutting (between May 24 and June 8), concentrations of nitrogen, phosphorus and potassium (mg g^{-1} dry wt) and C:N and C:P ratios.*

Plot name	Plant community (all fragmentary or trunk communities)	Bio-mass	N conc.	P conc.	K conc.	C conc.	C:N ratio	C:P ratio
Dodewaard	*Ranunculo-Alopecuretum geniculati*	2.3	17.5	3.0	19.8	421	24.1	140
Nijmegen I	*Ranunculo-Alopecuretum geniculati*	4.8	15.0	2.6	16.8	427	28.4	164
Nijmegen II	*Ranunculo-Alopecuretum geniculati*	1.2	14.7	2.7	16.9	429	29.2	161
Zetten	*Ranunculo-Alopecuretum geniculati*	1.5	20.7	3.6	18.5	425	20.5	118
Rossum west	*Arrhenatheretum elatioris*	2.2	12.7	2.3	12.9	419	33.0	181
Rossum east	*Arrhenatheretum elatioris*	1.0	13.5	1.8	8.1	429	31.9	236
Heerewaarden	*Arrhenatheretum elatioris*	3.3	13.1	2.1	15.8	417	31.8	201
Almelo	*Ericion tetralicis*	0.9	9.0	0.5	3.6	387	42.9	824

Table 2. *Characteristics of the plant communities involved in the experimental study. A short soil description, species with relatively high cover (bold) and some characteristic species (underlined) are presented. Community names follow Schaminée* et al. *(1995, 1996). Species names follow Van der Meijden (1996).*

Ranunculo-Alopecuretum:	Nutrient rich clay soils, extremely wet in winter/spring but very dry in summer. Species: ***Agrostis stolonifera***, ***Ranunculus repens***, ***Holcus lanatus***, ***Alopecurus pratensis***, ***Lolium perenne***, ***Carex hirta***, ***Arrhenatherum elatius***, *Alopecurus geniculatus*, *Potentilla anserina*, *Carex otrubae*.
Arrhenatheretum:	Moderately nutrient rich, moderately moist, loamy soils. Species: ***Arrhenatherum elatius***, ***Trisetum flavescens***, ***Crepis biennis***, ***Festuca rubra***, ***Poa trivialis***, ***Poa pratensis***, ***Achillea millefolium***, *Daucus carota*, *Ranunculus bulbosus*, *Trifolium dubium*, *Leucanthemum vulgare*.
Ericion:	Wet, nutrient poor and acid, sandy soil. Species: ***Molinia caerulea***, ***Holcus lanatus***, ***Carex nigra***, ***Agrostis capillaris***, ***Juncus acutiflorus***, *Erica tetralix*, *Rhynchospora fusca*.

Between May 24 and 8 June the plots were cut at 1 cm above the soil surface. Long stems were reduced to pieces of 10 cm length at most and the material was thoroughly mixed. Half of the fresh cut material of each plot was evenly distributed between 25 litterbags (20 for the grass-heath plot), each measuring 15x15 cm with a mesh size of 1 mm, allowing soil microflora and microfauna and most of the soil mesofauna to enter (Swift *et al.* 1979). The litterbags were returned to the field the same day and were laid out in the plot, evenly spread between the remaining part of the cut material.

At 1 to 2 week intervals during the next 5 to 6 weeks, sets of five litterbags per plot were randomly collected. The first set of litterbags was collected on the day of cutting itself ($t=0$). After collection, the content of each bag was dried at 70 °C during 48 h, weighed and stored for later chemical analysis.

At a weather-station near some of the plots (Herwijnen) 75 mm of rainfall was measured during the 43 days of the experiment (the 30-year average for this period was ±96 mm). Slight differences among plots and between plots and the weather-station could not be avoided. The average air temperature at 1.5 m height was ±16 °C (the 30-year average for this time of year was ±15 °C).

Chemical analysis and initial data handling

The concentration of nitrogen, phosphorus and potassium in each litterbag was determined after digestion with H_2O_2 at 100 °C followed by digestion with concentrated sulphuric acid at 300 °C under the influence of selenium as a catalyst (Walinga *et al.* 1995). Salicylic acid was added to prevent the loss of nitrate. Nitrogen and phosphorus were measured spectrophotometrically using an autoanalyzer (EPOS 5060, Eppendorf, Hamburg, Germany). Potassium was measured using a flame atomic emission spectrometer (ELEX 6361, Eppendorf). Carbon contents were measured in the litterbags at $t=0$ only, using an element analyzer (EA 1108, Fisons Instruments, Rodano/Milan, Italy).

Multiplication of measured concentrations with dry weights yielded an estimate of the amount of each nutrient present in the litterbags. The results will be presented as fractions of the initial amount. Because the true initial dry weight and initial amount of nutrients could only be determined for the five litterbags collected at $t=0$, their mean value (per plot) was taken to be the initial value for the other litterbags. As each cutting had been thoroughly mixed and as all the litterbags of a plot had been filled with the same weight of fresh material, this assumption is unlikely to lead to significant errors.

Statistical analysis

The fractions of nitrogen, phosphorus, potassium and dry weight remaining in the litterbags were plotted against time and fitted to an asymptotic exponential model (Howard & Howard 1974; Wieder & Lang 1982). This model has the general form:

$$\mathrm{Y}(t) = a + (1-a)\,\mathrm{e}^{-kt}$$

in which $\mathrm{Y}(t)$ denotes the remaining fraction at a specific time (t). It contains two parameters: a representing the asymptotic remaining fraction and k characterizing the rate at which the asymptotic fraction is approached.

The model allows the fractions remaining after 0, 1, 2, 3, 4, 5 and 6 weeks to be calculated for each plot. These remaining fractions (as well as the model parameters themselves) constitute the basic data used for further analysis. If no reliable fit to the model could be obtained (the grass-heath plot only), linear interpolation between surrounding sample dates was used to avoid missing values.

Wilcoxon's signed-ranks test (Sokal & Rohlf 1995) was used to investigate differences between the remaining fractions of the three nutrients. Analysis of variance was used to investigate differences between the two grassland plant communities.

Fractional data were converted using an arcsine transformation ($\arcsin(\sqrt{x})$) before analysis of variance (Sokal & Rohlf 1995).

The above-ground biomass and chemical composition of the vegetation at the time of cutting were evaluated as possible explanatory variables for differences in remaining fractions (Table 1). The chemical measures included the initial N, P and K concentrations, the initial carbon content, and the initial C:N, C:P, and C:K ratios (calculated as the mean of the five litterbags at $t=0$). Also the total amounts of N, P, K and C present at time of cutting were considered, as were the percentages of grass and herb weights, and the percentages of leaf and stem weights.

Stepwise multiple regression was used to detect the factors that best explain the differences between plots (Sokal & Rohlf 1995). The analysis was performed for each nutrient for each successive week after cutting. In cases where only one factor proved significant, simple linear regressions resulted. In these cases non-linear (exponential) regressions were also checked for a possible better explanation of the observed variation.

During the analysis of possible explanatory variables the grass-heath (*Ericion*) plot was omitted initially because it showed outlying values for many of the variables and would thus heavily determine the results of regressions. This would be particularly undesirable as the results from this plot may be less reliable because of the lack of fit to the asymptotic model. The data from this plot were only used at a later stage, as a check on the suitability of the regressions obtained with the other seven plots (grasslands). When two different regression models (for instance a linear and an exponential one) performed equally well, the data of the grass-heath plot was used to decide which one performed best.

Experiment results

Fitting asymptotic loss curve

In general, the experimental data fit the asymptotic exponential model well (Fig. 1, Table 3). Only the grass-heath plot (*Ericion*) does not conform to the exponential model for all nutrients. In this plot, after an initial fall during the first week, the nitrogen and phosphorus fractions rose again during the second week. For nitrogen, the fractions even rose to more than 1 after 2 weeks, indicating net immobilization of nitrogen. For potassium, the data for this plot do fit an asymptotic decrease, but the fit is relatively poor and the remaining fractions are considerably higher than in the other plots. The different behaviour of this plot (*Ericion*) was expected as the plot was selected for its contrasting nature. The cuttings contain a small amount of woody (Ericaceous) material and the chemical composition also differs from the other plots, showing lower concentrations of the three nutrients and higher C:nutrient ratios (Table 1).

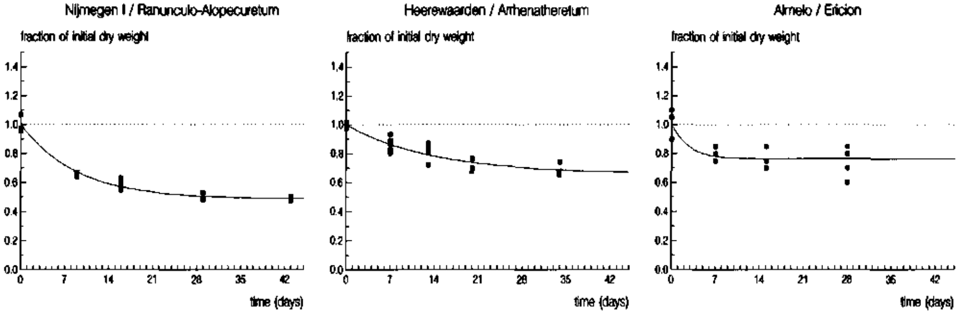
Focusing attention on the seven grassland plots (*Ranunculo-Alopecuretum* and *Arrhenatheretum*), it can be seen from Table 3 that mass loss is described best. The explained variation (R^2) ranges from 0.77 to 0.97 (0.88 on average). Phosphorus and potassium losses can also be described well by the asymptotic model. For phosphorus the R^2 ranges from 0.50 to 0.93 (0.76 on average) and for potassium from 0.54 to 0.98 (0.82 on average). Nitrogen loss is described least well by the asymptotic model, the R^2 ranging from 0.08 to 0.74 (average value 0.44). However, no other simple regression model could be found that better described the nitrogen data.

Differences between nutrients

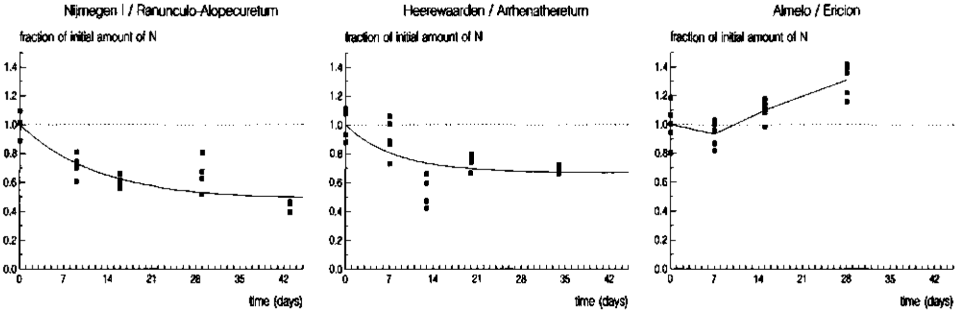
Large amounts of nutrients were lost from the litterbags during the experiment. The amounts clearly differ for the three nutrients (Table 3). The losses were relatively small for nitrogen, the remaining fractions after for instance 4 weeks ranged from 0.52 to 0.89 (considering the seven grassland plots only). Phosphorus showed larger losses, remaining fractions after 4 weeks ranged from 0.36 to 0.66 for the grassland plots.

***Figure 1** (opposite). Remaining fractions of dry weight, nitrogen, phosphorus and potassium in relation to time since cutting for three plots as examples (Nijmegen I, Heerewaarden and Almelo). Fitted asymptotic exponential models are plotted. If no fit to the exponential model could be obtained (*Ericion *only), linear interpolation between means at sample dates was applied.*

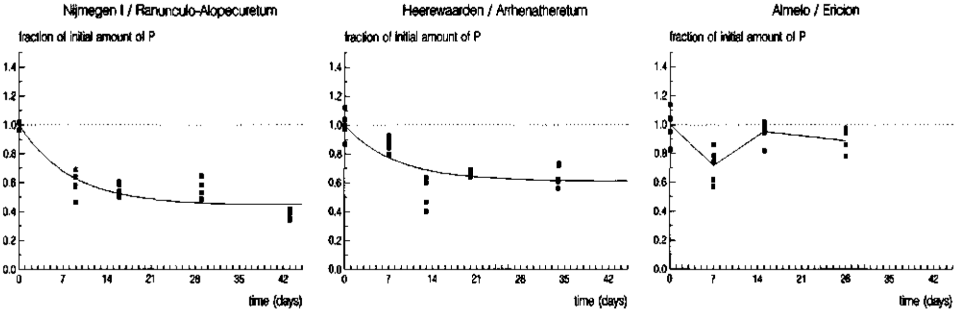
Dry weight



Nitrogen



Phosphorus



Potassium

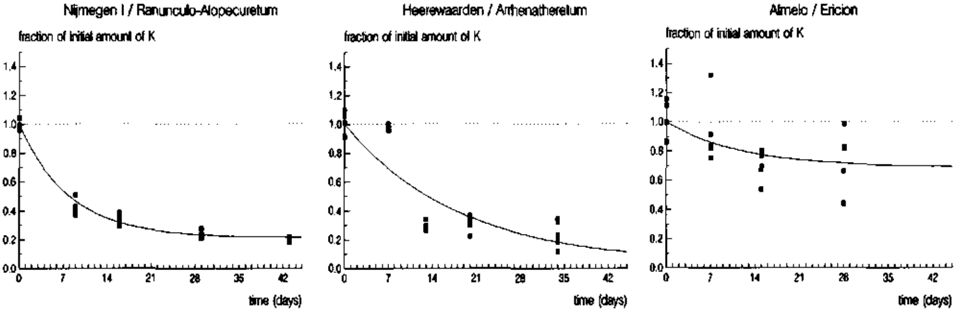


Table 3. *Parameters (*a *and* k*) and explained variation (*R^2*) of the asymptotic exponential models describing the remaining fraction of dry weight, nitrogen, phosphorus and potassium.* R^2 *values larger than 0.55 are significant at* $p < 0.001$*, values between 0.40 and 0.55 at* $p < 0.01$*.* R^2 *values below 0.32 are not significant (*$p > 0.05$*).*

Plot	Dry weight			Nitrogen			Phosphorus			Potassium		
name	*a*	*k*	R^2	*a*	*k*	R^2	*a*	*k*	R^2	*a*	*k*	R^2
Dodewaard	0.54	0.083	0.97	0.48	0.038	0.43	0.50	0.160	0.86	0.07	0.044	0.80
Nijmegen I	0.49	0.114	0.97	0.48	0.082	0.74	0.44	0.123	0.83	0.21	0.125	0.97
Nijmegen II	0.55	0.078	0.81	0.60	0.054	0.42	0.33	0.117	0.93	0.11	0.114	0.98
Zetten	0.39	0.065	0.87	0.45	0.074	0.71	0.36	0.110	0.92	0.01	0.080	0.93
Rossum west	0.64	0.062	0.77	0.78	0.055	0.08	0.65	0.175	0.50	0.13	0.068	0.76
Rossum east	0.59	0.064	0.87	0.54*	0.024*	0.20	0.57	0.098	0.62	0.00	0.038	0.54
Heerewaarden	0.66	0.073	0.87	0.67	0.124	0.47	0.61	0.125	0.66	0.03	0.055	0.76
Almelo	0.76	0.368	0.66	-	-	-	-	-	-	0.69	0.083	0.31

* marks a case with a very small value of *k*. Here, the asymptotic remaining fraction will only be approached long after the end of the experiment making the actual value debatable. The parameters themselves are therefore excluded from statistical analysis and are only used for the calculation of remaining fractions at specific moments within the experiment.

Potassium clearly showed the largest losses. In the grassland plots most of the potassium has already been lost from the material within 4 weeks, the remaining fractions ranged from only 0.11 to 0.35.

The differences between any pair of nutrients were statistically significant ($p < 0.05$) after 2 weeks and remained so from then on. The differences between remaining fractions of nitrogen and those of the other two nutrients were even significant after 1 week. The *Ericion* plot confirmed these results. Including this plot in the analyses improved the levels of significance, in some cases to $p < 0.01$.

The model parameter *k* is significantly larger for phosphorus as compared with nitrogen and potassium ($p < 0.05$). This implies that the decline in phosphorus takes place more rapidly in the first weeks of the experiment than the decline in the amounts of nitrogen and potassium. The difference between the nitrogen and potassium *k*-values was not significant.

Differences between the grassland communities

Analyses of variance reveal that the two studied grassland communities differ significantly in the fractions of dry weight, nitrogen and phosphorus that are lost from the cuttings (Table 4). The remaining fractions are smaller for the *Ranunculo-Alopecuretum* than for the *Arrhenatheretum* community. The differences are already

Table 4. *The average percentages of dry weight and N, P and K remaining in the two grassland communities (Ran =* Ranunculo-Alopecuretum*; Arrh =* Arrhenatheretum*) over a period of 6 weeks, together with the estimated asymptotic fraction remaining (*a*) and the model parameter* k. *Significant differences between the two communities, based on analysis of variance, are indicated by* * $p < 0.05$, ** $p < 0.01$.

	Dry weight			Nitrogen			Phosphorus			Potassium	
Plant community	**Ran**	**Arrh**		**Ran**	**Arrh**		**Ran**	**Arrh**		**Ran**	**Arrh**
Fraction after 1 week	77.5	86.2	*	82.6	88.8		65.6	77.1	**	59.6	71.0
Fraction after 2 weeks	65.2	77.7	**	71.7	82.5		51.4	68.0	**	38.7	51.2
Fraction after 3 weeks	58.3	72.2	**	64.7	78.6		45.3	64.1	**	27.5	37.7
Fraction after 4 weeks	54.4	68.7	**	60.1	76.0		42.8	62.4	**	21.1	28.3
Fraction after 5 weeks	52.2	66.6	*	57.1	74.0	*	41.7	61.7	**	17.3	21.7
Fraction after 6 weeks	50.9	65.2	*	55.1	72.6	*	41.2	61.3	**	15.0	17.1
Fraction asymptotic (a)	49.0	62.9	*	50.5	72.4	*	40.8	61.0	**	10.1	5.4
Model-parameter k	0.085	0.066		0.062	0.090		0.128	0.133		0.091	0.054

significant from the first week onward after cutting for dry weight and phosphorus. For nitrogen the differences are only significant from 5 weeks onward after cutting. For potassium the differences between the two grassland communities are not significant, although the same trend of lower remaining fractions for the *Ranunculo-Alopecuretum* does exist.

No significant differences between the two communities could be found for the model parameter k.

Explanatory variables

From the set of possible explanatory variables only a few show significant relationships. These are all chemical characteristics of the vegetation at the moment it was cut. The remaining fractions of dry weight and nitrogen can best be explained by the C:N ratio or (slightly less well) the initial nitrogen concentration, whereas the remaining fractions of phosphorus and potassium can best be explained by the initial phosphorus concentration or (less well) by the C:P ratio. The regression models producing the highest coefficients of determination (Table 5) all prove to be simple regressions, using one explanatory variable only. A linear regression proves best for the remaining fraction of dry weight. For the remaining fractions of the three nutrients an exponential model is best. The model parameter k cannot be explained satisfactorily by any of the available variables.

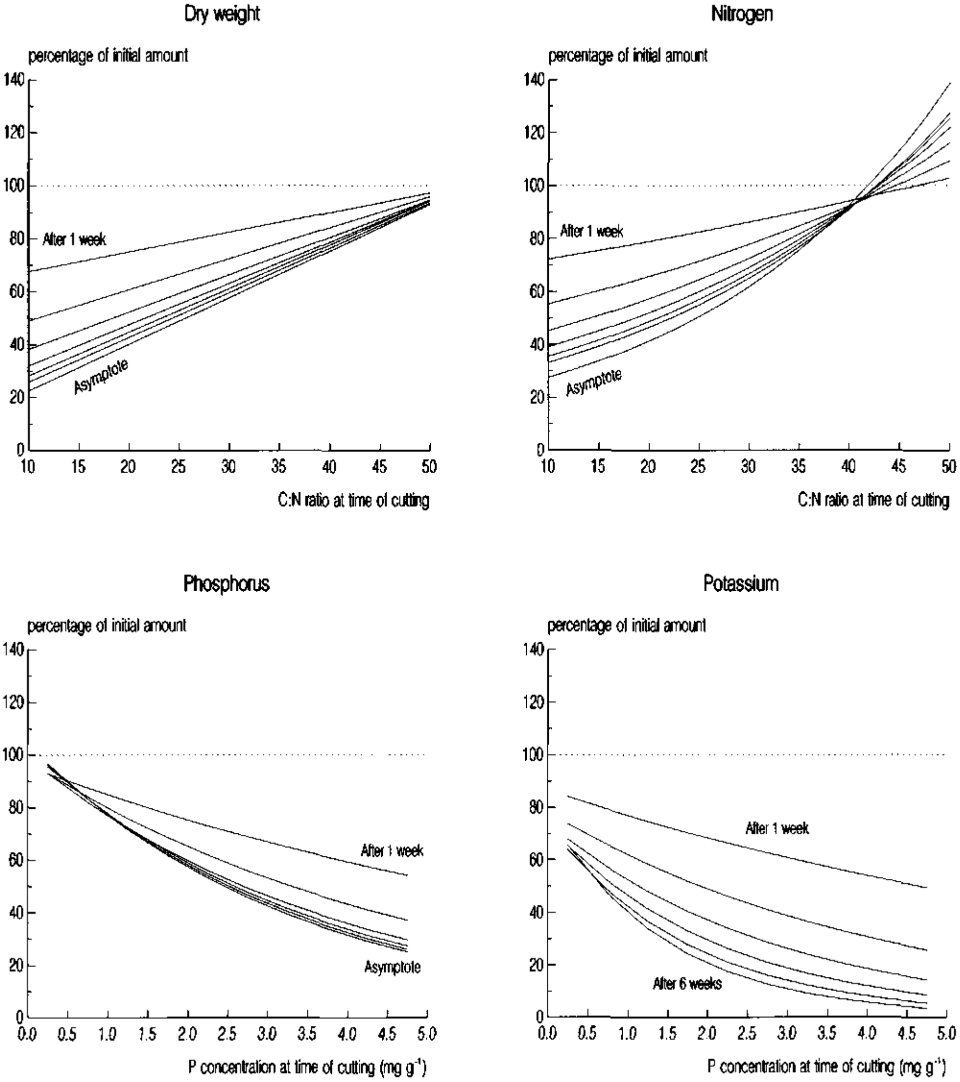
Table 5. *Regression models for the remaining percentages of dry weight, nitrogen, phosphorus and potassium at various weeks after cutting. CN = initial C:N ratio; P = initial phosphorus concentration (mg P g^{-1} dry wt);* b,c *= regression coefficients;* R^2 *= fraction of variation explained;* p *= significance.*

Variable	Dry weight				Nitrogen			
Regression model	$c + (b \cdot \mathrm{CN})$				$c \cdot b^{\mathrm{CN}}$			
	b	c	R^2	p	b	c	R^2	p
Remaining % after 1 week	0.74	60.3	0.38	0.143	1.0089	66.2	0.27	0.236
Remaining % after 2 weeks	1.17	37.3	0.50	0.075	1.0172	46.7	0.38	0.141
Remaining % after 3 weeks	1.41	24.1	0.61	0.039	1.0239	35.7	0.48	0.085
Remaining % after 4 weeks	1.56	16.3	0.68	0.023	1.0289	29.4	0.57	0.051
Remaining % after 5 weeks	1.65	11.6	0.72	0.015	1.0321	25.9	0.63	0.033
Remaining % after 6 weeks	1.69	8.89	0.75	0.012	1.0342	23.7	0.68	0.023
Remaining % asymptotic (*a*)	1.76	4.88	0.78	0.009	1.0413	18.4	0.78	0.019

Variable	Phosphorus				Potassium			
Regression model	$c \cdot b^{\mathrm{P}}$				$c \cdot b^{\mathrm{P}}$			
	b	c	R^2	p	b	c	R^2	p
Remaining % after 1 week	0.877	95.8	0.62	0.036	0.888	86.7	0.19	0.326
Remaining % after 2 weeks	0.815	98.0	0.57	0.051	0.791	78.3	0.26	0.245
Remaining % after 3 weeks	0.776	100.8	0.52	0.067	0.707	74.0	0.34	0.166
Remaining % after 4 weeks	0.757	102.6	0.50	0.074	0.635	73.1	0.42	0.113
Remaining % after 5 weeks	0.748	103.6	0.48	0.083	0.575	73.3	0.44	0.102
Remaining % after 6 weeks	0.745	103.9	0.48	0.086	0.517	77.4	0.42	0.115
Remaining % asymptotic (*a*)	0.741	104.3	0.47	0.088	-	-	-	-

The regression models explain the remaining percentages very well for dry weight and quite well for nitrogen (C:N ratio being the explaining variable). In both cases accuracy increases with increasing time passed since cutting (Table 5). For phosphorus, the regressions also explain the remaining percentages well, although in this case the accuracy of the model decreases slightly with time since cutting.

For potassium, the remaining fractions can only be poorly explained. The regression models never reach significance (Table 5) and for the asymptotic remaining fraction no satisfactory fit could be obtained at all. Though not significant at $p < 0.05$, the regression models for potassium are none the less presented. The resemblance to the models for other nutrients instills extra confidence in the presented relationships but it should be stressed that the relationships are poor for potassium and may be unjustified.



Dry weight

Nitrogen

Phosphorus

Potassium

Figure 2. *Regression models (see Table 5) explaining the remaining percentages of dry weight, nitrogen, phosphorus and potassium (after 1, 2, 3, 4, 5, 6 weeks and the asymptote) in terms of the initial chemical composition of the cutting. (For potassium no suitable regression model could be obtained for the asymptotic values.)*

The regression models from Table 5 are visualized in Fig. 2. It can be seen how low initial C:N ratios (high nitrogen concentrations) and high initial phosphorus concentrations correspond to large relative losses of dry weight and nutrients. For low initial nitrogen and phosphorus concentrations, the relative losses are small.

For nitrogen it can be seen in Fig. 2 how immobilization is predicted at high initial C:N ratios (above 42). This corresponds to the actual results for the *Ericion* plot with its relatively high C:N ratio (42.9). Remaining percentages at higher initial C:N ratios concern extrapolations, so the predicted values at the extreme right of the figure should be treated with some care. For phosphorus no immobilization is predicted within the studied period, given the studied range of initial chemical compositions. Nevertheless, a slight increase in remaining percentage is predicted after an initial drop when very low phosphorus concentrations (below 0.5 to 1.0 mg P g^1) exist at time of cutting. This also corresponds to the actual results for the *Ericion* plot with its very low initial phosphorus concentration.

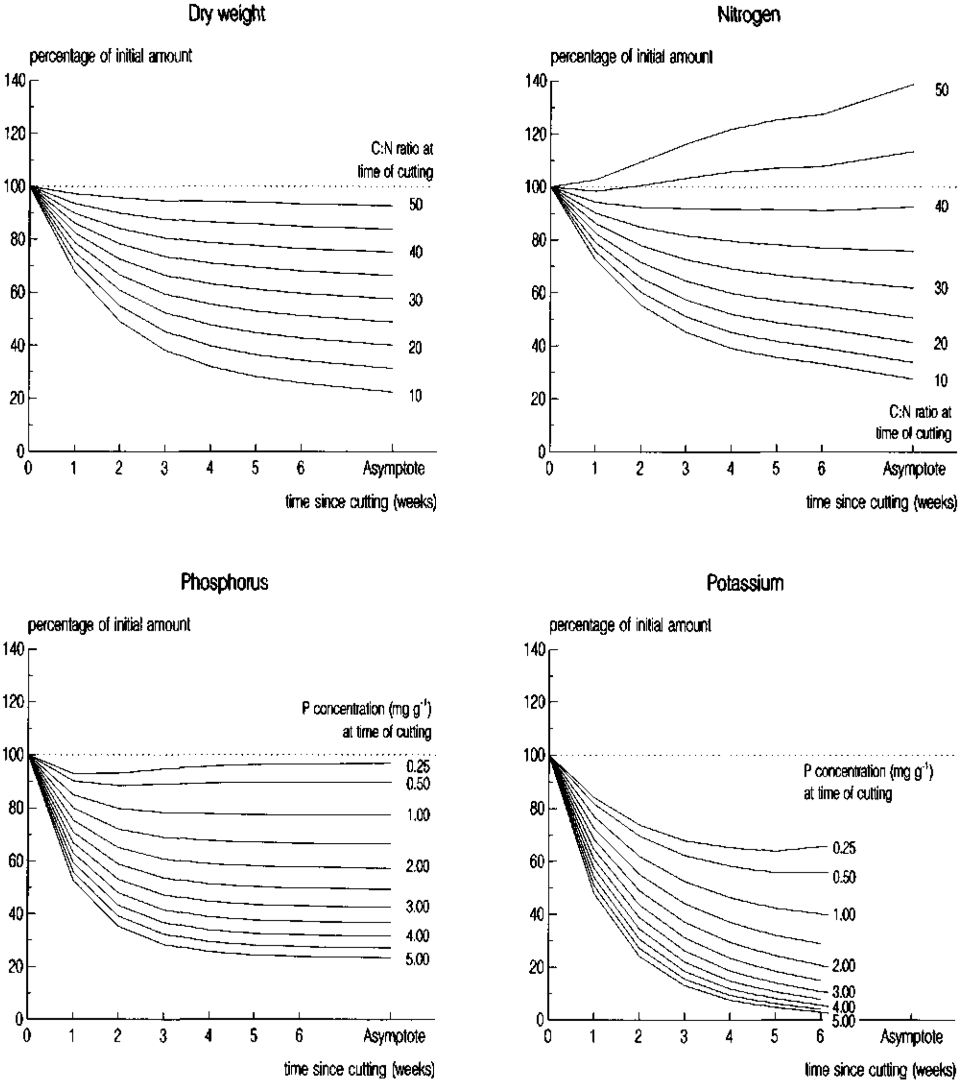
The results of the regression models can also be presented with time on the abscissa for a selection of different initial chemical compositions (Fig. 3). Presented in this way, graphs appear resembling the asymptotic exponential loss curves. However, at high initial C:N ratios and low phosphorus concentrations the curves now also show the predicted (and observed) immobilization of nitrogen and the slight increase of remaining phosphorus after the initial drop.

Model description

Amounts removed in different plant communities

Using the empirical relationships as predictors, remaining fractions can be calculated for any vegetation and removal delay time, provided the initial chemical composition is known. If total biomass of each cut is also known, remaining total amounts can be calculated, representing the quantities that can still be removed after a specific period.

We applied this procedure to model the annual removal of nutrients and biomass in several plant communities from road verges by using existing data on cuttings in Dutch roadside plant communities (Chapters 2 & 4). These data comprise information on biomass and chemical composition of all the cuttings during a 2-year period (1993 and 1994) in 56 plots, involving 12 plant communities (Table 6). Two of these communities contain trees, but only the herb layer was considered as only this layer was mown. Data on late autumn regrowths (usually absent or very little) were treated as extra cuts



Dry weight

Nitrogen

Phosphorus

Potassium

Figure 3. *Relation between time and remaining percentages of dry weight, nitrogen, phosphorus and potassium as derived from the regression models (see Table 5). (For potassium the asymptote could not be calculated.)*

although in reality this material was seldom cut. This way, amounts removed yearly could be compared in a fair way to the actual yearly above-ground production. Also, it ensured that the amounts removed would be safe maximum estimates causing the calculated losses to be safe minimum estimates.

The amounts removed were modelled for eight different management regimes, i.e. removal after 0 weeks for every cut (immediate removal), removal after 1, 2, 3, 4, 5 or 6 weeks for every cut, or removal always after a period notably longer than 6 weeks (representing the asymptotic value which for practical purposes can be imagined to represent roughly 2 months). The calculations were performed individually for each cut for each plot. Totals for each year were determined and an average yearly removal was calculated for each plot. Subsequently the average yearly removal was calculated per plant community.

Amounts removed versus atmospheric deposition

The amounts of nutrients removed (ecosystem output) were compared with the total atmospheric depositions (ecosystem input) for the Dutch situation. Ranges of atmospheric depositions for the Netherlands were obtained from the literature (Van de Meent *et al.* 1984; Van Breemen *et al.* 1988; Kleijn *et al.* 1989; Bobbink *et al.* 1990; Van Dam 1990; Ivens 1990; Houdijk & Roelofs 1991; Bobbink *et al.* 1992; Heij & Schneider 1995).

For nitrogen, a total deposition range of 30 to 75 kg N ha^{-1} $year^{-1}$ was adopted. In areas of intensive farming however these values may even be exceeded. In forests in these areas, depositions of 100 to 150 kg N ha^{-1} $year^{-1}$ have been observed (Ivens 1990; Houdijk & Roelofs 1991).

For phosphorus, total deposition data are scarce and vary greatly. Based on various sources, a total deposition range of 0.3 to 3.0 kg P ha^{-1} $year^{-1}$ was assumed in the present study. Higher values may be expected regionally (Bobbink *et al.* 1990; Houdijk & Roelofs 1991), but Newman (1995) concluded that most of the higher phosphorus deposition rates reported in the literature are incorrect.

For potassium, accurate total deposition data are hard to obtain, mainly because the interception part of the deposition is difficult to assess as potassium shows strong canopy leaching. Based on the collected data, the average deposition range for potassium was assumed to be 5 to 20 kg K ha^{-1} $year^{-1}$, but higher regional values can not be excluded (Bobbink *et al.* 1990).

Table 6. *Plant communities used in modelling the removed amounts of nutrients. Community names follow Sýkora* et al. *(1993), Westhoff & Den Held (1969) and Schaminée* et al. *(1995, 1996). The number of plots, a short description and the customary form of management are presented. Species with relatively high cover (bold) and some characteristic species (underlined) are indicated. Species names follow Van der Meijden (1996).*

Code	**Plant community**
Filip	*Valeriano-Filipenduletum*, 5 plots. Tall-herb grassland on moist to wet, moderately fertile soils. Species: ***Phragmites australis***, ***Carex acutiformis***, ***Calamagrostis canescens***, ***Lysimachia vulgaris***, *Valeriana officinalis*, *Filipendula ulmaria*, *Eupatorium cannabinum*, *Thalictrum flavum*, *Lythrum salicaria*. Management: cutting with removal once per year.
Aego	*Agropyro repentis-Aegopodietum podagrariae*, 4 plots. Vegetation of woodland- and hedge-margins, usually semi-shaded. On nitrate rich, moderately moist soils. Species: ***Aegopodium podagraria***, ***Urtica dioica***, ***Anthriscus sylvestris***, ***Glechoma hederacea***. Management: cutting (usually with removal) of herb layer once or twice per year.
Chaer	*Alliario-Chaerophylletum temuli*, 5 plots. Much like previous community but on drier, more sandy soils. Species: ***Chaerophyllum temulum***, ***Bromus sterilis***, *Alliaria petiolata*. Management: Irregular (herb layer only).
Calth	*Calthion palustris* trunk community, 6 plots. Hay-meadow on moderately fertile, continuously wet soils. Species: ***Holcus lanatus***, ***Anthoxanthum odoratum***, ***Rumex acetosa***, ***Carex disticha***, *Lychnis flos-cuculi*, *Lotus pedunculatus*, *Cirsium palustre*, *Angelica sylvestris*. Management: cutting with removal twice per year, sometimes once or three times.
Frit	*Fritillario-Alopecuretum pratensis*, 5 plots.
/f	- fragmentary, 2 plots
/w	- well developed, 3 plots
	Hay-meadow on moderately fertile, moderately wet soils (preferably flooded seasonally). Species: ***Alopecurus pratensis***, ***Plantago lanceolata***, ***Anthoxanthum odoratum***, ***Agrostis stolonifera***, *Sanguisorba officinalis*. In well developed form also: *Fritillaria meleagris*, *Alchemilla glabra*. Management: cutting with removal twice per year.
Ran-A	Fragmentary *Ranunculo-Alopecuretum geniculati*, 5 plots. Grassland on nutrient rich soils, flooded in winter and spring. In summer groundwater is deep and soils dry out. Species: ***Agrostis stolonifera***, ***Ranunculus repens***, ***Holcus lanatus***, ***Carex hirta***, *Alopecurus geniculatus*, *Carex otrubae*, *Potentilla anserina*. Management: cutting with removal twice per year.
Tri-A	Fragmentary *Triglochino-Agrostietum juncetosum gerardi*, 7 plots. Grassland on moderately nutrient-poor, moderately acid, often flooded soils which remain moist year-round. Species: ***Agrostis stolonifera***, ***Juncus articulatus***, ***Hydrocotyle vulgaris***, ***Potentilla anserina***, *Triglochin palustris*, *Juncus gerardi*, *Carex distans*. Management: cutting with removal once per year.
Ar s.B	Fragmentary *Arrhenatheretum elatioris* subassociationgroup B (Westhoff & Den Held 1969), 5 plots. Hay-meadow on moderately nutrient rich, relatively dry, circum-neutral soils. Species: ***Arrhenatherum elatius***, ***Trisetum flavescens***, ***Festuca rubra***, ***Achillea millefolium***, *Ranunculus bulbosus*, *Knautia arvensis*, *Pimpinella saxifraga*, *Galium verum*, *Plantago media*. Management: cutting with removal twice per year, sometimes once.
Ar pic	*Arrhenatheretum picridetosum*, 5 plots. Slightly ruderalized *Arrhenatheretum* on moderately nutrient rich, relatively dry calcareous soils. Many species in common with previous community. ***Arrhenatherum elatius***, ***Brachypodium pinnatum***, *Helictotrichon pubescens*, *Origanum vulgare*, *Agrimonia eupatoria*, *Picris hieracioides*. Management: cutting with removal once per year.
Meso	*Mesobromion* trunk community, 5 plots. Chalk grassland, i.e. grassland on calcium rich, dry soils. Species: ***Brachypodium pinnatum***, ***Centaurea scabiosa***, *Briza media*, *Carex flacca*, *Linum catharticum*, *Galium pumilum*, *Thymus pulegioides*. Management: cutting with removal once per year.
Erici	*Ericion tetralicis* (fragmentary *Lycopodio-Rhynchosporetum albo-fuscae)*, 4 plots. Grass-heath vegetation on wet, nutrient poor, very acid soils. Species: ***Erica tetralix***, ***Molinia caerulea***, ***Agrostis capillaris***, *Lycopodiella inundatum*, *Drosera intermedia*, *Rhynchospora fusca*. Management: cutting with removal once per year.

Model results

Amounts removed in different plant communities

The modelled amounts of removed dry weight and nutrients under different removal regimes are presented in Fig. 4 for the different plant communities. In this figure the first bar for each community represents the amount removed annually when the cuttings are immediately removed. The first bar thus represents the total annual above-ground production. This is the maximum amount that can be removed each year. The difference between any bar and the first one represents the loss: the amount that might have been removed had removal been immediate.

It is clear from Fig. 4 how, for all nutrients, large losses already occur in the first 2 to 3 weeks. For phosphorus the largest losses even occur within the first 2 weeks. When, in the more productive communities, removal always takes place after e.g. 4 weeks, the losses (the amounts not removed) range from 2 to 5 ton dry wt ha^{-1} $year^{-1}$, 25 to 100 kg N ha^{-1} $year^{-1}$, 2 to almost 10 kg P ha^{-1} $year^{-1}$ and 40 to 200 kg K ha^{-1} $year^{-1}$.

Amounts removed versus *atmospheric deposition*

When the amounts removed are compared with the atmospheric deposition (Fig. 4) it can be seen that after a few weeks delay the amounts removed may often drop below the deposition levels.

For nitrogen, this can easily happen for many communities. Only for the *Valeriano-Filipenduletum*, the fragmentary *Fritillario-Alopecuretum* and maybe also the *Calthion* community does this risk not exist, although it should be noted again that in areas of intensive farming depositions up to 150 kg N ha^{-1} $year^{-1}$ have been observed in forests (Ivens 1990; Houdijk & Roelofs 1991). For four communities the removed amounts of nitrogen appear to be almost always lower than the atmospheric deposition, regardless of the regime of removal: the *Triglochino-Agrostietum, Arrhenatheretum picriditosum, Mesobromion* and *Ericion* communities. In some regions this may also be true for the herb layer of the *Agropyro-Aegopodietum* community.

Although for phosphorus the losses can also be substantial, the amounts removed exceed the relatively low deposition levels in most communities whatever the regime of removal. For some low productive communities, however, the amounts removed may not always exceed atmospheric deposition, but in these communities the differences between removal regimes are small anyway, suggesting that the removal regime is not very important to the nutrient balance. The communities concerned are the same four where

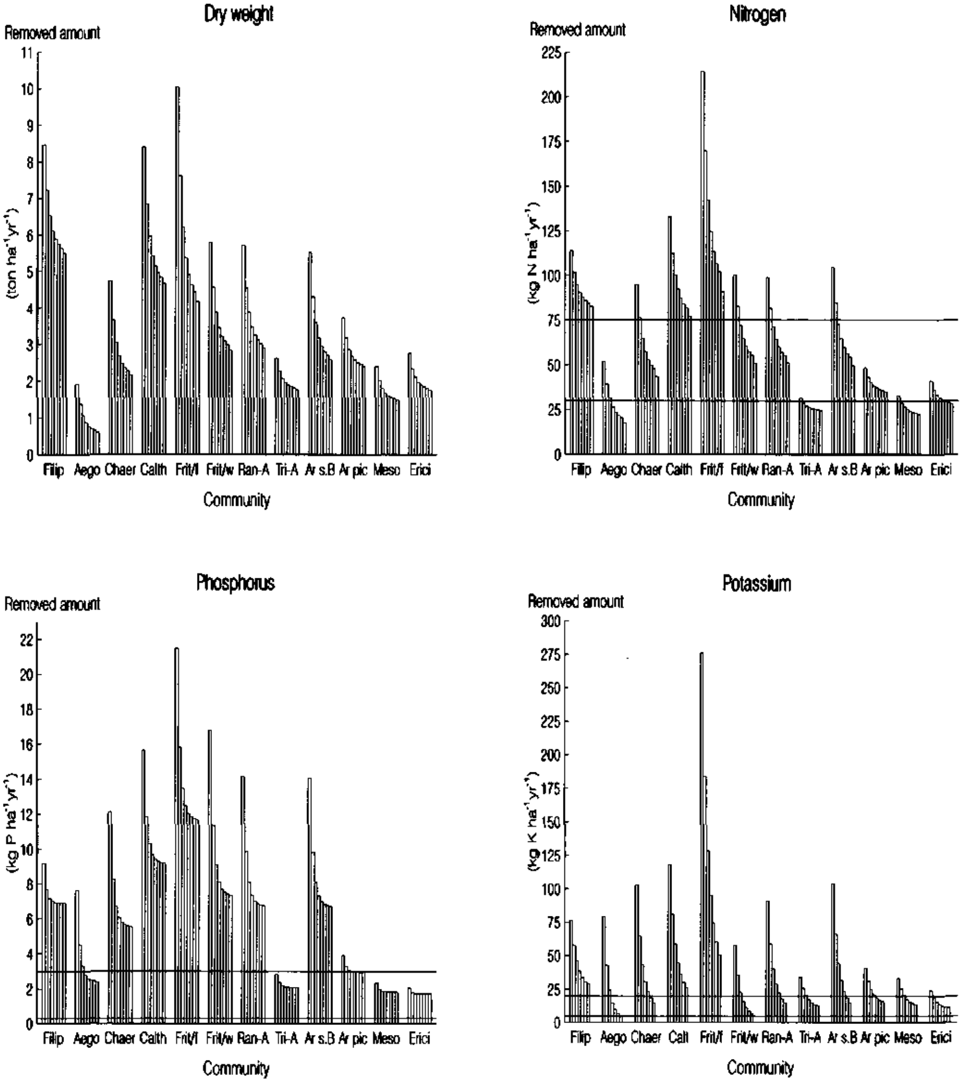


Figure 4. *Annually removed amounts (dry weight, nitrogen, phosphorus and potassium) per plant community in relation to the amount of time the cuttings are left in the field before removal. For each community the bars represent: removal following every cut after 0, 1, 2, 3, 4, 5, 6 weeks, or considerably longer than 6 weeks, respectively. For potassium the last bar could not be calculated. Solid horizontal lines indicate average maximum and minimum annual atmospheric deposition for the Dutch situation. (For explanation of the community-codes: see Table 6. The* Aegopodietum *and* Chaerophylletum *usually contain trees, but only the herb layer is taken into consideration here.)*

nitrogen deposition almost always exceeds nitrogen removal: *Triglochino-Agrostietum*, *Arrhenatheretum picriditosum*, *Mesobromion* and *Ericion*.

For potassium the level of deposition is also low compared to the above-ground production in most cases. But as potassium is most rapidly lost from the cuttings, in most communities the amounts actually removed can easily drop below the atmospheric input after some weeks. Again, only the *Valeriano-Filipenduletum*, the *Calthion* and the fragmentary *Fritillario-Alopecuretum* communities appear to be free from this risk.

Discussion

Magnitude of losses

It may be surprising that such substantial proportions of the initial dry weight and nutrients were lost within a few weeks. Clearly not only microbial decomposition and leaching, but also comminution (reduction in particle size) will have contributed to this result as small particles will be lost from the litterbags. In many decomposition studies particle losses as well as initial leaching losses are regarded as an error. In this study however, these losses represent genuine losses from the cuttings. Particle losses may even be larger in actual management practice than from the litterbags with 1 mm mesh size.

Asymptotic loss curve

In this study an asymptotic exponential model is used to describe the mass and nutrient losses whereas most often exponential models approaching zero are used to describe decomposition processes (Swift *et al.* 1979; Wieder & Lang 1982). An exponential model approaching zero is what one might expect, as no plant material can resist total decay given a sufficiently long period of time. This model is not, however, as probable as it may seem at first glance. Decomposition processes act on a complex mixture of different plant parts and different chemical structures at the same time, each component having its own decay rate (Swift *et al.* 1979). It can easily be shown empirically that the resulting curve when modelling decomposition of a substrate containing components with different decay rates, can resemble an asymptotic model during the first stage. As soon as the easily decomposable components have almost disappeared, the first relatively steep part of the curve bends towards a relatively gradual part induced by the remaining more resistant components. This way, asymptotic models can be expected to fit the data well for parts of the decay process.

Moreover, not only are different substances involved, decomposition itself consists of different processes that are of an entirely different nature. Swift *et al.* (1979) divide decay processes into three distinct groups: leaching, comminution and catabolism. The relative importance of these processes may be different in different stages of decomposition. Thus, the asymptotic nature of the curves may also originate in the combined action of different processes with changing relative importances.

Decomposition processes

It is not easy to discriminate between the different decomposition processes on the basis of the data presented. A dominating influence of the leaching process might be expected in the first days to weeks and losses through comminution may also be important in this period.

However, the losses of dry weight, nitrogen and phosphorus in our short-term study could be explained adequately by the initial chemical composition of the material. These findings are supported by some long-term decomposition experiments in which the relationships between initial chemical composition and loss rates were found to be strongest during the first part of the decomposition curve (Berg & Staaf 1980; Staaf 1980). This suggests that for some elements catabolism does already play an important role during the first few weeks. C:N and C:P ratios (nitrogen and phosphorus concentrations) are known to influence microbial metabolism (Floate 1970; Alexander 1977; Swift *et al.* 1979; Taylor *et al.* 1989; Tian *et al.* 1992;). Of course, we cannot assume for certain that leaching and comminution are unaffected by chemical composition. At higher concentrations a larger part of the element may be present in leachable form for instance. However, the observed immobilization of nitrogen within 2 weeks after cutting in one plot strongly points to the importance of catabolism during the first weeks.

In addition, percentage nitrogen losses were found to be smaller than phosphorus losses. This may indicate that in our material nitrogen limits microbial decomposition more than phosphorus, which is in line with the observed N:P ratios of our material. These ratios vary between 5.5 to 7.3 (average value 6.0) for the grassland plots. This is considerably lower than the N:P ratio of an average microbial population in soils, which is believed to be relatively constant around 10 (Alexander 1977). This would indicate a relative shortage of nitrogen in our materials as compared with microbial requirements, which may account for the smaller losses. The relative abundance of phosphorus may also explain why phosphorus losses are significantly more concentrated in the first few weeks of the experiment than losses of nitrogen.

Swift *et al.* (1979) discuss the fact that rapid initial mass losses in long-term studies are often ascribed to the leaching of soluble constituents. They also argue that this may equally be explained by microbial catabolism of these substances. Howard & Howard (1974) noticed an initial rapid mass loss in their experiment which they ascribed not to leaching, but to microbial decomposition of readily-soluble substances (partly based on unpublished work of O.W. Heal *et al.*).

Leaching studies have shown repeatedly that nitrogen and phosphorus are not easily lost by leaching whereas potassium is easily lost (Nykvist 1959a&b & 1961a&b; Carlisle *et al.* 1966; Morton 1977; review by Tukey 1970). This is in accordance with the fact that potassium was the one element in this study where a relation between the (large) losses and the initial chemical composition could not be confirmed significantly. It suggests that leaching plays a dominant role for potassium, but not for nitrogen and phosphorus.

Initial chemical composition

Although initial nutrient concentrations (C:nutrient ratios) have traditionally been established as the main factors controlling decomposition (Floate 1970; Alexander 1977; Swift *et al.* 1979), more recently lignin has also been mentioned as an important factor (Berendse *et al.* 1987a; Berg & McClaugherty 1989; Aber *et al.* 1990). In our study we did not measure actual lignin concentrations. Several studies however, have examined both factors (Berg & Staaf 1980; Berendse *et al.* 1987a; Taylor *et al.* 1989; Tian *et al.* 1992). From these studies it can be concluded that at relatively low lignin concentrations and in relatively early decomposition stages C:N ratio will be a better predictor of decomposition than lignin.

In this present study two aspects of the initial chemical composition appear to be important: the C:N ratio explaining dry weight and nitrogen loss, and the phosphorus concentration explaining phosphorus and potassium loss. It should be noted, however, that the initial nitrogen and phosphorus concentrations are highly correlated. Their correlation is 0.93 when only the seven grassland plots are considered, and 0.94 if the *Ericion* plot is also included. None the less, a relation between initial phosphorus concentration and phosphorus loss rate is not inconceivable and has been reported by many authors (Floate 1970; Gosz *et al.* 1973; Staaf 1980; Berg & Staaf 1980).

Nutrient balance

In unfertilized grasslands under hay-making management regimes in the Netherlands, nutrient fluxes such as denitrification, N_2-fixation and leaching from the soil are thought to be relatively small compared to atmospheric deposition and removal with cuttings (Berendse *et al.* 1994). Some attention should be paid to this assumption and to other possible nutrient inputs and outputs.

Although leaching of elements from the soil usually concerns only minor amounts, larger quantities may possibly be leached from the soil if the cutting releases large amounts in a short period of time. This would represent an extra output, but it is not easy to determine whether this effect really occurs and to what extent. This will probably depend strongly on the local situation.

Additional inputs into the ecosystem may occur through run-off rainwater from road surfaces, debris, plant uptake by roots extending to nearby eutrophic water bodies, inundations, etc. It should also be noted that the interception part of the atmospheric deposition strongly depends on vegetation structure (e.g. Leaf Area Index, LAI: Heil *et al.* 1988) and therefore also on the above-ground biomass. Consequently, the actual deposition ranges may be only subranges of the adopted ones depending on the plant community concerned. Also, cutting the vegetation strongly reduces the LAI and thus temporarily reduces the interception part of the deposition.

The role of potassium

In the four low productive plant communities in road verges (*Triglochino-Agrostietum, Arrhenatheretum picriditosum, Mesobromion,* and *Ericion*) the total annual production of nitrogen is usually lower than the annual atmospheric nitrogen input (Fig. 4). The atmospheric deposition of nitrogen, therefore, can never be counteracted by the removal of cuttings. This would imply that production must be limited by one or more of the other major elements, otherwise these communities with low productivity would have disappeared already. Phosphorus can hardly play this limiting role as the amounts produced in these communities are either below the atmospheric deposition already or approach the deposition level closely. It does appear that potassium is the most probable limiting nutrient in these communities because the removable amounts are always larger than the deposition levels. However, this only holds if the cuttings are removed within 1 week (or maybe 2 weeks). If not, the amounts of potassium removed may also fall below the atmospheric deposition as potassium is the element most rapidly lost from the cuttings.

Apparently, potassium may be an important nutrient in low productive communities when management consists of hay-making. But potassium may also be a key element in many other communities when management aims at soil impoverishment. Support for this idea can be found in other studies. Most authors agree that only about one to a few per cent of the total ecosystem nutrient pool is removed annually with cuttings (Dickinson 1984; Bakker 1989). For many elements (nitrogen and phosphorus in particular) the effect of hay-making during several years cannot be detected in chemical soil analysis (Oomes & Mooi 1985; Bobbink & Willems 1988; Parr & Way 1988; Bakker 1987, 1989) although mineralization of these elements may possibly be affected (Bobbink & Willems 1988). None the less, hay-making usually leads to a rapid decline in biomass during the first few years (Dickinson & Polwart 1982; Bakker 1989; Oomes 1990), and although changes in nitrogen and phosphorus status of the soil can hardly be detected, some authors do report lower potassium levels in the soil (Parr & Way 1988; Bobbink & Willems 1988). Other authors report lower potassium levels in the vegetation after a few years (Bakker 1989; Oomes 1990). Oomes (1990) reports that potassium becomes the limiting nutrient within 3 years of hay-making on sandy soils, but no indication in this direction was obtained on clay.

These results all suggest that the removal of cuttings may primarily reduce the supply of potassium, at least on sandy soils with a low cation exchange capacity. As indicated before, potassium shows strong leaching from living tissues as well as from litter and cut material. It thus tends to cycle mainly through the vegetation (Van Dam 1990) and may, therefore, be affected most by removal of the cut material, provided there is little delay in removal.

Implications for management

It is clear that cuttings do lose large amounts of nutrients during the first few weeks. Hence, if soil impoverishment is an objective, the cuttings should be removed within 1 or 2 weeks. If not, the amounts removed can easily drop below the annual atmospheric deposition, especially for nitrogen and potassium. In plant communities where yearly productions are low, rapid removal of the cuttings may be the only way to maintain at least potassium at a limiting level.

One might conclude that cuttings are best removed instantly. Machinery does exist which cuts and at the same time removes the material by means of air suction. Although the use of such equipment certainly would be ideal from a nutrient balance point of view there are several disadvantages connected to this practice. First of all, large numbers of plant seeds will be removed this way. This also includes unripe seeds which might otherwise have been able to ripen and fall from the cuttings within a few days. This may influence the reproduction of certain species to a considerable extent and may lead to unwanted changes in composition of the vegetation. In addition, many insects and other arthropods or their eggs, pupae or nymphs may be removed by this type of machinery. These disadvantages should be carefully weighed against the benefits of additional soil impoverishment.

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4

Soil, biomass, and management of semi-natural vegetation

I. Mutual soil - biomass relationships

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Soil, biomass, and management of semi-natural vegetation

I. Mutual soil - biomass relationships

Abstract. Mutual relationships between biomass characteristics and soil properties (including *in situ* annual nitrogen mineralization) were investigated over a broad range of plant communities in unfertilized road verges. Not only the dependence of biomass characteristics on soil properties was investigated, but also the possibility of inferring soil nutrient availability from biomass characteristics was considered. Possible effects of overstory trees (shading) and vegetation management (mowing) were accounted for.

Annual aboveground biomass production depended mainly on: annual N mineralization, average soil moisture content, shading intensity, and soil pH (optimum at pH-$CaCl_2$ 5.7). Average tissue nutrient concentrations were primarily explained by: mowing frequency, shading intensity, the availability of the corresponding soil nutrient, and pH (optima between 5.5 and 6.0). Results also implied that hay-making twice per year removes more nutrients than a single cut at the end of the season.

N mineralization may be inferred from the aboveground biomass production, but only under comparable moisture and shading conditions (partial $r=0.74$). In general, it is concluded that nutrient availability can only be deduced from biomass characteristics if sites with equal moisture content are compared. Only K availability forms an exception to this general rule. Its availability was mainly indicated by the tissue K concentration (partial $r=0.80$), and the confounding effect of other factors was small (bivariate r was still 0.71). Soil available P could not be satisfactorily indicated, even under equal moisture and shading conditions. Also, different nutrients appeared to interact, and should not be considered independent of each other.

K was the only element with a strong relationship between its soil and tissue concentration. For the other nutrients, tissue concentrations did not depend predominately on the soil availability. Most likely, the species occurring in (semi-)natural vegetation are adapted to the local fertility through an adjusted physiology and growth rate. It is concluded that, with the possible exception of K, simple relationships between soil properties and biomass characteristics cannot be expected over wide environmental gradients.

Key-words: *environmental gradient, nitrogen mineralization, nutrient availability, plant communities, productivity, tissue concentrations.*

Introduction

Soil properties are considered the prime determinants for biomass characteristics such as production and tissue nutrient concentrations. The dependence of biomass production on physical and chemical soil properties has been studied before (*e.g.* Vermeer & Berendse 1983; Vermeer 1986; Bobbink *et al.* 1989; Bobbink 1991; Berendse 1990; Thormann & Bayley 1997), but the way in which biomass chemical composition depends on soil properties has been studied less frequently (*e.g.* Vermeer & Verhoeven 1985,1987; Thormann & Bayley 1997; Ertsen 1998; Waughman 1980; Hayati & Proctor 1990). These studies usually deal with a specific plant community or related community-types. Whether or not the reported relationships are meaningful over a much broader range is unclear, nor do we know the role of other environmental factors and management.

Since biomass characteristics depend on soil properties, the reverse question, whether or not soil properties can be inferred from biomass characteristics, may also be asked. Oomes & Mooi (1985) and Oomes (1990) concluded that the soil nutrient status may better be described by the vegetation than by soil analysis. This notion forms the basis for bioassay techniques such as the use of phytometers, either in field studies (Roem & Berendse 2000), or under greenhouse conditions (Van Duuren *et al.* 1997a,b; Pegtel *et al.* 1996; Van der Woude *et al.* 1994). Some authors argue that tissue nutrient concentrations (or their ratios) may provide a meaningful alternative for measurements of soil nutrient availability (*e.g.* Pegtel 1987; Güsewell *et al.* 1998). This matter has received considerable attention (*e.g.* Hayati & Proctor 1990,1991), especially in cases where efforts are directed towards detection of the nutrients that limit vegetation growth (Wassen *et al.* 1995; Pegtel *et al.* 1996; Boeye *et al.* 1997; Van Duuren *et al.* 1997a,b; Güsewell *et al.* 1998; Shaver & Chapin 1995; Esselink & Van Gils 1994). Although bioassays have their limitations (Chapin 1980; Pegtel *et al.* 1996), we may nevertheless expect a more or less clear relationship between the tissue concentration of a nutrients and its availability in the soil. Whether or not such expectations hold over a wide range of conditions and community-types will be addressed here.

The present study aims to investigate, over a wide range of unfertilized, semi-natural plant communities:

a) the dependence of biomass characteristics on soil properties;
b) the possibility of obtaining indications on soil nutrient availability from biomass characteristics.

Effects of management and other site conditions will be considered where necessary.

In part II (Chapter 5) the relevance of the studied variables for species diversity will be investigated. Fig. 1 visualises the central perspectives.

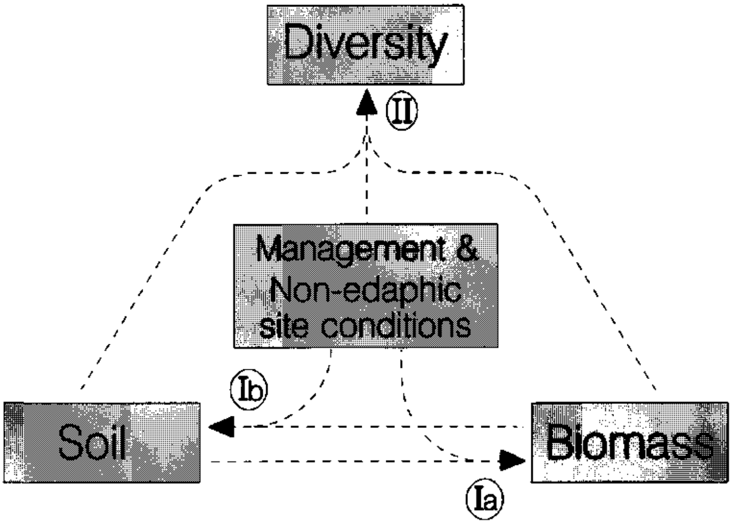

Figure 1. *Visualisation of the central perspectives of the study.* (Ia) *How are biomass characteristics (chemical composition and aboveground production) affected by soil properties (chemical and physical), and what is the role of non-edaphic site conditions and management?* (Ib) *Can soil chemical properties be deduced from biomass characteristics?* (II) *How is species diversity (richness, evenness, rareness) related to soil properties and biomass characteristics, and what is the role of non-edaphic site conditions and management? This second part of the study will be dealt with in Chapter 5.*

***Table 1** (opposite). Plant communities involved. Names of vegetation-types follow Schaminée* et al. *(1995, 1996), Stortelder* et al. *(1999), and Sýkora* et al. *(1993). The number of sites, average number of species (bryophytes and terrestrial lichens included), a short ecological description, and the customary form of management are presented. Species with relatively high cover (bold) and some characteristic species (underlined) are indicated. Nomenclature for vascular plants according to Van der Meijden (1996), for bryophytes according to Margadant & During (1982).*

Methods

Sites investigated

The study involves 74 sites scattered over roadside locations in the Netherlands. The sites belong to 14 different semi-natural, unfertilized vegetation-types and reflect a wide range of edaphic conditions (Table 1). The variation includes: open pioneer vegetation on very dry and nutrient-poor sandy substrates (both at low and high soil pH); grassland communities on dry and nutrient-poor calcareous soils, on loamy soils, and on wet or poorly drained clay or peat; tall-herb grasslands on (often peaty) soils with permanently high groundwater levels; partly-shaded herb communities on light clay or sand; and dry and wet heath and grass-heath vegetation on nutrient-poor, acid sand or loam. The sites differ in management. Many were mown once or twice annually, and in most cases the cuttings were removed (hay-making). Each community-type was represented by at least five sites, occasionally six or eight. Each site was recorded by a single 25 m^2 plot.

Biomass characteristics

Annual aboveground biomass production, average tissue nutrient concentrations and annual nutrient accumulation in the aboveground herb-layer were determined in 1993 and 1994 by clipping sub-plots just before the vegetation was mown by the road authorities, or when peak standing crop was assumed to have been reached. Biomass of an overstory tree or shrub layer (only at the two semi-shaded vegetation types) was omitted. In sites grazed by rabbits, exclosures were used. Late autumn regrowth, if present, was also assessed.

For each sample, five sub-plots of 0.5x0.5 m were cut at ground level. The cut material included living biomass and standing dead material. Surface litter was not collected; its amount was usually small due to hay-making. The sub-samples were bulked, dried at 70 °C for 48 hours, and weighed. The concentrations of N, P and K were

Valeriano-Filipenduletum, 5 sites (45 species).

Tall-herb grassland on moist to wet, moderately fertile soils. Species: ***Phragmites australis***, ***Carex acutiformis***, ***Calamagrostis canescens***, ***Lysimachia vulgaris***, ***Calystegia sepium***, *Valeriana officinalis*, *Filipendula ulmaria*, *Eupatorium cannabinum*, *Thalictrum flavum*. Management: cutting (with /without removal) once per yr, or none.

Urtico-Aegopodietum, 5 sites (32 species).

Vegetation of woodland- and hedge-margins, usually semi-shaded. On nitrate-rich, moderately moist soils. Species: ***Aegopodium podagraria***, ***Urtica dioica***, ***Anthriscus sylvestris***, ***Glechoma hederacea***, *Rumex obtusifolius*. Management: cutting (with or without removal) of herb layer once or twice per yr, or unmanaged.

Alliario-Chaerophylletum temuli, 5 sites (28 species).

Much like previous community but on drier, more sandy soils. Species: ***Chaerophyllum temulum***, ***Bromus sterilis***, *Alliaria petiolata*, *Poa nemoralis*. Often unmanaged, or cut once per yr with or without removal.

Calthion palustris trunk communities, 5 sites (44 species).

Hay-meadow on moderately fertile, continuously wet soils. Species: ***Holcus lanatus***, ***Anthoxanthum odoratum***, ***Rumex acetosa***, ***Carex disticha***, ***Calliergonella cuspidatum***, *Lychnis flos-cuculi*, *Lotus pedunculatus*, *Cirsium palustre*, *Angelica sylvestris*. Management: cutting (typically with removal) once or twice per yr.

Fritillario-Alopecuretum pratensis, 5 sites. Fragmentary form: 2 sites (38 spp.), well-developed form: 3 sites (52 spp.).

Hay-meadow on moderately fertile, moderately wet soils (preferably flooded seasonally). Species: ***Alopecurus pratensis***, ***Plantago lanceolata***, ***Anthoxanthum odoratum***, ***Agrostis stolonifera***, *Sanguisorba officinalis*. In well-developed form also: *Fritillaria meleagris* and *Alchemilla glabra*. Management: cutting with removal twice per yr.

Ranunculo-Alopecuretum geniculati, 5 sites (32 species).

Grassland on nutrient-rich soils, flooded in winter and spring. In summer groundwater is deep and soils dry out. Species: ***Agrostis stolonifera***, ***Ranunculus repens***, ***Holcus lanatus***, ***Carex hirta***, *Alopecurus geniculatus*, *Carex otrubae*, *Potentilla anserina*. Management: cutting with removal twice per yr, rarely without removal.

Fragmentary *Triglochino-Agrostietum stoloniferae* (including *juncetosum gerardi*), 8 sites (41 species).

Grassland on moderately nutrient-poor, moderately acid, often flooded soils that remain moist year-round. Species: ***Agrostis stolonifera***, ***Calliergonella cuspidatum***, ***Juncus articulatus***, ***Hydrocotyle vulgaris***, ***Potentilla anserina***, *Triglochin palustris*, *Eleocharis uniglumis*. Management: cutting (usually with removal) once per yr.

Fragmentary *Phleo-Tortuletum ruraliformis*, 5 sites (43 species).

Pioneer community on dry, relatively calcareous dune sand. Species: ***Tortula ruralis* var. *ruraliformis***, ***Brachythecium albicans***, ***Carex arenaria***, ***Hypnum cupressiforme* var. *lacunosum***, *Phleum arenarium*, *Erodium cicutarium* ssp. *dunense*, *Sedum acre*, *Saxifraga tridactylites*. No management, but grazed by rabbits.

Arrhenatheretum elatioris (excluding *festucetosum arundinaceae*), 5 sites (47 species).

Hay-meadow on moderately nutrient-rich, relatively dry soils. Species: ***Arrhenatherum elatius***, ***Festuca rubra***, ***Achillea millefolium***, ***Trisetum flavescens***, *Crepis biennis*, *Knautia arvensis*, *Ranunculus bulbosus*, *Pimpinella saxifraga*, *Plantago media*. Management: cutting with removal twice per yr, sometimes once.

Arrhenatheretum elatioris festucetosum arundinaceae, 5 sites (38 species).

Slightly ruderalized *Arrhenatheretum* on moderately nutrient-rich, relatively dry, calcareous soils. Many species in common with previous community. ***Arrhenatherum elatius***, ***Brachypodium pinnatum***, *Helictotrichon pubescens*, *Origanum vulgare*, *Agrimonia eupatoria*, *Picris hieracioides*. Cut once per yr, usually with removal.

Mesobromion erecti trunk communities, 5 sites (44 species).

Chalk grassland, *i.e.* grassland on calcium-rich, dry soils. Species: ***Brachypodium pinnatum***, ***Centaurea scabiosa***, *Briza media*, *Scabiosa columbaria*, *Galium pumilum*, *Cirsium acaule*, *Thymus pulegioides*, *Fissidens cristatus*, *Campylium chrysophyllum*. Management: cutting with removal once per yr.

Ericion tetralicis (trunk communities and *Lycopodio-Rhynchosporetum*), 6 sites (31 species).

Heath or grass-heath vegetation on wet, nutrient-poor, very acid soils. Species: ***Erica tetralix***, ***Molinia caerulea***, ***Agrostis capillaris***, *Lycopodiella inundatum*, *Drosera intermedia*, *Rhynchospora fusca*. Management: cutting with removal once per year or once per many years, or none.

Genisto anglicae-Callunetum, 5 sites (25 species).

Heath or grass-heath vegetation on relatively dry, nutrient-poor, very acid soils. Species: ***Calluna vulgaris***, ***Hypnum jutlandicum***, ***Empetrum nigrum***, ***Deschampsia flexuosa***, ***Festuca ovina***, ***Dicranum scoparium***, *Genista anglica*, *Genista pilosa*, *Lycopodium clavatum*, *Diphasiastrum tristachyum*. No management.

Spergulo-Corynephoretum, 5 sites (31 species).

Pioneer community on dry, acid, nutrient-poor, humus-poor, sandy soils. Species: ***Corynephorus canescens***, ***Polytrichum piliferum***, various ***Cladonia*** spp., *Agrostis vinealis*, *Spergula morisonii*. No management.

determined after digestion with H_2O_2 at 100 °C followed by a digestion with concentrated sulphuric acid at 300 °C using selenium as a catalyst (Walinga *et al.* 1995). Salicylic acid was added to prevent the loss of nitrate. N and P were measured spectrophotometrically, K using a flame atomic emission spectrometer.

Annual aboveground production was determined as the sum of the standing biomass values at the cuts, including any late autumn regrowth. At unmanaged sites and in cases where only a single (late) cut would take place, peak standing crop was used as an estimate. The amounts of N, P and K annually accumulating in the aboveground biomass were calculated using the nutrient concentrations in the cuts. Production and nutrient accumulation values were averaged over the two years of study to cover some of the between-year variability.

Tissue nutrient concentrations were averaged over all the clippings from a site, using the biomass of the clipping as weights during averaging. The obtained average can be considered the mean tissue concentration of the aboveground vegetation biomass at the times of cutting (or at peak standing crop if unmanaged).

The biomass measurements were obtained for 72 out of 74 plots. Annual production and nutrient accumulation could only be determined for 66 of these, since six sites were dominated by ericaceous dwarf-shrubs. These sites were unmanaged or cut only once every few years, causing the standing crop to reflect the production of several years, not of one.

Soil properties

From January 1993 to January 1995 various soil properties were measured, including *in situ* nitrogen (N) mineralization. All soil measurements refer to the top 10 cm of the soil, unless stated otherwise. Bulked samples consisting of five subsamples taken in a regular pattern were used. Samples were kept cool during transport to the laboratory, stored at 1 - 4° C (for 2.5 days at most), dried at 40 °C, and sieved using a 1 mm mesh. Material remaining in the sieve was weighed so that results could be adjusted to the complete sample-size. Bulk densities were measured by taking five random samples of exactly 0.2 l undisturbed soil using a specially designed auger 10 cm long. Chemical results were expressed on a volume basis (amount ha^{-1} [0-10 cm depth]).

Net annual N mineralization rates were assessed during two full years, by *in situ* incubation during 16 consecutive incubation periods (8 per year). Incubation was achieved using polyvinyl chloride tubes with sharpened lower rims (length 15 cm, inside diameter 2.5 cm) allowing undisturbed soil cores to be obtained (*cf.* Raison *et al.* 1987; Adams *et al.* 1989). The incubated cores were capped only at the top in order to enable the moisture content in the cores to adapt to changes in moisture content outside the tubes to some extent. During each incubation period five pairs of soil cores were used per plot, distributed in a regular pattern. One of each pair served as initial sample, the other remained incubated in the field. The five initial samples were bulked, and the same was done with the five incubated samples after retrieval.

Dried samples were extracted using 0.01*M* $CaCl_2$, which is a weak extraction solution approaching the average concentration of many soil solutions (Houba *et al.* 1986, 1994, 1996). Extraction was performed using 3 g soil in 30 ml of extraction solution by shaking for two hours. After centrifuging for 10 minutes at 3000 g, the centrifugate was used for spectrophotometric determination of NO_3-N and NH_4-N by a Segmented Flow Analyzer (Skalar, Breda, the Netherlands). N mineralization rate per incubation interval was defined as the amount of mineral N (NO_3-N + NH_4-N) in the incubated sample minus the amount of mineral N in the reference sample. Annual mineralization rates were calculated for both years and averaged.

Available amounts of NO_3, NH_4, PO_4 and K were determined at regular intervals (8 times per year, 17 sampling dates in total). $CaCl_2$ extraction was used as described above. Mineral N was taken to be the sum of NO_3-N and NH_4-N, and overall average amounts were calculated. The fraction of mineral N occurring as NO_3 was labelled the nitrification degree (not to be confused with the actual rate of the nitrification process). The available N:P ratio was expressed as the ratio between the average amounts of mineral N and PO_4-P.

Soil pH was measured twice, once in winter (early January) and once in summer (August). Both values were averaged as differences were generally small. Measurement took place in the settling suspension of the $CaCl_2$ extracts, before centrifuging (Houba *et al.* 1994; Schofield & Taylor 1955). The resulting pH-$CaCl_2$ usually takes values approximately halfway between pH-H_20 and pH-KCl (Gupta & Rorison 1975).

Total amounts of N and P were determined once, following the method described above for plant material. Carbon content was determined according to Kurmies (Houba *et al.* 1995), by oxidizing the organic matter with $K_2Cr_2O_7$ in very strong sulphuric acid for 1.5 h at 100 °C. The concentration of Cr^{3+} formed was measured spectrophotometrically. C:N ratios were calculated. The amount of carbonates and bicarbonates was determined by treating the samples with HCl and measuring the volume of CO_2 that evolved. Cation exchange capacity (CEC) was assessed at the actual soil pH and at a low ionic strength using unbuffered $BaCl_2$ (Houba *et al.* 1995). Granular composition was determined using a method based on differences in sedimentation velocity. Measured were the percentages of clay ($<2\mu$), fine silt ($2-16\mu$), coarse silt ($16-65\mu$), and sand ($>65\mu$). Organic matter contents were measured by weight-loss on ignition at 550 °C and were corrected for the loss of water bound to clay minerals using the soil clay content (Houba *et al.* 1995).

Soil moisture content was measured at all 17 sampling dates, and expressed on a volume basis. Groundwater level up to 1.5 m below surface was also determined at these dates. Soil pF values at each of these 17 sampling dates were estimated on the basis of matric potential characteristics obtained from literature (Wösten *et al.* 1994), using the soil moisture content, granular composition and organic matter content. For each of these three variables (moisture, groundwater, and pF), the annual average, the average highest, and the average lowest value over the two years of study were also calculated.

Other site conditions and management

Two non-edaphic site conditions are used in this study, both related to the overstory tree- or shrub-layer present at some sites. The variable 'tree presence' describes the presence or absence of such an overstory layer. A zero value indicates no trees/shrubs are present (no shading), value 1 indicates there are (some form of shading is present). The second variable indicates the number of roadsides with trees. As this translates into a crude indicator of the amount or duration of shading, the variable is tentatively labelled 'shading intensity'. Value 0 indicates no trees (unshaded). Value 1 indicates trees were present on the studied roadside only (shading from one side only). Value 2 indicates trees are present on both roadsides (shading from both sides). The two non-zero values largely parallel the two community-types containing overstory trees and/or shrubs: the *Alliario-Chaerophylletum* (shading intensity always 1) and the *Urtico-Aegopodietum* (shading intensity generally 2).

The main management variable describes the frequency of mowing (0/1/2 cuts per year). Related variables indicate the presence/absence of mowing, and whether or not mowing took place in May/June (early summer) in addition to a cutting later in the year (autumn). A third variable indicates whether or not the cuttings were removed. In one vegetation-type (*Phleo-Tortuletum*) no management took place, but the sites were grazed by rabbits. Here, management was regarded as equivalent to mowing with removal. Mowing frequency was coded as 1 (the intermediate value).

Data analysis

Stepwise multiple regression (Sokal & Rohlf 1995) was used to determine the best set of explanatory variables for each dependent variable under study. First, individual biomass characteristics were analysed. In this case, other biomass characteristics were not allowed as explanatory variables, only variables belonging to the categories: soil properties, management, and non-edaphic site conditions. To meet the second objective of this study, soil nutrient availability variables were used as the dependent variables to be explained. Here, other soil chemical properties were not allowed as explanatory variables, only variables belonging to the remaining categories (preferably biomass characteristics). See Fig. 1 for a schematic visualization.

At first, this combination of approaches may seem peculiar, as the impression may arise that a simple exchange between dependent and independent variables will be achieved. However, matters are not as simple as that in stepwise multiple regression where the new model variables are again selected from the pool of available variables. More fundamentally, the restrictions imposed on the selected variables (the categories to which they should belong), further prevent such simple exchanges. For instance, the model explaining a particular biomass characteristic may contain several soil properties, but if one of these soil properties is subsequently analysed as the dependent variable, other soil chemical properties are no longer allowed as predictors. However, various biomass characteristics can be selected from, and more than one may be selected. Thus, the two approaches cannot be considered reversed versions of the same analysis. Their aims are different, and they are not intended as a validations of each other.

Due to multicollinearity, the inclusion of one particular variable into the model often prohibits the inclusion of another. Sometimes the best statistical result (highest coefficient of determination) is reached using a particular variable, whereas almost the same result (indicated by an R^2 that is only slightly lower) may be obtained with one or two other variables offering a more meaningful interpretation. Therefore, stepwise regression with manually controlled inclusion or removal of variables was performed as well, to find alternative models with similar R^2. This way, not only the ecologically most interpretable regression models could be identified, but also a consistent subset of variables could be searched for, with which the variables under study could be explained satisfactorily. Table 2 presents the ranges for the studied variables and the transformations applied. Up to third order polynomials were allowed in the models.

Table 2. *Range, unit and applied transformation for the studied variables. Soil variables refer to a depth of 0-10 cm.*

Variable	n	Minimum	Maximum	Unit	Transformation
BIOMASS					
Aboveground production	66	0.4	11.6	ton ha^{-1} yr^{-1}	Log(x+0.6)
Aboveground N accumulation	66	4.1	249.3	kg ha^{-1} yr^{-1}	Log(x)
Aboveground P accumulation	66	0.3	32.8	kg ha^{-1} yr^{-1}	Log(x)
Aboveground K accumulation	66	1.7	370.9	kg ha^{-1} yr^{-1}	Log(x)
Tissue-N concentration	72	7.7	26.7	g kg^{-1}	Log(x)
Tissue-P concentration	72	0.4	4.5	g kg^{-1}	Log(x)
Tissue-K concentration	72	2.9	47.4	g kg^{-1}	Log(x)
Tissue N:P ratio	72	4.5	23.0	-	Log(x)
Tissue N:K ratio	72	0.5	3.7	-	Log(x)
Tissue K:P ratio	72	2.5	17.0	-	Log(x)
SOIL					
N mineralization	74	1.4	348	kg ha^{-1} yr^{-1}	Log(x+5.0)
Soil mineral N	74	1.3	24.8	kg ha^{-1}	Log(x)
Soil available P	74	0.01	11.1	kg ha^{-1}	Log(x)
Soil available K	74	4.7	187	kg ha^{-1}	Log(x)
Soil NO$_3$	74	0.14	18.8	kg ha^{-1}	Log(x)
Soil NH$_4$	74	0.79	12.2	kg ha^{-1}	Log(x)
Nitrification degree	74	0.03	0.76	-	Arcsine(√x)
Available N:P ratio	74	1.4	538	-	Log(x)
pH-CaCl$_2$	74	3.7	7.6	-	-
Avg. spring water level	74	≪ -150	-2	cm	classes
Avg. highest water level	74	≪ -150	11	cm	classes
Avg. lowest water level	74	≪ -150	-14	cm	classes
Avg. soil moisture content	74	6.7	86.8	% (v/v)	Arcsine(√(x/100))
Avg. highest moisture content	74	10.0	97.9	% (v/v)	Arcsine(√(x/100))
Avg. lowest moisture content	74	1.2	76.3	% (v/v)	Arcsine(√(x/100))
Avg. soil pF	74	< 1	4.1	-	<1 ➡ 1
Avg. lowest soil pF	74	< 1	2.9	-	<1 ⇒ 1
Avg. highest soil pF	74	< 1	6.0	-	<1 ⇒ 1
Soil total N	74	0.17	8.8	ton ha^{-1}	Log(x)
Soil total P	74	0.08	1.9	ton ha^{-1}	Log(x)
C:N ratio	74	9.4	44.4	-	Log(x)
Cation Exchange Capacity	74	16.5	432.6	kmol + ha^{-1}	Log(x)
Organic matter content	74	0.6	60.9	% (w/w)	Log(x)
CaCO$_3$ content	74	0.0	64.8	% (w/w)	Log(x+0.1)
Percentage clay (<2μ)	74	0.4	46.4	% (w/w)	Log(x)
Percentage particles < 16μ	74	1.3	77.6	% (w/w)	Log(x)
Percentage silt (2-65μ)	74	0.2	65.1	% (w/w)	Arcsine(√x)
Percentage sand (>65μ)	74	3.9	97.0	% (w/w)	Arcsine(√x)
NON-EDAPHIC SITE CONDITIONS					
Tree presence	74	0	1	absent/present	-
Shading intensity	74	0	2	nr. of sides	-
MANAGEMENT					
Mowing frequency	74	0	2	times yr^{-1}	-
Mowing	74	0	1	no/yes	-
Early summer cut	74	0	1	no/yes	-
Removal	74	0	1	no/yes	-

Although the presence of trees was statistically accounted for by the tree variable, the variables accepted in the final regression models were required to show significant relations also when the sites with an overstory tree layer were eliminated from the analysis. For all regression models, analysis of the residuals was performed to ensure that regression requirements (especially the homogeneity of variances) were satisfied.

The performance of the explanatory variables was primarily inspected using their beta coefficients (*i.e.* the *standardized* regression coefficients), which may be considered measures of the relative importance of the explanatory variables. For comparison with bivariate correlation coefficients, partial correlation coefficients (*i.e.* the correlation between an explanatory and the dependent variable when the effects of the other variables in the model are accounted for) were also calculated.

If both a linear and a quadratic term proved significant, two coefficients were connected with the variable, making it impossible to judge the relative importance of the variable from a single coefficient. To facilitate presentation and interpretation in these cases, a simple procedure was applied to obtain a single beta related to the variable. The regression terms ($a\mathrm{x}+b\mathrm{x}^2$) were rewritten to $b(\mathrm{x}-q)^2+c$; where $q = -a/2b$, representing the value at which the optimum or minimum is reached. The new variable $(\mathrm{x}-q)^2$ now reflects the squared deviation from q, and can be used instead of x and x^2 in the regression. Effectively, the same fitted curve is reproduced in an alternative model, but now a single beta associated with the variable is obtained. The beta coefficients of the other variables remain unchanged, as does the coefficient of determination. To obtain significance levels and the adjusted R^2 the original variables were used, since for these purposes q should remain the result of the parameterisation process.

Results

Biomass characteristics

In the model explaining annual aboveground biomass production (Table 3), the only explanatory variable not being a soil property was the intensity of shading. Higher shading intensities (through overstory trees/shrubs) were related to a lower aboveground production of the herb layer. Of the soil properties, particularly the annual N mineralization and the average soil moisture content had important positive effects. Soil pH showed an optimum relation: highest production (under equal conditions concerning the other variables) occurred near pH-$CaCl_2$ 5.7. Finally, an additional independent contribution to the explanation of aboveground production was provided by the amount of soil particles smaller than 16μ (the clay plus fine silt fraction). Its relative contribution (positive) was smallest of all the variables in the model. If, instead of N mineralization, the soil mineral N pool was used in the model, the R^2 value decreased considerably (from 80% to 74%).

Tissue N concentration (average for the vegetation biomass) appeared to be influenced most by the frequency of mowing; higher frequencies were related to higher tissue N concentrations. Shading intensity showed the second large influence, with higher shading intensities related to higher N concentrations. Both variables appeared to be of more importance than any of the soil variables. The most important soil variable was the N mineralization. Soil pH again demonstrated a quadratic relationship showing an optimum at pH-$CaCl_2$ 5.9. The fraction of variance explained by the model was 71% (or 68% without pH).

Tissue P concentration also appeared to be influenced most by the frequency of mowing. In this case its relative importance was much higher than that of any other variable. Shading intensity did not show a significant contribution (although a weak positive partial relation may be indicated at $p=0.108$). The most important soil variable was pH. Again the relationship was quadratic, with the optimum at pH-$CaCl_2$ 5.5. Other explanatory soil variables included the amount of available P (positive relation), the amount of mineral N (negative), and the nitrification degree (positive). Also the average soil moisture content contributed significantly (negative).

The model for tissue K concentration resembled the model for tissue P, the explanatory variable soil available P being replaced by soil available K. However, the relative contributions of the variables were different. Soil available K was by far the most important variable explaining tissue K concentration. Soil moisture content did not

Table 3. *Factors affecting biomass characteristics. Regression models obtained by stepwise multiple regression using as possible explanatory variables: soil properties, non-edaphic site conditions and vegetation management. For each variable the standardized regression coefficient (beta coefficient), the partial correlation coefficient (small typeset), and the significance are presented. Most important variables in bold.*

CATEGORY	Variable	Above-ground production	Tissue N conc.	Tissue P conc.	Tissue K conc.	Tissue N:P ratio
SOIL PROPERTIES	N mineralization	**+0.61 +0.71** **<0.0001**	+0.30 +0.43 0.0002			
	Soil available P			+0.34 +0.41 0.0007		**−0.65 −0.57** **<0.0001**
	Soil available K				**+0.58 +0.65** **<0.0001**	
	Soil mineral N			−0.16 −0.27 0.0273	−0.24 −0.33 0.0065	+0.46 +0.55 <0.0001
	Nitrification degree			+0.35 +0.53 <0.0001	+0.24 +0.42 0.0004	
	Moisture content	**+0.57 +0.62** **<0.0001**		−0.28 −0.42 0.0004		+0.31 +0.38 0.0015
	Particles <16μ	+0.23 +0.37 0.0036				−0.21 −0.29 0.0164
	$(\text{pH}-\text{optimum})^2$	−0.32 −0.49	−0.21 −0.31	**−0.44 −0.72**	−0.21 −0.43	+0.39 +0.60
	p quadratic term	0.0005	0.0098*	**<0.0001**	0.0003	<0.0001
	p linear term	0.0007	0.0105*	**<0.0001**	0.0003	0.0001
	optimum / minimum	5.73 (opt)	5.85 (opt)	**5.50 (opt)**	5.97 (opt)	5.62 (min)
NON-EDAPHIC	Shading intensity	−0.42 −0.60 <0.0001	+0.37 +0.49 <0.0001		+0.27 +0.50 <0.0001	
MANAGEMENT	Mowing frequency		**+0.44 +0.55** **<0.0001**	**+0.64 +0.76** **<0.0001**	+0.26 +0.51 <0.0001	
	Early summer cut					**−0.57 −0.70** **<0.0001**
	R^2	0.798	0.707	0.845	0.884	0.761
	R^2_{adj}	0.778	0.685	0.828	0.872	0.735
	Nr. of variables	5	4	6	6	6
	Nr. of plots	66	72	72	72	72

*: Not significant at $p=0.05$ when sites with a tree/shrub layer are omitted. At $p=0.06$ significance is retained.

Table 4. *Factors needed to infer soil nutrient availability. Regression models obtained by stepwise multiple regression, with other chemical soil properties excluded as possible explanatory variables. Management variables never contributed significantly. For soil available P and N:P ratio no satisfactory models could be obtained (coefficients of determination below 0.50). For each variable the standardized regression coefficient (beta coefficient), the partial correlation coefficient (small typeset), and the significance are presented. Most important variables in bold.*

CATEGORY	Variable	N mineralization	Mineral N pool	Available P pool	Available K pool	Available N:P ratio
BIOMASS	Aboveground production	**+0.74 +0.74** **<0.0001**	+0.49 +0.46 0.0001		+0.35 +0.42 0.0007	
	Tissue K concentration		**+0.75 +0.63** **<0.0001**		**+0.98 +0.80** **<0.0001**	
	Tissue P concentration		−0.34 −0.34 0.0060		−0.46 −0.52 <0.0001	
NON-EDAPHIC	Shading intensity	+0.45 +0.64 <0.0001				
SOIL (physical)	Soil moisture content	**−0.80 −0.76** **<0.0001**	−0.52 −0.49 <0.0001		−0.27 −0.34 0.0068	
	R^2	0.717	0.531	<0.50	0.693	<0.50
	R^2_{adj}	0.704	0.500		0.673	
	Nr. of variables	3	4		4	
	Nr. of plots	66	66		66	

contribute significantly to the model, but shading intensity again did. Tissue K also showed a quadratic relationship with pH, with optimum values reached at pH-$CaCl_2$ 6.0.

The models explaining the amounts of N, P and K annually accumulating in the aboveground biomass were largely identical to the model for aboveground production (data not shown). However, the fraction of fine particles did not contribute to the explanation of the K accumulation. In addition, the models for the P or K accumulation required as explanatory variables soil available P or soil available K, respectively (positive relations). All three nutrient accumulations also showed an additional significantly positive relation with the presence of an early cut (May/June mowing in addition to a cutting later in the year). The R^2 values were 83, 87 and 86% for the N, P and K accumulation, respectively.

When explaining tissue N:P ratio, both soil available N and P showed significant relationships. However, the relation for soil available P (negative) was stronger than that for soil mineral N (positive). Consequently, a better model was obtained using soil available P and N as individual explanatory variables, than when using the soil available N:P ratio. Other variables showing strongly significant contributions were soil moisture (positive), soil pH (minimum at 5.6), the fraction of fine particles (negative), and the presence of an additional early cutting in May/June (negative). In all, 76% of the variation in tissue N:P ratios was explained.

Summarizing, aboveground production could be explained by a simple model using five variables and explaining 80% of the variation (Table 3). For tissue N the model was most simple of all, involving only four variables, but the variation explained was less (71%). Explanation of the other tissue nutrients required more complex models, but the variation explained was generally higher as well. Tissue K concentrations could be explained best (88% using six variables), mainly due to the strong influence of soil available K.

Soil properties

Soil chemical properties could not be inferred from biomass characteristics only (Table 4). In all cases, the average soil moisture content was needed to obtain acceptable levels of explanation ($R^2 > 50\%$). Since moisture content is not a chemical but a physical property it was allowed in the models, if only to show how this variable complicated the indication of soil nutrient availability by non-edaphic factors. In some cases, shading intensity was needed as an additional explanatory variable as well. Management did not complicate the models further.

Net annual N mineralization could be explained for 72% by three variables (Table 4). Most important were soil moisture content (negative relation) and the annual aboveground production (positive relation). If, instead of production, the annual N accumulation was used, the R^2 was slightly lower (0.5%). Shading intensity showed a significant positive relation, but its contribution was smaller than that of the other variables.

The variation in the pool of soil mineral N was less easily explained. Four variables were needed and the fraction of variation accounted for was 53% only. Again, moisture content and annual production were present in the model, but also tissue P and K concentrations were required. Tissue K (positive relation) was the most important variable in the model, tissue P (negative relation) only played a minor role. Instead of biomass production, N accumulation could be used, yielding a similar R^2 value.

Production was preferred in the presented model, in order to maintain consistency with the other models.

Soil available P could not be explained in a satisfactory way. R^2 values above 50% could only be obtained when next to management also soil pH would be included in the model, but other soil chemical properties were not allowed for the inference of soil available nutrients. The analyses were repeated with subsets including only sites with tissue N:P ratios above or below various threshold values, in an attempt to confine the analysis to sites potentially limited by either P or N. However, no improvement was obtained.

Soil available K could be explained fairly well. The R^2 amounted to 69%, using the same four variables that explained the variation in soil mineral N. Also the signs of the partial relationships were identical, but relative importances changed. Although tissue K concentration was again the most important variable, its relative importance was now substantially larger than that of the other explanatory variables. The importance of soil moisture content was only small. If this variable was omitted an R^2 value of 65% was still maintained. Instead of biomass production, K accumulation could be used in the model, yielding a similar R^2 value.

The soil available N:P ratio could not be explained satisfactory. Weak partial relations appeared to exist with the tissue N:P ratio (positive) and shading intensity (negative). Also management variables showed weak partial relationships, but despite this the variation explained remained below 50%. Like the situation for soil available P, more variation could only be explained if also soil pH would be introduced in the model.

Bivariate correlations

Since multiple regression showed that mutual relationships between soil nutrients and biomass characteristics were generally complicated by other variables, bivariate correlation coefficients were calculated to judge the strength of the mutual relations when these confounding factors are ignored (Table 5). Calculations were performed using all plots ($n=74$), as well as using only the plots without overstory trees ($n=64$).

Although aboveground production was an important variable in multiple regression, its bivariate correlations were only moderate to low. As could be expected, these correlations rose slightly when only the sites without trees (unshaded plots) were considered, but all remained well below $r=0.50$.

Table 5. *Bivariate correlation coefficients between soil nutrient availability and biomass characteristics. Correlations between the average tissue nutrient concentrations and aboveground production are also reported. Top half of the table concerns all plots, bottom half concerns only the plots without overstory trees or shrubs. Significances: *: < 0.01; **: < 0.001 (two-tailed; pairwise deletion of missing values). All values ≥ 0.26 in this table are significant at* p = *0.05. Relatively strong correlations (≥ 0.50) in bold.*

CATEGORY		**SOIL NUTRIENT AVAILABILITY**					**BIOMASS**
Variable		**N mineralization**	**N mineral**	**P available**	**K available**	**N:P ratio**	**Aboveground production**
ALL SITES	*n*	74	74	74	74	74	66
Tissue N concentration	72	.49**	.48**	.44**	.48**	-.30	.28
Tissue P concentration	72	.39**	.28	.49**	.31 *	-.46**	.30
Tissue K concentration	72	.37 *	**.53****	**.54****	**.71****	-.40**	.31
Tissue N:P ratio	72	-.22	-.07	-.41**	-.12	.48**	-.23
Aboveground production	66	.19	.30	.01	.35 *	.17	---
UNSHADED ONLY	*n*	64	64	64	64	64	57
Tissue N concentration	63	.34 *	.30	.18	.33 *	-.05	.48**
Tissue P concentration	63	.17	.04	.26	.12	-.28	.43**
Tissue K concentration	63	.10	.36 *	.31	**.65****	-.18	**.53****
Tissue N:P ratio	63	-.02	.13	-.25	.03	.37 *	-.27
Aboveground production	57	.24	.38 *	.02	.43**	.20	---

The correlations between the availability of a nutrient in the soil and the concentration of the corresponding nutrient in the tissues were just below r=0.50 for N and P, and even dropped to lower values when only the sites without trees (unshaded plots) were considered. The same holds for the available N:P ratio.

The only relatively strong bivariate correlations involve the tissue K concentration. Its correlation with soil available K amounted to 0.71 using all plots, and remained relatively high when only the unshaded plots were considered r=0.65). With soil mineral N and available P correlations were also relatively strong (r just above 0.50), but these dropped substantially when only the unshaded plots were considered ($r \leq 0.36$).

Discussion

Biomass characteristics

Over the wide range of unfertilized ecosystems studied, aboveground biomass production appeared to be affected most by the soil N mineralization. This agrees with the results of other studies. Berendse *et al.* (1987, 1994), showed that mineralization accounts for 70-80% of the vegetation N uptake in unfertilized meadow and heathland ecosystems in the Netherlands. Olff *et al.* (1994) showed grassland regrowth after cutting to be correlated well with annual N mineralization. Mineral N supply is known to limit plant growth in many natural environments (Runge 1983). In the present study, N mineralization explained a larger part of the variation in aboveground biomass production than the pool of soil mineral N. As the mineral N pool is relatively small compared to the N fluxes, this pool is generally thought to supply little information on the amounts of N that can be taken up by the vegetation (Binkley & Hart 1989). The present result confirms this conviction, although over the same wide range of conditions, the pool of soil mineral N was shown to correlate strongly with the annual N mineralization rate in Chapter 7 ($r=0.75$; Schaffers 2000).

Soil moisture content emerged as a factor almost equally important for the explanation of aboveground production. This may not be surprising, although we might have expected an optimum relation caused by oxygen shortage in the rooting zone at the higher soil moisture levels. However, no indication of reduced production at high moisture contents was found within the studied range (including plots with groundwater levels less than 20 cm below ground surface for most of the growing season, and inundated in winter and early spring). This agrees with Thormann & Bayley (1997), who studied peatlands representing the wet end of the range included in the present study, and marshes from even wetter conditions. It may be concluded that species growing naturally under wet conditions are well adapted to low oxygen levels in the rooting zone, and that their production is not hampered by this.

The amount of fine soil particles ($< 16\mu$) also showed a significant positive relation with aboveground production. Soil texture is known to be strongly related to many soil properties, for instance the CEC and the organic matter content. However, many of these properties were explicitly measured, and did not perform better in the model. It is assumed that the effect of soil texture also relates to its effect on moisture fluctuations. Soils with a smaller amount of fine particles may be more prone to moisture fluctuations that hamper production.

Soil pH showed an optimum relationship (under equal conditions concerning the other variables), with maximum aboveground production near pH-$CaCl_2$ 5.7. Most likely, this relationship is not due to pH as such. The concentration of H^+ ions is only of secondary importance for plant growth, except at low pH where the H^+ ion itself may become harmful (Kinzel 1983). However, pH regulates a large number of soil processes (see *e.g.* Scheffer & Schachtschabel 1989). Many of these are related to the solubility of macro- and micronutrients, some of which may become toxic at higher concentrations. Most macronutrients reach maximum availability at intermediate pH, where also the activity of micro-organisms is highest (*e.g.* Rieley & Page 1990). Although a large number of pH related soil properties were explicitly measured, pH nevertheless performed best in this study. Most likely, pH effectively summarizes the effect of a complex of soil chemical properties related to it.

The negative effect of shading (overstory trees) on aboveground production was expected, since only herb-layers were studied. Mowing did not affect the aboveground production.

When explaining tissue nutrient concentrations, it appeared that relationships with the corresponding soil nutrients were present in all cases, but strong only for K. Mutual relations of this kind will be considered in more detail when discussing indication of soil nutrient availability by biomass characteristics.

A remarkable similarity between the models describing the tissue concentrations is the important role of mowing frequency. Its positive effect may be attributed to maintaining the vegetation in a physiologically young state, causing smaller amounts of structural tissues and/or storage polysaccharides (Chapin 1980). In addition, a higher frequency of mowing may reduce reallocation of nutrients to the root system (Goodman & Perkins 1959; Morton 1977; Berendse *et al.* 1987b; Ernst 1975), and also implies less leaching of nutrients from living tissues (Tukey 1970; Morton 1977; Carlisle *et al.* 1966; see also Chapter 3: Schaffers *et al.* 1998). Since biomass production was *not* affected by the frequency of mowing, higher mowing frequencies will lead to higher aboveground nutrient accumulations. This agrees with the positive partial relationships obtained between the annual nutrient accumulations and the presence of an early summer cut in addition to a later cut. Hay-making twice per year will thus remove more nutrients than if hay-making is performed only once at the end of the season. A similar conclusion may be drawn from the results of Oomes & Mooi (1985).

All tissue nutrient concentrations appeared positively affected by the intensity of shading, although not significantly so for P. The higher shading intensities in this study also imply tree-leaf litterfall, moisture and nutrient competition by tree-roots, and other tree-related factors that influence soil properties. However, most of these soil properties were measured, and some were selected in the models. Nevertheless, shading intensity provided highly significant additional information, indicating that direct effects of shading are involved.

Only tissue P was significantly related to soil moisture content. The reason for this should probably be sought in the relationship between soil moisture and P mineralization. P mineralization is likely to be more important than the available P pool, as was already demonstrated for N. Mineralization rates for P are hard to measure, however, and such measurements were not available in the present study. Consequently, soil available P was the variable selected during stepwise regression. The additional selection of soil moisture content may serve to better approximate the actual mineralization of P. The negative sign of the partial relation for moisture may seem puzzling. However, it only holds for situations with similar amounts of available P (since this variable is also present in the model). If P mineralization is assumed to be the actual factor represented by the combination of soil available P and moisture, the implication is that *if* sites have maintained similar pools of available P, the dry sites must have had higher mineralization rates. A parallel situation has been found for N in Chapter 7 (Schaffers 2000), where the annual N mineralization rate appeared to be well described in multiple regression by the pool of soil mineral N (positive), soil moisture content (negative), and soil pH (optimum relation with peak near pH-$CaCl_2$ 5.5). Note that, if soil mineral N is replaced by soil available P, these variables are all involved in the present model for tissue P, with the same signs attached to them and with a very similar pH optimum. Given these considerations the models for tissue P and tissue N may be more similar than they appear at first sight.

For all nutrients, the highest tissue concentrations occurred at pH-$CaCl_2$ values between 5.5 and 6.0. The reasons are probably similar to those discussed for biomass production. For tissue P, however, the relative importance of the optimum pH relationship is remarkably high. This could imply that the mineralization of P is particularly pH dependent. It may also be regarded an expression of the well established fact that especially the solubility of P is highest at intermediate soil pH (*e.g.* Scheffer & Schachtschabel 1989). However, this implicitly puts doubt on the suitability of the available P measurement, since this variable was already present in the model. Possibly, not all the P measured as being 'available' can be used by the vegetation. Measured available P comprises different forms (H_xPO_4 with $x = 0$ to 3). Schachtman *et al.* (1998) suggest that P is taken up only in the monovalent form ($H_2PO_4^-$), based on many studies showing that P uptake rate is highest between pH 5.0 and 6.0 (where the monovalent form dominates). This pH range corresponds remarkably well with the optimum found in the present study.

The effects of soil nutrients cannot always be considered independent of each other. The models for both tissue P and tissue K include not only the available amounts of the corresponding nutrient, but also the amount of mineral N. The negative sign for this relation may imply a 'dilution effect', where higher amounts of soil mineral N (at otherwise comparable soil P or K levels) may stimulate growth and thus dilute the tissue concentrations of P and K. In addition to the negative partial relation for soil mineral N, the models also show a positive partial relation with the degree of nitrification (the fraction of mineral N occurring as NO_3). The combined effect implies a positive partial relation for soil NO_3 (at fixed NH_4) and a negative partial relation for NH_4 (at fixed NO_3), which was confirmed by additional regression analyses. Higher soil NO_3 levels are apparently correlated with higher tissue P and K concentrations whereas higher soil NH_4 levels restrain the tissue concentrations of P and K. This most likely is a consequence of physiological processes associated with NO_3 or NH_4 nutrition. Cation and anion contents have been shown to be much lower in plants supplied exclusively with NH_4, than in NO_3 supplied plants (Kirkby & Mengel 1967; Kirkby 1969). NH_4 may compete with K during uptake (De Wit *et al.* 1963), while an increased uptake of cations with NO_3 nutrition has been shown in many studies (see review by Runge 1983).

The model for the tissue N:P ratio most resembled that for tissue P (with signs reversed). Additional analyses showed tissue N:P to be correlated more strongly with tissue P than tissue N, which may explain this resemblance. Curiously, both correlations are negative (also that for tissue N), implying that for a certain relative change in tissue P, tissue N changes in the same direction, but less. Of the explanatory variables, soil available P was more important than soil mineral N. These results show that particularly P (both in the soil and in the tissues) determines the variation in tissue N:P ratios. This may also indicate that the effects of P-limitation on tissue N:P ratios are stronger than those of N-limitation. Both N- and P-limited vegetation were represented in the study, as judged from the wide range of tissue N:P ratios (4.5 - 23.0; Table 2).

Soil properties

It was demonstrated that, over a wide range of edaphic conditions and plant communities, soil nutrient availability could not be inferred from biomass characteristics only. The average soil moisture content was also needed to obtain acceptable models, and shading intensity was sometimes needed as well. The negative sign of the partial relation for moisture suggests that, *given equal values for the other variables in the model*, soil nutrient measurements are lower if moisture content is higher. For instance, given equal production and shading levels, N mineralization is lower if the average soil moisture content is higher. Apparently, under wet conditions lower mineralization rates suffice to attain similar production levels. Under dryer conditions, higher mineralization rates are needed to attain a similar production. This conclusion may also be drawn from the model explaining aboveground production, presented in Table 3. The possibility that a methodological artifact is involved may be considered here. It could be hypothesized that the incubated soil cores in the wettest sites are susceptible to a rinsing effect due to groundwater level fluctuations, since the incubation tubes were only capped at the top. However, the models for other soil nutrient measurements that do not involve incubation, show similar significant negative partial relations for soil moisture. Apparently, under wetter conditions, also smaller pools of mineral N and K suffice to maintain similar production levels and tissue concentrations.

The consequence is that biomass characteristics *alone*, can only provide information on the soil nutrient status if sites with equal moisture conditions are compared. The one possible exception to this general rule is K, where the confounding effect of moisture is weak. If we seek an indication of the N mineralization, sites should be equally shaded as well. This last restriction may be self-evident, since biomass production (the predictor variable) does not take place in the herb-layer only in sites shaded by trees.

If moisture and shading are similar, N mineralization can be indicated simply by the aboveground production of the herb-layer (partial $r=0.74$). Obtaining an accurate indication of the soil available N and P pools is much less easy, even under equal moisture and shading conditions. For soil mineral N, only slightly more than 50% of the variation could be explained. Soil available P (and also N:P) could not even be adequately inferred at all. The model explaining soil available N also included tissue K and P concentrations. This again shows that nutrients cannot be considered independent of each other.

Evidently, aboveground production is of distinct importance when aiming to infer soil nutrient availability, since it features in all the models, most notably the one explaining N mineralization. Although we might have expected the annual accumulation of nutrients to be more informative (Oomes & Mooi 1985), biomass production appeared equally informative or even slightly better. Also Oomes (1990) concluded that, for practical applications, aboveground production can be used. We should, however, be aware that if soil moisture and shading are *not* accounted for (bivariate correlations), aboveground production never explained more than 12.5% of the variation in any of the soil measurements (up to 19% when only unshaded plots are considered).

An initial expectation was that the availability of a particular nutrient in the soil would largely be reflected by the concentration of that nutrient in the tissues. When analyzing tissue concentrations (Table 3), partial relationships of this kind were indeed present for all three nutrients, although relatively strong only for K. When actually trying to infer soil availability (Table 4), the corresponding tissue nutrient appeared as a predictor variable only for K. In this case, it also proved to be the most informative factor (partial r=0.80). Since the bivariate correlation was still 0.71 (for the unshaded plots 0.65), K availability may be indicated to some extent using its tissue concentration only, even in situations where shading intensities, moisture conditions, and production levels differ. K is known to show strong leaching from living tissues as well as from litter and cut material (Tukey 1970), and it tends to cycle rapidly between the vegetation and the soil (Chapter 3: Schaffers *et al.* 1998). This may explain the close relationship between the soil and tissue concentration of this nutrient.

From several other studies in natural ecosystems, positive relationships between tissue concentrations and the corresponding soil nutrients may be deduced. These include both relationships with total soil amounts (Vermeer & Verhoeven 1985; Diemont 1994; Van Duuren *et al.* 1997a,b; Waughman 1980), and with measures reflecting nutrient availability (Boller-Elmer 1977; Boeye *et al.* 1997; Beltman *et al.* 1992; Wassen *et al.* 1995; Thormann & Bayley 1997; Ertsen 1998; Hayati & Proctor 1990,1991). However, the relationships are seldom very clear and consistent. Hayati & Proctor (1990) reported that variations in tissue concentrations are not necessarily related in a simple way to nutrient availability as measured by conventional soil analysis. In addition, Hayati & Proctor (1991) concluded that "chemical analysis of plant material may be of only limited value as an indication of nutrient availability under natural conditions". The present result confirms this opinion for a wide range of conditions (with the possible exception of K).

The expectation that tissue nutrient concentrations should be related to the soil nutrient status, partly originates in agricultural practice and forestry where it is common to use foliar analysis to assess the nutrient status of crops and stands of trees (De Wit *et al.* 1963; Van den Driessche 1974). Several reasons exist why clear relationships need not be present in natural ecosystems. Many of these are well described elsewhere (Chapin 1980; Van den Driessche 1974; Pegtel *et al.* 1996; Hayati & Proctor 1990,1991) and will not be discussed here. Above all, however, it should be noted that plant communities developing through natural succession are likely to be adapted to the local conditions. Under unfavourable conditions, such communities will consist of species (or ecotypes) capable of maintaining sufficiently high nutrient levels in their biomass. Apart from other physiological adaptations, this may involve a low growth rate, preventing the sparse nutrients from being diluted in the biomass. Therefore, we should not simply expect (semi-)natural vegetation to show low tissue concentrations under unfavourable conditions and high concentrations in fertile situations. Productivity is likely to be more important, which the present study confirms.

Considerable weight is often attached to tissue nutrient ratios, especially in many recent studies on nutrient limitation (*e.g.* Güsewell *et al.* 1998; Koerselman & Meuleman 1996; Pegtel *et al.* 1996; Van Duuren *et al.* 1997a,b; Ertsen 1998; Esselink & Van Gils 1994; Shaver & Chapin 1995). Given the result that nutrients should not be considered independent of each other, this may be appreciated. However, their usefulness is likely to be restricted to the detection of limiting factors, *i.e.* relative nutrient availability. The present study has provided no indication that tissue nutrient ratios can be informative on absolute levels of nutrient availability.

Core relationships

The strongest mutual relationship between soil and biomass characteristics appears to exist between soil and tissue K concentrations. The explanation of tissue K requires information on soil available K (Table 3), the inference of soil available K requires information on tissue K (Table 4), and the mutual relationship is relatively little confounded by other variables (Table 5).

Aboveground production features in all the models explaining soil nutrient availability, most notably that of N mineralization. If the models for aboveground production (Table 3) and N mineralization (Table 4) are compared, a strong resemblance can be noted in the variables involved. We may conclude that important between-category relations involve: biomass production, N mineralization, moisture content, and shading. Secondary variables are soil pH and mowing frequency.

Although relations between biomass characteristics and soil chemical properties are evident, the importance of other variables indicates that such relationship should not be interpreted in a simplified way. In general, they may be obvious only under comparable moisture and/or shading conditions, and sometimes a comparable management may be required as well. Even then, different nutrients do not behave independently. With the possible exception of K, simple relationships between soil properties and biomass characteristics cannot be expected over wide environmental gradients.

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5

Soil, biomass, and management of semi-natural vegetation

II. Factors controlling species diversity

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Soil, biomass, and management of semi-natural vegetation

II. Factors controlling species diversity

Abstract. Using a wide range of unfertilized conditions and plant community types, species diversity was investigated in relation to edaphic and non-edaphic site conditions, management, and biomass characteristics. Both standing biomass and aboveground production were investigated, and their effects compared. Three taxonomic assemblages were studied: vascular plants only, bryophytes included, and terrestrial lichens included as well.

Using a multivariate approach, both species richness and evenness could be explained best for the vascular plants only, emphasising the importance of taxonomic restrictions. The models best explaining species richness required only abiotic conditions. This supports recent theories emphasising the importance of an environmental regulation of the pool of (adapted) species from which the actual species are recruited. Explanatory soil properties were moisture content and pH (both unimodal), and the available N:P ratio. Overstory trees (shading) affected richness negatively. Plots with large perimeter:area ratios had significantly more species than those with low ratios, indicating the importance of consistency in quadrat shape.

Hump-shaped species richness relationships could be identified for both standing biomass and productivity, but they only explained a small part of the variation and were apparent only if soil and management effects were not accounted for. Unimodality (and notably the decreasing phase) was most pronounced for maximum standing biomass, suggesting that competition for light is the key-factor. Productivity as such (*i.e.* without its effect through standing crop) is likely to be favourable for species richness. At intermediate levels of the maximum standing biomass, the positive effect of productivity and the negative effects of standing biomass balance, and high species numbers may be expected.

Hump-shaped biomass relationships were no longer confirmed when soil or management variables were allowed in the models, suggesting that such relationships may arise from the covariation of biomass with other factors. Management explained a much larger part of the variation than the hump-shaped biomass relationship, suggesting that mowing and hay removal (showing independent positive effects) regulate species richness in other ways than through a control of the maximum standing biomass only. In the best explaining models without soil variables, biomass only showed a weak, but significantly positive relationship with species richness. Apparently, high biomass sites need not necessarily be species-poor, as is often assumed.

Species evenness was positively related to the frequency of mowing. In addition, significantly higher evenness values were obtained at sites with low maximum biomass values, but only for the vascular plants.

The numbers of both rare and endangered species were strongly curtailed by high standing biomass, suggesting that these species are more susceptible to competitive exclusion than others. Through its direct as well as indirect effects, management is confirmed to be beneficial not only for general species richness, but also for the occurrence of rare and endangered species.

Key-words: *environmental gradient, maximum standing biomass, mowing, plant communities, productivity, rarity.*

Introduction

The existence of a hump-shaped relationship between plant species richness and biomass or productivity (*e.g.* Grime 1973a,b 1979) has been much debated. Although unimodal relationships have been observed to fit many empirical data sets, much discussion remains about the generality of the relation and the theory behind it (see *e.g.* Petraites *et al.* 1989; Rozenzweig & Abramsky 1993; Tilman 1993; Tilman & Pacala 1993; Abrams 1995; Oksanen 1996; Tilman *et al.* 1996; Aarssen 1997; Rapson *et al.* 1997; Grace 1999).

In one of the first studies proposing the hump-shaped relationship, Al-Mufti *et al.* (1977) compared high biomass sites (each almost completely dominated by a single species like *Urtica dioica, Pteridium aquilinum, Chamaenerion angustifolium, Filipendula ulmaria* or *Petasites hybridus*), with intermediate biomass sites (extremely species-rich limestone grasslands), and low biomass sites (shaded herb-layers of woodlands; species-poor). Although all sites were reported to have been stable during a long period, this choice of sites may not have been very fortunate as we can ask ourselves whether anything else than a hump-shaped curve could have transpired using these data. In the present study a similar wide range of plant communities is studied. However, in an attempt to avoid artefacts and to keep the range of possible explanations broad, several precautions are taken and some additional aspects considered.

First of all, only plant communities are studied that are relatively 'saturated' in a syntaxonomical sense (see Kopecký & Hejný 1974,1978). Also, statistical allowances are made for the presence of a tree-layer.

Since biomass related variables have usually been found to explain only a limited proportion of the variation in species richness (Grace 1999), other factors may be equally or more important. Several authors have argued in favour of multivariate approaches, incorporating not only community attributes, but also environmental factors (Gough *et al.* 1994; Grace & Pugesek 1997; Grace 1999). In the present study, a large number of soil and management variables was therefore included as well.

Rozenzweig & Abramsky (1993) pointed out that different taxonomic groups may reach their peak diversity at different levels of productivity. Abrams (1995) argued that taxonomic restrictions may even be responsible for unimodal relationships. Many studies on diversity of terrestrial vegetation focus on vascular plants. Some also include bryophytes (Pollock *et al.* 1998; Wheeler & Giller 1982; Wheeler & Shaw 1991). Often, however, taxonomic boundaries are not stated and we have to assume that only vascular plants were included (*e.g.* Puerto *et al.* 1990; Oomes 1990, 1992). In the present study species richness was examined using three different taxonomic assemblages: (1) vascular plants only, (2) bryophytes included, and (3) terrestrial lichens included as well. The incentive was to be prepared for possible effects of the applied taxonomic boundary on the relationships observed; not to study individual species groups.

Partly because a of lack of agreement on the mechanisms involved in species richness - productivity relations, some authors focus on the relation with productivity, others on the relation with standing crop. Often, standing crop is used as a substitute for productivity (*e.g.* Tilman *et al.* 1996), and the terms are frequently used interchangeably (Vermeer & Berendse 1983; Zobel & Liira 1997). Actual measurements of production have rarely been used in studies of species diversity (but see Pollock *et al.* 1998). Sometimes surrogate variables have been used (*e.g.* Whittaker & Niering 1975; Huston 1980; Richerson & Lum 1980). Although standing crop will usually correlate strongly with productivity, these variables may relate to different mechanisms and one may be causal, the other not (Rozenzweig & Abramsky 1993). In a recent review, Grace (1999) proposed a theoretical model yielding the expectation that species richness is correlated stronger with biomass than with productivity, and hoped that "the recognition of this important distinction will clarify some of the confusion in the literature on diversity which commonly refers to habitat productivity in vague and undefined ways". In the present study, both standing biomass and productivity were measured, and their relevance for species diversity was compared. For terrestrial systems a similar comparison has only been reported by Wheeler & Shaw (1991) and Wheeler & Giller (1982), for British fens.

The central objective of the present study is to investigate the relationships between species diversity on the one hand, and biomass characteristics, soil properties, vegetation management and other non-edaphic site conditions on the other hand, over a wide range of unfertilized, semi-natural plant communities. Both species richness and evenness will be considered. Next to overall species richness, also the number of rare and endangered species will be studied. The main aim is to establish the factors most strongly related to species diversity. However, special attention will be paid to possible unimodal relationships with standing biomass and aboveground production, their differences, and implications thereof.

Methods

Sites investigated

As part of a synecological study on Dutch roadside plant communities, 74 sites were studied. The sites, scattered over the Netherlands, belong to 14 different semi-natural, unfertilized vegetation types (syntaxa) and reflect a wide range of edaphic conditions. The variation includes: open pioneer vegetation on very dry and nutrient-poor sandy substrates (both at low and high soil pH); grassland communities respectively on dry and nutrient-poor calcareous soils, on loamy soils, and on wet or poorly drained clay or peat; tall-herb grassland communities on (often peaty) soils with permanently high groundwater levels; partly shaded herb communities on light clay or sand; and dry and wet heath and grass-heath vegetation on nutrient-poor, acid sand or loam. The sites differ in the way they were managed by the road authorities. Many sites were mown regularly and in many of these cases the cuttings were removed (hay-making management). For an overview of the studied syntaxa consult Table 1 in Chapter 4.

Site selection was based on syntaxonomic criteria and aimed at obtaining sites that were appropriate representations of the 14 different syntaxa. This entails that, given the constraints of the roadside habitat, sites were required to contain as many species characteristic of the vegetation type as possible, and as few species indicating other syntaxa as possible. Species richness as such was not a selection criterion. Each community type was represented by at least five sites; occasionally six or eight sites were available. The sites had been free of significant disturbances other than vegetation management during the preceding years. The species composition of each site was described by a single 25 m^2 plot. This size was assumed to be large enough to serve as the basis for a total inventory (the community pool in terms of Zobel *et al.* 1998; see also Pärtel *et al.* 1996) and small enough to avoid homogeneity problems.

Species composition

Species composition was recorded in summer 1992. For each species the cover and/or the abundance was noted, using a nine point modified Braun-Blanquet scale (Table 1). In this ordinal scale, cover and abundance are integrated into one figure that may be viewed as a crude logarithmic transformation of the species cover, weighted by the species abundance.

***Table 1.** Ordinal cover/abundance scale after Van der Maarel (1979). The abundance values presented denote the values applied in the present study (plot-size 25 m^2).*

Value	Cover %	Abundance
1	< 5	1
2	< 5	2-50
3	< 5	50-250
4	< 5	> 250
5	5 - 12.5	any
6	12.5 - 25	any
7	25 - 50	any
8	50 - 75	any
9	75 - 100	any

Apart from vascular plants, bryophytes (mosses and hepatics) were also recorded, as well as terrestrial lichens. Epiphytic lichens and lichens growing on dead stems and branches were not recorded. Overstory tree- and shrub-layers (only present in the two communities of woodland- and hedge-margins and usually planted) were disregarded, as well as all juvenile trees and shrubs, as they were considered to occur due to the presence of planted adult specimens. Dwarf shrubs, climbers and lianes were not excluded. A total of 458 species were recorded: 362 vascular plants, 64 bryophytes and 32 lichen species.

Species diversity was investigated using three taxonomic assemblages: 1) vascular plant species exclusively, 2) vascular plants and bryophytes, 3) vascular plants, bryophytes, and terrestrial lichens. Species richness was defined as the number of species per 25 m^2. Species evenness was determined as $E_{2,1}$ (Hill 1973). This evenness statistic is the ratio between Hill's N_2 and N_1 diversity indices. It can be defined alternatively as $e^{H'}/S$ (in which H' is the Shannon-Weiner diversity index, and S is Simpson's diversity index). It is entirely independent of species richness in a mathematical sense when applying the test criteria used by Smith & Wilson (1996). Also $(N_2-1)/(N_1-1)$ was considered as evenness statistic, being Alatalo's (1981) revision of Hill's (1973) original N_2/N_1 ratio, but results were comparable and will not be reported.

Species richness, being a simple species count, gives equal weight to all taxa. Therefore, species rareness was also studied. Rare species are defined here as the species (vascular plants only) occurring in less than 190 of the 1677 grid squares (5x5 km) in the Netherlands (CBS 1991: situation 1990). For each plot the number of endangered species was also counted, *i.e.* species mentioned on the red list of vascular plants for the Netherlands (CBS 1991). This list is based on an integration of the rarity of a species and its rate of decrease.

Biomass characteristics

Biomass characteristics of the aboveground herb-layer were determined in 1993 and 1994 by clipping sub-plots just before the vegetation was mown by the road authorities, or when peak standing crop was assumed to be reached. In sites subject to grazing by rabbits, exclosures were used. Late autumn regrowth, if present, was also sampled. For each sample, five sub-plots of 0.5x0.5 m were cut at ground level. The cut material included living biomass as well as standing dead material. Surface litter was not collected; its amount was small in most cases due to hay-making. The five sub-samples were bulked, dried at 70 °C for 48 hours, and weighed.

Annual aboveground biomass production was determined as the sum of the amounts of standing biomass at each of the cuts during a single year, including any late autumn regrowth. At unmanaged sites and in cases where only a single (late) cut would take place, peak standing crop was used as an estimate. Given the wide range of productivities studied, losses to insects or litterfall were considered negligible.

Maximum standing biomass was defined as the highest amount of standing biomass present at any time during the year. For most sites this is the amount reached just before one of the cuts by the road authorities. I do not refer to this amount as peak standing crop, as this term usually refers to unmanaged situations or exclosures, and as such is often used as an indication of productivity. At unmanaged sites and in cases where only a single (late) cut would take place, maximum standing biomass was equal to the peak standing crop.

Average tissue nutrient concentrations and annual aboveground nutrient accumulation were also assessed, provided no extra information in the present study. See Chapter 4 for further details.

Values for the two years were averaged to cover some of the between-year variability. Biomass measurements were available for 72 out of the 74 plots. Annual aboveground production could only be determined for 66 of these, since the ‘herb-layer’ of six sites was dominated by (woody) ericaceous dwarf-shrubs. These sites were unmanaged or managed only once every few years, causing biomass measurements to reflect the production of several years, not of one.

Soil properties

From January 1993 to January 1995 various soil properties were measured, including *in situ* annual nitrogen (N) mineralization, NO_3-N, NH_4-N, the amount of mineral N (NO_3 + NH_4), the degree of nitrification (NO_3/mineral N), available P (PO_4), available K, available N:P ratio, pH ($CaCl_2$), total N, total P, carbon content, C:N ratio, % organic matter, % $CaCO_3$, % sand, % silt, % clay, CEC, seasonal groundwater levels, seasonal moisture contents, and seasonal pF values. All measurements (except groundwater) refer to the top 10 cm of the soil. Using measured bulk densities, all chemical results were expressed on a volume-wise basis (amount ha^{-1} [0-10 cm depth]), as this was considered the most suitable approach from the plant availability point of view. A detailed description of the analysis procedures followed is given in Chapter 4.

Other site conditions and management

The main management variable describes the mowing frequency (0/1/2 cuts per year). Other management variables indicate the presence/absence of mowing, and whether or not the cuttings were removed. In one vegetation type (*Phleo-Tortuletum*: pioneer communities in sand-dune areas) no actual management took place, but these communities were grazed by rabbits. Here, management was regarded as equivalent to mowing with removal. Mowing frequency was coded as 1, this being the intermediate value.

The main non-edaphic site condition variable distinguishes between the two levels of structural complexity present among the investigated sites, *i.e.* the presence or absence of an overstory tree- or shrub-layer. The variable is labelled 'tree presence', but shading will often be the main factor through which it operates. A zero value indicates no trees are present (no shading), value 1 indicates there are (and thus some form of shading is also present). Value 1 also indicates that all biomass and diversity related variables only concern the herb-layer, and not the total biomass or the total number of species. For these reasons the tree variable was considered a fundamental site condition. A related variable indicates the number of roadsides with trees. As this translates into a crude indicator of the amount or duration of shading, the variable is tentatively labelled 'shading intensity'. Value 0 indicates no trees (unshaded conditions). Value 1 indicates shading from one roadside only. Value 2 indicates trees are present on both roadsides (shading from both sides).

Another non-edaphic site condition variable describes the shape of the plot, through the ratio between the perimeter length and the plot area. Plots were always

25 m^2 and square plots were preferably used, but in some verges plots were forced to be long and narrow.

Data analysis

The dependent variables all belong to the category of diversity measures (richness, evenness and rareness). The explanatory variables belong to four different categories: biomass characteristics (annual aboveground biomass production, maximum standing biomass, annual nutrient accumulation, tissue chemical composition), soil properties (physical and chemical soil measurements), vegetation management (mowing frequency, removal of cuttings), and non-edaphic site conditions (presence/absence of trees, shading intensity, perimeter:area ratio).

Stepwise multiple regression (Sokal & Rohlf 1995) was used to determine the best set of explanatory variables, allowing up to 3rd order polynomials in the models. For all regression models an analysis of the residuals was performed to ensure that regression requirements (especially concerning the homogeneity of variances) were satisfied. Table 2 presents the ranges for the main variables and the transformations applied to them. Only a selection of the explanatory variables is presented. Variables absent in Table 2 (mostly soil properties) provided no additional information on species diversity.

Although the presence of trees was statistically accounted for by the tree variable, the variables accepted in the final models were required to show significant relations also when the sites with an overstory tree-layer were eliminated. This way, it was ensured that the results are not spurious relationships resulting from comparing structurally different communities. In the occasional event where presented results do not comply to this requirement, this will be stated.

The performance of the explanatory variables was primarily inspected using their beta coefficients (standardized regression coefficients), which may be considered measures of the relative importances. If both a linear and a quadratic term proved significant, a simple procedure was applied to obtain a single beta related to the variable. The regression terms $ax+bx^2$ were rewritten to $b(x-q)^2+c$; where $q = -a/2b$ representing the value at which the optimum (peak) or minimum of the relation is reached. The new variable $(x-q)^2$ reflects the squared deviation from q, and a single beta is now associated with it. To obtain significance levels and the adjusted R^2, the original variables were used (see also Chapter 4).

Table 2. *Range, unit and applied transformation for the main variables. Units for soil variables refer to a depth of 0-10 cm. For species richness and evenness, the three presented values denote (in order of appearance): vascular plants only, bryophytes included, terrestrial lichens included as well. For species evenness, the minimum value is equal for all taxonomic assemblages.*

Variable	*n*	Minimum	Maximum	Unit	Transformation
SPECIES DIVERSITY					
Species richness	74	7 11 15	62 67 67	-	-
Evenness ($E_{2,1}$)	74	0.871	.959 .946 .946	-	-
Nr. of endangered species	74	0	10	-	Log(x+1)
Nr. of rare species	74	0	13	-	Log(x+1)
BIOMASS[•]					
Max. standing biomass	72	0.4	13.3	ton ha^{-1}	Log(x+0.6)
Aboveground production	66	0.4	11.6	ton ha^{-1} yr^{-1}	Log(x+0.6)
NON-EDAPHIC SITE CONDITIONS[•]					
Perimeter:area ratio	74	0.8	2.91	m m^{-2}	Log(x)
Tree presence	74	0	1	no / yes	-
MANAGEMENT[•]					
Mowing frequency	74	0	2	times yr^{-1}	-
Removal	74	0	1	no / yes	-
SOIL[•]					
Soil moisture content	74	6.7	86.8	% (v/v)	Arcsine(√(x/100))
pH-$CaCl_2$	74	3.7	7.6	-	-
N:P ratio (available fractions)	74	1.4	538	-	Log(x)

[•] For a more extensive list of variables available during stepwise multiple regression see Chapter 4. Other biomass characteristics included: tissue N, P and K concentrations; tissue N:P, N:K, and K:P ratios; and annual aboveground N, P and K accumulations. Other non-edaphic site conditions included the shading intensity (0/1/2). Other management variables included the presence/absence of mowing and the presence/absence of a spring or early summer cutting in addition to a later cut. Other soil properties included: *in situ* net annual N mineralization; mineral N; available NO_3-N, NH_4-N, PO_4-P, and K; nitrification degree; total N and P; C:N ratio; CEC; % organic matter; % $CaCO_3$; % sand, silt, clay, and particles <16μ; highest and lowest moisture contents; average, highest and lowest groundwater levels; and average, highest and lowest pF.

Some variables appeared to show an interaction with the presence of trees. The effects of these variables were significant only in the sites without trees (unshaded sites), while in the sites with overstory trees the effects were not significant (and trends were of opposite sign). Statistically, the most appropriate way to implement interactions in multiple regression would be the use of product variables. However, the resulting models are not easily interpreted, nor presented. Therefore, variables interacting with tree presence were incorporated using variables that are not true product variables but closely resemble them. These variables (here labelled interaction variables) retained their original value for the unshaded sites, and received a constant value (the overall variable mean) for the sites with overstory trees/shrubs. The resulting variable thus represents the original variable under unshaded conditions (64 sites), and loses its variation (and thus its meaning) for the 10 semi-shaded sites. An inconvenience may be that the applied constant could be considered slightly arbitrary, but nevertheless affects the significance of the tree variable. Since the importance of the tree variable was usually beyond doubt ($p< 0.01$) and further emphasised by the significant existence of the interaction, this can be considered a minor inconvenience. The significance of the interaction variable itself does not depend on the constant (as long as the tree variable is also included in the model), although its beta coefficient does. Results for the other variables are not affected, and neither are the R^2 values. In the presented models, values depending on the constant used in interaction variables will be marked. The adopted implementation slightly overestimated the R^2 values compared to the use of true product variables, but differences were less than 2.5% in all cases. Interpretation of the results was essentially identical, though much simplified.

Straightforward multiple regression (not stepwise) was also used. While stepwise regression aims to determine the most important explanatory variables and their relative importance, straightforward multiple regression was used to uncover the relationship with a particular variable while accounting for the confounding effects of a small number of other variables. Because in these cases the aim no longer is to establish the relative importances of the independent variables, unstandardized coefficients will be presented.

Results

Species richness

The best performing models only contained soil properties and non-edaphic site conditions. However, since it is conceivable that biomass characteristics and/or management may summarize the influence of soil properties to some extent, attempts were also made to determine the most important factors when only specific categories of variables were allowed in the explanatory models. This procedure was started using only the non-edaphic site conditions since these were considered to reflect essential differences within the data, and also appeared to be most important of all statistically. Through examination of the differences in R^2, a crude partitioning of the explained variation among different categories of variables could be obtained.

When only the non-edaphic site conditions were allowed in the models (Table 3a), the perimeter:area ratio appeared to be the most important variable explaining the richness of vascular plant species. The larger this ratio (*i.e.* the more narrow the site), the larger the number of species. Also the presence of a tree- or shrub-layer contributed significantly (negative) to the explanation of the species richness (herb-layer only). The variation explained by the two variables is 21%. When other taxonomic groups were included in the species count, the same two variables remained important. The fraction of variation explained steadily increased to 28 and 35%, mainly due to an increase in the relative importance of tree presence (shading).

Next, also management variables were allowed to enter the models (Table 3b). In addition to the two non-edaphic site conditions, mowing frequency and the removal of cuttings appeared to be important variables. However, for both variables a significant interaction with tree presence emerged. The effect of both was significantly positive only for the unshaded sites. For the sites with overstory trees, no significant relations were present; the trends being negative. (Interactions were incorporated using 'interaction variables', retaining their original value and meaning for treeless sites, being constant in shaded sites: see section 'Data analysis'). Due to the introduction of management, the R^2 values improved considerably. Since the same two non-edaphic site condition variables are still present in the models, the increase can be considered a measure of the importance of the two management variables. The importance of management appears largest for the number of vascular plant species. Here the R^2 increased by 38%. Its contribution is smaller if more taxonomic groups are included (29% with bryophytes included, and 12% with lichens included as well). The total R^2 value is now largest for the vascular plant richness (59%), only slightly smaller for the richness when bryophytes

***Table 3** (opposite). Factors affecting species richness. For each variable the standardized regression coefficient (beta) and the significance are presented, respectively. For quadratic relations, the value (back-transformed) at which the optimum is reached is also presented. Models obtained by stepwise multiple regression using different categories of explanatory variables: (A) only non-edaphic site conditions, (B) also management allowed, (C) also biomass characteristics allowed, (D) soil properties permitted as well. Species richness concerns either vascular plants only, or vascular plants and bryophytes, or vascular plants, bryophytes and terrestrial lichens.*

are included (58%), but notably lower (47%) when terrestrial lichens are included too, due to the absence of a significant contribution by the mowing frequency. Since the explanatory variables reflect independent contributions, both mowing and hay removal appear to independently affect species richness in a positive way.

Next, also biomass characteristics were allowed as explanatory variables (Table 3c). Maximum standing biomass appeared to show an additional contribution to the models, although only for the unshaded sites and not when both bryophytes and lichens were also included in the species counts. The non-edaphic site conditions and management variables already included before remained significant, and their relative importances changed only slightly. Compared to the models when biomass variables were not allowed, the gain in explanatory power is relatively small, ca. 4% only. Vascular plant richness still is the variable that can be explained best, as it obtains the highest R^2 value (63%). The percentage of variance explained again decreases with each successive taxonomic group included (62% and 49% respectively).

It should be noted that maximum standing biomass is the biomass characteristic selected, not aboveground production. Annual aboveground production could have been used but it clearly performed less well. Although data on aboveground production were available for only 66 sites (instead of 72), maximum standing biomass still performed better when using the same subset of 66 sites. The R^2 values were higher and the contributions to the models were consistently more significant. Tissue nutrient concentration or aboveground nutrient accumulation never contributed to the species richness models.

When also the soil properties were allowed in the models, the results changed substantially (Table 3d). Both management and biomass variables disappeared from the models entirely and were replaced by soil properties. Tree presence and perimeter:area ratio remained present in the models, and even appeared to be the most important variables now. As before, the relative importance of these variables (especially tree presence) increased when bryophytes or also lichens are included in the species count.

		SPECIES RICHNESS		
CATEGORIES PERMITTED	**Variables**	**VASCULAR PLANTS**	**BRYOPHYTES INCLUDED**	**LICHENS AS WELL**
(A)				
NON-EDAPHIC SITE CONDITIONS	Perimeter:Area ratio	+0.51 0.0001	+0.56 <0.0001	+0.57 <0.0001
	Tree presence	−0.33 0.0069	−0.47 0.0001	−0.58 <0.0001
74 plots	R^2 (R^2_{adj})	0.213 (0.191)	0.284 (0.264)	0.350 (0.332)
(B)				
NON-EDAPHIC SITE CONDITIONS & MANAGEMENT	Perimeter:Area ratio	+0.40 <0.0001	+0.47 <0.0001	+0.56 <0.0001
	Tree presence	$-0.26^{\#}$ $0.0038^{\#}$	$-0.41^{\#}$ $<0.0001^{\#}$	$-0.55^{\#}$ $<0.0001^{\#}$
	Mowing frequency (if no trees)	$+0.40^{\#}$ <0.0001	$+0.31^{\#}$ 0.0009	
	Hay removal (if no trees)	$+0.33^{\#}$ 0.0003	$+0.34^{\#}$ 0.0002	$+0.35^{\#}$ 0.0001
74 plots	R^2 (R^2_{adj})	0.589 (0.565)	0.578 (0.554)	0.473 (0.451)
(C)				
NON-EDAPHIC SITE CONDITIONS, MANAGEMENT & BIOMASS CHARACTERISTICS	Perimeter:Area ratio	+0.38 <0.0001	+0.45 <0.0001	+0.56 <0.0001
	Tree presence	$-0.24^{\#}$ $0.0054^{\#}$	$-0.39^{\#}$ $<0.0001^{\#}$	$-0.54^{\#}$ $<0.0001^{\#}$
	Mowing frequency (if no trees)	$+0.36^{\#}$ 0.0001	$+0.26^{\#}$ 0.0040	
	Hay removal (if no trees)	$+0.40^{\#}$ <0.0001	$+0.41^{\#}$ <0.0001	$+0.36^{\#}$ 0.0001
	Max. standing biomass (if no trees)	$+0.19^{\#}$ 0.0175	$+0.19^{\#}$ 0.0212	
72 plots	R^2 (R^2_{adj})	0.626 (0.598)	0.618 (0.589)	0.487 (0.465)
(D)				
ALL	Perimeter:Area ratio	+0.51 <0.0001	+0.56 <0.0001	+0.59 <0.0001
	Tree presence	−0.55 <0.0001	−0.67 <0.0001	−0.78 <0.0001
(but biomass characteristics and management showed no effects)	$(\text{pH}-\text{optimum})^2$	−0.42 pH 6.31	−0.34 pH 6.33	
	p quadratic term	0.0045	0.0374^{*}	
	p linear term	0.0025	0.0259^{*}	
	$(\text{Moisture}-\text{optimum})^2$	−0.46 53.8 %	−0.46 51.9 %	−0.41 57.9 %
	p quadratic term	<0.0001	<0.0001	0.0057
	p linear term	<0.0001	<0.0001	0.0008
	Soil available N:P	−0.24 0.0286	−0.24 0.0446	−0.45 <0.0001
74 plots	R^2 (R^2_{adj})	0.761 (0.736)	0.724 (0.695)	0.553 (0.520)

[*] : Not significant when sites with trees (semi-shaded sites) are omitted.

[#] : Value depends on the constant applied for the sites with trees in the interaction variable (overall variable mean used).

The soil properties that appeared as important explanatory variables are pH, moisture content, and the available N:P ratio. For the richness of vascular plants only, moisture and pH are the soil variables with the highest relative importance. When bryophytes are included, soil pH still contributes significantly, but significance is lost if the sites with a tree-layer are omitted from the analysis. With the lichens included as well, soil pH no longer contributes significantly, but the relative importance of the available N:P ratio increases. For both soil pH and moisture content the established relations are significantly unimodal and represent optimum relations. For pH the optimum is at 6.3 (pH-$CaCl_2$), and for moisture at 51-58% (v/v). The contribution of the soil available N:P ratio has a negative sign, implying higher species numbers at lower values.

The coefficients of determination improved distinctly with the introduction of the soil properties, especially when lichens are not included in the species count. Again, species richness can be explained best for the vascular plants only: the R^2 amounts to 76%. The variation explained decreases when other species groups are included (72% with bryophytes included, and 55% with lichens included as well). As the models still contain the same two non-edaphic variables already present in Table 3a, the difference in R^2 represents the additional variation explained due to the introduction of the soil variables. It appears that also this contribution is clearly largest for the vascular plants (55%), and decreases if other taxonomic groups are included (44% with bryophytes included and only 20% with lichens also included).

Hump-shaped biomass/productivity relations

In the present section, species richness relationships will be studied for standing biomass and productivity specifically. Instead of relating the variables directly, there is a clear need to filter out the above established effects of plot shape and structural complexity, the effects of which are partly associated with the sampling method. The shape of the plot (perimeter:area ratio) was largely forced by the shape of the roadside habitat, and the structural complexity (tree presence) is associated with the omission of part of the vegetation data: *i.e.* both biomass and species of the overstory tree-layer. By incorporating these variables in the regression, their effect is statistically controlled for. This causes the resulting relations with biomass or productivity to be the relations as they would occur if all sites would have had the same shape and the same basic vegetation structure. This seems a reasonable prerequisite for a meaningful interpretation of the relationships, as well as for a fair comparison with other studies. Since the aim no

Table 4. *Unimodal relationships between species richness and (A) maximum standing biomass or (B) aboveground production, in polynomial multiple regression models. These regressions do not aim to establish the best explaining variables (for this see Table 3) but serve to uncover the bivariate species richness - biomass relationships, while accounting for the confounding effects of plot shape (perimeter:area ratio) and basic vegetation structure (presence/absence of trees). Presented are the unstandardized regression coefficients and their significance, respectively (for units and applied transformations see Table 2). 'BioMax' indicates maximum standing biomass. 'R^2 variable-name' indicates the rise in R^2_{adj} attributable to the addition of the variable in its polynomial form. 'Opt. variable-name' indicates the value of the variable at which peak species richness is reached (back-transformed). Species richness concerns either vascular plants only, or vascular plants and bryophytes, or vascular plants, bryophytes and terrestrial lichens.*

		SPECIES RICHNESS		
CATEGORIES INCLUDED	Variables	VASCULAR PLANTS	BRYOPHYTES INCLUDED	LICHENS AS WELL
(A)				
NON-EDAPHIC SITE CONDITIONS &	Perimeter:Area ratio	+40.8 <0.0001	+43.7 <0.0001	+39.4 <0.0001
	Tree presence	−13.3 0.0016	−17.7 <0.0001	−18.3 <0.0001
MAX. STANDING BIOMASS	BioMax	+72.5 0.0001	+66.6 0.0002	+32.1 0.0299
	BioMax^2	−59.6 0.0002	−55.1 0.0003	−29.9 0.0179
72 plots	R^2 (R^2_{adj})	0.369 (0.331)	0.422 (0.388)	0.410 (0.375)
	R^2 BioMax	0.139	0.121	0.037
	Opt. BioMax (ton ha^{-1})	3.45	3.42	2.84
(B)				
NON-EDAPHIC SITE CONDITIONS &	Perimeter:Area ratio	+32.8 0.0002	+39.0 <0.0001	+36.6 <0.0001
	Tree presence	−13.6 0.0007	−19.0 <0.0001	−19.3 <0.0001
ABOVEGROUND PRODUCTION	Production	+61.0 0.0009	+66.1 0.0003	+34.0 0.0249
	Production^2	−40.3 0.0078	−47.5 0.0014	−26.5 0.0362
66 plots	R^2 (R^2_{adj})	0.408 (0.369)	0.463 (0.428)	0.442 (0.405)
	R^2 Production	0.177	0.161	0.067
	Opt. Prod. (ton ha^{-1} yr^{-1})	5.11	4.36	3.78

longer is to find the most important variables, unstandardized coefficients will be presented instead of beta coefficients.

For both maximum standing biomass and aboveground production, second order terms proved to be significant (Table 4), indicating unimodal relationships. Second order coefficients were particularly large when lichens were not included in the species count.

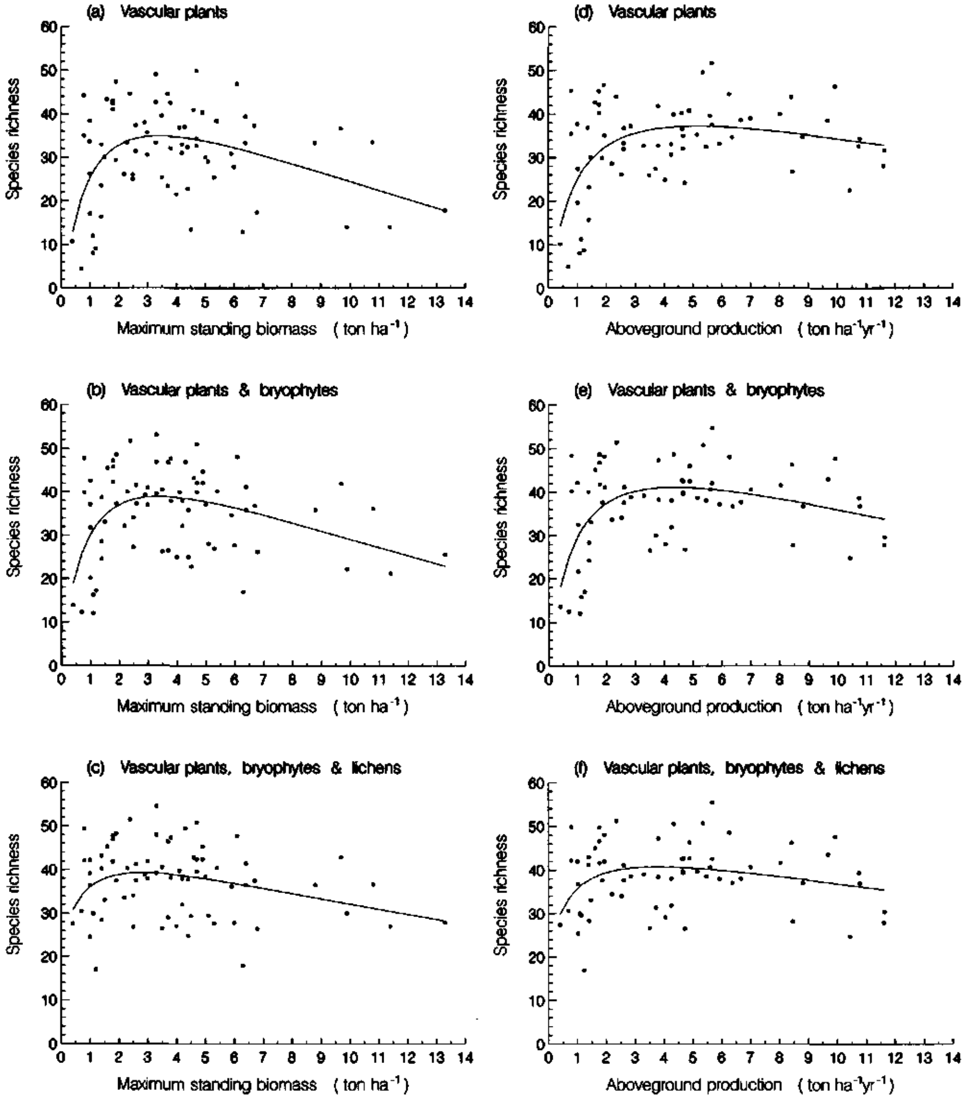

Figure 1. Effects of maximum standing biomass (a-c; left-hand side) and aboveground production (d-f; right-hand side) on species richness. Lines represent the fitted relation (back-transformed) when species richness is adjusted to unshaded conditions (no trees) and a perimeter:area ratio of 1.0 (implying 10 x 2.5 m plots). Dots represent the fitted values plus the residuals for individual plots. For full models: see Table 4.

This signifies that the curvature of the relation is strongest (the hump shape clearest) when lichens are not included.

The variation explained by the hump-shaped biomass or productivity relationships (the rise in R^2_{adj} with their introduction in the models) is largest for the richness of vascular plants only (14% for maximum standing biomass, 18% for aboveground production). It is slightly lower when bryophytes are included in the species count (12 and 16%), and much lower when terrestrial lichens are included as well (4 and 7%, respectively).

Although production contributes more to the explanation of species richness than maximum standing biomass, second order coefficients are consistently larger (and more significant) for the latter. This indicates a stronger curvature and thus a more pronounced hump shape for maximum standing biomass (Fig. 1: a-c *versus* d-f). Differences are clearest for the decreasing part of the curves: species richness decreases much more with increasing maximum biomass than with increasing productivity. The strongest decrease is observed for vascular plants only, where the decreasing part covers 17 species in the relationship with maximum biomass (4.4 with productivity). If bryophytes are included, the decline covers 16 species for maximum biomass (7.3 for productivity). If terrestrial lichens are included in the species count as well, the decrease covers only 11 species for maximum biomass (5.3 for productivity).

Considering the increasing part of the curves, differences are clearest when comparing the different taxonomic restrictions. The increasing part covers the largest span when only vascular plants are included (22 for maximum biomass and 23 for productivity). This range is similar when bryophytes are included (20 and 23), but is much reduced if lichens are included as well (8.6 and 11, respectively).

The values at which species richness peaks also differ (Table 4). For maximum biomass this value decreases from 3.5 ton ha^{-1} if only vascular plants are considered, to 3.4 ton ha^{-1} when bryophytes are included, to 2.8 ton ha^{-1} when terrestrial lichens are included in the species count as well. Aboveground productivities at which the peak is reached are substantially higher: 5.1, 4.4 and 3.8 ton ha^{-1} yr^{-1}, respectively.

Species evenness

Species evenness could only be explained to a considerable extent for vascular plants only (Table 5). If bryophytes are included (or lichens as well) the R^2 remained below 15%. Mowing frequency was the best correlate in these cases. Its correlation was positive, indicating an increase in species evenness with increasing mowing frequencies.

For the evenness of vascular plants only, mowing frequency is similarly involved. However, in this case the maximum standing biomass appeared to play an important additional role. Initial results showed first, second and third order terms to be significant. When this third order polynomial was graphically inspected, however, it appeared to consist mainly of a sharply decreasing segment for maximum biomass values below 1.2 ton ha^{-1}, after which only a very weak increase occurred followed by a similarly weak decrease. The amount of scatter around this fitted line did not warrant a true third order relationship. Effectively, this third order relation only served to distinguish sites with very low biomass (high evenness) from those with higher biomass values (low evenness; Fig. 2). Therefore, a new *ad hoc* variable was introduced, separating the sites with maximum standing biomass below 1.2 ton ha^{-1} (value 0) from those with higher biomass (value 1). This new variable even performed better than the original polynomial, and also appeared to be more important than mowing frequency (beta coefficients; Table 5). Together, both variables explained 55% of the variation in vascular plant evenness.

Maximum standing biomass again performed better than productivity, but the difference is very small. For a comparable *ad hoc* variable for productivity, the classification below/ above 1.2 ton ha^{-1} yr^{-1} only differed for one site.

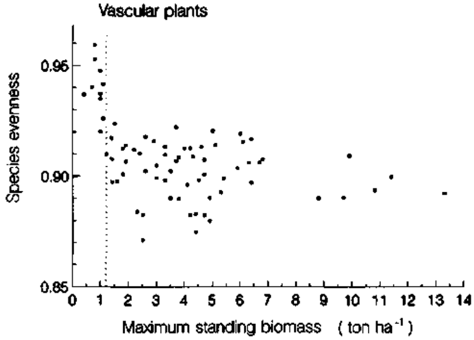

Figure 2. *Effect of maximum standing biomass on the evenness of vascular plant species, after accounting for the effects of mowing (by adjustment to a mowing frequency of 1 for all plots). Dotted line: 1.2 ton ha^{-1}. For full model: see Table 5.*

Table 5. *Factors affecting species evenness. For each variable the standardized regression (beta) coefficient and the significance are presented, respectively. 'BioMax' indicates maximum standing biomass. Evenness concerns either vascular plants only, or vascular plants and bryophytes, or vascular plants and bryophytes and terrestrial lichens. Only management and biomass characteristics exhibit explanatory qualities. Soil properties and/or non-edaphic site condition variables do not possess additional explanatory value.*

		EVENNESS		
CATEGORIES PERMITTED	Variables	VASCULAR PLANTS	BRYOPHYTES INCLUDED	LICHENS AS WELL
ALL	Mowing frequency	+0.37 <0.0001	+0.34 0.0030	+0.37 0.0010
	BioMax $\geq$1.2 (ton ha^{-1})	−0.71 <0.0001		
	R^2 (R^2_{adj})	0.551 (0.538)	0.116 (0.104)	0.140 (0.128)
	Nr. of plots	72	74	74

Rare and endangered species

Both rare and endangered species clearly occurred most in sites on limestone (*Arrhenatheretum festucetosum* and *Mesobromion* communities). Therefore, a distinction will be made between limestone and other sites in this section. An *ad hoc* variable (limestone: 0/1) was introduced for this purpose. In stepwise multiple regression this variable was always selected. Its explanatory power was not exceeded by any combination of other soil factors, including the actual soil $CaCO_3$ content. Almost 57% of the variation in the number of endangered species was explained by it. For the rare species this was ca. 42%.

For the number of endangered species, an additional positive contribution could be established for the removal variable (p=0.0035, R^2 improved from 57 to 62%). Thus, mown sites where cuttings are removed contain significantly more endangered species. For the rare species this relation also existed (p=0.0265, R^2 improved from 42 to 46%), but in this case it appeared to be caused mainly by a few sites all belonging to a single community (*Phleo-Tortuletum*), where removal was atypical as the sites were grazed by rabbits.

When biomass characteristics were also allowed in the models, maximum standing biomass appeared to play a significant role for both endangered and rare species (Table 6a). If, for comparison, aboveground production was used (Table 6b), the amounts of variation explained were slightly smaller. The removal variable still showed an effect additional to those of maximum standing biomass and limestone, but only for the endangered species (total R^2 ca. 67%), and significance was lost when only the unshaded sites were considered.

For the endangered species, first, second and third order terms for maximum standing biomass all proved significant (Table 6a). This polynomial (after back-transformation) effectively represents a steep rise to a maximum around 1.8 ton ha^{-1} followed by a slightly less steep decline, after which the relationship becomes virtually horizontal over the remainder of the studied range. Endangered species thus occur most frequently at relatively low to intermediate levels of maximum standing biomass. For aboveground production (Table 6b), only first and second order terms appeared significant. This corresponds to a wider (less pronounced) hump, and a higher value at which the peak number of endangered species is reached. This difference may also be discerned from simple scatterplots. For maximum standing biomass (Fig. 3a), the sites on limestone (crosses) agree well with the other sites (triangles) concerning the biomass at which most endangered species occur (roughly between 1 and 4 ton ha^{-1}). Using aboveground production (Fig. 3c) the range with highest potentials is less narrowly defined. This can be seen most clearly for the sites not situated on limestone (triangles), showing more than a single endangered species up to production levels of 6 ton ha^{-1} yr^{-1}.

For the rare species, only negative relations with biomass and production appeared (Table 6). This indicates that best potentials for rare species occur at low biomass or production values. For maximum standing biomass, the relationship is steeper (regression coefficients), explains more variation, and is more significant, than for production. Thus, the confinement of rare species to the lowest range is stronger for maximum standing biomass. The difference may be also be discerned from scatterplots (Figs 3b&d). Sites not situated on limestone contain five rare species or more only at maximum biomass values below 3.5 ton ha^{-1}, whereas a similar number can still be found for production values up to 6 ton ha^{-1} yr^{-1}. Three or more rare species only occur at maximum biomass values below 6 ton ha^{-1}, whereas the same number still occurs in a site with a production of 10 ton ha^{-1} yr^{-1}.

Table 6. *Unimodal relationships between the numbers of endangered or rare species and (A) maximum standing biomass or (B) aboveground production, in polynomial multiple regression while accounting for the effects of limestone. To enable the comparison of slopes and shapes, unstandardized regression coefficients are presented (for units and applied transformations see Table 2). The coefficients are followed by their significance. The models under (A) correspond to the best performing models (but see footnote[*] for the endangered species). 'BioMax' indicates maximum standing biomass. 'R^2 variable-name' indicates the rise in R^2_{adj} attributable to the addition of the variable in its polynomial form. 'Opt. variable-name' indicates the value (back-transformed) at which the optimum number of rare or endangered species is reached.*

		RARENESS	
CATEGORIES INCLUDED	**Variables**	**ENDANGERED SPECIES**	**RARE SPECIES**
(A)			
LIMESTONE & MAX. STANDING BIOMASS	Limestone	+0.626 <0.0001	+0.708 <0.0001
	BioMax	+2.844 0.0026	−0.269 0.0396
	BioMax^2	−5.244 0.0028	
	BioMax^3	+2.619 0.0066	
72 plots	R^2 (R^2_{adj})	0.647[*] (0.626)	0.475 (0.460)
	R^2 BioMax	0.065	0.026
	Opt. BioMax (ton ha^{-1})	1.79	very low
(B)			
LIMESTONE & ABOVEGROUND PRODUCTION	Limestone	+0.600 <0.0001	+0.691 <0.0001
	Production	+0.888 0.0220	−0.251 0.0502[#]
	Production^2	−0.897 0.0059	
66 plots	R^2 (R^2_{adj})	0.641 (0.624)	0.473 (0.456)
	R^2 Production	0.057	0.025
	Opt. Prod. (ton ha^{-1} yr^{-1})	2.53	very low

[*]: In this case, also the removal variable contributes significantly ($p=0.0460$), raising the R^2 to 0.668 ($R^2_{adj} = 0.643$; Opt. BioMax = 1.76 ton ha^{-1}). This would subsequently be the best possible model, but the removal variable loses significance when only the sites without trees are considered. Disregarding removal also simplifies comparison with the model under (B).

[#]: When the sites with overstory trees are omitted: $p=0.0162$.

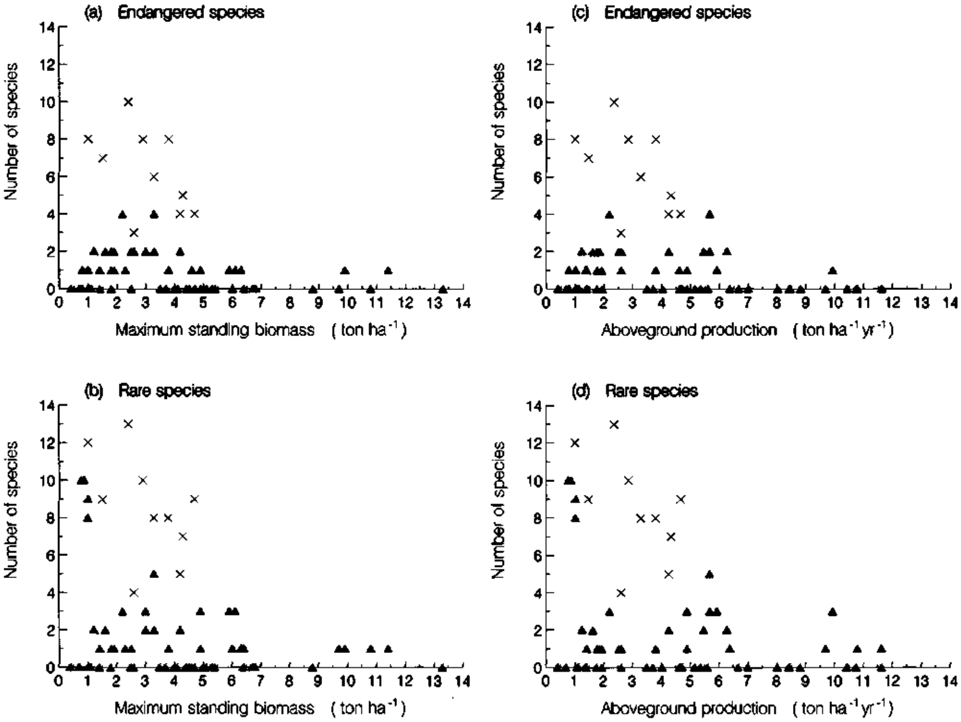

Figure 3. *Scatterplots for the number of endangered species and the number of rare species in relation to maximum standing biomass (a-b; left-hand side) and aboveground production (c-d; right-hand side). Effects of other variables not accounted for. Cross marks represent plots on limestone (Arrhenatheretum festucetosum and Mesobromion communities); other plots represented by triangles. In the limestone plots, aboveground production equals maximum standing biomass as both were estimated by the peak standing crop in these cases.*

Discussion

Species richness

The much debated hump-shaped relationship between biomass (or productivity) and species richness also existed in the present data. The unimodal nature appeared to be most pronounced when using maximum standing biomass instead of aboveground production, which was demonstrated by the stronger effect of the quadratic term and a more distinct decreasing phase (Table 4; Fig. 1).

Few other studies exist that have measured both standing crop and productivity. Wheeler & Giller (1982), studying fen vegetation, indeed found species richness to be more strongly related to standing crop at the end of summer than to their measure of productivity (the April-September biomass increase), but differences were small. Wheeler & Shaw (1991), however, reported a more abrupt decrease in species richness with productivity than with standing crop, but they included litter. For standing crop without litter, their regression equations suggest a slightly steeper relation than for productivity, which is in line with the current results.

The stronger unimodal relation for maximum standing biomass may be an important result, indicating that high biomass values are more detrimental for species richness than high productivity levels as such. Apparently, highly productive sites may still be relatively species-rich if maximum standing biomass values remain low (*e.g.* through disturbances or management). This suggests that particularly competition for space and light may be the cause of the decreasing part of the hump shape. This agrees with the notion that competition for space and light is likely to be of a stronger interspecific nature than competition for belowground resources (Abrams 1988; Newman 1973). Light availability also determines opportunities for germination and seedling establishment. In a fertilization experiment, Tilman (1993) observed that species richness indeed depended strongly on light penetration, and also Grace & Pugesek (1997) showed a clear effect of biomass through the availability of light. Grytnes (2000) showed species richness to be better correlated with vegetation cover than with biomass, again indicating light to be the important factor. These, as well as the present results, confirm the expectation of Grace (1999) that species richness is related more directly to biomass than to productivity.

Environmental stress (productivity) and disturbance (management) have often been considered in relation to species richness (*e.g.* Grime 1973a,b; Huston 1979; Fox 1979). However, both factors also regulate the maximum standing biomass. This may help to understand why the hump-shaped relationship is clearest for maximum standing biomass. If productivity is low (or disturbance high), both standing biomass and species richness will be low. Many species will simply not be able to persist under these stress levels. When environmental stress levels (or disturbance rates) decrease, species richness will increase, but so will maximum standing biomass. Gradually, a shift will occur from belowground competition to aboveground competition for space and light. At a certain point, maximum standing biomass itself becomes the causal factor limiting species richness. It sets its own constraints as soon as space and light competition begin to outweigh the, now reduced, environmental stress and disturbance. Competitive exclusion will now cause species richness to decrease again, and in addition, many species will not be able to germinate and (re-)establish themselves. Highest species richness may thus be expected if a balance exists between environmental stress and disturbance on the one hand, and light and space competition on the other. Such situations exist at intermediate levels of maximum standing biomass. Fig. 4 schematically illustrates this. Note that, at similar disturbance levels, a positive monotonic relation is assumed with productivity as such (*i.e.* without the effect it has through the standing biomass). A negative monotonic relation is assumed for maximum standing biomass as such (*i.e.* without the effects of the factors regulating it). It may be noted that this argument is consistent with the general model described by Grime in 1979, and supports his original decision to use maximum standing biomass on the horizontal axis in his hump-shaped model, not productivity.

The unimodal shape was clearest when only vascular plants were considered. This indicates that different taxonomic groups differ with respect to the standing biomass or productivity at which they reach peak species richness (Rozenzweig & Abramsky 1993). The existence of unimodal relationships may therefore be related, at least partly, to the taxonomic restrictions applied (see also Abrams 1995).

The standing biomass (or aboveground production) at which highest species richness was reached in a number of terrestrial studies are presented in Table 7. These studies were performed in different vegetation types, different countries and have used different plot sizes. Some included bryophytes, and methods also differ with respect to the in- or exclusion of litter. Nevertheless, most studies agree fairly well on an optimum species richness at biomass values between 2 and 6 ton ha^{-1}. The average biomass at which richness peaks is ca. 3.25 ton ha^{-1}, which is in very good agreement with the present results.

We should be aware that a very specific form of covariation exists between maximum standing biomass and vegetation management. Management affects the standing biomass, but reversed, management is also partly guided by the site productivity. Unmown sites will either have very low standing biomass values (when unmown because of low productivity), or very high values as the result of the absence of mowing (sometimes even if productivity is low; for instance in ericaceous dwarf-shrub communities accumulating biomass over several years). Mown sites, especially if mown twice, will generally obtain intermediate values for the maximum standing biomass. Their productivity is high enough to justify mowing, and the cuts prevent the amounts of standing biomass from becoming very large. Unless rather high mowing frequencies are also present, this leads to a unimodal form of covariation where the frequency of

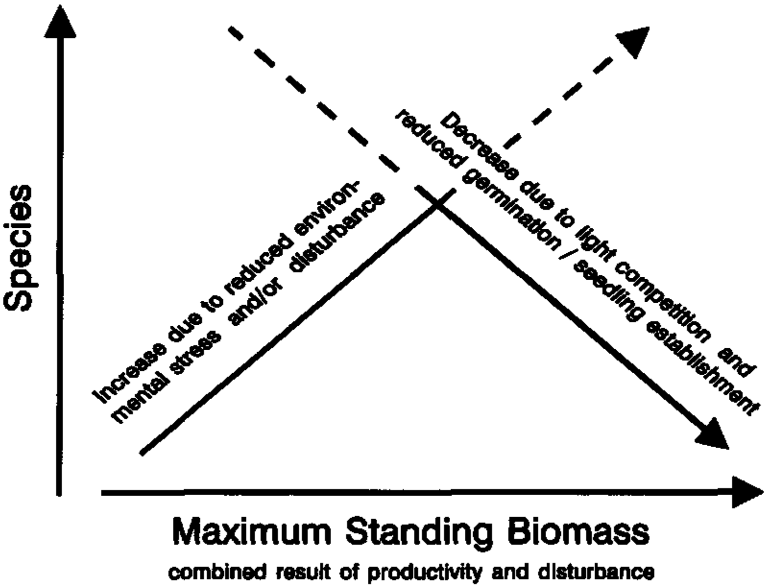

Figure 4. *Conceptual model for the hump-shaped relationship between species richness and maximum standing biomass. Richness is presumed to be limited by two opposite sets of mechanisms: environmental stress and disturbance on the one hand, and space/light competition and reduced germination/seedling establishment on the other. Both are related to the maximum standing biomass: environmental stress and disturbance determine the maximum standing biomass, and maximum standing biomass in turn determines space and light competition. In the left-hand part of the diagram, few species can cope with the high environmental stress levels and/or the high disturbance rates. As standing biomass is low here, light competition and seedling establishment will not limit species richness. If environmental stress and/or disturbance rate is relaxed, maximum standing biomass will increase. This will cause more space and light competition, and at a certain level this will start to limit richness. By then, environmental stress levels and/or disturbance rates are low and no longer limiting. Peak richness is reached at intermediate values for the maximum standing biomass, when both limiting processes balance.*

***Table** 7 (opposite). Standing crop and/or aboveground production at maximum species richness, as inferred from other studies. Presented are the author(s) and year of publication, vegetation types and country of study, plot size used, whether or not bryophytes were included in the species count, and whether or not litter was included in the reported biomass values. If possible, both a range (estimated visually) and a single optimum value (preferably estimated using presented equations) are given, for standing biomass and/or productivity at maximum species richness.*

mowing effectively displays an optimum relation with maximum standing biomass. Since removal of cuttings can only take place if a site is mown, a similar (but weaker) situation exists for the removal variable.

Consequently, we need not be surprised that mowing frequency and hay removal can be used in the regression models (Table 3b) instead of the maximum standing biomass polynomial (Table 4). Remarkably, however, the models using management explain a much larger part of the variation in species richness (59 *versus* 37% for vascular plants). Additional analyses even show the increase in R^2 caused by mowing frequency alone, to considerably exceed that of the maximum standing biomass polynomial (29 instead of 14% for vascular plants). This indicates that effects of management should not be considered only as the result of a general covariation between management and standing biomass, or only as an indirect effect through the control of maximum standing biomass and light regime (*e.g.* Hansson & Fogelfors 2000).

Positive effects of mowing on species richness have been demonstrated in several experimental studies (Oomes & Mooi 1981; Bakker & De Vries 1985; Bobbink *et al.* 1987; Parr & Way 1988; Van Schaik & Van den Hengel 1994; Hansson & Fogelfors 2000). In most of these, independent effects of management cannot be distinguished from the effects through modification of the maximum standing biomass and light regime. However, possible independent effects are many. The actual mowing operation may disturb the upper soil-layer, creating small open patches and various other microhabitats (Parr & Way 1988). The increased heterogeneity may offer possibilities for the establishment of new species and the persistence of others. Moreover, Bakker *et al.* (1995) demonstrated a strong potential for enhanced seed dispersal through the large amounts of seeds that become attached to the mowing machinery. Mowing may even stimulate flowering and seed production in some species. In addition, it strongly impedes succession towards less species-rich shrub communities.

The present results not only indicate a positive effect of mowing, but an independent positive effect of hay removal as well (Tables 3b&c). In many studies, the effects of mowing cannot be distinguished from the effects of removing the cuttings.

Authors	Vegetation types; Country	Plot size (m^2)	Bryophytes incl.	Litter incl.	Standing biomass (ton ha^{-1})	Aboveground production (ton ha^{-1} yr^{-1})
Al-Mufti *et al.* 1977	Woodland herb-layers, limestone grasslands & tall-herb communities; Great Britain	0.25	No	Yes	(3.5) 5.4 (7.5)	
Day, Keddy & McNeill 1988	Marshes; Canada	0.25	No	Yes	(1.5) 2.5 (4.0)	
Dodd *et al.* 1994	Park grass experiment; Great Britain	80 -500	No?	No	≤3.5 (....)	
García *et al.* 1993	Upper salt marsh; Spain	0.25	No?	No?	(1.5) 3.0 (5.0)	
Moore & Keddy 1989	Wetlands; Canada	0.25	No?	No?	(0.6) 1.1 (5.0)	
Olff & Bakker 1991	Grassland; The Netherlands	4.0	No	No?	≤4.0 (....)	
Oomes 1990	Grassland; The Netherlands	100	No?	No?	< (5-6)	
Oomes 1992	Grasslands; The Netherlands	150	No?	No?	(4.6) 5.3 (6.0)	
Pollock, Naiman & Hanley 1998	Riparian wetlands; Alaska	1000	Yes	No?		(1.2) 2.5 (4.0)
Puerto *et al.* 1990	Mediterranean grasslands; Spain	2.5	No?	No?	(1.4) 2.3 (3.4)	
Schaffers (present study)	Woodmargin herb-layers, grasslands, heath-, pioneer-, & tall-herb communities; The Netherlands	25	No Yes	No No	(0.7) 3.5 (6.5) (0.7) 3.4 (6.5)	(0.7) 5.1 (10) (0.7) 4.4 (10)
Vermeer & Berendse 1983	Grass-, wetlands & fens; The Netherlands	0.01 - 0.04	No	No	(4.0) 4.3 (5.0)	
Vermeer & Verhoeven 1987	Fens; The Netherlands	0.4	No	No	(4.5) .... (6.5)	
Walker & Peet 1983	Savannas; United States	0.25 - 625	No	No	(....) 2.8 (....)	
Wheeler & Giller 1982	Fens; Great Britain	0.25	Yes Yes	Yes No	< (14-17) < (7-10)	
Wheeler & Shaw 1991	Fens; Great Britain	4.0	Yes	Yes	(4.0) .... (17)	(0.5) 3.3 (6.0)
Willems 1980	Limestone grassland; The Netherlands	2.25	No	No	(1.5) .... (3.5)	
Wilson & Keddy 1988	Lakeshores; Canada	0.25	No	??	(0.2) 2.8 (3.5)	
Wisheu & Keddy 1989	Lakeshores; Canada	0.25	No	Yes	(0.6) 3.2 (4.0)	
Zobel & Liira 1997	Forest ground-layers & grasslands; Estonia	1.0	No	No?	(1.8) 2.9 (5.0)	

Parr & Way (1988), however, differentiated between these factors in a long term experiment. They first of all showed lowest species richness in the uncut sites and highest richness in the sites mown twice per year. Secondly, they demonstrated an independent positive effect of hay removal, in addition to the effects of mowing. This entirely corresponds to the present results.

Nutrient removal is an important factor associated with hay removal (Oomes & Mooi 1985; Oomes 1990; Bobbink & Willems 1988; Bakker 1987,1989). The amounts annually removed can be substantial and constitute an important component in the soil nutrient balance of mown ecosystems (Berendse *et al.* 1994; Schaffers *et al.* 1998: see Chapter 3). However, nutrient removal likely affects species richness mainly through changes in productivity and standing biomass, which were available as alternatives during regression (Table 3c).

Prevention of litter accumulation is probably the most important independent effect of hay removal. Dickinson (1984) described a large surface accumulation of litter after the cessation of mowing. A dense litter-layer affects seed germination and seedling establishment, as well as the outcome of competition between existing species (Carson & Peterson 1990; Tilman 1993; Foster & Goss 1998; Berendse 1999). Hay removal alleviates the smothering effect caused by leaving cuttings on the site (Parr & Way 1988), which can be considered an extreme case of litter accumulation. Personal field observations suggest this factor to be of much importance due to its sudden nature and the large amounts involved.

It is interesting to note the significant interaction between the effects of management and tree presence. Positive effects of mowing and removal were only present for the sites not shaded by trees. This emphasizes the role of both light and litter in the effects of management, since positive effects on species richness could no longer be confirmed in situation where light is low already, and litter accumulation is high already.

With the effects of management accounted for, the remaining relationship between maximum standing biomass and species richness is monotonic (Table 3c). This relation only holds for unshaded sites and is not very strong, but significantly positive. This positive relationship may be discerned in Fig. 1 as well. While the hump shape itself can (apparently) be described also through the effects of mowing and removal, the fact that this hump shape is slightly tilted reflects the positive relationship with maximum standing biomass.

The implied increase in species richness with increasing standing biomass is well conceivable at very low biomass values. In such habitats only a few species may be adapted to the associated high levels of environmental stress or disturbance (Rozenzweig & Abramsky 1993); an assumption that constitutes the general basis for the increasing part of hump-shaped relationships. However, in the present data the relation remains positive, even in an additional analysis using only sites with maximum standing biomass values above 3 ton ha^{-1} (although no longer significant).

A positive relationship between biomass and species richness that is not restricted to the range of low biomass values only, is not without theoretical support. Tilman *et al.* (1996) experimentally controlled species richness and found standing biomass to be positively related to it. They theorize that a more diverse vegetation may be able to exploit the environment more completely due to complementary resource utilization, which they confirmed for nitrogen. This could even hold to some extent for aboveground resources like space and light. In a low biomass vegetation, little space is available for different aboveground growth strategies or light requirements. In a vegetation with high standing biomass, species with high light requirements as well as species able to endure under shaded conditions may find suitable micro-habitats. This form of niche differentiation could explain why it is standing biomass that is selected for this positive relationship, rather than productivity.

It may be true that high biomass situations are often species-poor and that it is more difficult to find high biomass habitats that are at the same time rich in species. However, the present results indicate that, under equal management conditions, high standing biomass sites need not necessarily species-poor. A clear example from our data are the *Valeriano-Filipenduletum* sites. These tall-herb communities occurring in wet and fertile situations show maximum standing biomass values between 6 and 11 ton ha^{-1} (mown once per year at most), but nevertheless contain 45 species per 25 m^2 on average (38 if adjusted to a standard perimeter:area ratio of 1.0).

The failure of biomass characteristics to explain a considerable part of the variation in species richness has been noted in many studies, even across broad ranges of habitat conditions (*e.g.* Gough *et al.* 1994). The amount of variation explained by biomass parameters is only 25%, over a number of studies (review by Grace 1999). It has been suggested that the species richness of a site first of all depends on an environmental control of the 'species pool' for that site ('potential richness' in terms of Gough *et al.* 1994). Biomass characteristics are assumed to subsequently regulate the richness that is actually realized (see Grace 1999). Using abiotic as well as biomass variables, Grace & Pugesek (1997) were able to explain 45% of the species richness.

In the present study, the use of soil variables made biomass variables entirely dispensable. More than 75% of the vascular plant richness could be explained using habitat conditions only (Table 3d), suggesting environmental determination of the species pool to be of paramount importance. The absence of biomass variables need not necessarily imply that subsequent regulation by standing biomass is unimportant. The most important soil variables in this study were soil moisture and pH, and both appeared to be strong determinants of the aboveground production (Chapter 4). This suggests that environmental factors determining the species pool may often correspond to a considerable extent with the factors governing biomass parameters.

Both soil moisture content and pH showed significantly unimodal relationships (Table 3d). Apparently species richness is highest at intermediate levels. This confirms what is generally expected of species richness along environmental gradients (Odum 1963; Huston 1980). The unimodality of these relations can be understood using the concept of potential richness. The largest pools of well adapted species can be expected in those environments where the evolutionary history of most species was spent. These likely were intermediate ones, simply because most environments are intermediate by definition (as the endpoints of gradients are defined by the presence/absence of living species with their biological restrictions: Abrams 1995). In addition, sites near the endpoint of an environmental gradient can obtain migrants from adjacent species pools in only one direction, while intermediate sites may gain immigrants from pools on both parts of the gradient (Abrams 1995).

A unimodal relation for moisture was previously reported by Whittaker & Niering (1975), although in their case the moisture classes used were based on differences in precipitation along an elevational gradient. Optimum species richness in the present study was at ca. 50-60% soil moisture (v/v), within a total range of 6.5-87%. For soil pH the optimum was also reached at a relatively high value in relation to the total range: ca. 6.3 (pH-$CaCl_2$) within a range from 3.7-7.6. The established relationship signifies that the main decrease in species richness occurs at pH-$CaCl_2$ levels below 5. Grime (1973b,1979) presented a similar result.

One might have expected nutrient availability variables like N mineralization to have been among the most important soil variables for species richness. Again, the established relationships for moisture, pH, and tree presence may already summarize nutrient availability sufficiently (see also part I). The only variable in the models directly related to soil nutrients was the available N:P ratio. Its negative partial relation implies lower species richness at higher N:P ratios (given equal pH and moisture levels). Atmospheric N deposition is causing a shift in the N:P balance in many habitats in the Netherlands, which has been shown to affect species richness (Roem & Berendse 2000). A shift toward high N:P ratios suggests that growth is less likely to be limited by both N and P, while co-limitation by different nutrients is usually considered beneficial for species richness (Braakhekke 1980; Braakhekke & Hooftman 1999).

Tree presence was a strong and constant factor in the richness models. Apparently, the number of species being able to coexist under (semi-)shaded conditions is smaller than that in open situations. This is probably due to increased competition for light, and to negative effects of low light levels and litterfall on germination and seedling establishment (see Foster & Gross 1998). Belowground competition with tree and shrub species may also play a role. The negative effect on species richness was stronger when bryophytes were included in the species count, and strongest when also the lichens were included. Apparently, the numbers of bryophytes and terrestrial lichens are more sensitive to shading than the number of vascular plant species.

The distinct importance of the perimeter:area ratio for plot species richness can be considered a striking result, especially since considerable attention was paid to the aspect of homogeneity in species composition during plot selection. Relatively long and narrow sites were only selected when forced to do so because of the nature of the site. This, however, may also indicate the vicinity of other plant communities with other species. The higher species richness of narrow plots could thus be due to neighbourhood effects (vicinism). On the other hand, it can also be hypothesised that the existence of a long border truly implies better possibilities for colonization and recolonization, resulting in an increase in species richness. The result can further be explained by assuming a certain amount of spatial autocorrelation. This would cause the vegetation of plots with smaller distances between all its parts to be more homogeneous (less species rich) than the vegetation in plots containing longer distances between its parts (more narrow plots). Whatever the cause, the strength of the relationship is remarkable and indicates the importance of consistency in quadrat shape in ecological studies.

A clear trend may be recognised when comparing the results for different taxonomic assemblages. The more taxonomic groups are included in the species count, the smaller the variation that can be explained (Table 3d). Apparently, different taxonomic groups respond to environmental conditions in different ways, making it harder to detect general relationships when too many different groups are included. This emphasises the importance of the taxonomic boundaries applied in studies, and (again) the need for consistency.

Species evenness

Species evenness appeared to be positively related to the frequency of mowing. Since evenness can be seen as a measure of the extent to which a few species dominate, higher mowing frequencies imply less dominance. It is tempting to assume that higher mowing frequencies reduce the intensity of competition and competitive exclusion, and thus reduce the occurrence of strong dominance. If so, the effect is not likely to be mediated through standing biomass. In that case, maximum standing biomass would have been present in the models instead. However, with mosses or also lichens included, maximum standing biomass appeared not to be related to evenness (in an additional analysis it could not even replace mowing frequency). For vascular plants, the effect of mowing was *additional* to an effect of maximum standing biomass (Table 5). We therefore have to assume that the effects of mowing on species evenness are mediated through other mechanisms, most likely similar to the ones affecting species richness. Particularly an increase in small-scale heterogeneity may be an important factor precluding the dominance of one or a few species.

For the vascular plants only, evenness also appeared to be related to the maximum standing biomass. Very few studies exist relating evenness to biomass. Drobner *et al.* (1998) reported a negative relationship which, however, they claim to be an artefact caused by the way abundance values are usually distributed in natural plant communities. This conclusion was cautiously questioned by Weiher & Keddy (1999), who also reported a negative relationship. The present data again show a negative relationship, but its shape does not resemble any of those reported in the previous studies. It rather shows an abrupt decline in vascular plant evenness when maximum standing biomass rises above 1.2 ton ha^{-1}, above which value a weak but not significant negative relationship may be discerned (Fig. 2). This second part possibly corresponds to the artefact reported by Drobner *et al.* (1998). The initial abrupt decline most likely relates to effects of competition for space and light, and probably indicates that there is little interspecific competition between vascular plant species in low biomass situations. When the bryophytes were included (or the lichens as well) evenness was no longer higher in the low biomass sites, suggesting that interspecific competition is important also in low biomass situations for these species. The fact that many bryophyte and lichen species are well adapted to conditions unfavourable for most higher plants may correspond to this observation.

Rare and endangered species

The largest numbers of both rare and endangered species were found at the sites on limestone. To a large extent this will be due to the scarcity of this habitat in the Netherlands, and not to specific ecological processes.

The occurrence of endangered species was positively related to hay removal. Mechanisms comparable to those discussed for general species richness probably apply her. For the rare species this relation was also present but less clear, and could not be confirmed when biomass variables were also allowed in the models.

Best potentials for endangered species existed at relatively low to intermediate values for maximum standing biomass (1 to 4 ton ha^{-1}). Such a range was less narrowly defined using aboveground production. For the rare species, monotonically decreasing relations were obtained, indicating highest potentials at the lowest levels (< 3.5 ton ha^{-1}). Again, this region was less narrow when using productivity.

Since standing biomass was already identified as the factor showing a unimodal effect on general species richness, we need not be surprised that this factor also relates strongly to the numbers of rare and endangered species. However, the effect on these particular species is much more distinct than the effect on general species richness. For the endangered species, the hump shape is more pronounced (compare Fig. 3a and 1a). For the rare species, the decrease is steeper (Fig. 3b *versus* 1a). For both, the range with best potentials is confined to lower biomass values. We may conclude that a poor competitive ability most likely causes these species to be rare or endangered. Fertilization, atmospheric deposition, and other environmental disturbances are widespread phenomena in countries with heavy industrialization or intensive agriculture, promoting the occurrence of species with more superior competitive abilities.

General conclusion

Since: (1) low maximum standing biomass values are particularly important for the occurrence of rare and endangered species, (2) management can prevent large amounts of standing biomass from accumulating, (3) management was shown to be an important factor for general species diversity through more direct effects as well, we may conclude that given the constraints set by the environment, providing or maintaining opportunities for high species diversity in semi-natural vegetation is strongly aided by management.

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6

Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements

Schaffers, A.P. & Sýkora, K.V. (2000). Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. *Journal of Vegetation Science* **11**: 225-244.

Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements

Abstract. Ellenberg indicator values for moisture, nitrogen and soil reaction were correlated with measured soil and vegetation parameters. Relationships were studied through between-species and between-site comparisons, using data from 74 roadside plots in 14 different plant communities in the Netherlands forming a wide range.

Ellenberg moisture values correlated best with the average lowest moisture contents in summer. Correlations with the annual average groundwater level and the average spring level were also good. Ellenberg N values appeared to be only weakly correlated with soil parameters, including N mineralization and available mineral N. Instead, there was a strong relation with biomass production. We therefore endorse Hill & Carey's (1997) suggestion that the term N values be replaced by 'productivity values'. For soil reaction, many species values appeared to need regional adjustment. The relationship with soil pH was unsatisfactory; mean indicator values were similar for all sites at pH>4.75 because of wide species tolerances for intermediate pH levels. Site mean reaction values correlated best (*r* up to 0.92) with the total amount of calcium (exchangeable Ca^{2+} plus Ca from carbonates). It is therefore suggested that reaction values are better referred to as 'calcium values'.

Using abundance values as weights when calculating mean indicator values generally improved results, but, over the wide range of conditions studied, differences were small. Indicator values for bryophytes appeared well in line with those for vascular plants. It was noted that the frequency distributions of indicator values are quite uneven. This creates a tendency for site mean values to converge to the value most common in the regional species pool. Although the effect on overall correlations is small, relationships tended to be less linear. Uneven distributions also cause the site mean indicator values at which species have their optimum to deviate from the actual Ellenberg values of these species. Suggestions for improvements are made.

It is concluded that the Ellenberg indicator system provides a very valuable tool for habitat calibration, provided the appropriate parameters are considered.

Key-words: *calcium, lime, nutrients, pH, productivity, weighted averaging, soil reaction, Zeigerwerte.*

Nomenclature: Van der Meijden (1996) for vascular plants. Margadant & During (1982) for bryophytes. Sýkora *et al.* (1993), Schaminée *et al.* (1995, 1996) and Stortelder *et al.* (1999) for syntaxa.

Introduction

The occurrence and abundance of different plant species enables ecologists to make statements about the prevailing environmental conditions. One formalized and extensively used system of indicator values is that of Ellenberg *et al.* (1992). They assigned indicator values to 2726 Central European vascular plant species, with respect to moisture, soil nitrogen status, soil reaction (acidity / lime content), soil chloride concentration, light regime, temperature and continentality. The values were developed mainly on the basis of field experience, and quantification generally follows a nine-point scale. For some factors, the system also provides indicator values for bryophytes and lichens. The indicator values reflect the ecological behaviour of species, not their physiological preferences (Ellenberg *et al.* 1992). They summarize complex environmental factors (*e.g.* groundwater level, soil moisture content, precipitation, humidity, etc.) in one figure. Values do not refer to conditions at a specific moment but present an integration over time.

Although Ellenberg indicator values were designed for Central Europe, they have also been used outside that region, *e.g.* the Netherlands (Van der Maarel *et al.* 1985), Norway (Vevle & Aase 1980), Sweden (Diekmann 1995), Estonia (Pärtel *et al.* 1996, 1999), Poland (Roo-Zielińska & Solon 1988), Great Britain (Hawkes *et al.* 1997), Northeast France (Thimonier *et al.* 1994) and Central Italy (Celesti Grapow *et al.* 1993). They have been used to interpret indirect ordination results (Persson 1981), to relate vegetation change to environmental changes (Persson 1980), to assess the synecology of plant communities (Jurko 1984), to evaluate the humus form or soil quality in forests (Möller 1997), to study the ecology of urban floras (Wittig & Durwen 1982), to compile the regional pool of potential species for a specific community (Pärtel *et al.* 1996), to estimate the probability of occurrence of species (Dupré & Diekmann 1998), for ecological risk assessment (Latour *et al.* 1994), and many other purposes.

Ellenberg values are most commonly used in calculations based on the complete species composition of plant communities. Because of the ordinal character of indicator values, only a few methods are free from mathematical problems. Examples of such problem-free methods include the use of so-called indicator spectra for sites (Ellenberg *et al.* 1992; Dierschke 1994; Wittig & Durwen 1982), and calculation of the site median (Möller 1987). Nonetheless, the calculation of weighted average indicator values has established itself as an extremely useful technique. Although its mathematical inappropriateness has been stressed repeatedly (Möller 1992, 1997; Dierschke 1994; Melman *et al.* 1988), studies by Ter Braak & Barendregt (1986) and Ter Braak (1995)

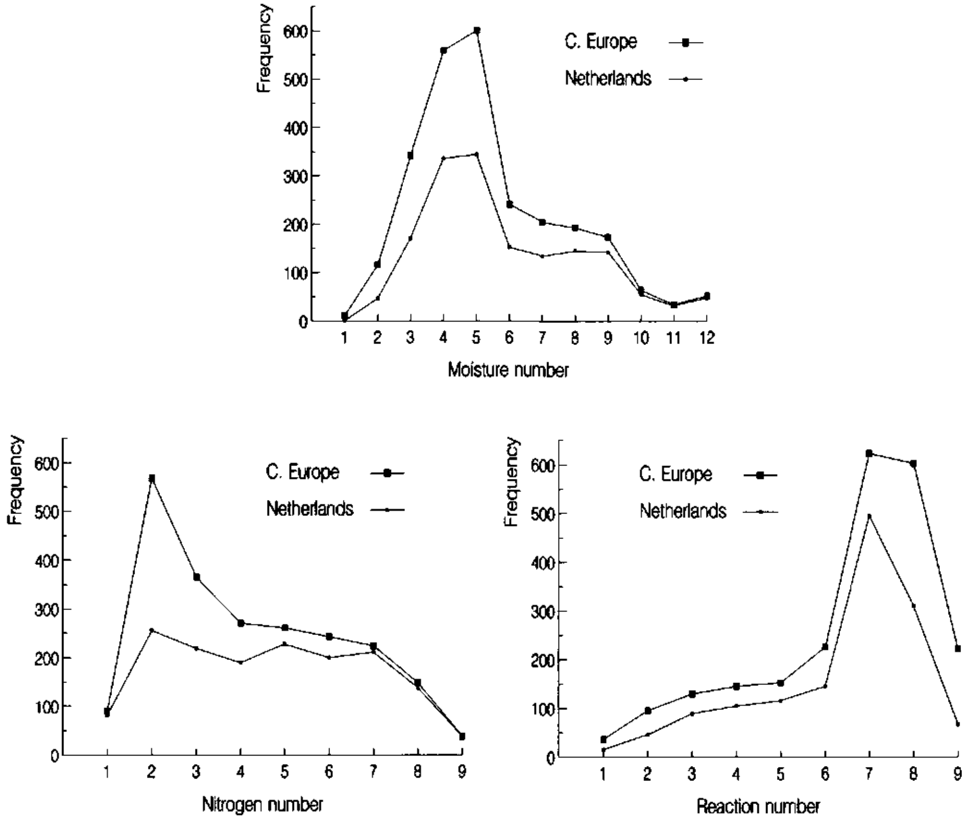


Figure 1. *Frequency distribution (number of species) for the indicator values of vascular plants according to Ellenberg* et al. *(1992) for moisture, nitrogen and soil reaction, respectively. The distributions for both Central Europe and for the Netherlands are presented.*

provided it with a sound theoretical basis. Although restrictions do apply, these studies showed that the calculation of weighted average indicator values can be considered an effective form of calibration.

One aspect which has never received much attention is the uneven distribution of indicator values for the species of a given region (see Fig. 1; also reported by Ellenberg *et al.* 1992). Site mean indicator values may be affected by this frequency distribution. This can be shown using the indicator values for moisture as an example (Fig. 1). The number of species rises from only a few with moisture values 1 and 2, to a very large reservoir of species with indicator values 4 and 5. Since the species pool of a particular community depends on the regional species pool (Pärtel *et al.* 1996) - a notion which also forms the basis for many studies on assembly rules (*e.g.* Law & Morton 1996) - it is more likely for a site with moisture conditions best reflected by indicator value 3 that co-occurring species at that site will have indicator values 4 and 5 rather than values 1 and 2. This may lead to biassed results, a loss of indicative ability, and misinterpretations.

The consistency of the Ellenberg indicator values (not their relation to field measurements) has been studied by others. Van der Maarel (1993) reported that the sociological-ecological species-groups defined for the Netherlands contain species with very similar indicator values. Ter Braak & Gremmen (1987) showed that the moisture values have a reasonable internal consistency in the Netherlands.

Our main objective was to test the reliability of the Ellenberg indicator values for moisture, soil reaction and nitrogen for the Netherlands, using *measured* parameters. We also aimed to establish which environmental parameter is indicated best, as this was never made explicit by Ellenberg (Ter Braak & Gremmen 1987). Other studies showing correlations between indicator values and measured parameters have generally been restricted to specific forest or grassland types, to specific soil types, or to a small number of measured parameters. These studies will be addressed in more detail in the discussion. The present study included a wide range of soil types and plant communities, and a large variety of measurements.

A secondary objective was to examine whether indicator values for bryophytes may be used in combination with those for vascular plants - Ellenberg *et al.* (1992) advocated treating them separately. We also examined whether species abundance values provide extra information compared to using presence/absence data only. Since we hypothesized that the uneven regional frequency distribution of indicator values leads to biassed results, we developed a method to remove this effect enabling us to assess its importance.

Sites and measurements

Sites investigated

As part of a synecological study on Dutch roadside plant communities, 74 sites were studied. The sites (scattered over the Netherlands) belong to 14 different semi-natural

Table 1. *Plant communities involved in the study: number of sites and short description. The term 'trunk community' refers to both basal and derivate communities (Kopecký & Hejný 1974).*

Valeriano-Filipenduletum, 5 sites.
Tall-herb grassland on moist to wet, moderately fertile soils.

Urtico-Aegopodietum podagrariae, 5 sites.
Vegetation of woodland- and hedge-margins, usually semi-shaded. Nitrate-rich, moderately moist soils.

Alliario-Chaerophylletum, 5 sites.
Much like previous community but on drier, more sandy soils.

***Calthion palustris* trunk communities**, 5 sites.
Hay-meadow on moderately fertile, continuously wet soils.

Fritillario-Alopecuretum pratensis, 5 sites. (Fragmentary form, 2 sites; well-developed form, 3 sites).
Hay-meadow on moderately fertile, moderately wet soils (preferably flooded seasonally).

Ranunculo-Alopecuretum geniculati, 5 sites.
Grassland on nutrient-rich soils, flooded in winter and spring. In summer groundwater is deep and soils dry out.

Fragmentary *Triglochino-Agrostietum stoloniferae* (including *juncetosum gerardi*), 8 sites.
Grassland on moderately nutrient-poor, moderately acid, often flooded soils which remain moist year-round.

Fragmentary *Phleo-Tortuletum ruraliformis*, 5 sites.
Pioneer community on dry, relatively calcareous dune sand.

Arrhenatheretum elatioris (excluding *festucetosum arundinaceae*), 5 sites.
Hay-meadow on moderately nutrient-rich, relatively dry soils.

Arrhenatheretum elatioris festucetosum arundinaceae, 5 sites.
Slightly ruderalized *Arrhenatheretum* on moderately nutrient-rich, relatively dry, calcareous soils.

***Mesobromion erecti* trunk communities**, 5 sites.
Chalk grassland, *i.e.* grassland on lime-rich, dry soils.

Ericion tetralicis (trunk communities and *Lycopodio-Rhynchosporetum*), 6 sites.
Heath or grass-heath vegetation on wet, nutrient-poor, very acid soils.

Genisto anglicae-Callunetum, 5 sites.
Heath or grass-heath vegetation on relatively dry, nutrient-poor, very acid soils.

Sperguло-Corynephoretum, 5 sites.
Pioneer community on dry, acid, nutrient-poor, humus-poor, sandy soils.

unfertilized communities, reflecting a wide range of environmental conditions (Table 1). The variation includes open pioneer vegetation on extremely dry and poor sandy substrates (both at low and high soil pH), grassland communities on dry and poor lime-rich soils, on loamy soils, and on wet or poorly drained clay or peat, tall-herb grasslands on soils (often peaty) with permanently high groundwater levels, partly shaded tall-herb grassland communities on clay or sand, and dry and wet heath and grass-heath vegetation on poor, acid sand or loam. Each community was represented by five sites; occasionally six or eight sites were available. Each site was described by a single plot of 25 m^2.

Species composition

The relevés were made in summer 1992 using a nine-point modified Braun-Blanquet scale (Table 2), which combines cover and abundance. In the remainder of this chapter the term 'abundance' will be used to denote values on this combined scale. Both vascular plants and bryophytes were recorded.

The tree and shrub layers in the two partly shaded communities were not considered, as these had usually been planted.

Soil measurements

From January 1993 to January 1995 various soil parameters were measured. All soil measurements refer to the top 10 cm of the soil. Bulked samples consisting of five subsamples were used in all cases. Samples were kept cool during transport to the laboratory, stored at 1 - 4° C (for 2.5 days at most), dried at 40 °C, and sieved using a 1-mm sieve. The material remaining in the sieve was weighed so that the results could be adjusted to the complete sample size. Bulk density was measured by taking 5 random samples of exactly 0.2 1 undisturbed soil using a specially designed auger 10 cm long. Chemical results were expressed on a volume basis (amount ha^{-1}; 0-10 cm depth), as very different soils were to be compared.

Table 2. *Ordinal cover/abundance scale after Van der Maarel (1979). The abundance values presented denote the values applied in the present study (plot-size 25 m^2).*

Value	Cover %	Abundance
1	< 5	1
2	< 5	2-50
3	< 5	50-250
4	< 5	> 250
5	5 - 12.5	any
6	12.5 - 25	any
7	25 - 50	any
8	50 - 75	any
9	75 - 100	any

Net annual N mineralization rates were assessed during two full years. Assessment took place by *in situ* incubation during 16 consecutive incubation periods (8 per year). Incubation was achieved using polyvinyl chloride tubes with sharpened lower rims (length 15 cm, inside diameter 2.5 cm) allowing undisturbed soil cores to be obtained (*cf.* Raison *et al.* 1987; Adams *et al.* 1989). During each incubation period five pairs of soil cores were used per plot, distributed in a regular pattern. One sample of each pair served as initial sample, the other remained incubated in the field. The five initial samples were bulked, and the same was done with the five incubated samples after retrieval.

Dried samples were extracted using 0.01*M* $CaCl_2$ which is a weak extraction solution approaching the average concentration of many soil solutions (Houba *et al.* 1994, 1996). Extraction was performed using 3 g soil in 30 ml of extraction solution by shaking during two hours. After centrifuging for 10 minutes at 3000 g, the centrifugate was used for spectrophotometric determination of NO_3-N and NH_4-N by a Segmented Flow Analyzer (Skalar, Breda, the Netherlands). N mineralization rate per incubation interval was defined as the amount of mineral N (NO_3-N + NH_4-N) in the incubated sample minus the amount of mineral N in the reference sample. Annual mineralization rates were calculated for both years and averaged.

Available amounts of NO_3, NH_4, PO_4 and K were determined at regular intervals (8 times per year, 17 sampling dates in total). $CaCl_2$ extraction was used as described above. Mineral N was taken to be the sum of NO_3-N and NH_4-N, and average amounts were calculated. The nitrification degree was expressed as the fraction of mineral N occurring as NO_3.

Total amounts of N and P were determined once, after digestion with H_2O_2 at 100 °C, followed by digestion with concentrated sulphuric acid at 300 °C under the influence of selenium as a catalyst (Houba *et al.* 1995). Salicylic acid was added to prevent the loss of nitrate. N and P were measured spectrophotometrically using a Segmented Flow Analyzer.

Carbon contents were determined once, according to Kurmies (Houba *et al.* 1995) by oxidizing the organic matter with $K_2Cr_2O_7$ in very strong sulphuric acid for 1½ h at 100 °C. The concentration of Cr^{3+} formed was measured spectrophotometrically. C:N ratios were subsequently calculated.

Soil pH was measured twice, once in winter (early January) and once in summer (August). Measurement took place in the settling suspension of the $CaCl_2$ extracts, before centrifuging (Houba *et al.* 1994; Schofield & Taylor 1955). The resulting pH-$CaCl_2$ usually takes values approximately halfway between pH-H_20 and pH-KCl (Gupta & Rorison 1975).

The amounts of carbonates were determined once by adding HCl and measuring the volume of CO_2 produced. This volume was compared to the volume that developed from pure $CaCO_3$ (the Scheibler method; see Houba *et al.* 1995).

Cation exchange capacities (CEC) were determined once, at the actual soil pH and at a low ionic strength using unbuffered $BaCl_2$ (Houba *et al.* 1995). Samples were equilibrated with a 0.01 *M* $BaCl_2$ solution after saturation with Ba^{2+} by three extractions with 0.1 *M* $BaCl_2$. Subsequently, a known excess of 0.02 *M* $MgSO_4$ was added, causing all Ba^{2+} to precipitate as $BaSO_4$ and causing all sites with exchangeable ions to be occupied by Mg^{2+}. The excess of Mg was measured by flame atomic absorption spectrometry. Exchangeable amounts of the individual bases Ca, Mg, K and Na were analysed in the 0.1 *M* $BaCl_2$ extracts. Ca and Mg were determined by flame atomic absorption spectrometry, K and Na by flame emission spectrometry.

Both individual and total base saturation levels were defined as the ratio of exchangeable positive charges of the bases (Ca, Mg, K and Na; in kmol+ ha^{-1}) relative to the total CEC (kmol+ ha^{-1}). As the results for the total CEC appeared to be unreliable for the peaty soils, only data from the sites with an organic matter content below 15% were used (62 sites).

The absolute amounts of the individual exchangeable bases (Ca, Mg, K and Na) as well as their combined amount (kmol ha^{-1}; ions, not charge), were also used as soil parameters. For Ca, the total amounts present were calculated also, including Ca in the exchangeable form as well as in the form of carbonates. These data were available for all sites except one (73 sites).

Groundwater levels were determined at regular intervals (8 times per year, 17 sampling dates in total), up to 1.5 m below surface. Average levels, average spring levels (March and April), average highest levels (winter) and average lowest levels (summer) were calculated. At several sites groundwater level was permanently below 1.5 m. To circumvent missing values, average depths were transformed to 8 groundwater level classes as shown in Table 3.

Table 3. *Transformation of groundwater depth to groundwater level as applied in this study.*

Level	Groundwater depth (cm)
0	Inundation
-1	+1 to -2
-2	-3 to -30
-3	-31 to -60
-4	-61 to -90
-5	-91 to -120
-6	-121 to -150
-7	-151 or below

Soil moisture contents were also determined at all 17 sampling dates. These were expressed on a volume basis. Annual average, average highest (winter) and average lowest (summer) contents were deduced.

Granular composition was determined once, using a method based on differences in sedimentation velocity (Houba *et al.* 1995). Organic matter contents were determined by weight-loss on ignition at 550 °C and corrected for the loss of water bound to clay minerals using the soil clay content (Houba *et al.* 1995).

Using moisture content, granular composition and organic matter content, soil pF values at all sampling dates were estimated on the basis of matric potential characteristics obtained from literature (Wösten *et al.* 1994). Annual averages, average lowest (winter) and average highest (summer) values were calculated.

Vegetation measurements

Aboveground annual biomass production was determined in both years by clipping subplots just before the vegetation was mowed by the road authorities. This usually took place twice per year (early summer and autumn) or only once (autumn). Any late autumn regrowth (if present) was also determined. At unmanaged sites biomass production was estimated by clipping the peak standing crop in late summer. Per plot, five subplots (0.5mx0.5m) were cut at ground level, bulked, dried at 70 °C for 48 h, and weighed. Tissue concentrations of N, P and K were determined as described for total soil N and P (Walinga *et al.* 1995). Average nutrient concentrations were calculated as a weighted average using the dry matter of each clipping as the weighting factor. Annual aboveground nutrient accumulations were computed.

For two sites, biomass measurements failed in both years. Tissue nutrient concentrations were therefore only available for 72 sites. Annual biomass production and nutrient accumulation could not be measured at some heathland sites containing Ericaceous dwarf shrubs as these sites were managed only once every few years and standing crop measurements therefore reflect the production of several years, not of one. These measurements were also not available for the partly shaded situations where, although part of the actual biomass production consisted of tree biomass, only the herb layer had been clipped. Thus, suitable biomass production and nutrient accumulation figures were available for 57 sites only.

Data analysis

Two weighted averaging approaches were used to relate Ellenberg indicator values to actual measurements: one species-based and the other site-based. In the species-based method, the optima with regard to the measured parameters were calculated for all species, and correlations between these optima and the species indicator values were calculated. In the site-based method, average indicator values per site were calculated, and correlated with the actual measurements for the sites. Many parameters were log-transformed before analysis, some were arcsine-transformed (Table 4).

Table 4. *Ranges, transformations applied, and number of sites used for the variables reported in tables and figures. Units for soil variables refer to a depth of 0-10 cm.*

Variable	Sites	Minimum	Maximum	Unit	Transformation
MOISTURE					
Average groundwater	74	-7	-1	classes	Table 3
Lowest moisture	74	0.012	0.763	(v/v)	Arcsine($\sqrt{x}$)
Highest pF	74	< 1.0	6.0	-	-
NITROGEN					
Soil C:N ratio	74	9.4	44.4	-	Log(x)
Soil total N	74	0.17	8.76	ton ha^{-1}	Log(x)
N mineralization	74	1.45	347.8	kg ha^{-1} yr^{-1}	Log (x+5.0)
Soil mineral N	74	1.31	24.78	kg ha^{-1}	Log(x)
Soil NO_3-N	74	0.14	18.77	kg ha^{-1}	Log(x)
Nitrification degree	74	0.03	0.76	-	Arcsine($\sqrt{x}$)
Soil available PO_4-P	74	0.01	11.10	kg ha^{-1}	Log(x)
Soil available K	74	4.7	187.5	kg ha^{-1}	Log(x)
Tissue N concentration	72	7.74	26.69	g kg^{-1}	Log(x)
N accumulation	57	4.1	249.3	kg ha^{-1}	Log(x)
Biomass production	57	0.4	11.6	ton ha^{-1} yr^{-1}	Log(x)
SOIL REACTION					
pH-$CaCl_2$	74	3.72	7.60	-	-
Base saturation	62	0.00	0.864	-	-
Ca^{2+} saturation	62	0.00	0.817	-	-
Ca^{2+} amount	73	0.0	221.2	kmol ha^{-1}	Log (x+2.5)
Total calcium	73	0.0	7446.3	kmol ha^{-1}	Log (x+0.5)

Species-based correlations

For each species the optimum O for a measured parameter X can be determined by averaging the parameter values X_i for the sites (i=1 to n) in which this species occurs, weighted by the species abundances a_i. The species tolerance T can likewise be estimated by the weighted standard deviation. However, for weighted averaging to yield an effective estimate of the species optimum, the values of the measured parameter should be distributed reasonably uniformly over the sites (Ter Braak & Looman 1986, 1995). As this requirement can never be fulfilled when many different parameters are studied, the optima O_f and tolerance T_f were calculated while compensating for uneven sampling distributions by introducing an extra weighting factor f. For this purpose, the range of each measured parameter was partitioned into eight equally-sized regions and the frequency of samples f_i in the region in which i lies was calculated. The inverse of this frequency was then applied as an extra weighting factor during weighted averaging:

$$O_f = \frac{\Sigma \frac{a_i}{f_i} X_i}{\Sigma \frac{a_i}{f_i}} \quad (1) \qquad T_f = \sqrt{\frac{\Sigma \frac{a_i}{f_i} (X_i - O_f)^2}{\Sigma \frac{a_i}{f_i}}} \quad (2)$$

Including f_i in the equations effectively downweights the influence of oversampled parameter regions and gives more weight to ranges that were rare in our data.

The calculated species optima were correlated with the species indicator values for moisture, nitrogen and soil reaction as given by Ellenberg *et al.* (1992). Correlation coefficients were calculated for two sets, one containing only vascular plants and one including the bryophytes too. Ellenberg N values were not available for bryophytes. Juvenile trees and shrubs were omitted from the species-based analysis as these usually originated from planted specimens nearby. This left a total of 413 species (including 64 bryophytes). An Ellenberg value for at least one ecological characteristic was available for 399 species (including 61 bryophytes).

As calculated optima are less reliable for species occurring only once or twice than for species which occur more frequently, we restricted the correlation analyses to species with a specific minimum number of occurrences. Instead of using the actual number of occurrences (as would be suitable for normal, unweighted averages), the effective number of occurrences n_e (defined analogous to Ter Braak 1887-1992 and to the N_2-diversity index for sites as described by Hill 1973) was calculated:

$$n_e = \frac{\left(\Sigma \frac{a_i}{f_i} \right)^2}{\Sigma \left(\frac{a_i}{f_i} \right)^2} \quad (3)$$

If the weights (a_i / f_i) for a species are equal, then n_e equals the actual number of occurrences of the species. The more uneven the weights, the more n_e decreases to 1. Correlation coefficients were calculated using all species, using only the species with $n_e > 2$, and using only species with $n_e > 4$.

Table 5. *Species-based correlation coefficients for a selection of the parameters measured. Species optima were calculated according to Eq. 1, and correlated with their Ellenberg indicator values. Different species selections were used for the calculation of the correlation, based on the type of species (vascular plants only or bryophytes as well), and on the effective number of occurrences (*n_e*: Eq. 3). Correlation type was either normal, or weighted by the inverse of the standard errors of the calculated optima (Eq. 4). Coefficients* ≥ 0.30 *are significant at* $p = 0.001$*; all coefficients presented are at least significant at* $p = 0.01$ *(one-tailed).*

SPECIES INCLUDED	VASCULAR PLANTS				BRYOPHYTES ALSO			
Selection	All	$n_e>2$	$n_e>4$	$n_e>4$	All	$n_e>2$	$n_e>4$	$n_e>4$
Correlation type	----- Normal -----			Wght 1/SE	----- Normal -----			Wght 1/SE
MOISTURE								
Avgerage groundwater	.72	.79	.79	.84	.70	.78	.78	.82
Lowest moisture	.73	.79	.77	.82	.72	.79	.78	.81
Highest pF	-.73	-.78	-.76	-.74	-.72	-.77	-.76	-.75
NITROGEN								
Soil C:N ratio	-.40	-.36	-.30	-.23	..	..	..	..
Soil total N	.31	.47	.45	.40	..	..	..	..
N mineralization	.39	.39	.41	.47	..	..	..	..
Soil mineral N	.32	.31	.31	.48	..	..	..	..
Soil NO_3	.53	.54	.56	.63	..	..	..	..
Nitrification degree	.57	.57	.59	.60	..	..	..	..
Soil available PO_4	.44	.38	.37	.23	..	..	..	..
Soil available K	.34	.40	.35	.42	..	..	..	..
Tissue N concentration	.52	.56	.64	.62	..	..	..	..
N accumulation	.41	.63	.62	.62	..	..	..	..
Biomass production	.38	.59	.56	.59	..	..	..	..
SOIL REACTION								
pH-$CaCl_2$	.65	.69	.73	.85	.70	.75	.79	.89
Base saturation	.68	.72	.78	.91	.73	.77	.82	.91
Ca^{2+} saturation	.66	.69	.83	.94	.72	.75	.86	.93
Ca^{2+} amount	.66	.73	.81	.87	.72	.77	.86	.92
Total calcium	.63	.70	.76	.71	.69	.75	.81	.79
Number of species								
maximum	310	196	134	134	363	222	148	148
minimum	229	119	54	54	279	142	64	64

We further refined our analysis by using a weighted correlation technique. For this the weighted standard errors of the weighted optima were calculated:

$$SE_{O_f} = \frac{T_f}{\sqrt{n_e - 1}} \qquad (4)$$

Since T_f actually represents a population statistic and not the sample standard deviation, a division by $\sqrt{(n_e - 1)}$ was needed in Eq. 4 instead of a division by $\sqrt{(n_e)}$ in order to obtain an unbiased estimate. The inverse of the calculated SE_{O_f} values were applied as weights during the correlation analysis, thus downweighting the influence of species with less reliable optima. Only species with $n_e > 4$ were used for this procedure.

Site-based correlations

Site mean indicator values were calculated by weighted averaging using different methods. The first approach comprises the conventional ways of calculating the mean indicator values. Here, site mean indicator values mI are calculated by averaging the indicator values I_j of the species ($j = 1$ to k) which occur at the site, either using the species abundances a_j as weights, or simply using presence/absence values.

The other approach aims to compensate for uneven frequency distributions of indicator values in the regional species pool. This was achieved in a similar way as when compensating for uneven sampling distribution in the species-based approach (Eq. 1). An extra weighting factor F_j was introduced, representing the total frequency of I_j (the indicator value of species j) within the regional flora. The site mean indicator value corrected for the distribution of indicator values in a given region was calculated as:

$$mI_F = \frac{\Sigma \frac{a_j}{F_j} I_j}{\Sigma \frac{a_j}{F_j}} \qquad (5)$$

In the present study F_j refers to the whole flora of the Netherlands (Fig. 1). Again, the calculations were performed either using the species abundances a_j as weights, or simply using presence/absence values. All calculations of site mean indicator values were performed twice; once using only the vascular plant species, and once using the bryophytes as well. Ellenberg N values for bryophytes were not available.

***Table 6** (opposite). Site-based correlation coefficients for a selection of the measured parameters. Site mean indicator values were correlated with the values measured at the sites. The site mean indicator values were calculated either using vascular plants only or also using bryophytes, either as normal weighted averages (Normal) or using an extra weight factor to correct for the number of each indicator value present in the total Dutch flora (Eq. 5; Frequency wt.), and either using*

The calculated site mean indicator values were subsequently correlated with the parameter values as measured at the sites. Weighted correlation analyses were not carried out, nor were the analyses restricted to sites with a specific minimum for the effective number of species. We intended to test the site mean values regardless of the number of species, and regardless of the standard deviation of the indicator values present.

Results

Moisture: species-based

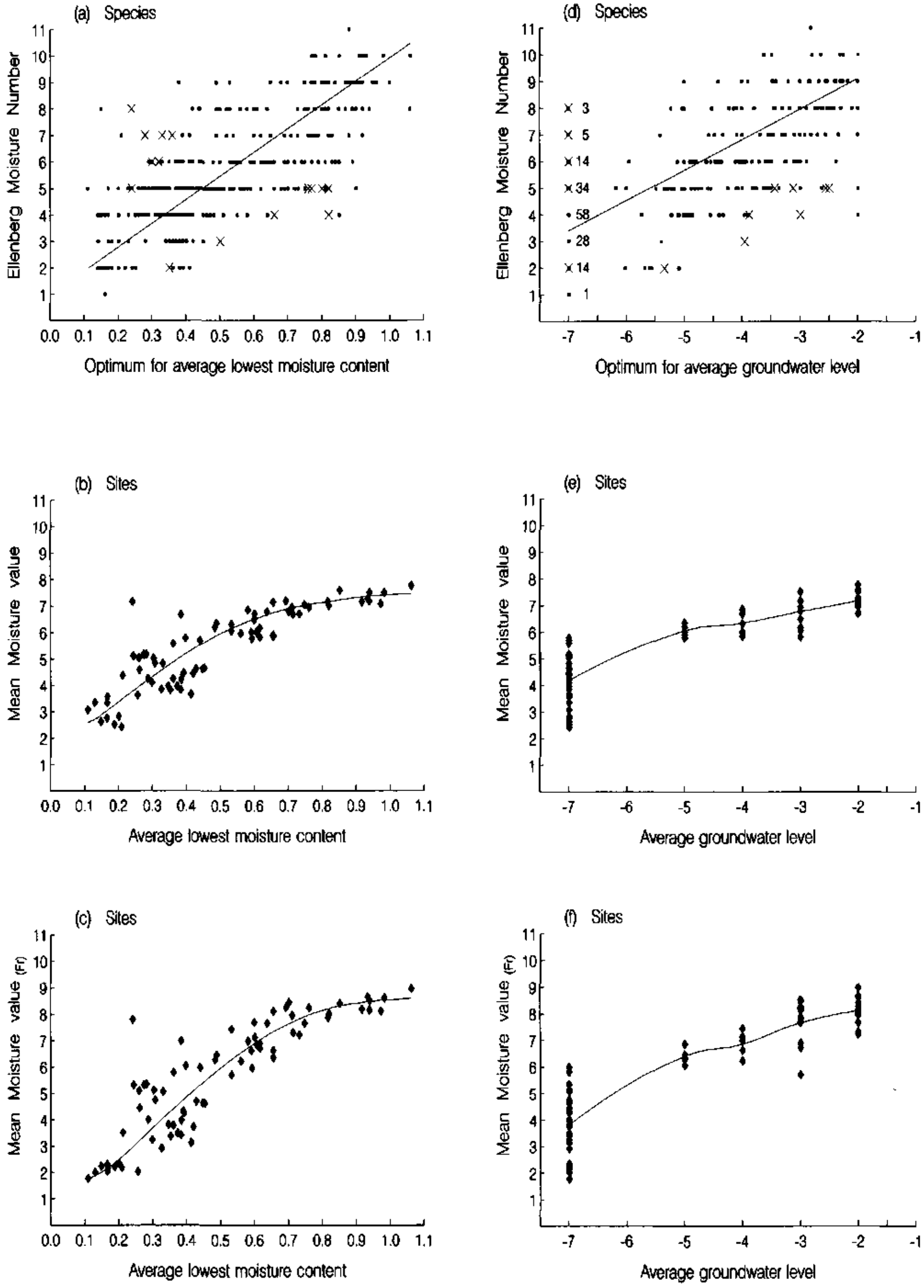
Indicator values for moisture performed very well (Table 5). In general, correlations were strongest with the average annual groundwater level and the average lowest moisture content of the soil in summer (r = 0.72 to 0.73 for vascular plants). When species with a low effective number of occurrences (n_e) were omitted these correlations improved (0.77 to 0.79). Additional weighting by the standard error of the calculated optima further improved the correlations (0.82 to 0.84). For comparison, correlations with the average highest pF are also presented. However, this variable performs slightly less well. If bryophytes are included, correlations were similar, although sometimes slightly lower.

Figs 2a and 2d visualize the results for the average lowest moisture content and the average groundwater level. For several species the indicator values did not match the calculated optima. We more closely investigated all species outside the 90% prediction limits obtained from both a regression of the indicator values on the calculated optima and a regression of the calculated optima on the indicator values. Many of these outliers could easily be explained as species whose actual optima were not sampled as their optima occur outside the plant communities investigated. For other species, however, we suggest an adjusted indicator value would better reflect the Dutch situation (Table 7). These species have been indicated by a cross in the figures.

*presence/absence data (Pres) or using species abundance values as weights (Abun). 'Species adjusted' denotes that the reaction values for 17 vascular plant species were adjusted to the Dutch situation (as in Table 7). 'pH > 5.25' refers to a subset of the data (calculations were performed using the adjusted reaction values in this case). 'ns' denotes not significant (*p *= 0.05; one-tailed). All coefficients calculated using the entire set are at least significant at* p *= 0.0005 (one-tailed).*

SPECIES INCLUDED		VASCULAR PLANTS				BRYOPHYTES ALSO[a]			
Calculation type		Normal		Frequency wt.		Normal		Frequency wt.	
Transformation	*n*	Pres	Abun	Pres	Abun	Pres	Abun	Pres	Abun
MOISTURE									
Avgerage groundwater	74	.87	.87	.88	.88	.88	.88	.88	.88
Lowest moisture	74	.84	.84	.87	.86	.85	.86	.87	.87
Highest pF	74	-.77	-.76	-.77	-.76	-.78	-.77	-.77	-.76
NITROGEN									
Soil C:N ratio	74	-.54	-.54	-.52	-.50	..	..	..	..
Soil total N	74	.61	.61	.62	.61	..	..	..	..
N mineralization	74	.39	.40	.41	.42	..	..	..	..
Soil mineral N	74	.50	.51	.53	.54	..	..	..	..
Soil NO$_3$	74	.68	.69	.69	.69	..	..	..	..
Nitrification degree	74	.66	.67	.65	.65	..	..	..	..
Soil available PO$_4$	74	.51	.51	.53	.52	..	..	..	..
Soil available K	74	.59	.60	.60	.59	..	..	..	..
Tissue N concentration	72	.71	.72	.69	.70	..	..	..	..
N accumulation	57	.83	.85	.83	.85	..	..	..	..
Biomass production	57	.82	.85	.84	.86	..	..	..	..
SOIL REACTION									
pH-CaCl$_2$	74	.79	.79	.78	.78	.79	.80	.79	.80
Base saturation	62	.94	.94	.87	.86	.94	.94	.91	.91
Ca^{2+} saturation	62	.94	.94	.88	.87	.94	.94	.91	.91
Ca^{2+} amount	73	.92	.92	.90	.90	.92	.93	.91	.91
Total calcium	73	.90	.90	.86	.86	.90	.90	.89	.88
Species adjusted									
pH-CaCl$_2$	74	.81	.82	.84	.84	.82	.83	.84	.85
Base saturation	62	.95	.95	.90	.90	.95	.95	.92	.92
Ca^{2+} saturation	62	.95	.95	.92	.92	.96	.96	.94	.94
Ca^{2+} amount	73	.91	.91	.87	.87	.91	.91	.89	.88
Total calcium	73	.92	.92	.91	.92	.92	.92	.92	.93
pH > 5.25									
pH-CaCl$_2$	45	.36	.37	.32	.36	.35	.36	.33	.37
Base saturation	37	.38	.39	.31	.37	.39	.41	.36	.41
Ca^{2+} saturation	37	.43	.45	.37	.43	.43	.46	.41	.47
Ca^{2+} amount	44	ns	ns	ns	ns	ns	ns	ns	ns
Total calcium	44	.60	.65	.60.	.68	.58	.62	.60	.67

[a] Bryophytes constituted between 0 and 80% of the total number of species with indicator values; the average value was only 14-15%.


(a) Species
Ellenberg Moisture Number
1
2
3
4
5
6
7
8
9
10
11
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1
Optimum for average lowest moisture content
(d) Species
Ellenberg Moisture Number
× 3
× 5
× 14
× 34
• 58
• 28
× 14
• 1
-7
-6
-5
-4
-3
-2
-1
Optimum for average groundwater level
(b) Sites
Mean Moisture value
Average lowest moisture content
(e) Sites
Mean Moisture value
Average groundwater level
(c) Sites
Mean Moisture value (Fr)
Average lowest moisture content
(f) Sites
Mean Moisture value (Fr)
Average groundwater level

Moisture: site-based

Site-based correlations for moisture variables (Table 6) were considerably higher than the species-based correlations. Correlations were again strongest for the average annual groundwater level and the average lowest moisture content (summer), reaching values of 0.84 to 0.88. Although the average highest pF might be expected to show stronger correlations than the average lowest moisture content, correlations were lower (0.76 to 0.78). Average highest and average spring groundwater level (not in Table 6) performed almost equal to the annual average groundwater level, but the average lowest groundwater level showed lower correlations (0.76 to 0.82). Compared to the lowest moisture content, the annual average moisture content (not in Table 6) showed lower correlations (0.82 to 0.85), while correlations for the highest moisture content were lower still (0.78 to 0.82).

Using abundance values instead of presence/absence data had virtually no effect. The inclusion of bryophytes in the calculations slightly improved some of the correlations, leaving others unaffected.

The relationships were relatively linear (Figs 2b and 2e), although at higher values there was a tendency to level off. Fig. 2b (moisture content) contains an outlier. This site is situated on artificially deposited loose sand with low moisture content, on a slope extending to open water. The vegetation fully depends on groundwater and the nearby open water, and does not behave as an outlier in Fig. 2e (average groundwater level). If the site is omitted, the correlations for the average lowest moisture content rise to values between 0.87 and 0.90 and this parameter subsequently performs best of all.

Accounting for the frequency of occurrence of the indicator values in the Dutch flora (Eq. 5), increased correlations negligibly. Differences are more pronounced if we visually compare Fig. 2b with 2c, and 2e with 2f. The relationships become significantly steeper ($p<0.0001$ one-tailed; $F_{[1,144]}$ with assumed linearity), and cover a larger total range. In Fig. 2c the relationship now levels off only at the highest moisture contents.

***Figure 2** (opposite). Relation between moisture indicator values and measured values. Figures on the left: average lowest moisture content (arcsine transformed). Figures on the right: average annual groundwater level (see Table 3). Figs (a) and (d): Species-based. Calculated species optima* versus *species indicator values. Included are vascular plants as well as bryophytes. Species with low occurrence not excluded. Trend line fitted by geometric mean regression (Sokal & Rohlf 1995). Crosses indicate species with indicator values considered inappropriate for the Dutch situation (Table 7). Values inside Fig. (d): number of data points with same position in diagram. Figs (b) and (e): Site-based. Calculated mean site indicator values* versus *measured values. Abundance values used as weights, bryophytes included. Trend lines were fitted by hand and have no statistical status. Figs (c) and (f): As previous two, but mean site indicator values calculated taking the frequency distribution of the indicator values in the Dutch flora into account (Eq. 5).*

Table 7. *Suggested species adjustments of Ellenberg indicator values for the Dutch situation, based partly on the species position in Figs 2a/d, 3a/d and 4a/d, and partly on own judgements. 'O' indicates original values; 'A' denotes adjusted values. Species adjusted to higher values are presented before the species rated lower. Differences larger than 1 unit: in bold. 'X' indicates indifferent behaviour.*

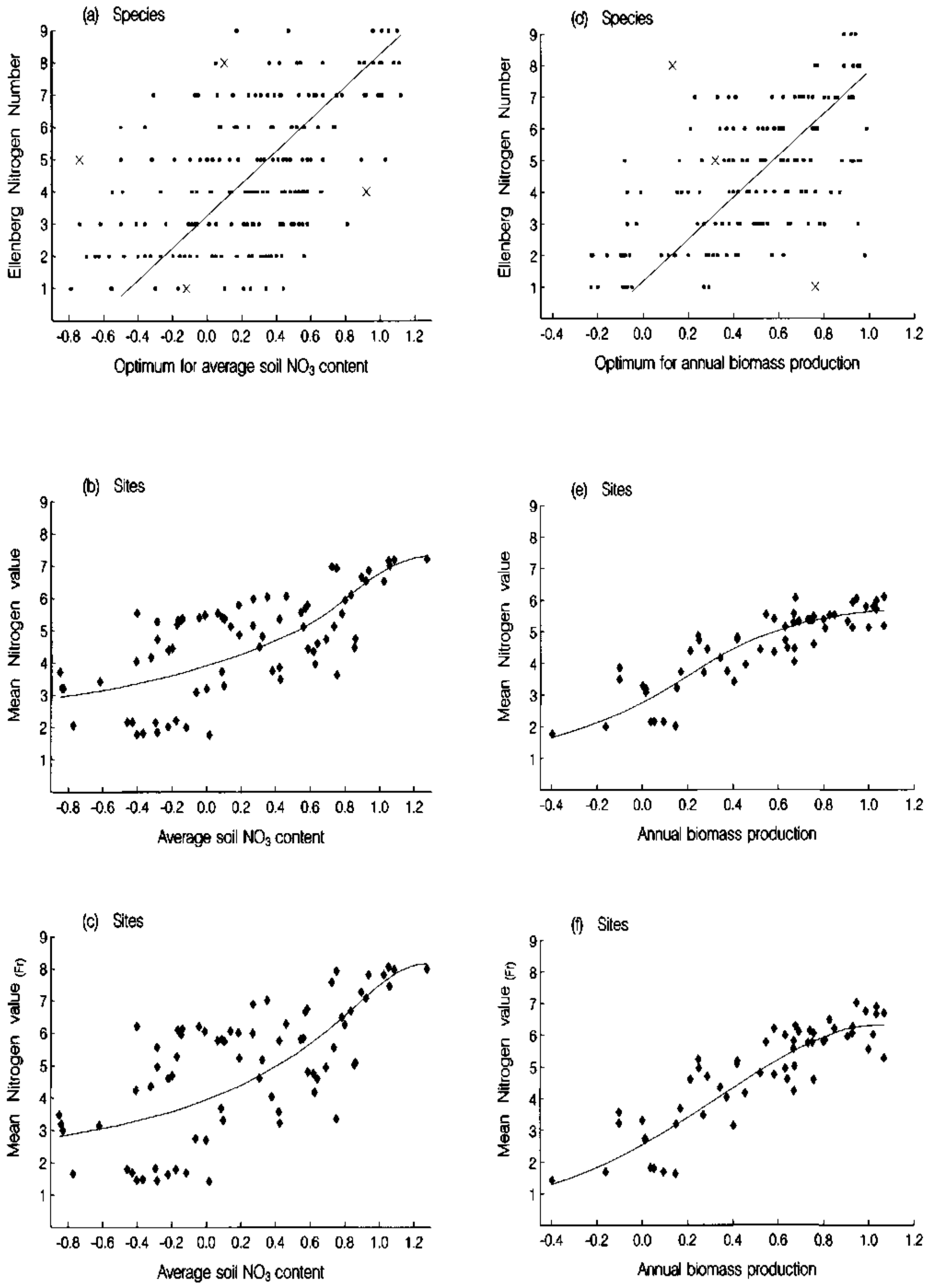
MOISTURE	O	A	NITROGEN	O	A	SOIL REACTION	O	A
Barbula unguiculata	2	X	*Poa nemoralis*	4	5	***Aira praecox***	**2**	**4**
Brachythecium rutabulum	4	5	***Triglochin palustris***	**1**	**5**	***Arabidopsis thaliana***	**4**	**6**
Cynosurus cristatus	5	6				***Brachypodium pinnatum***[b]	**7**	**9**
Galeopsis bifida	**5**	**6/7**				*Carex arenaria*[a]	2	X
Hypmum jutlandicum	2	3				*Carlina vulgaris*[b]	7	8
Luzula multiflora	**5**	**6/7**				*Cirsium acaule*[b]	8	9
Myosotis discolor	4	X				***Galium pumilum***	**4**	**9**
Prunella vulgaris	5	6				***Helictotrichon pratense***[b]	**X**	**9**
Senecio erucifolius	3	5				***Polygala vulgaris***	**3**	**5**
						Senecio aquaticus	4	5
						Trifolium arvense	**2**	**4**
Allium scorodoprasum	**7**	**5/6**				***Vicia lathyroides***	**3**	**6**
Artemisia vulgaris	6	5						
Bryonia dioica	5	4				*Carex disticha*	8	7
Cruciata laevipes	6	5				*Juncus subnodulosus*	9	8
Humulus lupulus	8	7	*Cynoglossum officinale*	7	6	***Potentilla anglica***	**8**	**5**
Leucobryum glaucum	7	X	*Juncus tenuis*	5	4			
Medicago sativa	6	5	*Mercurialis annua*	8	7	*Schoenoplectus tabernaemontani*	9	8
Melilotus altissimus	7	6	*Senecio vulgaris*	8	7	*Thalictrum flavum*	8	7

[a] Optimum is bimodal. [b] Not a clear outlier in the graphs.

Nitrogen: species-based

Ellenberg *et al.* (1992) loosely defined the N values as indicating the amount of N available during the growing season, but added that the values may also be interpreted as indicating the general nutrient supply. One could therefore expect the available amount of mineral N and the annual N mineralization to be parameters with high correlations, but both N mineralization and the mineral N pool showed correlation coefficients < 0.50 (Table 5). The same holds for soil total N and the C:N ratio, as well as for available PO_4 and K. Of the soil parameters, only the amount of NO_3 and the degree of nitrification showed higher correlations (up to 0.60 to 0.63). Similar correlations (up to 0.59 to 0.64) were obtained for vegetation parameters like annual biomass production, tissue N concentration and annual N accumulation in the plant biomass.

Figs 3a and 3d visualize the results for soil NO_3 and for the annual aboveground biomass production. It was not easy to verify the species values because of the mentioned uncertainty about which measured parameter should be indicated. We judged the indicator value to be inappropriate for the Dutch situation for only a few species (Table 7), most notably *Triglochin palustris.* That species was assigned indicator value 1 by Ellenberg *et al.* (1992), but in the Netherlands it prefers moderately productive, slightly nutrient-poor to moderately nutrient-rich situations best reflected by indicator value 5.


(a) Species
Ellenberg Nitrogen Number
1
2
3
4
5
6
7
8
9
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
1.2
Optimum for average soil NO_3 content
(d) Species
Ellenberg Nitrogen Number
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
1.2
Optimum for annual biomass production
(b) Sites
Mean Nitrogen value
Average soil NO_3 content
(e) Sites
Mean Nitrogen value
Annual biomass production
(c) Sites
Mean Nitrogen value (Fr)
Average soil NO_3 content
(f) Sites
Mean Nitrogen value (Fr)
Annual biomass production

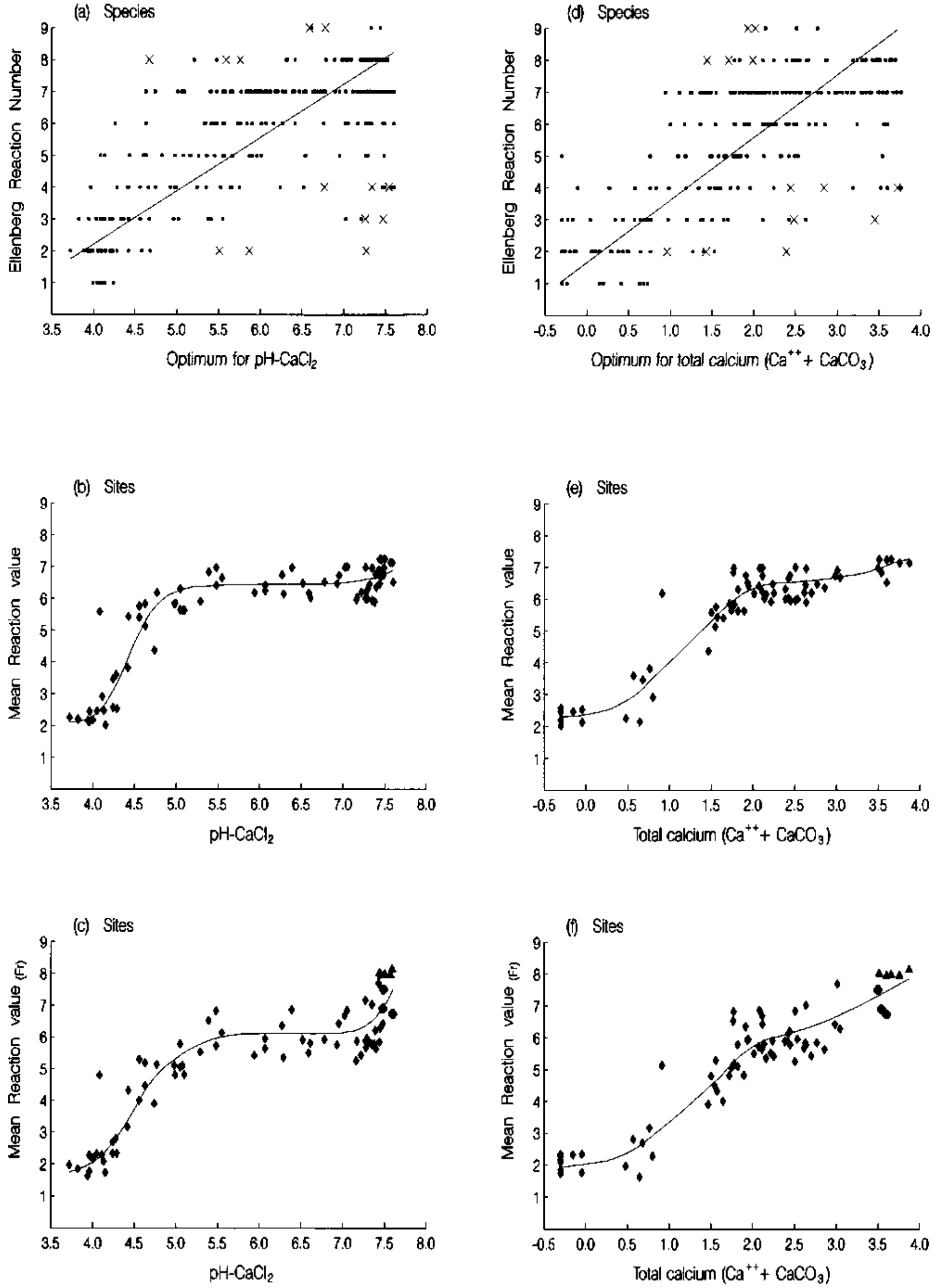
Nitrogen: site-based

For most measured N parameters, the site-based correlations (Table 6) were higher than the species-based correlations. Soil parameters were indicated considerably less well than measured vegetation parameters. Soil N mineralization appeared most unsuitable of all. Of the soil parameters, NO_3 content performed best, but still considerably less than vegetation N accumulation and biomass production. Correlations obtained using one of the latter two were surprisingly high (0.85 to 0.86), given that the 17 sites which were excluded for lack of production data represent extremes in nutrient status. They include both the low-productive heath locations as well as the highly productive semi-shaded locations. This can be observed in Fig. 3, where the highest mean indicator values are missing in the graph of biomass production (compare 3e with 3b), and there are fewer extremely low mean indicator values. If all correlations were calculated with these sites omitted, correlations for the soil parameters dropped substantially and differences with the vegetation parameters became even larger.

Applying abundance values as weights instead of using presence/absence data, negligibly improved correlations for the biomass parameters and the best performing soil parameters (NO_3 and nitrification degree).

The relationships appeared to be fairly linear, although most parameters tended towards an S-curved relationship. Taking the frequencies of occurrence of indicator values in the Dutch flora into account (Eq. 5), barely influenced correlations. This may be explained by the relatively homogeneous distribution of the N values in the Netherlands (Fig. 1). Nevertheless, if we compare Fig. 3b with 3c, and 3e with 3f, the same effects can be observed as were obtained for moisture. The range of mean indicator values has increased and slopes have become steeper. For biomass production this effect was significant at $p<0.05$ (one-tailed; $F_{[1,110]}$), for soil NO_3 it was not significant. For biomass production (Fig. 3f) the tendency to level off has been somewhat reduced and now only takes place at the highest values.

***Figure 3** (opposite). Relation between nitrogen indicator values and measured values. Figures on the left: soil NO_3 content (kg N ha^{-1}; log-transformed). Figures on the right: annual aboveground biomass production (ton dry weight ha^{-1} yr^{-1}; log-transformed). Figs (a) and (d): Species-based. Calculated species optima* versus *species indicator values. Only species with effective number of occurrences n_e > 2 are included. Species with indicator values deemed inappropriate for the Dutch situation are shown as a cross (Table 7). Trend line fitted by geometric mean regression (Sokal & Rohlf 1995). Figs (b) and (e): Site-based. Calculated mean site indicator values* versus *measured values. Abundance values used as weights. Trend lines fitted by hand. Figs (c) and (f): As previous two, but mean site indicator values calculated taking the frequency distribution of the indicator values in the Dutch flora into account (Eq. 5).*


(a) Species
Ellenberg Reaction Number
Optimum for pH-CaCl₂
(d) Species
Ellenberg Reaction Number
Optimum for total calcium (Ca⁺⁺+ CaCO₃)
(b) Sites
Mean Reaction value
pH-CaCl₂
(e) Sites
Mean Reaction value
Total calcium (Ca⁺⁺+ CaCO₃)
(c) Sites
Mean Reaction value (Fr)
pH-CaCl₂
(f) Sites
Mean Reaction value (Fr)
Total calcium (Ca⁺⁺+ CaCO₃)
1
2
3
4
5
6
7
8
9
3.5
4.0
4.5
5.0
5.5
6.0
6.5
7.0
7.5
8.0
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0

Soil reaction: species-based

Ellenberg reaction values correlated very well with soil chemical parameters (Table 5). For soil pH the correlation was 0.65 (using vascular plants only), steadily increasing to 0.73 when species with a low effective number of occurrences (n_e) were omitted. A strong additional increase to 0.85 was obtained using the standard error of the calculated optima as weights during correlation analysis. Other measured parameters performed even better, with weighted correlations reaching 0.87 to 0.94 for base saturation, Ca^{2+} saturation and the amount of exchangeable Ca^{2+}. Including bryophytes improved most correlations appreciably.

Nevertheless, for several species the reaction values do not match the calculated optima very well (Figs 4a and 4d). For most reaction values a bimodal frequency distribution may be discerned concerning the actual pH optima (Fig. 5). For all reaction values between 1 and 8, a second group is present at the very right. This indicates the existence of a large group of species showing optimal occurrence at high pH values in our data, although their indicator value is lower. This second group is especially large for reaction value 7 (40 out of the 108 species have their pH optimum between 7.2 and 7.7). For value 8 only a single group appears, but even in this case most species are clustered at the very right (30 out of 49 species have pH optimum 7.2 to 7.7).

These systematic deviations from the expected pattern will be considered in more detail in the discussion. It is most notable for *Galium pumilum* which has a published reaction value of 4 whereas we believe that 9 would best describe its behaviour in the Netherlands. Other examples are presented in the upper section of Table 7, but Fig. 5 indicates that many more may require adjustment for the Netherlands.

A second group of outlier species with inappropriate reaction values includes species from wet locations with high reaction values. Some of these may indeed prefer

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***Figure 4** (opposite). Relation between indicator values for soil reaction and measured values. Figures on the left: soil pH-$CaCl_2$. Figures on the right: total calcium (exchangeable amount of Ca^{2+} including Ca from carbonates [kmol ha^{-1} + 0.5; log-transformed]). Figs (a) and (d): Species-based. Calculated species optima* versus *species indicator values. Included are vascular plants as well as bryophytes. Species with low occurrence not excluded. Species with indicator values deemed inappropriate for the Dutch situation are shown as a cross (Table 7). Trend line fitted by geometric mean regression (Sokal & Rohlf 1995). Figs (b) and (e): Site-based. Calculated mean site indicator values* versus *measured values. Abundance values used as weights, bryophytes included. Trend lines fitted by hand. Figs (c) and (f): As previous two, but mean site indicator values calculated taking the frequency distribution of indicator values in the Dutch flora into account (Eq. 5), and after adjustment of some indicator values for the Dutch situation (see Table 7). Circles: $CaCO_3$ content > 20%; triangles: > 35%.*

calcareous fens or peat on calcareous soils. However, as these situations do not exist in the Netherlands, their reaction values are too high to correctly reflect their actual behaviour in the Netherlands (Table 7; lower part).

Soil reaction: site-based

As with moisture and nitrogen, site-based correlations for soil reaction (Table 6) were generally higher than species-based correlations. Using abundance values instead of presence/absence data only had minor effects. Including bryophytes generally improved the results, as was also noticed for the species-based relations.

Although for soil pH a high correlation was obtained (0.79 to 0.80), the relation appeared by no means linear (Fig. 4b). After a steep initial rise, site mean indicator values did not increase further, and the relation became virtually horizontal. Similar site mean indicator values were obtained for all pH-$CaCl_2$ values above ca. 4.75, which may be considered a serious complication.

Correcting for the frequency distribution (Fig. 4c) caused the site mean values in the most acid region to become lower. More importantly, the mean indicator values of several sites at pH 4.5 to 5.0 also decreased considerably, causing them to fit the increasing part much better. It now became possible to distinguish sites with pH above 5.25 from sites with lower values. In Fig. 4c the debatable reaction values mentioned above were also adjusted. Additional analyses showed the separate effect of this to be largely restricted to the sites with lime-rich soils at high soil pH, where higher mean indicator values were obtained (Fig. 4c: circles indicating more than 20% $CaCO_3$, triangles more than 35% $CaCO_3$).

Base saturation, Ca^{2+} saturation, the amount of Ca^{2+}, and the total amount of calcium all performed much better than pH because these relations were markedly more linear. For the log-transformed amount of total calcium (exchangeable Ca^{2+} plus Ca from carbonates) a fairly linear relationship was obtained, but at higher values the relation still levelled off (Fig. 4e; $r=0.90$). Adjusting species values to the Dutch situation clearly improved this relation; correlations rose to 0.92 because there was less tendency to level off at high values. Additional correction for the frequency distribution further improved the relationship. The combined result is shown in Fig. 4f. The relationship has become significantly steeper ($p<0.05$ one-tailed; $F_{[1,142]}$) also in the critical middle range, and approaches linearity fairly well. The correlation (bryophytes included) is 0.93.

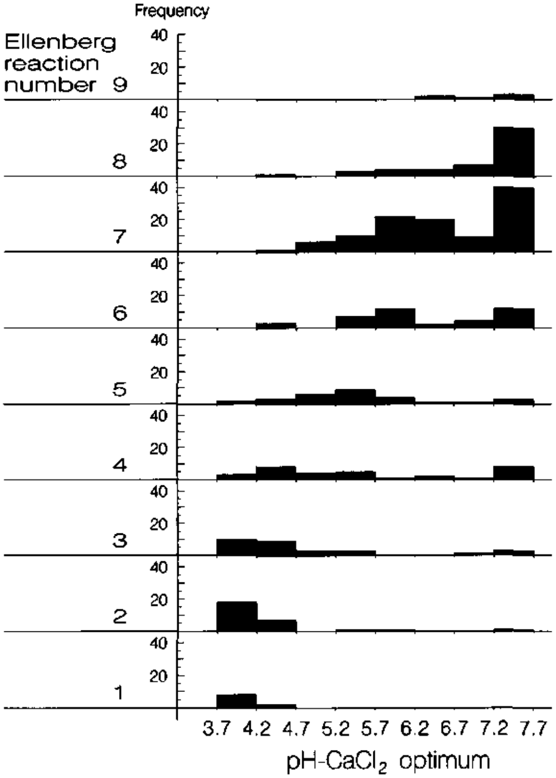

Figure 5. *Frequency of species (bryophytes included) in eight classes of pH optimum values, for each of the nine Ellenberg reaction values.*

Correlations up to 0.95 and 0.96 were obtained for base saturation and Ca^{2+} saturation (Table 6). These parameters therefore seem to explain a larger part of the variation than total calcium. However, graphical inspection (not presented) revealed that at higher levels, the relation between saturation parameters and site mean indicator values breaks down. The amount of scatter becomes large and a wide region of indiscrimination develops. The parameter suffering least from these problems was total calcium.

This was confirmed by correlation analyses when only the sites with $pH > 5.25$ were considered (Table 6). It appeared that within this critical range the strongest correlation was found with total calcium (up to $r = 0.67$ or 0.68). The amount of exchangeable Ca^{2+} showed no significant correlations in this range, indicating that calcium in the form of carbonates should also be taken into account when explaining site mean reaction values. Ca^{2+} saturation also performed much less than total calcium (r up to 0.47 only), and base saturation even less, although both performed better than soil pH.

Discussion

Weighted averaging

Calculating species optima can be regarded as a regression problem (Jongman *et al.* 1995). The weighted averaging approach to this problem assumes species to have a higher probability of occurrence closer to their optima. Specifically, it assumes unimodal response curves but circumvents the need to assume a more specific distribution. It has been shown (Ter Braak & Looman 1986, 1995) that weighted averaging efficiently estimates the optimum of a Gaussian response curve if the measured parameter is distributed reasonably homogeneously among the sites over the full range of occurrence of the species.

We compensated for uneven sampling distributions by using as weights the inverse of the frequency of sampling in eight equal subranges of the measured parameter (Eqs 1 and 2). This procedure introduces some arbitrariness, as the defined number of regions influences the frequency values. Increasing the number of regions might suggest a higher resolution but would result in regions containing very few sites, annulling the function of the frequencies as weights. By using only eight regions, some species occur exclusively in a single region and calculation of their optima does not benefit from the extra weighting. For these species, however, the requirement of a homogenous distribution is much less important, as the narrow ecological amplitude of these species already promotes accurate estimation of their optima (Ter Braak & Looman 1986, 1995). For our set of 74 sites, eight regions appeared a good compromise between resolution and effectiveness.

Calculating site mean indicator values can be regarded as a problem of calibration (Jongman *et al.* 1995). The weighted averaging approach assumes that, if a species is very abundant, the site mean indicator value should be close to the indicator value for that species. However, as pointed out in the introduction, different frequencies of indicator values in the regional species pool may cause different probabilities for specific indicator values to occur in a particular community, and may thus lead to biassed results. A modified equation was derived (Eq. 5), in symmetry with the formula used to compensate for the distribution of sampling when calculating species optima (Eq. 1).

To retain complete symmetry we might be tempted to use for the additional weights (F_j) the frequency of species with indicator value j present *in our data.* If we do so, the results for each individual site become dependent on the species in the other sites in the data. What actually needs to be corrected for, however, is the distribution of indicator values in the total reservoir of species the sites draw upon. Our practical solution was to equate this reservoir to the total flora of the Netherlands, since the sites in our study were distributed over the whole country and over a wide range of environmental conditions and plant communities. This approach essentially includes all potential species in our data, the extra species implicitly occurring with zero abundance. Viewed this way F_j still refers to the species 'present' in our data and a large degree of symmetry is retained with the species-based technique (Eq. 1).

For Central Europe, the frequency distribution of all species published by Ellenberg *et al.* (1992) may be used (Fig. 1). Of course, it remains debatable whether a site in a Central European alpine region draws species from the same reservoir as a site in a Central European lowland region. We nevertheless feel that using large regions (*e.g.* whole countries) presents the most practical and efficient solution.

It has been shown (Ter Braak & Barendregt 1986; Ter Braak 1995) that calibration by weighted averaging is almost as efficient as a recursive maximum likelihood estimation if certain conditions hold. First, species response curves should resemble Gaussian (symmetrical) curves. For moisture, fairly symmetrical response curves have been affirmed by Ter Braak & Gremmen (1987). Three other requirements should hold as well (Ter Braak & Barendregt 1986):

1. Species response curves should have equal tolerances.
2. Species response curves should have equal maxima.
3. Species optima should be evenly distributed over a large interval around the conditions to be indicated.

Conflicts with these requirements may arise from the general characteristics of the indicator system as well as from our species data (and transformations thereof), but also from the responses of species to the various ecological parameters studied. We will consider these conflicts during the discussion of each of the three ecological factors. Subsequently, we will consider each of the three requirements separately. The requirement of equal tolerances will be discussed in relation to the indifferent behaviour of species, the requirement of an even distribution in relation to the frequency correction we applied, and the requirement of equal maxima in relation to the use of abundance values *versus* the use of presence/absence data.

Moisture indication

Although the moisture indicator values are generally considered to lie at the heart of the Ellenberg system (Böcker *et al.* 1983), the actual relation with values as measured in the field has never received much attention. Ter Braak & Gremmen (1987) tested the consistency of the moisture values between different species (which was found to be reasonably good), but they did not correlate with measured parameters. In Great Britain, Thompson *et al.* (1993) found a close relation between Ellenberg moisture values and the affiliation of species with dry or moist habitats or wetlands. Böcker *et al.* (1983) assert that groundwater level is the parameter that can be expected to show the closest relation to moisture values. However, none of these authors measured soil moisture or groundwater.

Using field measurements, Mountford and Chapman (1993) reported moisture indicator values to be correlated with the mean groundwater level and its degree of fluctuation, with the height above ditch water level, and with ditch depth, but their study was rather fragmentary. Ertsen *et al.* (1998) found site mean indicator values to be related to the mean spring groundwater level, but the study only included sites with relatively high groundwater levels. Their results show clear differences between sandy, clayey and peaty soils. This indicates that groundwater level itself may not always be indicated in a simple way. Unfortunately, they did not measure other soil moisture parameters for comparison. Given the different relations for different soil types, and given our results, better performances might be expected if soil moisture content or pF had been measured. These variables clearly depend on both groundwater level and soil type. In our study, soil pF values did not perform as well as moisture contents, but this was probably because the pF values were not actually measured, but estimated from the measured soil moisture content and texture. Diekmann (1995) correlated site mean indicator values with measured soil moisture contents in deciduous Swedish forests, but only found low correlations. This was probably due to a relatively small range of moisture contents present, as also the author suggested. Moreover, the measurements were taken only once. He found stronger correlations if soil moisture contents were measured on a very dry day, which is in agreement with our finding that the average *lowest* moisture content was the best correlated moisture content parameter. This suggests that the Ellenberg moisture values are sensitive to the soil's drought susceptibility in summer.

Ellenberg moisture values most probably integrate both groundwater level and soil moisture content. At low moisture content, a high groundwater level may still supply deeper plant roots with sufficient water. At low groundwater level a high moisture content may still be retained if physical soil characteristics are favourable.

Nitrogen indication

Vegetation-derived parameters appeared to reflect the Ellenberg N values much better than soil measurements. Strong correlations with vegetation-derived parameters have also been reported in other studies. Thompson *et al.* (1993) found a clear correlation ($r=0.78$) between the Ellenberg N value of plants and their foliar N concentration in the field. Melman *et al.* (1988) present a correlation of ca. 0.84 between site mean N indicator values and biomass production. Neither of these studies, however, made comparisons with soil measurements. Boller-Elmer (1977) and Briemle (1986), in agreement with the present results, found site mean N values to be correlated better with biomass production than with N mineralization rates, although both only used a very limited number of sites. Ertsen *et al.* (1998) showed site mean N values to be more closely related to standing crop and N stock than to chemical soil measurements, but their soil data included total amounts of N, P and K only, not the amounts available. Hill & Carey (1997) reported that site mean indicator values correlated better with hay yield ($r=0.91$) than with N fertilization ($r=0.85$).

The strong correlations reported with vegetation parameters and most notably with aboveground biomass production, demonstrate that Ellenberg N values provide an effective integration of several ecological parameters and do not reflect the availability of nutrients only. Various other factors determine productivity, such as moisture availability, soil aeration, soil acidity, and disturbance. Productivity can be regarded as a measure of fertility as ‘perceived’ by the vegetation. Our results and those of other studies indicate that - as also Hill & Carey (1997) have suggested - Ellenberg N values should rather be called ‘productivity values’.

Soil reaction

Ellenberg soil reaction values appear to be most problematical when they are related to measured parameters. Our research revealed two main problems:
- Individual species appear to suffer from geographical changes in species preferences.
- Site mean reaction values appear not to indicate soil pH satisfactorily.

Both aspects will be considered in more detail.

Geographical variations in the ecological preferences of species for soil acidity and lime content were already reported over a century ago (Flahault 1893 in Braun-

Blanquet 1929; Salisbury 1920; Steele 1955; Clymo 1962). Ellenberg was well aware of these shifts in preferences (Ellenberg 1958) and suggested regional checks before applying the reaction values (Ellenberg *et al.* 1992).

The phenomenon was clearly described by Holzner (1978), for weed species. He distinguished two groups. One group consists of thermophilous species of southern origin, which are indifferent toward soil pH at the centre of their distribution. However, at the northern, western, or upper limits of their distribution they prefer calcareous soil. A second group concerns species with an oceanic-suboceanic distribution which (because of their physiology) need to avoid calcareous soils. At the centre of their distribution these species will be able to compete on acid to even neutral soils. In continental and subcontinental areas, however, they are only competitive on very acid soils. For both groups, reaction values based on Central Europe will be too low to reflect preferences in more northern or western regions. One example from our data of a species showing geographical variation in ecological preference may be *Polygala vulgaris* (reaction value 3, suggested value for the Netherlands 5). This species was also mentioned by Thompson *et al.* (1993) to be an outlier in their study in Britain. In Central England it is almost exclusively restricted to highly calcareous soils. Another such species is *Carlina vulgaris* (reaction value 7, suggested value for the Netherlands 8), which shows a clear preference for limestone in southern England (Steele 1955) whereas it has a much broader distribution in Central Europe.

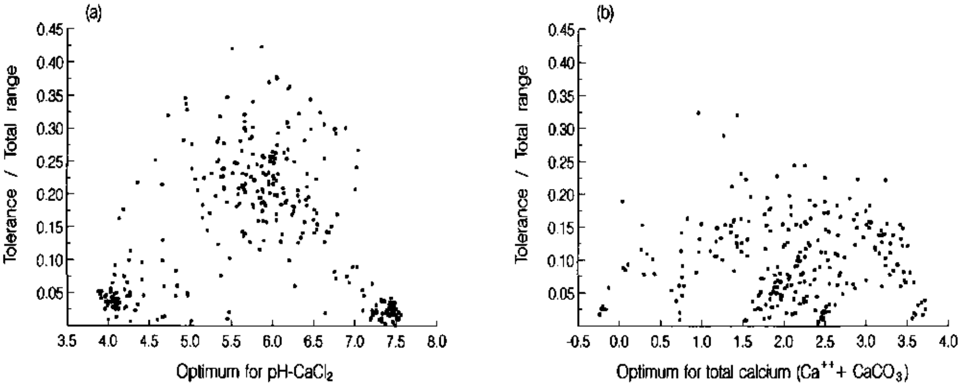

Figure 6. *Relation between species optima and tolerances: (a) for soil pH-CaCl$_2$, and (b) for total calcium. Tolerances expressed as fractions of the total range sampled. Included are vascular plants as well as bryophytes.*

A disproportionate number of species with reaction values 8 or 9 appear not to occur in the Netherlands (Fig. 1). This may simply be because there are very few lime-rich habitats in the Netherlands. However, it may also suggest that many of these species are thermophilous, reaching the limit of their geographical distribution in Central Europe, which may be why they behave as lime indicators in Central Europe in the first place.

For these reasons, particularly the indication of lime may become problematic north/west of Central Europe. Many species with high indicator values no longer occur. Many species characteristic of limestone (in these regions) have indicator values that are too low (for these regions). Our results confirm that the indication of lime improves if reaction values are adjusted (Figs 4c and 4f). Shifts in ecological preferences should thus be given serious consideration before applying Ellenberg reaction values outside Central Europe.

Although soil pH is generally considered to be the factor indicated by the Ellenberg reaction values, the relation between soil pH and site mean reaction values appeared to be virtually horizontal at pH-$CaCl_2 > 4.75$. A similar pattern can be discerned in many other studies (*e.g.* Ellenberg 1948; Ellenberg *et al.* 1992; Seidling & Rohner 1993; Möller 1997; Persson 1980; Hill & Carey 1997; Diekmann 1995; Ertsen *et al.* 1998). In studies where no tendency to level off could be observed, only sites with pH-$CaCl_2$ levels below ca. 5.5 were involved (Rodenkirchen 1982, Vevle & Aase 1980). The problem has never been fully recognised because of small numbers of sites, small pH ranges, and/or the expectation of linear relationships.

As the undesirable form of the relationship was absent in the species-based approach, we suspect that the problem largely arises because the requirement of equal tolerances is violated. We therefore investigated the relation between species pH optima and their pH tolerance. Species with pH optima near the extremes appeared to show remarkably narrow tolerances while species with intermediate pH optima very often showed wide tolerances (Fig. 6a). We are very aware that part of this relation can be attributed to an artifact due to edge-effects. However, we did not observe such distinct differences in tolerances for total calcium, which is susceptible to the same edge-effect (Fig. 6b). This demonstrates that the requirement of equal tolerances is much less violated if total calcium is used as the indicated parameter. It is also apparent that there is more indifference to intermediate pH levels than to intermediate levels of total calcium (Fig. 6a *versus* 6b).

The results presented in Fig. 6 explain why site mean reaction values do not indicate pH very well. This problem might be solved if detailed information on pH tolerances, which could be used as an additional weighting factor (Ter Braak & Barendregt 1986; Melman *et al.* 1988), were available. Until such data become available, the ability of site mean reaction values to indicate soil pH is limited. We conclude that site mean reaction values should not be used to indicate soil pH as such (especially not if a linear relationship is required), unless it is certain that the pH-$CaCl_2$ at all sites is below 5.5.

Failure to recognize the limitations concerning soil pH may lead to inappropriate application of site mean reaction values. For example, Jurko (1984) reported mean reaction values between 5 and 7.5 for most of the plant communities in his study area and concluded that the geology of the region permitted the occurrence of communities from somewhat acid to only slightly acid soils. Our findings cast doubt on this interpretation. Reif *et al.* (1985) calculated site mean indicator values for 94 communities containing *Urtica dioica* and concluded that this species has a surprisingly narrow amplitude for soil acidity. However, the small range of mean reaction values they obtained (between 5.6 and 7.5; once 8.0) may be expected for the whole range of pH-$CaCl_2$ values above 4.75. Wiertz *et al.* (1992) estimated the probability of occurrence of species as a function of moisture, nutrients, pH and salt, using site mean indicator values. However, using mean reaction values as a measure of soil pH may be inappropriate, given that most sites will give intermediate reaction values although the actual pH-$CaCl_2$ may range from anywhere between 4.75 and 7.5.

The fairly linear relationship between site mean reaction values and log-transformed total calcium corresponds with the findings that there is relatively little systematic variation in species tolerances for total calcium and that the general indifference to intermediate amounts of total calcium is relatively small (Fig. 6). We conclude that over a large range of conditions the Ellenberg reaction values accurately describe the total amount of calcium in the soil, *i.e.* both exchangeable Ca^{2+} as well calcium in the form of carbonates. We know of no other studies presenting relations with the total amount of calcium as defined in the present study.

Seidling & Rohner (1993) showed base saturation to correlate better with site mean reaction values than with pH in German forests, and Vevle & Aase (1980) showed high correlations for base saturation in Norwegian forest communities. The present study confirms these findings, but also shows that the relationship breaks down at higher values. Ca^{2+} saturation was indicated slightly better, although this relation too is weak at higher saturation values. As far as absolute amounts were concerned, exchangeable Ca^{2+} by itself also performed better than the combined exchangeable bases. We found a clear relationship with exchangeable Ca^{2+}, but only when pH was below 5.25. Vevle & Aase

(1980) presented data on this parameter, but no relation with mean reaction values was present. This may have been because of the presence of calcium carbonates, although reported pH levels would not allow large amounts. In a relatively acid Polish forest range, Degórski (1982) found that amounts of exchangeable Ca^{2+} were clearly correlated with site mean reaction values. He reported this relation to be stronger than when pH or base saturation was used, which is in general agreement with our findings. Using species-based data, Thompson *et al.* (1993) reported a positive correlation (r=0.72) between the Ellenberg reaction value of 24 species of dicotyledons collected in the field and their foliar Ca content.

It has long been established that pH itself is only of secondary importance in determining plant occurrence (Kinzel 1983), except in acid environments where the H^+ ion itself may become harmful. Calcium, however, is an essential nutritive element. Plant Ca status affects the integrity of cytoplasmic membranes, K uptake, osmotic regulation, and iron metabolism (Kinzel 1983). Clymo (1962) showed that requirements for Ca^{2+} varied for two related *Carex* species, one characteristic of Ca-rich fens and one less so. Steele (1955) experimentally showed that some species characteristic of lime-rich soils required a high supply of Ca^{2+} more than a high soil pH, while others demand high levels for both. Some of the species not characteristic of limestone regions appeared to be inhibited by Ca^{2+}. The experimental results were confirmed by field observations comparing regions with highly basic igneous rock (high in Mg but not Ca) with equally basic limestone areas (high in Ca). The results imply that it is not so much the soil pH or the collective bases that determines the occurrence of many plant species, but rather the calcium status of the soil.

Since site mean reaction values accurately indicate soil total calcium over a wide range of conditions, whereas the indication of soil pH is problematic, we suggest that the Ellenberg reaction values are better referred to as 'calcium values'.

Indifferent species and the equal tolerance requirement

The requirement of equal tolerances was reported by Ter Braak & Barendregt (1986) to be critical for the efficiency of weighted averaging. Our results for soil pH demonstrate that a violation of the equal tolerance requirement may indeed reduce the effectiveness of site mean indicator values.

It has been stated that calculation of site mean indicator values may benefit from additional information on species tolerances (Ter Braak & Barendregt 1986; Melman *et al.* 1988), since species with narrow tolerances are better indicators than species with wide ecological amplitudes. Our results, however, suggest that additional weighting with species tolerances is especially necessary to remove detrimental effects of violations of the equal tolerance requirement. Ideally, tolerances should be assessed relative to the indicator scale. There may be a strong potential in a recursive procedure: first estimating species tolerances using site mean indicator values, then using these tolerances to calculate improved site mean values that can be used to calculate improved tolerances, and so on until no significant changes occur.

At present, the status 'indifferent' is the only way in which the Ellenberg system provides information about species tolerances. This information should not fall prey to an overzealous effort to fill in what might be perceived as 'empty spaces'. Too many relatively indifferent species may already have been assigned indicator values. Until quantified information on species tolerances becomes available, no values should be assigned to species currently labelled indifferent, since this would further violate the condition of equal tolerances. Moreover, species now labelled indifferent would, by definition, receive fairly intermediate values. This would cause the frequency distributions of indicator values to become even more uneven than they are already, which compromises the requirement for an even distribution of indicator values as well.

Frequency correction and the even distribution requirement

The requirement of an even distribution of the species optima over a large interval around the conditions to be indicated is far from fulfilled by the Ellenberg system. It is violated not only by uneven frequency distributions of indicator values (Fig. 1), but also by a boundary problem, since species indicator values can only range from 1 to 9 (12 for moisture).

Our initial expectation was that uneven frequency distributions of indicator values in a region would lead to biased site mean values. Applying the suggested correction (Eq. 5) usually showed little effect on correlation coefficients, although the effect was generally positive for the best performing variables (and/or in the critical ranges). The shape of the relationships, however, was more markedly improved. The correction successfully reduced the tendency of site mean values to converge toward the indicator values common in the regional species pool, bringing about larger total ranges, steeper relationships, and less levelling off. An improved linearity is especially important when site mean values are to be used in calculations, and when quantitative statements about environmental conditions are to be made. We therefore recommend the frequency distribution weighting as standard procedure, particularly for the reaction values.

The boundary problem can be regarded as a special case of the violation of the even distribution requirement. Sites with extreme conditions may also contain species with less extreme indicator values, but there are no indicator values for more extreme conditions. As a result, site averages are predisposed toward intermediate values and tend to be confined to a smaller range than the full range of species values (Böcker *et al.* 1983). This implies that site mean indicator values cannot be interpreted in terms of species values, especially near the extremes. If the frequency correction is not applied this problem is aggravated, since the most common indicator values are generally the intermediate ones.

We carried out additional analyses to determine to what extent the species indicator values corresponded to the site mean values at which they had their optimum. These analyses did indeed show better correspondence when the frequency correction was applied. However, substantial systematic deviations that were not confined to the extremes still existed, even for the corrected means. It may be that the effects of the boundary problem are stronger than expected. We suspect, however, that other factors are involved as well, most notably a general indifference to intermediate values (a violation of the requirement of equal tolerances). The implication is that site mean values should not be interpreted in terms of the original species indicator values. In our opinion, this limitation is not always fully realized. It also puts severe restrictions on attempts to correct species indicator values on the basis of site mean indicator values (*e.g.* Wiertz *et al.* 1992).

Abundance weighting and the equal maxima requirement

Many - including Ellenberg - have recognized the problem of unequal maxima of species response curves. Some species never attain the maximum abundance reached by others (Olff & Bakker 1998), and will thus never be able to determine site mean values equally strong. Hypothetically, the abundance of each species could be expressed as a fraction of its average maximum abundance under natural circumstances (Noest *et al.* 1989; Van der Maarel 1993). This would not only require the estimation of these maxima for all species, but also has theoretical implications. The problem of unequal maxima is avoided when using presence/absence data.

In our study, correlations using abundance data as weights were generally only negligibly higher than those based on presence/absence data. The information added by using species abundances probably outweighs the detrimental effects. We assume that the cover/abundance scale applied (which can be considered a crude logarithmic transformation of the actual species cover) reduces the potential magnitude of violations.

Hill & Carey (1997) reported that site mean Ellenberg N performed better when presence/absence data were used. However, in their case, species biomass figures were applied as weights which, unless they were transformed first, may have strongly violated the requirement of equal species maxima.

Whether or not to use abundance values as weights will depend on the type of study and the type of vegetation involved. Using abundance values is recommended when sites are less species-rich than those included here, because it may be the only way to obtain significant discrimination (Böcker *et al.* 1983). We may also expect the use of abundance values to be beneficial when smaller ranges of environmental conditions are involved, since species composition in terms of presence/absence data may vary little in these cases, whereas species abundances may vary appreciably. In our data, correlations improved when using abundance values in the subrange of pH values above 5.25, whereas differences were negligible when the entire pH range was considered (Table 6). Melman *et al.* (1988) also reported better results for the abundance weighted method within each of their locations. When data for their locations were combined, presence/absence data performed slightly better but differences were relatively small.

Bryophytes

Our results show that indicator values for bryophytes may be used in combination with those for vascular plants. Site-based correlations generally increase slightly when bryophytes are included. Species-based correlations improved considerably for soil reaction, but for soil moisture they seemed to be affected slightly negatively. Indicator values for bryophytes may be especially useful in situations with a low number of vascular plant species. Ellenberg's hesitation to use the bryophyte indicator values in conjunction with those for vascular plants does not seem justified.

Species versus *sites*

Site-based correlations were consistently higher than species-based correlations, which indicates that species assemblages are capable of yielding more accurate indications than single species. The sites involved in the present study were relatively species-rich. This promotes accurate indication by site mean values and may explain why the site-based relationships showed relatively little scatter compared to many other studies.

Interactions

Ellenberg indicator values were primarily based on field observations in natural and semi-natural situations and are therefore subject to many interactions. Because of this, several authors have remarked that factors other than those under consideration may interfere (Melman *et al.* 1988; Thompson *et al.* 1993; Ter Braak & Gremmen 1987). Our results for the Ellenberg N values confirm this, by showing that measured soil parameters cannot be indicated accurately, since confounding factors (other limiting elements, moisture, pH) cause the measured amounts as such to be of only limited relevance. However, biomass production effectively integrates confounding factors in a way reflecting fertility as perceived by the vegetation, resulting in a strong correlation with the indicator values.

The results show that indicator values perform well when the appropriate parameters are considered. It is only necessary to account for confounding effects if indications are required of a factor which, *in an isolated form*, is not particularly relevant for species composition. For instance, if we seek to indicate N mineralization from Ellenberg N values (productivity values), interacting factors such as soil moisture and soil pH need to be allowed for. Trial analyses using multiple regression show that for N mineralization this may indeed result in reliable predictions. To a somewhat lesser extent this was even the case if Ellenberg moisture and reaction values were used as indicators of the confounding factors.

Those applying indicator values should be aware that, unless interactions are taken into account, only integrated information is obtained. Failure to recognize this may lead to incorrect conclusions. An example may illustrate this. Suppose a grassland section where (some years earlier) management has been changed to hay-making twice per year is compared with an unmown section, and suppose that for the mown section lower productivity (indicator) values are observed. We may conclude that hay-making has decreased productivity. However, indicator values merely indicate lower productivity *from the point of view of species composition.* It might well be that smaller amounts of standing crop during large parts of the growing season caused by the hay-making management simply allow species indicative of low productive situations to occur (Bakker 1987). The actual productivity need not have changed at all. From the vegetation point of view the indication is accurate, as competition for light is less in the hay-making site and this is a characteristic of sites with lower productivity.

General conclusions

We conclude that the Ellenberg indicator values studied are confirmed by field measurements, provided the appropriate parameters are considered. The values can be used in the Netherlands and probably in Northwest Europe as a whole, but care should be taken concerning the reaction values (calcium values). The correlations obtained are particularly high if we consider that they only relate to one single parameter at a time, whereas the indicator values summarize a complex of parameters associated to the factor indicated. The correlations may therefore be considered minimum estimates of the correlations with these complex environmental factors.

At a time when there is a strong call for expert systems, the Ellenberg indicator system deserves more attention than it has received so far. The loose description of what exactly the indicator values indicate may present a problem if we aim to relate the values to an isolated parameter. However, organisms rarely respond to the value of one particular parameter at one particular point in time. Therefore, the implicit nature of the Ellenberg indicator values and the integration over time they represent should not be seen as a disadvantage, but as the actual strength of the system.

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7

In situ annual nitrogen mineralization predicted by simple soil properties and short-period field incubation

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In situ annual nitrogen mineralization predicted by simple soil properties and short-period field incubation

Abstract. A typical method to determine nitrogen mineralization is year-round field incubation of undisturbed soil cores. As this technique is very laborious, the aim of the present study was to establish less time consuming methods to assess the annual N mineralization. Options considered were reducing the period of subsequent field incubations to less than a full year, and prediction using simple (direct) soil measurements.

In situ annual N mineralization was measured in 74 semi-natural, unfertilized sites under year-round vegetation cover by sequential incubation of undisturbed soil cores during two full years. The sites classify into 14 very different plant community types and encompass a wide range of edaphic conditions.

A high correlation with the annual N mineralization was maintained when sequential incubations were restricted to the period early March to mid August ($r=0.98$). Shorter periods may also be used, as long as they lie within the period early March to mid August and cover three months at least.

The average annual N mineralization could be predicted accurately using the soil mineral nitrogen pool (N_{min}), moisture content and pH as the predictor variables. In a multiple regression model based on log-transformed values, the R^2 was 0.835. Samples (preferably bulked) are best taken in early March, just before the start of the growing season. Higher N_{min} contents (moisture and pH assumed constant) indicated higher annual N mineralization rates. Higher moisture contents (at constant N_{min} and pH) generally indicated lower annual rates. Soil pH showed a quadratic relation (at fixed N_{min} and moisture) with maximum annual mineralization occurring at a pH-$CaCl_2$ value of 5.5 to 5.6.

N_{min} appeared to be the most important predictor variable. Even within plant community types (with a reduced range of conditions), its relationship with the annual N mineralization persisted. Frequently studied factors, such as total soil N, organic matter content, C:N ratio, soluble organic N, and particle size composition, only showed low and insignificant correlations, although stronger relationships have sometimes been reported. It is assumed this discrepancy is caused by the smaller range of conditions usually studied.

Key-words: *mineral N pool, moisture content, pH-$CaCl_2$, plant community, sampling date, vegetation.*

Introduction

Nitrogen (N) mineralization is generally regarded as a key-process in terrestrial ecosystems. Since N supply often limits plant growth in natural environments, N availability affects the outcome of species competition and consequently controls the development, persistence and decline of plant communities in many areas (Runge 1983). In unfertilized meadow ecosystems and heathlands in the Netherlands, N mineralization was shown to account for 70-80% of the N uptake by the vegetation (Berendse *et al.* 1987, 1994). As the pool of mineral N in soils is small compared to the N fluxes, the pool size is thought to supply little information on N availability (Binkley & Hart 1989). Measuring N mineralization has therefore become an important objective in many ecological studies.

However, measuring mineralization is not an easy task. Several methods have been devised. Laboratory methods usually determine the mineralization potential under controlled conditions (Hassink 1994; Morecroft *et al.* 1992; Robertson & Vitousek 1981; Stanford & Smith 1972; Troelstra *et al.* 1990a,b, 1995). It is difficult, however, to extrapolate potential mineralization rates to the field situation (*e.g.* Honeycutt 1999), although good correlations are sometimes obtained (Carlyle *et al.* 1999). Various methods exist to measure N mineralization *in situ*. Of these, field incubation of undisturbed soil cores is among the best presently available (Adams *et al.* 1989; Raison *et al.* 1987). This method has been used in many ecological studies (*e.g.* Berendse 1990; Berendse *et al.* 1987, 1994; Olff *et al.* 1994; Van Vuuren *et al.* 1992). Another method that has been applied less frequently uses ion exchange resins (Bhogal *et al.* 1999; Hart & Gunther 1989). Since *in situ* methods generally require year-round sampling, they are very laborious and time consuming, which can be considered their major drawback.

Various studies have tried to relate N mineralization to other soil factors, including soil total N, C:N ratio, soluble organic N, nitrate, particle size distribution, organic matter content, moisture and pH (*e.g.* Alexander 1977; Appel & Mengel 1990, 1993, 1998; Berendse 1990; Berendse *et al.* 1994; Groot & Houba 1995; Hassink 1994; Myers *et al.* 1982; Nyborg & Hoyt 1978; Pastor *et al.* 1987; Robertson & Vitousek 1981; Troelstra *et al.* 1995; Zöttl 1960a,b). The results of these studies are often contradictory, suggesting that the relationships, so developed, may only apply to a small range of soil types or to specific circumstances (Runge 1983).

The objective of the present study was to find reliable estimators for the average annual N mineralization (as measured using consecutive *in situ* incubations of undisturbed soil cores during two years), over a wide range of undisturbed soil types and unfertilized, semi-natural plant community types. First, correlations were examined with *in situ* mineralization rates as measured during periods shorter than a full year. The second aim was to find a set of simple instantaneous soil properties (*i.e.* properties which only need to be measured at one particular time), from which the average annual N mineralization could be predicted. Such predictions should benefit plant and vegetation ecologists in cases where the actual measurement of net annual N mineralization is too time consuming and/or expensive.

Table 1. *The 14 plant community types into which the 74 studied sites were classified. Community names follow Schaminée* et al. *(1995, 1996), Stortelder* et al. *(1999) and Sýkora* et al. *(1993). A short ecological description is provided.*

1 ***Urtico-Aegopodietum***, 5 sites.
  Vegetation of woodland- and hedge-margins, usually semi-shaded. On nitrate-rich, moderately moist soils.

2 ***Alliario-Chaerophylletum temuli***, 5 sites.
  Much like previous community but on drier, more sandy soils.

3 ***Valeriano-Filipenduletum***, 5 sites.
  Tall-herb grassland on moist to wet, moderately fertile soils.

4 ***Fritillario-Alopecuretum pratensis***, 5 sites (fragmentary form: 2 sites, well-developed form: 3 sites).
  Hay-meadow on moderately fertile, moderately wet soils (preferably flooded seasonally).

5 ***Calthion palustris* trunk communities**, 5 sites.
  Hay-meadow on moderately fertile, continuously wet soils.

6 **Fragmentary *Triglochino-Agrostietum stoloniferae***, 8 sites (including *juncetosum gerardi*, 3 sites).
  Grassland on moderately nutrient-poor, moderately acid, often flooded soils which remain moist year-round.

7 ***Ranunculo-Alopecuretum geniculati***, 5 sites.
  Grassland on nutrient-rich soils, flooded in winter/spring. In summer, groundwater is deep and soils dry out.

8 ***Arrhenatheretum elatioris*** (excluding *festucetosum arundinaceae*), 5 sites.
  Hay-meadow on moderately nutrient-rich, relatively dry soils.

9 ***Arrhenatheretum elatioris festucetosum arundinaceae***, 5 sites.
  Slightly ruderalized *Arrhenatheretum* on moderately nutrient-rich, relatively dry, calcium-rich soils.

10 ***Mesobromion erecti* trunk communities**, 5 sites.
  Chalk grassland, *i.e.* grassland on dry, calcareous soils.

11 **Fragmentary *Phleo-Tortuletum ruraliformis***, 5 sites.
  Pioneer community on dry, relatively calcium-rich dune sand.

12 ***Spergulo-Corynephoretum***, 5 sites.
  Pioneer community on dry, acid, nutrient-poor, humus-poor, sandy soils.

13 ***Genisto anglicae-Callunetum***, 5 sites.
  Heath or grass-heath vegetation on relatively dry, nutrient-poor, very acid soils.

14 ***Ericion tetralicis*** (trunk communities and *Lycopodio-Rhynchosporetum*), 6 sites.
  Heath or grass-heath vegetation on wet, nutrient-poor, very acid soils.

Materials and methods

Investigated sites

As part of a study on Dutch roadside ecology, 74 sites were selected, scattered across the Netherlands. Within each site a single plot of 25 m^2 was studied. The sites reflected a wide range of undisturbed, semi-natural conditions, including: pure sand to heavy clay to peat, pH-$CaCl_2$ levels from 3.6 to 7.6, extremely nutrient-poor to very nutrient-rich, and groundwater levels from near the surface during long periods, to well out of reach of the roots for the entire year. The sites were unfertilized and under vegetation cover also in winter, although many were mown once or twice per year (usually with removal of the cuttings).

The vegetation at the sites was classified into 14 very different plant community types (Table 1), with approximately equal numbers per type. The community types reflected the variation in edaphic conditions to a considerable extent, since plant community types can be considered to summarize a complex of ecological requirements. However, even within community types, the values for specific soil properties sometimes varied considerably, and the ranges for the different community types often overlapped partially.

Climate and weather

Climate in the Netherlands can be categorized as temperate Atlantic. On average (as measured during 1961-1990), the mean annual temperature is 9.4 °C, with average monthly means varying between 2.2 °C in January, and 16.8 °C in July. The actual mean annual temperatures in 1993 and 1994 were 9.6 and 10.6 °C, respectively. The monthly values are presented in Fig. 1.

Average annual precipitation in the Netherlands is 803 mm (1961-1990), with average monthly values varying between ca. 50 mm in February and April, to ca. 80 mm in November and December. 1993 and 1994 were relatively wet: at the centre of the country (De Bilt) precipitation amounted to 880 mm in 1993 and 1023 mm in 1994. Monthly values are presented in Fig. 1.

The average annual amount of direct radiation (sunshine) in the Netherlands is 1477 h (1961-1990). Both 1993 and 1994 were relatively sunny with 1493 and 1548 h, respectively. Monthly values presented in Fig. 1 (data from the Royal Dutch Meteorological Institute: Heijboer 1994/1995).

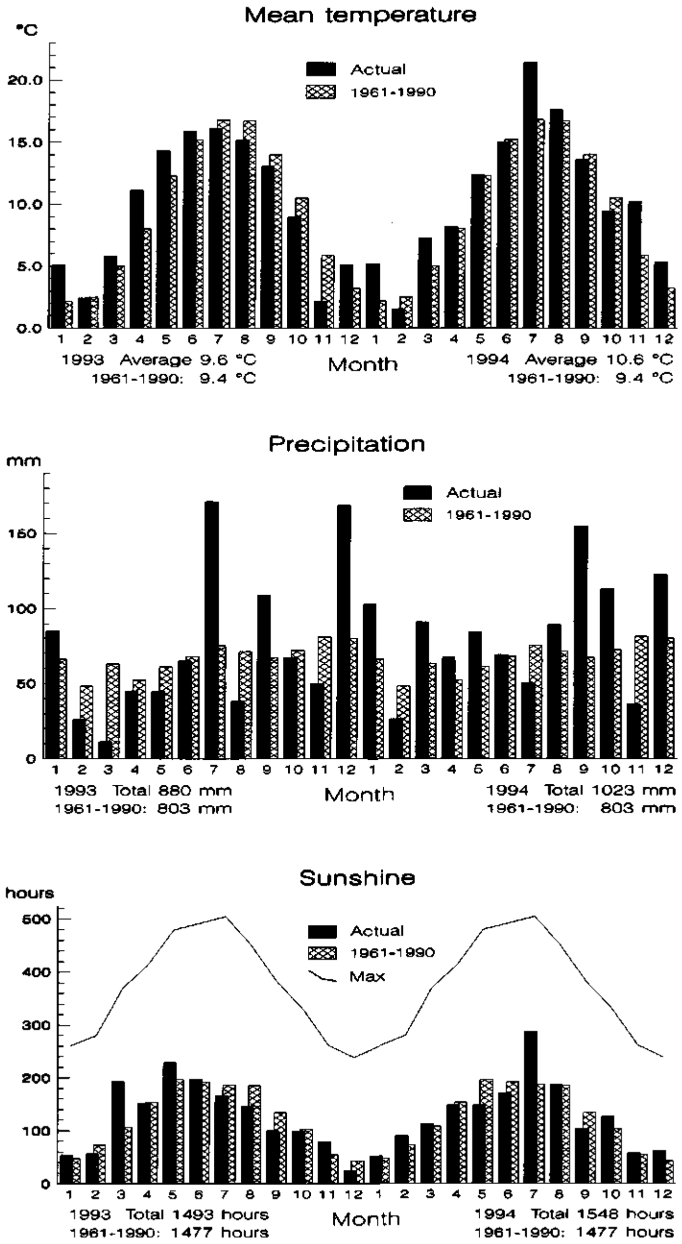

Figure 1. *Monthly and annual values for mean temperature, precipitation and amount of sunshine over the full two year period of consecutive field-incubations (1993 & 1994). Data for 'De Bilt' (approximately in the centre of the Netherlands). Mean values for 1961-1990 also presented.*

Table 2. *Correlations between the average mineralization rate over specific periods of different length, and the annual N mineralization rate, for both 1993 and 1994. The percentage of variation explained by the minimum correlation in the two years is given separately (in bold for the best periods of a specific length). To put the data into perspective, the percentage of the total annual mineralization realised during each period, as well as the soil temperature sum over each period, is indicated (two year averages). Temperature sums were calculated by adding the mean daily soil temperatures above 0 °C (using measurements from the Wageningen weather station at -0.05 m depth in grass covered soil).*

Combined incubation (period numbers)	Mean start date	Mean end date	Average period length (days)	Average temperature sum (°C days)	Average % of annual temperature sum	Average % of annual mineralization	Correlation with annual mineralization		R^2 (%) of the minimum correlation
							1993	1994	
1 incubation									
1	05 Jan[a]	- 05 Mar	59	222	6	7	.67	.76	44.4
2	05 Mar	- 10 Apr	36	239	6	10	.73	.72	51.6
3	10 Apr	- 22 May	42	521	13	20	.90	.83	68.3
4	22 May	- 05 July	44	728	18	20	.86	.82	66.8
5	05 July	- 16 Aug	42	821	20	13	.85	.78	60.2
6	16 Aug	- 03 Oct	48	753	19	13	.84	.82	67.9
7	03 Oct	- 16 Nov	44	452	11	11	.82	.87	67.9
8	16 Nov	- 05 Jan	50	284	7	6	.70	.68	45.9
2 incubations									
2-3	05 Mar	- 22 May	78	760	19	30	.94	.90	**81.5**
3-4	10 Apr	- 05 July	86	1249	31	40	.95	.90	**81.1**
4-5	22 May	- 16 Aug	86	1549	39	33	.91	.91	**82.0**
5-6	05 July	- 03 Oct	90	1574	39	26	.92	.89	79.3
6-7	16 Aug	- 16 Nov	92	1205	30	24	.89	.92	79.8
3 incubations									
2-4	05 Mar	- 05 July	122	1488	37	50	.97	.95	**89.5**
3-5	10 Apr	- 16 Aug	128	2070	51	53	.97	.96	**92.7**
4-6	22 May	- 03 Oct	134	2302	57	46	.95	.93	86.9
5-7	05 July	- 16 Nov	134	2026	50	37	.93	.95	86.5
4 incubations									
2-5	05 Mar	- 16 Aug	164	2309	57	63	.98	.98	**95.5**
3-6	10 Apr	- 03 Oct	176	2823	70	67	.99	.97	94.9
4-7	22 May	- 16 Nov	178	2754	69	57	.96	.96	92.2
5 incubations									
2-6	05 Mar	- 03 Oct	212	3063	76	76	.99	.98	96.9
3-7	10 Apr	- 16 Nov	220	3275	81	77	.99	.98	96.5
6 incubations									
2-7	05 Mar	- 16 Nov	256	3514	87	87	.99	.99	98.0

[a] Due to solidly frozen soils, the start of the very first incubation period (1993) had to be postponed for 1.5 weeks but, as mineralization in the frozen soils was assumed to have been negligible, the first incubation was taken to have started at the planned earlier date.

Soil bulk density

Bulk density was determined using five random soil cores per plot. Each core was obtained with a 100 mm long auger capable of collecting exactly 0.2 L of undisturbed soil. Drying took place at 40 °C. All chemical results were expressed on a volume of soil basis (*i.e.* amount ha^{-1} to 0.10 m depth).

Mineralization assessment

During two successive years (1993 and 1994), net N mineralization in the top 0.10 m of the soil was assessed by incubation *in situ*. Incubation took place during 16 successive periods (*i.e.* 8 periods per year; see Table 2). Individual incubation periods lasted ca. 6 to 7 weeks. Incubation periods were shorter in spring (5 weeks), and longer during the winter (up to 8.5 weeks). Similar sampling dates were used in both years. Visiting all sites took between 9 and 12 days: the dates presented in Table 2 are averages.

Undisturbed soil cores were incubated (see also Raison *et al.* 1987) using polyvinyl chloride tubes with sharpened lower rims (length 150 mm, inner diameter 25 mm). These tubes were driven 0.10 m into the soil. Loose litter was removed before sampling, but the decomposed layer was left undisturbed. Five paired samples per plot were obtained. One tube of each pair was taken back to the laboratory immediately after sampling (reference samples). The other was left in the soil, covered with a lid which left a few small side holes open for gaseous exchange. No cover was used on the bottom end of the tube, in order to enable the cores to adapt to changes in soil moisture content to some extent. The incubated cores were collected at the end of the incubation period, this being the start of the next period.

The five incubated samples of each site were bulked and the same was done with the five reference samples. Thus, one bulked incubated sample and one bulked reference sample was obtained for each individual incubation period at each site. In the remainder of this study, these bulked samples will simply be referred to as the 'samples'. Incubated samples and reference samples were treated identically. They were kept cool during transportation and sometimes needed to be stored cold (1 - 4 °C) for 1 to 2.5 days.

Due to the relatively large amount of time involved in collecting all samples from their scattered locations and the inevitable storage associated, analysing fresh samples was not feasible. Samples were dried at 40 °C for ca. 48 h, and fresh and dry weights were recorded. The samples were subsequently sieved using a 1 mm sieve to obtain a homogeneous sample. The material remaining on the sieve was weighed for adjustment of the results to the original sample size. The dry samples were sometimes stored (for 1 to 10 weeks) in plastic bags in a cool, dry place until chemical analysis. Storage under these conditions, as well as sieving, hardly affect extractable N fractions (Houba & Novozamsky 1998; Houba *et al.* 1993).

Three g of each dry sample were extracted by shaking for 2 h in 30 ml of 0.01 *M* $CaCl_2$ (Houba *et al.* 1986, 1990, 1996). After centrifuging for 10 min at 3000 g, NO_3-N and NH_4-N were determined spectrophotometrically using a Segmented Flow Analyzer (Skalar, Breda, the Netherlands). Mineral N was taken to be the sum of NO_3-N and NH_4-N. The incubated and the associated reference sample were always analysed in pairs. N mineralization was calculated as the amount of mineral N in the incubated sample minus the amount in the reference sample. This measure of the net N mineralization will simply be referred to as 'N mineralization' in the remainder of this chapter. Summation of the N mineralized in all the incubation periods of each year, yielded annual mineralization rates for 1993 and 1994. From these, average annual rates were calculated. Results were expressed as N mineralized in kg N ha^{-1} yr^{-1} (to 0.10 m depth).

Direct soil measurements

The amounts of NO_3-N, NH_4-N, and mineral N (N_{min}) directly extractable from the soil at each of the sampling dates were already available from the $CaCl_2$ extracts of the reference samples. In addition, these extracts were analysed for: soluble organic N (N_{org}), total extractable N (N_{min} + N_{org}), the fraction of N_{min} available as NO_3-N, available phosphorus (PO_4-P), and available potassium (K^+). Moisture contents were also determined in all reference samples (by drying at 40 °C), and were expressed on a gravimetric and volumetric basis. All the above results were therefore obtained for each of the sampling dates (Table 2).

Soil pH was measured in the 0.01 *M* $CaCl_2$ extracts, in the settling suspension, before centrifuging the extracts for further analysis (Houba *et al.* 1990, 1996; Schofield & Taylor 1955). The resulting pH-$CaCl_2$ usually takes values 0.3 - 0.8 lower than the frequently used pH-H_2O (Gupta & Rorison 1975). Compared to pH-KCl, values are generally 0.5 higher in very acid soils, and similar in slightly alkaline soils (Fotyma *et al.* 1998). Soil pH was determined in the reference samples from January and August 1994. The average value was used, as differences were generally small and showed no consistent seasonal trend.

Total soil N, P and K were determined by digestion with H_2O_2 at 100 °C, followed by digestion with concentrated sulphuric acid at 300 °C, using selenium as a catalyst and salicylic acid to improve the recovery of nitrate. The amount of carbonates and bicarbonates was determined by treating the samples with HCl and measuring the volume of CO_2 which evolved. Organic matter content was determined by loss on ignition at 550 °C. Carbon contents were determined by oxidizing the organic matter in the samples with $K_2Cr_2O_7$ in very strong sulphuric acid for 1.5 h at 100 °C, and measuring the concentration of Cr^{+3} that was formed. Cation exchange capacity was determined at the actual soil pH and at a low ionic strength using unbuffered $BaCl_2$. Clay content ($<2\mu$) and the content of fine particles ($<16\mu$) were determined using a method based on differences in sedimentation velocity. The sand-fraction ($>65\mu$) was determined by sieving, before determination of the other fractions. The silt content ($2\text{-}65\mu$) and the fine and course silt fractions (2-16 and $16\text{-}65\mu$), were calculated from the other fractions.

Groundwater levels (to a depth of 1.5 m) were determined at all sampling dates. Soil pF values for all sampling dates were estimated on the basis of matric potential characteristics obtained from the literature (Wösten *et al.* 1994) using soil moisture content and particle size composition.

Data analysis

Average mineralization rates for combined periods of different lengths (*i.e.* periods consisting of different numbers of individual incubation periods) were calculated using the amount of N mineralized during the combined periods and the combined length. These rates were subsequently correlated with the annual mineralization rate. The correlations were based on log-transformed data, with mineralization rates expressed as kg N ha^{-1} d^{-1} (to 0.10 m depth), after the addition of 0.5 kg N ha^{-1} d^{-1} to eliminate negative values.

Stepwise multiple regression (Sokal & Rohlf 1995) was used to find a limited set of simple soil variables with which the average annual N mineralization might be predicted adequately. To conform to statistical requirements, regression was based on log-transformed data, with the annual mineralization expressed as kg N ha^{-1} yr^{-1} (to 0.10 m depth), after the addition of 5 kg N ha^{-1} yr^{-1} to eliminate negative values. All the soil properties previously described were considered as independent variables, allowing for possible second order polynomials. Also the plant community type was considered. Most independent variables were log-transformed before analysis. Fractional data, if not log-transformed, were arcsine-transformed (Table 3).

For the independent variables which were sampled at different dates, the overall average annual values were used initially. Since the most promising regression model appeared to include some of these seasonal variables, a cross-validation technique was applied to determine which sampling date performed best. For this, the data set was split in two: data from 1993 and data from 1994. The annual mineralization in the first year was regressed several times, each time using the values for the predictor variables as measured at a specific sampling date in the first year. The regression coefficients obtained for each of the sampling dates were subsequently used to predict the annual mineralization in the following year, using also the predictive measurements at the corresponding dates in that second year. The predicted mineralization rates were compared to the actual mineralization rates, and coefficients of determination calculated. Next, the procedure was reversed, now using data from the second year to obtain regression coefficients for each of the sampling dates, and using the first year data for validation of these coefficients. The best performing sampling date was considered to be the one which validated best in both years.

Results

Short-period field incubation

When using one incubation period only (ca. 6 weeks), correlations between the average mineralization rate during this period and the annual mineralization rate were relatively low (Table 2). However, when the period was extended to include two incubation periods (ca. 12 weeks), correlations of 0.90 or higher ($R^2 > 81\%$) were obtained, as long as the incubations were performed anywhere between early March and mid August (Table 2). If the combined period was extended to include three incubation periods (ca. 18 weeks), the best results again occurred for incubations performed between early March and mid August, with correlations amounting to 0.95 or higher ($R^2 > 89\%$). By using a combined period of four incubation periods (ca. 24 weeks) a noticeable improvement in the correlation was still obtained. The period between early March and mid August again appeared to be best; correlations of at least 0.98 (R^2 95.5%) were obtained for this (now entire) period. Extending the period of mineralization assessment to more than four incubation periods contributed only little in terms of correlations.

Direct soil measurements

Bivariate correlation analyses showed that, of all the measured soil variables, only the mineral N pool (N_{min}) correlated relatively well ($R^2 > 50\%$) with the average annual N mineralization over the wide range of conditions studied (Table 3). If we discard variables obviously related to N_{min} (*e.g.* NO_3, NH_4, total extractable N, and the fraction

Table 3. *Bivariate correlation coefficients (Pearson) for the measured soil properties with the average annual N mineralization. The associated coefficient of determination (*R^2*) and the two-tailed significance are indicated. For each of the studied variables, the range, unit, and applied transformation are given. Units other than for groundwater refer to a depth of 0.10 m.*

Variable	Min.	Max.	Unit	Transformation	r	R^2	Sign. (n=74)
Avg. annual N mineralization	1.4	348	kg ha^{-1} yr^{-1}	Log(x+5.0)	-	-	-
Avg. mineral N (N_{min})	1.3	24.8	kg ha^{-1}	Log(x)	0.753	0.567	<0.0001
Avg. NO_3-N	0.14	18.8	kg ha^{-1}	Log(x)	0.684	0.468	<0.0001
Avg. NH_4-N	0.79	12.2	kg ha^{-1}	Log(x)	0.606	0.367	<0.0001
Avg. soluble organic N (N_{org})	3.23	27.7	kg ha^{-1}	Log(x)	0.272	0.074	0.0193
Avg. extractable N (N_{min}+N_{org})	6.06	43.4	kg ha^{-1}	Log(x)	0.510	0.260	<0.0001
Avg. (NO_3-N / N_{min})	0.03	0.76	-	Arcsine(√x)	0.491	0.241	<0.0001
Avg. available P (PO_4-P)	0.01	11.1	kg ha^{-1}	Log(x)	0.599	0.358	<0.0001
Avg. available K	4.7	187	kg ha^{-1}	Log(x)	0.498	0.248	<0.0001
Soil pH (in 0.01 *M* $CaCl_2$)	3.7	7.6	-	-	−0.046	0.002	0.6998
Avg. groundwater level	<−1.50	−0.05	m	8 classes^a	−0.527	0.277	<0.0001
Avg. highest water level	<−1.50	+0.11	m	8 classes^a	−0.485	0.236	<0.0001
Avg. lowest water level	<−1.50	−0.14	m	8 classes^a	−0.429	0.184	0.0001
Avg. soil moisture content	0.0442	5.821	g g^{-1} dry	Log(x)	−0.348	0.121	0.0024
Avg. highest moisture content	0.0629	6.462	g g^{-1} dry	Log(x)	−0.338	0.114	0.0033
Avg. lowest moisture content	0.0076	5.036	g g^{-1} dry	Log(x)	−0.378	0.143	0.0009
Avg. soil pF	<1	4.1	-	<1 ⇒ 1	0.321	0.103	0.0053
Avg. lowest pF	<1	2.9	-	<1 ⇒ 1	0.304	0.092	0.0085
Avg. highest pF	<1	6.0	-	<1 ⇒ 1	0.234	0.055	0.0446
Total N	0.17	8.8	ton ha^{-1}	Log(x)	0.147	0.022	0.2117
Total P	0.08	1.9	ton ha^{-1}	Log(x)	0.352	0.124	0.0021
Total K	0.50	21.2	ton ha^{-1}	Log(x)	0.079	0.006	0.5012
C:N ratio	9.4	44.4	-	Log(x)	−0.189	0.036	0.1070
Cation Exchange Capacity	16.5	432.6	kmol+ ha^{-1}	Log(x)	0.044	0.002	0.7113
Organic matter content	0.006	0.609	g g^{-1}	Log(x)	−0.134	0.018	0.2538
$CaCO_3$ content	0.000	0.648	g g^{-1}	Log(x+0.001)	−0.080	0.006	0.4996
Clay fraction (<2μ)	0.004	0.464	g g^{-1}	Log(x)	−0.071	0.005	0.5470
Fine particle fraction (<16μ)	0.003	0.776	g g^{-1}	Log(x)	−0.062	0.004	0.6027
Silt fraction (2-65μ)	0.002	0.651	g g^{-1}	Arcsine(√x)	−0.022	0.000	0.8509
Sand fraction (>65μ)	0.039	0.970	g g^{-1}	Arcsine(√x)	0.223	0.050	0.0560

[a] <−1.50 m; −1.50 to −1.21; −1.20 to −0.91; −0.90 to −0.61; −0.60 to −0.31; −0.30 to −0.03; −0.02 to +0.01; >+0.01 m.

of N_{min} available as NO_3-N), as well as available P and K (which were highly correlated with N_{min}), then most of the remaining correlations are only relatively weak to insignificant. Also C:N ratio, total soil N, the organic matter content, and soluble organic N did not show significant correlations (at p=0.01). The only notable correlations remaining involve the groundwater level. Higher groundwater levels were to some extent related to lower annual mineralization rates ($R^2 \leq 28\%$).

Stepwise multiple regression analyses indicated that the set of variables best predicting the average annual N mineralization consisted of:

1. N_{min} (positive partial relation),
2. gravimetric moisture content (negative partial relation),
3. pH (second order polynomial; optimum at pH-$CaCl_2$ 5.5 to 5.6).

Because of the seasonal variation in moisture and N_{min}, attention was subsequently focussed on the different sampling dates using the cross-validation method (see 'Materials and methods'). It appeared that best results were consistently obtained using samples from early March (Table 4). For the calculated regression models analysing the 1994 data, the highest coefficient of determination was obtained when using early March measurements (77.2%). This early March model also validated best; when the obtained regression coefficients were used to predict the mineralization in 1993 (using soil measurements from March 1993), 70.8% of the variation in actual mineralization in that year was predicted. The calculated regression models for the 1993 data showed only the second best results when using early March measurements (76.3%), but the March model was again the one which validated best (predicting 72.7% of the variation in mineralization for 1994). The seemingly better model for the 1993 data (mid November) performed worst of all during validation in 1994. It can thus be concluded that the models using early March measurements validate best.

Table 4. *Cross-validation of different sampling dates in the regression models predicting the annual N mineralization. Presented are* R^2 *values (%) for the calculated models based on one-year data, followed by their predictive merit,* i.e. *the* R^2 *when using the regression coefficients to predict the mineralization in the other year using also the predictive measurements from that year (at the specific sampling date under investigation). The final column presents the* R^2 *for models using average values over both years. High values in bold, the final model (Table 5) underlined.*

Average date of sampling	Calculated model for 1993	Predictive merit in 1994	Calculated model for 1994	Predictive merit in 1993	Calculated average model
05 Jan	69.6	62.3	69.9	60.6	78.3
05 Mar	**76.3**	**72.7**	**77.2**	**70.8**	**83.5**
10 Apr	70.8	62.2	70.1	60.6	76.8
22 May	71.5	63.4	70.5	63.9	76.4
05 Jul	70.0	55.9	73.6	46.4	76.9
16 Aug	72.4	45.3	73.4	38.4	76.6
03 Oct	72.5	46.5	73.8	38.3	76.6
16 Nov	**81.5**	43.7	71.5	50.6	79.0

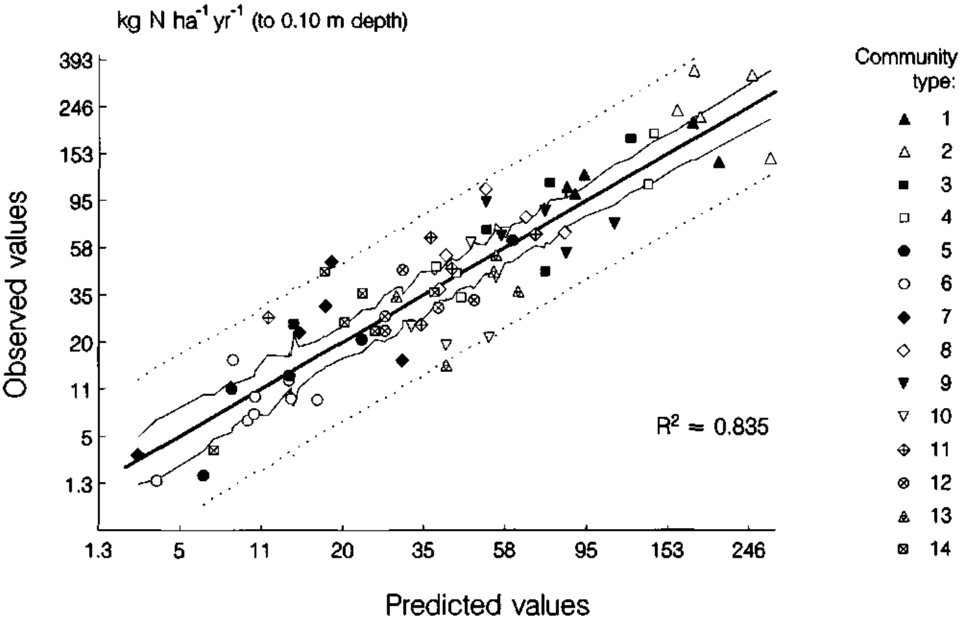

Figure 2. Average annual N mineralization as predicted by the multiple regression model (Table 5) versus *the actually observed amounts. 95% confidence limits connected by an unbroken line, 95% prediction limits for individual samples connected by a dotted line. Axes are log-transformed. Community types indicated; numbers according to Table 1.*

To obtain a final model predicting the *average* annual N mineralization, we may now use average values for early March from both years (Table 5). The variance explained is 83.5%, indicating a multiple correlation of 0.914. Fig. 2 shows the relation between predicted and observed values, the 95% confidence limits, and the 95% prediction limits for individual samples.

The final regression coefficients imply that an optimum exists at pH 5.54. Using this result, the final model may also be written in an alternative form (Table 5) using $(\mathrm{pH} - 5.54)^2$ instead of pH and pH^2. This new variable reflects the squared distance from the optimum at pH 5.54. The alternative form is more convenient for practical application and interpretation, as only a single pH-related variable remains.

We may use the alternative form of the regression model to obtain an impression of the relative importances of the three predictor variables involved, through inspection of the beta coefficients (Table 5). These standardized regression coefficients represent the relative slopes of the partial relationships. It appears that prediction of the N mineralization depends most on the amount of N_{min}. Moisture content comes next, showing only half as much influence. The pH-optimum variable $(\mathrm{pH} - 5.54)^2$ appears least important. The partial correlations (the correlation when the other variables present in the model are assumed constant) show a comparable order to that of the beta coefficients (Table 5).

The bivariate relationships between the four variables involved in the final regression model are presented in six scatterplots providing all possible bivariate combinations (Fig. 3). From the first three scatterplots (average annual N mineralization *versus* the independent variables) it can again be seen that only N_{min} (in March) shows a clear bivariate correlation with the annual N mineralization (R^2=56.4; two-tailed p<0.0001). The bivariate correlation for moisture content (in March) is only weak (R^2=9.7%; p=0.007). Soil pH only shows a very weak negative correlation (R^2=0.2%; p=0.700), and also the quadratic optimum variable can be shown to correlate only weakly (r=-0.209; R^2=4.4%; p=0.074).

From the last three scatterplots in Fig. 3 (mutual relationships between the three independent variables), it can be concluded that the model is based on data with a fairly even distribution of the values and their combinations.

Table 5. *Predictive multiple regression model for the average annual N mineralization (to 0.10 m depth) expressed as* ^{10}*Log(kg N* ha^{-1} yr^{-1} *+ 5). Presented are variable names, applied transformations, regression coefficients and their standard errors,* t-*values and significances. From the basic model (top), used for the calculation of significances, an alternative form (bottom) can be derived. For this more simple form, the standardized regression coefficients (Beta) and the partial correlation coefficients are presented. The* R^2 *of the model is 0.835 (0.825 when adjusted for degrees of freedom). The standard error of the estimate (the unexplained standard deviation) is 0.1642,* $n = 74$*. For 95% confidence limits: see Fig. 2.*

BASIC MODEL

Variable	Trans.	Coefficient	SE	T	*p*
Mineral N in early March (kg N ha^{-1} to 0.10 m depth)	^{10}Log	1.060	0.067	15.84	<0.0001
Moisture content in early March (g g^{-1} dry wt)	^{10}Log	−0.450	0.052	−8.62	<0.0001
pH^2 (in 0.01 *M* $CaCl_2$)	.....	−0.102	0.019	−5.40	<0.0001
pH (in 0.01 *M* $CaCl_2$)	.....	1.127	0.221	5.11	<0.0001
Constant	.....	−2.400	0.620	−3.87	0.0002

ALTERNATIVE FORM

Variable	Trans.	Coefficient	Beta	Partial *r*
Mineral N in early March (kg N ha^{-1} to 0.10 m depth)	^{10}Log	1.060	0.820	0.895
Moisture content in early March (g g^{-1} dry wt)	^{10}Log	−0.450	−0.472	−0.749
$(pH - 5.54)^2$ (in 0.01 *M* $CaCl_2$)	.....	−0.102	−0.342	−0.634
Constant	.....	0.723		

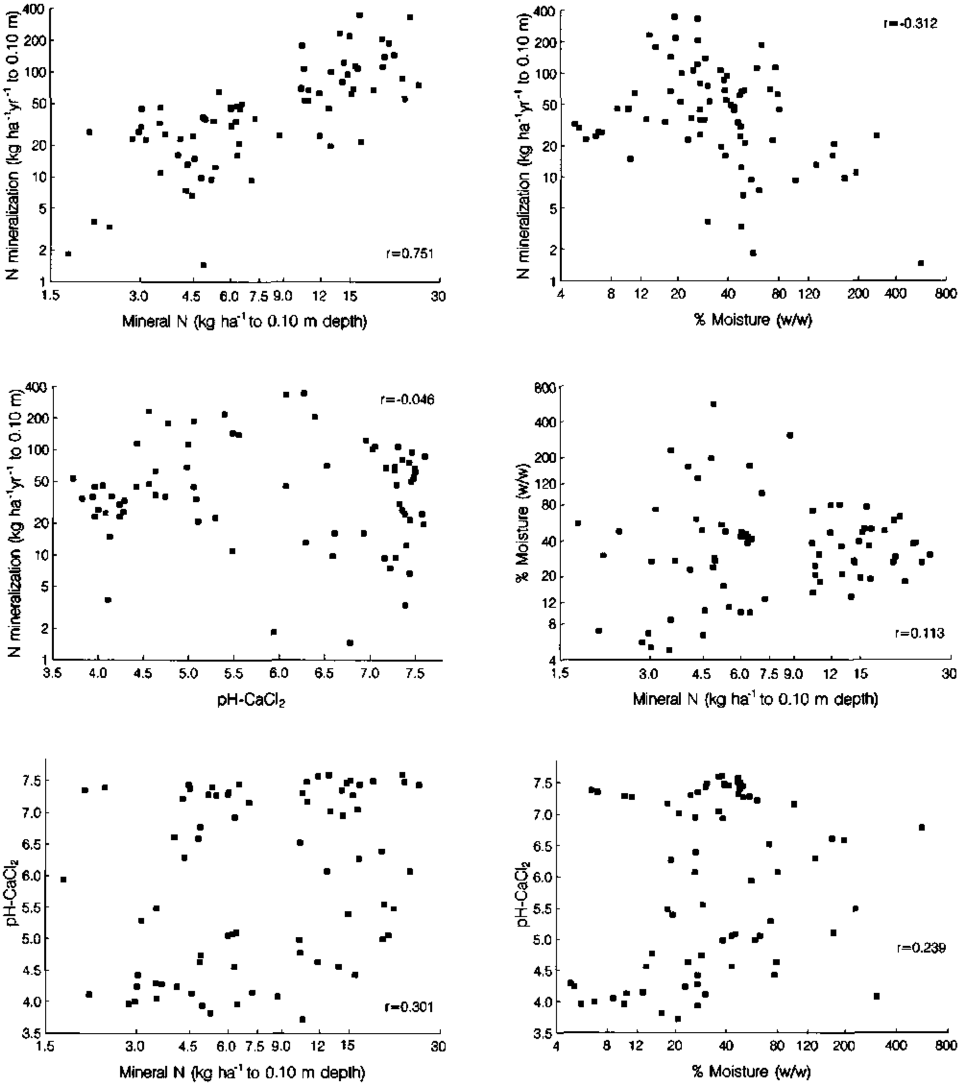

Figure 3. Bivariate scatterplots for the variables used in the multiple regression model: average annual N mineralization (log scale), N_{min} in early March (log scale), gravimetric moisture content in early March (log scale), and pH-CaCl$_2$. The first three plots present the average annual N mineralization versus *each of the independent variables, the last three plots illustrate the data structure for the independent variables mutually.*

If instead of soil properties, the plant community type was used to explain the N mineralization, a large part of the variation may also be explained (73.8%). To examine the relationships *within* the plant community types (where the lengths of the ecological gradients are relatively short), all 'between-community variation' was eliminated by subtracting the community average from the values at each site. This was done not only for the average annual N mineralization, but also for each of the three predictive variables, leaving only 'within-community variation' for further analysis. Even then, it appeared that sites with N_{min} values lower than the community average usually showed mineralization rates lower than the community average, and sites with N_{min} values higher than the community average usually showed annual rates higher than the community average (Fig. 4). The correlation, which can be considered the average correlation within the studied community types, amounted to 0.685 (R^2=47.0%; p<0.0001). For pH and moisture content the 'within-community variation' no longer contributed significantly.

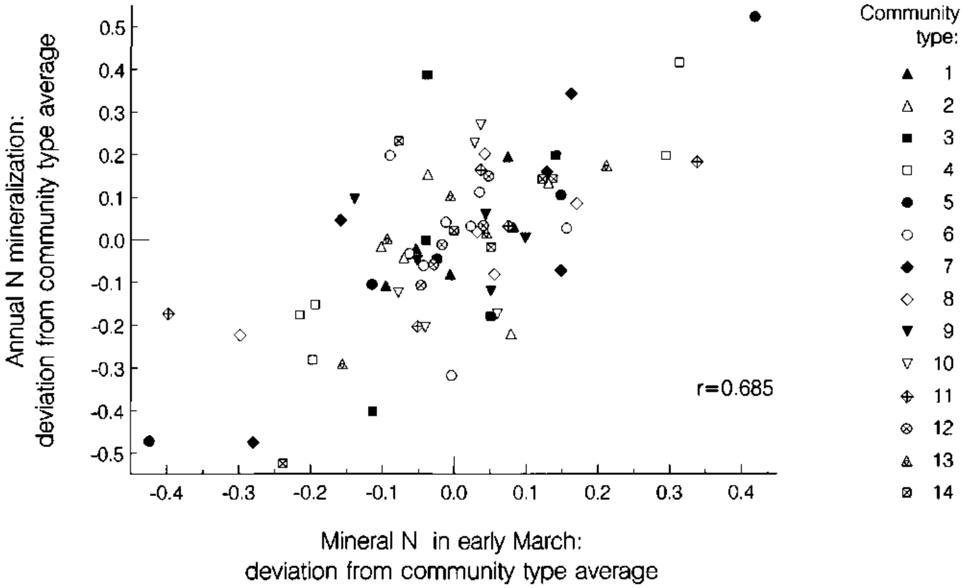

Figure 4. *The 'within plant community type' variation in average annual N mineralization presented in relation to the 'within plant community type' variation in N_{min} in early March. Values obtained by subtracting the community averages for both N mineralization and N_{min}, from the actual values at each of the sites (using transformed data). Community types indicated; numbers according to Table 1.*

Discussion

Early March to mid August appeared to be the best time for short-period field incubations aiming to evaluate the entire annual N mineralization. Within this period, successive incubations needed to be carried out for at least three months before a good correlation with the total annual mineralization could be expected. For shorter periods, the results most likely depended too much on the particular weather situation during and before the study. Using a three month period, a reasonable balance between precision and effort is obtained; the coefficient of determination was similar to the one obtained when using direct soil measurements from early March in a predictive regression model (R^2>80%). Increasing the number of sequential incubations naturally improved correlations, since the amount of N mineralized during a specific period is part of the amount mineralized during the whole year. When the entire period between early March and mid August was used (5.5 months), an R^2 of approximately 95% was achieved. Extending the period of sequential incubations any further provides relatively little extra information considering the extra investment.

These results are in accordance with the fact that a large part of the microbial activity can be expected to take place during the period early March to mid August. Of the total annual mineralization, ca. 63% was generally realised within this period, and the obtained correlations likely depend largely on this fraction. Although the realised mineralization will in turn depend on the temperature sum of specific periods, such a relationship was not as clear as might be expected (Table 2). The reason for this probably is the occurrence of moisture limitation in summer at many of the sites. The occurrence of a spring flush in mineralization may further interfere. Mineralization peaks in spring or early summer have frequently been reported (Runge 1978; Taylor *et al.* 1982; Williams 1969), and are probably caused by the availability of a relatively large and not yet depleted pool of readily decomposable components after the winter period. In the present study, the peak mineralization generally occurred in April, May, or June.

As an alternative for incubation methods, direct soil measurements can apparently be employed successfully to predict the average annual *in situ* N mineralization. A single (bulked) sample is needed, from which the three predictive soil properties (N_{min}, moisture content, and pH) can be measured using simple procedures. Best results can be expected when samples are collected just before the growing season (early March).

This result should be viewed in relation to the very wide range of environmental conditions involved (see Tables 1 and 3). This may explain why only low correlations were obtained for other (more frequently studied) properties such as total soil N, organic matter content, C:N ratio, particle size distribution, cation exchange capacity, and also soluble organic N (N_{org}) which has recently received considerable attention (*e.g.* Appel & Mengel 1998; Groot & Houba 1995; Mengel *et al.* 1999). The present results indicate that the reported relationships for these properties probably hold only within a relatively homogeneous set of soils.

One could, in theory, presume that the partial relationship between N_{min} and annual N mineralization constitutes a methodological artifact, caused by the use of dried samples (which was inevitable: see 'Methods' section). Drying at 40 °C is the standard pretreatment for the 0.01 *M* $CaCl_2$ extraction, but has been shown to increase the extractable amounts of some N fractions (particularly NH_4-N and N_{org}: Houba *et al.* 1989; Van Erp *et al.* 1998). This will have little effect on the mineralization assessment (as changes will be similar in the incubated and the reference sample and will thus largely cancel out), but N_{min} could be affected. Since changes in N_{min} during drying may involve easily mineralizable compounds, this could partially explain the relationship between N_{min} and the annual mineralization. However, this reasoning does not hold true when considering the range of N_{min} values studied, extending from 1.3 to 24.8 kg ha^{-1}. It is with respect to this variation (an almost 20-fold difference) that the established relationship should be considered. Possible effects of drying are too small to have had any significant influence on the predominant data structure.

Soil moisture content showed a negative partial relationship in the multiple regression model. Other studies generally agree that optimum conditions for mineralization exist between pF 2.0 and 2.7, when 10 to 20% of the soil pores are filled with air (Miller & Johnson 1964; Myers *et al.* 1982; Sierra 1997; Stanford & Epstein 1974). The present regression results seem to show no such optimum, even though pF values ranged from complete moisture saturation to pF 4.1 (annual averages). The relationship even remained negative when, during additional analyses, only the dry plots or the wet plots were considered. Although the present study makes comparisons between sites, whereas the above mentioned studies only showed that within specific sites optimal moisture contents exist, one would nevertheless expect lower annual mineralization rates also in extremely dry situations. This appears to be true also in the present study (Fig. 3), but at the same time, the extremely dry locations showed relatively low N_{min} contents, and here lies the solution to the paradox. The negative relation for moisture content should only be viewed as a partial relationship in the context of the multiple regression model. Thus, it only holds for situations with similar N_{min} and pH. The model merely predicts that, when dry locations have been able to maintain N_{min} and pH levels similar to those of moister sites, annual mineralization rates of these dry sites must have been higher.

Moisture content performed best in the regression model when expressed gravimetrically (as g moisture g^{-1} dry soil). Additional regression analyses showed that, even when only the dry or only the wet sites were considered, gravimetric moisture content (log-transformed) still performed better than volumetric moisture content (arcsine transformed). Apparently, gravimetric moisture content is better fitted to express the partial relationship than the (perhaps biologically more informative) volumetric moisture content.

It might be argued that the soil moisture content at a specific sampling date is far too prone to temporal variation to be used as a predictor variable for N mineralization. A similar concern might exist toward N_{min}, which is subject to spatial variation as well (Gupta & Rorison 1975; Taylor *et al.* 1982; Troelstra *et al.* 1990a, 1995). Because of this, Binkley & Hart (1989) concluded that extractable N fractions cannot give reliable information on N availability. The problem of spatial variability can effectively be reduced by the use of bulked samples. As for temporal variability, additional analyses showed that this type of variation was substantially smaller than the between-site variation, for both moisture content and N_{min}.

The robustness of N_{min} and moisture content as predictor variables (in spite of seasonal variation) was also demonstrated by Table 4. The regressions based on different sampling dates all explained ca. 70% or more of the variation in annual mineralization. Moreover, variation between years may be expected to be much smaller, particularly for samples collected in early March. At that time, between-year differences have probably levelled off during winter, when most soil and plant processes have been largely inactive. Given a wide range of edaphic conditions and plant communities, N_{min} and moisture content may be considered useful site characteristics, especially when sampling takes place in early spring. Of course, samples should not be taken during or shortly after heavy rain, but this may be regarded an obvious precaution.

Much of the variation in N mineralization appeared to consist of variation between plant community types, as revealed by the large amount of variation explained by this parameter (73.8%). This is less than was explained using soil parameters (83.5%). Since the occurrence of a particular plant community not only depends on soil factors but also on management activities, the lower fraction explained is not unexpected.

The large differences in mineralization between plant community types raises the question whether the established relationships are also present within plant community types. The wide range of conditions on which the model was based can be considered its strength, but it may constitute a weakness when predictions are desired for sites with relatively similar ecological conditions. Nevertheless, a clear correlation between N_{min} and the annual N mineralization could still be demonstrated within the community types (Fig. 4). N_{min} can therefore still be used as an indicator of the average annual mineralization when only sites with similar ecological conditions are compared. However, it is debatable whether moisture content and pH should also be used in the predictive model in such cases, since their contribution no longer remained significant.

In the agricultural practice, N_{min} is mainly regarded as a simple N pool. N uptake in crops is generally viewed as originating from three main sources: the N_{min} pool at the onset of the growing season, fertilization, and mineralization (*e.g.* Wild 1988). Fertilizer recommendations have long been based on the N_{min} content in early spring, although N_{min} is generally assessed using a relatively strong extraction solution and using fresh soil, often sampled up to 0.6 or 0.9 m depth. An example is the so-called N_{min}-method (Wehrmann & Scharpf 1979, 1986) which has found wide acceptance (see Appel & Mengel 1992; Mengel 1991). Such methods are based on studies of crop response, often showing clear relationships between N_{min} in early spring and fertilizer needs (Borst & Mulder 1971; Soper & Huang 1963; Wehrmann & Scharpf 1979, 1986), or plant N uptake (Appel & Mengel 1992; Németh *et al.* 1987).

Even though N_{min} is usually not considered for its possible information on N mineralization, laboratory studies demonstrating correlations between extractable N fractions and N mineralization do exist (Appel & Mengel 1993; Groot & Houba 1995; Soper & Huang 1963). References on the special status of early spring samples can also be found. When samples were taken in different seasons, extractable N fractions in early spring samples often correlated best with N mineralization as measured using laboratory incubation (Groot & Houba 1995), or with potentially mineralizable N (McTaggart & Smith 1993).

That N_{min} has never received much attention as a measure of N mineralization is probably due to the fact that it is not a causal factor for mineralization. It can, however, be viewed the other way round. N_{min} may be considered the direct result of mineralization, although modified by plant uptake, atmospheric deposition, and losses by leaching and denitrification (see also Rochester *et al.* 1991). These modifications notwithstanding, N_{min} apparently reflects the annual N mineralization well, at least under unfertilized conditions. Although in theory the N_{min} content (pool size) does not need to be related to the rate of its replenishment through mineralization (flux size), this nevertheless appears to be the case. It should be emphasised that this possibly holds only for undisturbed soils under year-round vegetation cover. Under cultivated conditions, the relationship could be different.

In conclusion, the mineral N pool should be considered a valuable soil parameter, indicative of the annual N mineralization in unfertilized ecosystems with undisturbed soils. Given a wide range of soil conditions or plant community types, a fairly accurate estimate of the average annual N mineralization may be obtained using soil mineral N, moisture content and pH as predictors. This way, the laborious technique of year-round field incubations can be circumvented.

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8

General discussion

General discussion

The previous chapters, although perhaps not strongly related at first sight (apart from referring to the same roadside locations), contain various links that deserve particular attention. The current chapter aims to identify the core relationships between plant communities and their environment, and attempts to identify the most important ecological factors. This central objective will be addressed from different starting points.

Synecology

In Chapter 2 the synecology of the plant communities was described. When the data were scrutinized for the variables best discriminating between the syntaxa, eight main variables were obtained. Although these variables primarily constitute the most suitable set of discriminating variables from a *statistical* point of view, they almost certainly include the *ecological* master factors in one way or another, either explicitly, or in a more or less indirect way. In addition, since the study was purely descriptive and involved relatively undisturbed (semi-natural) communities, most variables will depend on another to some extent. Several may even be strongly related. For these reasons, the eight discriminating variables should not be considered to simply represent eight individual ecological master factors. If we consider the list of main variables and try to identify the master factors they represent, the following picture emerges:

Statistically discriminating factors:	Ecological master factors:
1. intensity of shading	LIGHT
2. average spring groundwater level	MOISTURE
3. average lowest groundwater level	
4. percentage of $CaCO_3$	ACIDITY
5. soil pH	
6. percentage of fine soil particles	NUTRIENTS
7. degree of nitrification	
8. available K pool	

This of course is a simplified view. For instance, although not indicated above, some variables may also be considered representations of more than one ecological factor. This is most clear for the percentage of $CaCO_3$. The extremely high amounts of $CaCO_3$ occurring in some sites in this study (up to approx. 65%) not only indicate alkaline conditions, but also indicate the presence of a very shallow soil (because in these cases the $CaCO_3$ originates from blocks of limestone or marl already present within the top

10 cm of the soil). The shallowness of the soil in turn affects both the soil moisture status and the availability of nutrients. The percentage of fine soil particles is also partly related to moisture. It influences the capacity of the soil to retain moisture, and because of this it affects the amplitude and duration of short-term moisture fluctuations.

The three variables representing nutrient availability may need some further attention. As far as the three macronutrients N, P and K are concerned, only K availability is explicitly represented. P availability does not seem to be represented specifically. Some information on N dynamics is provided by one of the selected variables, although this does not concern the actual N availability (N mineralization or the pool of mineral N), but the fraction of the mineral N pool that occurs as NO_3 (labelled 'degree of nitrification'). It should be noted that in the study on Ellenberg indicator values reported in Chapter 6, this nitrification degree (and the strongly correlated size of the NO_3 pool) were the soil variables that correlated best with the Ellenberg N value, and (surprisingly) not the N mineralization or the mineral N pool. In addition, the Ellenberg N values were concluded not to indicate N availability as such, but rather the general soil fertility as perceived by the vegetation. Apparently, the degree of nitrification is closely associated with general soil fertility.

Regardless of interactions and complications, it nevertheless appears that the discriminating variables more or less clearly represent the fundamental ecological factors: light, moisture, acidity, and nutrient availability. Perhaps this is not surprising. The studied syntaxa cover an extensive range of ecological conditions, and it might therefore be considered only natural that these long established, principal ecological factors emerge. On the other hand, the fact that these four factors again surfaced also during this study, once more confirms their basic nature.

Indicator values

For several ecological factors indicator systems exist, using the species composition at a site to obtain information on these factors. In Chapter 6, the Ellenberg indicator system was studied. For three ecological master factors (moisture, acidity, and nutrients) the study tried to establish which *measurable* variables correlate best with the indicator values that more or less correspond to these factors.

As far as the Ellenberg moisture values were concerned, the best correlated variables appeared to be the average lowest soil moisture content in summer, and the annual average groundwater level or the average spring level. It should be noted that the latter also appeared as one of the main discriminating variables in the synecology study (Chapter 2).

For Ellenberg soil reaction (often interpreted as an acidity value) the situation was complicated. The study revealed that - contrary to expectations - soil pH was not indicated very well. It was only indicated effectively in the lower pH ranges. Moreover, also the amounts of $CaCO_3$ were not effectively indicated. However, it appeared that the total amount of calcium (including both exchangeable Ca^{2+} as well as calcium from carbonates) correlated very well with the Ellenberg reaction values. Total calcium may be understood as an integration of both soil pH and carbonate content. When little or no calcium carbonate is present the total calcium amount mainly consists of exchangeable Ca^{2+} and is therefore closely associated with soil pH. When calcium carbonate is present in considerable amounts, the relatively high soil pH level will usually vary little, but the total calcium amounts still do since in this range total calcium largely depends on the amount of carbonate calcium. The combined importance of both soil pH and $CaCO_3$ content thus demonstrated by this study, is neatly supported by the synecology study (Chapter 2), where pH *and* the $CaCO_3$ content both emerged as major discriminating factors. This again emphasises that they are both important, and supply complementary information related to different parts of the total range.

Concerning the Ellenberg nitrogen values, it appeared that soil variables were not indicated very well. The best correlated variable appeared to be the average annual aboveground production. From this it can be concluded that Ellenberg nitrogen values do not simply indicate nitrogen availability as such, but rather soil fertility in general as perceived by the vegetation. The indicator value effectively summarizes an unspecified number of variables regulating vegetation productivity. Aboveground productivity was closely studied in Chapter 4. Here, it appeared to depend on the N mineralization, but also on a number of other environmental factors: soil moisture content, shading intensity, soil pH, and the percentage of fine particles (in order of importance). It is therefore not surprising that the Ellenberg N values do not indicate the soil N mineralization as such. Interestingly, it may also be noted that the above mentioned variables explaining productivity (Chapter 4) may again be considered representations of the four fundamental ecological factors discussed before: nutrients, moisture, acidity, and light. The Ellenberg N figures apparently do not summarize the measurable nutrient availability as derived from soil chemical analysis, but instead provide an integration of various factors, representing different ecological master factors influencing the fertility of a site *as perceived by the vegetation* (and as demonstrated by its productivity).

N mineralization

Mineralization has received a lot of attention in this thesis. When it was attempted to infer the N mineralization from biomass characteristics (Chapter 4), productivity appeared to be the most important variable. However, it proved not to be possible to infer the N mineralization satisfactorily from biomass characteristics only. Given the number of variables that also affect vegetation productivity (see above) this is not surprising. It appeared that an acceptable inference of the N mineralization rate can be based on the aboveground production of the herb layer only if site conditions are similar with respect to the average soil moisture content and shading.

It is, however, possible to estimate the average annual N mineralization from other *soil* properties, as demonstrated in Chapter 7. Three simple variables appear to be needed: soil mineral N pool, soil moisture content, and soil pH; all as measured just before the growing season. Two aspects of this result are remarkable. First, the appearance of the soil mineral N pool as the most important predictor variable. This pool-size variable is generally deemed of limited relevance since N availability is considered to depend mainly on the N flux (mineralization). However, the results imply that there is a positive relationship between the two variables, and that the pool of mineral N can be a reliable indicator of the annual N mineralization as long as information on soil moisture and acidity is also available. The second remarkable aspect is that the three explanatory variables once again directly correspond to three ecological master factors that have emerged several times already: nutrients, moisture, and acidity.

Since Ellenberg indicator values exist for these three master factors (with a different degree of correspondence to the predictor variables), it is worthwhile to investigate whether N mineralization can be predicted adequately from the combined use of the three Ellenberg values. In the discussion of Chapter 6 it was already mentioned that trial analyses showed that fairly reliable predictions may indeed be obtained this way. To be more specific: 63% of the variation in average annual N mineralization could be explained using the three site mean Ellenberg values (applying abundance weighting, frequency weighting, adjusted reaction values, and including the mosses), and each of the three Ellenberg factors contributed significantly to this result ($p \leq 0.0001$). Although this may be promising, further research on this topic is required before this preliminary result can be put to practical use.

The role of K

A recurring aspect in the different chapters is the role of K. Although this nutrient usually receives considerably less attention than N and P, its ecological function may be equally important. In Chapter 3 it appeared that rapid hay removal is especially effective with regard to K. In low productive communities (often the target communities in roadside management or nature conservation), aboveground biomass production still contains more K than the amounts annually received by atmospheric deposition, in contrast to N and P. This implies that when low productivity is to be maintained through hay making, K may be the only element that can limit an unwanted increase in productivity. This, however, can only be achieved if hay removal is not delayed longer than one week, because the element is rapidly released from the cuttings to return to the soil (Chapter 3).

The rapid cycling of K between soil and vegetation was also demonstrated clearly in the study on the mutual relationships between soil and biomass characteristics (Chapter 4). The relationship between the availability of an element in the soil and the concentration of that particular element in the vegetation was most clear for K.

Given these considerations, it may be less surprising that during the synecology study (Chapter 2) soil available K was the only discriminating variable directly related to nutrient availability. The selection of this variable should not be considered as a mere statistical effect, but likely represents the true ecological significance of this element, at least within the range of communities studied.

For several of the syntaxa studied, the nutrient composition of vegetation biomass suggested a relative shortage of K (Chapter 2). In these syntaxa, K presumably is the limiting nutrient. K limitation is sometimes reported in other studies (*e.g.* Boeye et al. 1997; van Duuren et al. 1997a,b; Goodman & Perkins 1968; Oomes 1990; Verhoeven et al. 1996), but probably does not receive as much attention as it should. K limitation might be more common than indicated by fertilization experiments, as it has been suggested that K limitation may affect biomass allocation more than biomass increase (Shaver & Chapin 1995). Since an element is only defined limiting when it limits growth (*i.e.* biomass increase) this may underestimate the importance of K limitation.

Vegetation management

Effects of management have received repeated attention in this thesis. In Chapter 2 (synecology study) it has naturally been discussed on several occasions as an important tool in the maintenance or restoration of plant communities.

Chapter 3 is entirely devoted to management in the form of hay-making and showed that if hay removal is to be effective as a tool to achieve soil impoverishment, the cuttings are best removed within one or two weeks (a maximum of 10 days may perhaps be a practical guideline). If not, an increase in productivity may be inevitable due to atmospheric nutrient deposition. If management is not adjusted, this will cause an increase in the standing crop.

In Chapter 4, it emerged that hay-making twice per year causes more nutrients to be removed than a single cut at the end of the season. Although biomass production is not affected, the additional early summer cut causes the vegetation to remain in a physiologically young state for longer periods, signifying higher nutrient concentrations.

In Chapter 5, the importance of the maximum standing crop for species diversity was described. At high standing crop, increased competition for space and light may cause a decrease in species richness. Particularly the numbers of rare and endangered species were influenced negatively by high standing crop values. Management should therefore prevent high values of maximum standing biomass if species-rich plant communities are to be maintained, or if rare and endangered species are to be preserved. However, management appeared to affect species diversity not only through its effect on the maximum standing crop. Possible other mechanisms involved are the more direct effects of management activities such as small-scale disturbances of the upper soil-layer and (creating small open patches and other micro-habitats; Parr & Way 1988), and the prevention of litter accumulation (Foster & Gross 1998). Also, seed dispersal may be enhanced, through seeds that become attached to the applied machinery (Bakker et al. 1995). In some species mowing may even stimulate flowering and seed production. Naturally, an important effect of mowing also is the prevention of succession towards shrub communities of a less species-rich nature (as discussed for various communities in Chapter 2).

Chapter 6 showed that management has the potential to complicate the use of Ellenberg indicator values. The nitrogen values, for instance, were shown to indicate productivity rather than the soil nutrient status and management can simulate aspects of low productivity by maintaining a low standing biomass. In Chapter 4, mowing also appeared to obscure the relationships between soil nutrient availability and tissue nutrient concentrations (except for K).

Management apparently affects the vegetation through a number of ecological processes. It affects tissue nutrient concentrations, soil nutrient availability, standing biomass, litter accumulation, small-scale heterogeneity, competition, flowering and seed production, and seed dispersal. Through these it controls the succession of plant communities, and affects species diversity and the occurrence of rare or endangered species. Given these fundamental effects, vegetation management may well be considered an ecological master factor, in addition to light, moisture, nutrients and acidity.

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Summary

Summary

Ecological framework

The primary objective of this study was to provide an accurate ecological description for a cross-section of the relatively well-developed and/or species-rich plant communities (syntaxa) in roadside habitats in the Netherlands. The study covered a wide selection of syntaxa, reflecting a broad range of edaphic conditions, including: *Urtico-Aegopodietum*, *Alliario-Chaerophylletum temuli*, *Valeriano-Filipenduletum*, *Fritillario-Alopecuretum pratensis*, *Calthion palustris*, *Triglochino-Agrostietum stoloniferae*, *Ranunculo-Alopecuretum geniculati*, *Arrhenatheretum elatioris* (excluding *festucetosum*), *Arrhenatheretum elatioris festucetosum arundinaceae*, *Mesobromion erecti*, *Phleo-Tortuletum ruraliformis*, *Spergulo-Corynephoretum*, *Genisto anglicae-Callunetum*, and *Ericion tetralicis*. A large number of ecological variables was measured.

The resulting ecological framework was presented in Chapter 2. It is intended to serve as a reference for ecological management and construction of roadsides aiming at the development, maintenance or restoration of specific syntaxa in order to increase the ecological value of these habitats. Although primarily intended for roadsides, the results may well be applicable for management and (re-)construction of other infrastructure, such as canals and river dykes.

The ecological variables best discriminating between the syntaxa were: the intensity of shading, the average groundwater level in spring and the average lowest groundwater level in summer, soil pH and the percentage of $CaCO_3$, the amount of fine soil particles, the degree of nitrification, and the soil pool of available K. For most practical applications, measurement of these factors will provide an adequate basis for predictions to be made, or management and (re-)construction decisions to be taken.

The obtained set of best discriminating variables may also be regarded as the 'ecological master factors'. It should however be realized that they mainly represent the *statistically* most important variables, given the various inter-correlations between the studied variables. Specifying true ecological masterfactors is not an easy task since the measured variables are all strongly interrelated, and they generally also depend on each other causally. However, the emerging discriminating variables clearly represent four principal ecological factors: light, moisture, acidity, and nutrient availability. Vegetation management may be considered an additional master factor.

Hay removal and soil impoverishment

In Chapter 3 the effects of a delay in hay removal on the nutrient balance of the studied syntaxa were described. This study was motivated by the observation that cuttings in roadsides are often left in the field for a considerable time (mainly for pragmatic reasons), which may be in conflict with the objective of attaining soil impoverishment.

It was confirmed that a large quantity of the macronutrients N, P, and K return to the soil within a relatively short period if removal of the cuttings is delayed. Within a six weeks period, this may amount to more than 50%. The losses from the cuttings were positively related to the initial tissue nutrient concentrations at the time of cutting. N loss over time was best explained by the initial C:N ratio, P and K losses by the initial P concentration. K losses were particularly large (up to 90% of the amount initially present in the mown biomass). K is mainly lost from the cuttings by leaching, whereas the major N and P losses are most probably caused by rapid microbial decomposition of readily-soluble substances.

When modelling the nutrient losses for cuttings of various syntaxa and for different hay removal delay times, it became apparent that in most syntaxa the cuttings should be removed within 1 week (or 2 weeks at most) if soil impoverishment is aimed for. If removal is delayed longer, the amount of nutrients removed will often fall below the annual atmospheric input. In plant communities where annual accumulation of N and P in the aboveground biomass is lower than the annual input through atmospheric deposition already, rapid removal of the cuttings may be the only way to maintain at least K at a limiting level.

The study showed that K cycles rapidly between soil and vegetation. This is confirmed by the results presented in Chapter 4, showing that the relationship between soil and tissue concentration is strong for K, whereas it is relatively weak for the other macronutrients. Additional evidence for the importance of K can be found in Chapter 2, where soil available K emerged as one of the factors discriminating between syntaxa. It was the only selected variable directly representing the availability of a macronutrient. It may be concluded that one of the most important effects of hay-making on the soil nutrient status consists of a reduction of the potassium availability, at least on sandy soils with a low cation exchange capacity and provided there is little delay in hay removal.

Soil versus *biomass relationships*

When investigating mutual relationships between soil chemical properties and biomass characteristics over the range of edaphic conditions studied (Chapter 4), it appeared that these relationships were generally complicated by other variables, most notably soil moisture content, and non-edaphic site conditions such as shading and management.

The average annual aboveground production appeared to depend mainly on the average annual N mineralization, soil moisture content, and the intensity of shading by overstory trees or shrubs, but to a lesser extent also on soil pH (optimum at pH-$CaCl_2$ 5.7) and the percentage of fine soil particles. Management appeared not to confound this relationship further. For the tissue nutrient concentrations the explanatory models usually included: management (mowing frequency), shading intensity, the availability of the corresponding soil nutrient, and pH (optima between 5.5 and 6.0), but sometimes also soil moisture content and/or the degree of nitrification. It was noted that different nutrients can generally not be considered to be independent of each other. The results also show that hay-making twice per year causes more nutrients to be removed than a single cut at the end of the season.

Only for the macronutrient K was the mutual relationship between soil and biomass concentrations just little obscured by confounding factors. Consequently, the amount of soil available K can be deduced from the biomass concentration of K to some extent. For the pools of soil available P and N this is not as simple. Soil N mineralization can be inferred from the aboveground production, but the relationship is confounded by soil moisture content and shading intensity, and can therefore be of practical benefit only under similar moisture- and shading conditions.

It was concluded that, with the exception of K, simple relationships between soil properties and biomass characteristics cannot be expected over wide environmental gradients.

Species diversity

In Chapter 5 the significance of the previous soil, site and biomass variables was studied with respect to species diversity and the occurrence of rare and endangered species. Results depended on the number of taxonomic groups included (vascular plants only, bryophytes included, terrestrial lichens included as well). This can probably be attributed to different environmental responses of these taxonomic groups, and emphasises the importance of taxonomic restrictions.

Over the wide range of conditions studied, vascular plant species richness could be explained best. Although one might expect aboveground standing crop or management to be important variables, the best explaining regression models did not require biomass characteristics or management, but only soil properties and two non-edaphic site conditions (tree presence and plot shape). The strong effect of plot shape (perimeter: area ratio) was somewhat unexpected. Long and narrow plots contained significantly more species than those with a low perimeter:area ratio. Different mechanisms may be involved (vicinism, spatial autocorrelation, better possibilities for colonization and recolonization). Whatever the cause, however, this result emphasises the importance of consistency in quadrat shape in diversity studies. The presence of overstory trees/shrubs (shading) clearly affected species richness negatively. The most important soil properties were moisture content and pH (both showing unimodal optimum relationships), and to a lesser extent the soil available N:P ratio (negative relation).

The much debated hump-shaped relationships between species richness and biomass or productivity could also be confirmed in the present material, but only if it was specifically looked for; *e.g.* by excluding the soil and management variables from the models. The hump-shaped relationship was most pronounced for the vascular plants species only, and when using maximum standing biomass as the independent variable (peak species richness at approximately 3.5 ton ha^{-1}). Particularly the decreasing phase of the relationship was more distinct with standing biomass than when production was used.

Based on this result, maximum standing biomass is postulated to be a causal factor for the decreasing phase of hump-shaped relationships through its effect on competition for space and light. Higher productivities as such (*i.e.* without effects due to an increase in standing crop) are assumed to have a *positive* effect on species richness and cause the *rising* phase. At intermediate levels of the maximum standing biomass, the positive effects of productivity itself and the negative effects of the standing biomass balance, so that highest species numbers may be expected.

Strikingly, hump-shaped biomass relationships could no longer be confirmed when the soil and management variables were also allowed to enter the explanatory models. This suggests that unimodal species richness relationships for biomass and/or productivity may alternatively originate in the covariation of biomass with other variables (although this does not deny the existence of the hump-shaped relationship). Management appeared to explain a much larger part of the variation in species richness than the hump-shaped biomass relationship. This indicates that management affects species richness in other ways than through a control of the maximum standing biomass only, and indicates more direct positive effects of mowing and hay removal as well.

When the positive effects of mowing and hay removal (independent effects) were accounted for, maximum standing biomass still showed a weak but significant relationship with species richness. This relationship is no longer hump-shaped, but positive (linear). Apparently, sites with high standing biomass need not necessarily be species-poor, as is often assumed.

Species evenness was high (dominance low) if mowing frequency was high and if standing biomass was low. This suggests that high mowing frequency and low standing biomass reduce the intensity of competition and thus prevent dominance.

Since the occurrence of rare and endangered species was particularly curtailed by high standing biomass values, and since management was confirmed to be beneficial also for the occurrence of rare or endangered species, it was concluded that such species are more susceptible to competitive exclusion than others. Through direct as well as indirect (biomass) effects, management is an important aid in providing or preserving opportunities for rare and endangered species, or for the maintenance of high species diversity in general.

Ellenberg indicator values

Chapter 6 presents the results of a study on the usefulness of the Ellenberg indicator values for moisture, nitrogen, and soil reaction, on the basis of the wide range of conditions studied and the large number of measured variables available. The study was conducted both species-wise, as well as site-wise.

Ellenberg moisture values correlated best with the average lowest moisture contents in summer, but correlations with the annual average groundwater level and the average spring level were also good.

Ellenberg nitrogen values appeared to be only weakly correlated with soil parameters, including N mineralization and available mineral N. Instead, there was a strong relation with biomass production. Ellenberg nitrogen values apparently summarize a complex of variables regulating productivity, probably involving both nutrient availability variables, as well as moisture availability, soil acidity, etc. The Ellenberg nitrogen values thus reflect general site fertility, as perceived by the vegetation, not as measured by single soil parameters. Based on this result it is suggested to replace the term nitrogen values by 'productivity values'.

Ellenberg soil reaction appeared to be the most problematic indicator value of the three studied. The relationship with soil pH (generally expected to be the indicated factor) was unsatisfactory: site mean indicator values were similar for all sites with pH-$CaCl_2$ above 4.75. Only for lower values was the indication of soil pH effective.

The main reason for this was found to be the existence of wide pH tolerances in many species with their optimum at intermediate pH levels. Such systematic differences in tolerance constitute a violation of one of the most critical requirements for weighted averaging to be an effective method of calibration. However, reaction values appeared to be correlated strongly with the total amount of calcium (exchangeable Ca^{2+} plus Ca from carbonates). Partly, this will be due to the fact that systematic differences in species tolerances for total calcium were much less pronounced than for pH. Total calcium may be understood as an integration of both soil pH and carbonate content. If little or no calcium carbonate is present, total calcium mainly consists of exchangeable Ca^{2+} and is closely associated with soil pH. When a few percent of calcium carbonate (or more) is present, total calcium largely depends on the carbonates, whereas soil pH level will usually vary little. The combined importance of both soil pH and $CaCO_3$ content, is also indicated by Chapter 2, where pH and $CaCO_3$ both emerged as discriminating factors (each in addition to the other). They apparently supply information related to different parts of the total range. It is suggested that the Ellenberg reaction values are better referred to as 'calcium values'.

Several species indicator values appeared to need regional adjustment, most notably for soil reaction. For various species, reaction values based on Central Europe are too low to reflect preferences in more northern or western regions. This may particularly hamper the indication of lime in these regions. Many of the Central European species with high reaction values no longer occur more to the north and/or west, and the species actually characteristic of limestone in those regions often have Ellenberg values that are too low (for those regions). Geographic shifts in ecological preferences, particularly for soil reaction, should be given serious consideration before applying Ellenberg reaction values outside Central Europe.

One aspect which has never received much attention is the uneven distribution of indicator values over the members of the flora of a given region. For example, many more species with intermediate indicator values usually exist than species with more extreme values. Site mean indicator values are most probably affected by this, as the species pool of a particular community depends on the regional species pool. Thus, at a site with conditions best reflected by indicator value 3, the probability for species with indicator values 4 and 5 to be co-occurring at that site will generally be higher than for species with indicator values 1 and 2. This creates a tendency of site mean indicator values to converge to the value most common in the regional species pool (which adds to a boundary effect, causing site mean indicator values to stay away from the extreme ends of the scale). Therefore, a method was devised to compensate for uneven frequency distributions of indicator values. Although the positive effect of this correction on the overall correlations with measured variables was small, relationships tended to become more linear. Also, it caused the site mean indicator values at which species showed their optimum to deviate less from the actual Ellenberg values of these species. Thus, the correction was considered an improvement.

Indicator values for bryophytes appeared to be in line with those for vascular plants, and they may well be used in combination. Using abundance values as weights when calculating site mean indicator values generally improved results, but, over the wide range of conditions studied, differences were small.

The obtained correlations are remarkably high if it is realized that the indicator values were studied in relation to individual parameters only, whereas they most likely summarize a complex of parameters associated to the indicated factor. It was concluded that the Ellenberg indicator system provides a very valuable tool for habitat calibration, provided the appropriate parameters are considered. Its usefulness may be further enhanced by regional adjustments of indicator values (especially needed for the calcium values), by taking the regional frequency distribution of indicator values into account, and by the use of species tolerances as an additional weighting factor (when such tolerances would become available).

Estimating annual N mineralization

Chapter 7 focussed on methods to estimate the annual soil N mineralization. The most accurate method to determine the net annual mineralization of N is year-round field incubation of undisturbed soil cores. As this technique is very laborious, the study aimed to establish less time consuming methods to assess this important soil property.

When sequential incubations were restricted to periods shorter than a full year, high correlations with the *annual* N mineralization were maintained when the field incubations were performed from early March to mid August. Shorter periods may also be used, as long as they cover three months at last, and remain within the period early March to mid August.

Predicting the average annual N mineralization using simple soil measurements appeared to be possible with a large degree of accuracy (over the wide range of environmental conditions studied). Three soil measurements appeared to be needed as predictor variables: the soil mineral N content (N_{min}), moisture content, and pH. The samples should be taken in early March, just before the start of the growing season. Higher N_{min} values (moisture and pH assumed to be constant) indicate higher annual N mineralization rates. Higher moisture contents (at constant N_{min} and pH) indicate lower annual rates. Soil pH showed a quadratic relation (at fixed N_{min} and moisture) with maximum annual mineralization rate occurring at a pH-$CaCl_2$ value of 5.5 to 5.6.

N_{min} appeared to be the most important predictor variable. Even within plant community types (with a reduced range of conditions), its relationship with the annual N mineralization persisted. Other factors such as total soil N, organic matter content, C:N ratio, soluble organic N, and particle size distribution, only showed low and insignificant correlations, although stronger relationships have sometimes been reported. It is assumed that this discrepancy is caused by the smaller range of conditions usually studied.

It should be emphasised, that the results were established for undisturbed, unfertilized soils, under year-round vegetation cover. Under such conditions, N_{min} may be considered the direct result of net N mineralization, modified only by plant uptake, atmospheric deposition, and losses by leaching and denitrification. In theory, the soil mineral N content (pool size) does not need to be related to the rate of its replenishment through mineralization (flux size), but this does appear to be the case, at least under semi-natural conditions.

Vegetation management

Soil impoverishment is often an important aim of vegetation management. However, it appeared that a delay in the removal of cuttings counteracts this effort, as the amount of nutrients that can be removed with the cutting rapidly falls to a level below the atmospheric deposition in most cases (Chapter 3). In Chapter 4 it was further concluded that hay-making twice per year generally causes a stronger soil impoverishment than cutting the accumulated biomass at the end of the season only.

Effects of management on species diversity are partly caused by such effects on the nutrient balance, but there are various other aspects to mowing and hay removal (Chapter 5). The maintenance of a relatively low maximum standing biomass appeared to be important for species diversity in general, and crucial for the occurrence of rare or endangered species. But results even indicated more direct positive effects of management. Among these, an increase in small-scale heterogeneity, and the prevention of litter accumulation are suggested to be particularly important. Surface accumulation of litter negatively affects germination and seedling establishment of most species. Particularly cuttings that are not or not properly removed, and litter of unmanaged vegetation, cause a smothering effect that is detrimental for species diversity.

Most plant communities require some kind of management. In low productive communities mowing once per year may suffice, but in most other communities (particularly if they are species-rich or valuable otherwise) two cuts are usually needed.

If mowing has taken place, cuttings should be removed without much delay. Although delayed removal (or no removal at all) often occurs in roadsides due to practical or financial considerations, this should be considered a waste of previously invested time and resources, since it only has negative consequences for the vegetation. Even sloppy removal can undo some of the benefits of management, especially in the more valuable plant communities. If, however, ecological management is taken seriously, the prospects for species-rich or otherwise ecologically valuable plant communities (both in roadside verges and in other infrastructure related habitats) may well be enhanced substantially.

Samenvatting

Samenvatting

Oecologisch referentiekader

De belangrijkste doelstelling van het hier gepresenteerde onderzoek was het nauwkeurig beschrijven van de oecologie van een aantal relatief goed ontwikkelde en/of soortenrijke plantengemeenschappen (syntaxa) van Nederlandse wegbermen. De studie omvat een aantal zeer uiteenlopende gemeenschappen, en heeft daardoor betrekking op een breed scala van standplaatscondities. De onderzochte vegetatie behoort tot de volgende syntaxa: *Urtico-Aegopodietum*, *Alliario-Chaerophylletum temuli*, *Valeriano-Filipenduletum*, *Fritillario-Alopecuretum pratensis*, *Calthion palustris*, *Triglochino-Agrostietum stoloniferae*, *Ranunculo-Alopecuretum geniculati*, *Arrhenatheretum elatioris* (excluding *festucetosum*), *Arrhenatheretum elatioris festucetosum arundinaceae*, *Mesobromion erecti*, *Phleo-Tortuletum ruraliformis*, *Spergulo-Corynephoretum*, *Genisto anglicae-Callunetum*, en het *Ericion tetralicis*. Hierin werd een groot aantal omgevingsfactoren gemeten.

Het resultaat kan worden gebruikt als een referentiekader (hoofdstuk 2), en kan dienen als basismateriaal bij oecologische inrichting en beheer van wegbermen met als doel het ontwikkelen, herstellen of behouden van specifieke syntaxa en het verhogen van de oecologische waarde. Hoewel in eerste instantie bedoeld voor bermen, kan het ook van dienst zijn bij oecologische inrichting en beheer van andere infrastructuur, zoals sloten, kanalen en dijken.

De verschillende syntaxa konden van elkaar worden onderscheiden aan de hand van de mate van beschaduwing, de gemiddelde voorjaars-grondwaterstand, de gemiddelde laagste grondwaterstand, de bodem-pH en het percentage $CaCO_3$, de fractie bodemdeeltjes kleiner dan 16μ, de nitrificatie-graad, en de hoeveelheid beschikbaar K. In de meeste gevallen zal het meten van deze factoren voldoende zijn om een adequate voorspelling te kunnen doen over de te verwachten plantengemeenschap, of om beheers-, inrichtings- of reconstructie-beslissingen op te baseren.

De genoemde variabelen kunnen tevens worden beschouwd als '*master*'-factoren. Hierbij moet echter worden opgemerkt dat het gaat om de *statistisch* meest belangrijke variabelen. Het aanwijzen van de daadwerkelijke oecologische *master*-factoren is niet eenvoudig omdat de gemeten variabelen van nature met elkaar gecorreleerd zijn en veelal ook causaal met elkaar samenhangen. Toch vertegenwoordigen de discriminerende variabelen duidelijk de vier oecologische basis aspecten: licht, vocht, zuurgraad, en voedselrijkdom. Gezien de resultaten in andere hoofdstukken behoort ook het beheer tot de *master*-factoren.

Maaiselafvoer en bodemverschraling

In hoofdstuk 3 wordt het effect van vertraging in de maaisel-afvoer op de nutriëntenbalans van de bestudeerde syntaxa beschreven. De aanleiding tot deze deelstudie was het feit dat maaisel in wegbermen vaak lange tijd blijft liggen voordat het geruimd wordt (veelal vanwege praktische overwegingen), terwijl niet bekend was wat dit betekent voor de met het beheer nagestreefde bodemverschraling.

Het blijkt dat een groot gedeelte van de in het maaisel aanwezige N, P en K niet afgevoerd wordt wanneer het maaisel gedurende enkele weken blijft liggen. Deze voedingsstoffen keren zeer waarschijnlijk grotendeels naar de bodem terug. Na 6 weken kan dit oplopen tot meer dan 50% van de oorspronkelijk in het maaisel aanwezige hoeveelheid. De verliezen bleken positief gerelateerd te zijn aan de initiële nutriëntenconcentraties in het gewas op het tijdstip van maaien. Het verloop van het N verlies met de tijd bleek het beste te verklaren met de initiële C:N ratio, terwijl de verliezen aan P en K het best verklaard werden uit de initiële P concentratie in het gewas. Vooral voor K waren de verliezen groot (tot 90%). K verdwijnt voornamelijk door uitspoeling. De N en P verliezen worden echter waarschijnlijk grotendeels veroorzaakt door snelle microbiële decompositie van gemakkelijk oplosbare bestanddelen.

Wanneer de verliezen gemodelleerd werden voor de verschillende syntaxa en voor verschillende tijdsduren van vertraging in de afvoer, bleek dat in de meeste syntaxa het maaisel binnen 1 week (soms tot maximaal 2 weken) geruimd moet worden om bodem-verschraling mogelijk te maken. Wanneer het maaisel langer blijft liggen zal er minder worden afgevoerd dan er via atmosferische depositie wordt aangevoerd. In plantengemeenschappen waar de atmosferische depositie al hoger ligt dan de bovengrondse N en P productie, blijkt snelle afvoer van het maaisel de enige manier om tenminste de beschikbaarheid van K limiterend te houden.

De snelle uitspoeling van K wijst er op dat dit element snel kan circuleren tussen de bodem en de vegetatie. Dit wordt bevestigd door de resultaten in hoofdstuk 4, waar de onderlinge relatie tussen de bodem- en de gewas-concentratie sterk blijkt te zijn voor K en relatief zwak voor de andere twee macronutriënten. Een extra indicatie voor het belang van K wordt gevonden in hoofdstuk 2, waar de beschikbaarheid van K één van de factoren was uit de set waarmee de syntaxa het beste van elkaar te onderscheiden waren. Het was de enige variabele uit de set die direct gerelateerd was aan de beschikbaarheid van een macronutriënt. Hieruit kan worden geconcludeerd dat het belangrijkste bodemeffect van het afvoeren van maaisel een vermindering van de K beschikbaarheid is. Dit geldt vooral op zandige bodems met een lage CEC en onder de voorwaarde dat het maaisel snel wordt afgevoerd.

Bodem - biomassa relaties

Wanneer over het brede scala van standplaatscondities de onderlinge relaties tussen chemische bodemeigenschappen en biomassakenmerken onderzocht worden (hoofdstuk 4), blijkt dat deze relaties veelal vertroebelt worden door de belangrijke rol die andere factoren spelen. Met name het vochtgehalte van de bodem (een fysische bodemeigenschap), maar ook beschaduwing en het beheer, bleken van belang.

De gemiddelde jaarlijkse bovengrondse biomassaproductie bleek vooral af te hangen van de gemiddelde jaarlijkse netto N mineralisatie, het vochtgehalte van de bodem, de mate van beschaduwing, en voor een minder belangrijk deel van de bodem-pH (optimum bij pH-$CaCl_2$ 5.7) en de fractie bodemdeeltjes kleiner dan 16μ. Het beheer bleek niet van invloed. De nutriëntenconcentratie in het gewas bleek vooral af te hangen van: het beheer (maaifrequentie), de mate van beschaduwing, de beschikbaarheid van de betreffende nutriënt in de bodem, en pH (optima tussen 5.5 en 6.0), maar soms ook van het vochtgehalte van de bodem en/of de nitrificatiegraad. Ook bleek dat de gewasconcentratie van een nutriënt af kon hangen van de bodemconcentratie van een ander element. Verschillende nutriënten kunnen dus niet onafhankelijk van elkaar beschouwd worden. De resultaten laten ook zien dat 2x per jaar maaien plus afvoeren meer nutriënten verwijdert dan 1x maaien met afvoer laat in het seizoen of aan het einde daarvan.

Alleen voor K bleek er een sterke relatie te bestaan tussen de concentratie van het element in de bodem en de concentratie in het gewas; een relatie die slechts in geringe mate vertroebeld werd door andere factoren. De implicatie is dat alléén voor K de beschikbaarheid in de bodem in redelijke mate afgeleid kan worden uit de concentratie in het gewas. Voor de bodemconcentraties van N en P blijkt dit niet mogelijk. De jaarlijkse N mineralisatie kan in redelijke mate afgeleid worden uit de jaarlijkse bovengrondse biomassaproductie, maar deze relatie wordt vertroebeld door het vochtgehalte van de bodem en de intensiteit van beschaduwing, en kan daarom alleen praktisch nut hebben wanneer vocht- en schaduw-condities vergelijkbaar zijn.

Er kan geconcludeerd worden dat, met uitzondering van K, er *over een breed oecologisch gradiënt* geen eenvoudige relaties bestaan tussen chemische bodemeigenschappen en biomassakarakteristieken.

Soortsdiversiteit

In hoofdstuk 5 is de betekenis onderzocht van de hierboven beschreven bodem- en biomassa-variabelen voor de diversiteit (soortenaantal, *evenness,* en het voorkomen van zeldzame en rode-lijst soorten). De resultaten bleken af te hangen van het aantal taxonomische groepen dat in de analyse betrokken werd (ofwel alleen hogere planten, ofwel hogere planten inclusief de blad- en lever-mossen, ofwel ook de terrestrische lichenen inbegrepen). Dit kan zeer waarschijnlijk toegeschreven worden aan een verschil in oecologische respons van de verschillende taxonomische groepen, en onderstreept de rol van de taxonomische omgrenzing die in een studie gehanteerd wordt.

Over de brede reeks van standplaatscondities kon het aantal hogere plantensoorten het best verklaard worden. Hoewel men wellicht zou verwachten dat de bovengrondse staande biomassa en het beheer als belangrijke factoren naar voren zouden komen, bleken deze variabelen in de best verklarende regressiemodellen niet geselecteerd te worden. In deze modellen komen alleen bodemfactoren voor, plus het al of niet voorkomen van een boom-/struiklaag en de vorm van het proefvlak. Het grote belang van de proefvlak-vorm (lengte:breedte verhouding) was in enigszins onverwacht. Lange en smalle proefvlakken bleken significant meer soorten te bevatten dan proefvlakken met een lage lengte:breedte verhouding. Verschillende mechanismen kunnen hiervoor verantwoordelijk zijn (bv. vicinisme, ruimtelijke autocorrelatie, betere mogelijkheden voor kolonisatie en rekolonisatie). Los van de oorzaak onderstreept dit resultaat echter het belang van consistentie in proefvlak-vorm bij het bepalen van de diversiteit. Het voorkomen van een boom-/struiklaag (beschaduwing) beïnvloedt het aantal soorten in de kruidlaag duidelijk negatief. De meest belangrijke bodemfactoren waren de vochtigheidsgraad en pH (beide optimum relaties) en in mindere mate ook de ratio tussen de beschikbare (minerale) N en P fracties (negatief verband).

De veelbesproken unimodale (*'hump-shaped'*) relatie tussen soortenrijkdom en biomassa of productiviteit (maximale soortenrijkdom bij intermediaire biomassa of productiviteit) bleek inderdaad aangetoond te kunnen worden. Deze relatie was het duidelijkst voor de hogere planten, en met de maximale staande biomassa als onafhankelijke variabele (piek in soortenrijkdom bij ca. 3.5 ton ha^{-1}).

Vooral het dalende gedeelte van het unimodale verband was duidelijker voor de maximale staande biomassa dan wanneer de bovengrondse productie als onafhankelijke variabele gebruikt werd. Gebaseerd op dit resultaat wordt verondersteld dat de maximale staande biomassa een causale factor is voor het dalende gedeelte, via het effect op concurrentie om licht en ruimte. Productiviteit op zich (zonder de effecten die het gevolg zijn van een toename in staande biomassa) wordt verondersteld positief te zijn voor soortenrijkdom, en verklaart het stijgend gedeelte van het optimum-verband. Bij een intermediair biomassa-niveau zijn de positieve effecten van de productiviteit en de negatieve effecten van de staande biomassa zelf in evenwicht, en kunnen de hoogste aantallen soorten verwacht worden.

Opvallend was dat de unimodale biomassa relatie slechts een zeer gering gedeelte van de variatie in soortenrijkdom verklaarde, en ook alleen aangetoond kon worden wanneer er zeer direct naar gezocht werd door bodem- en beheers-variabelen bewust uit de verklarende regressiemodellen te weren (dus te pretenderen dat deze niet beschikbaar en/of gemeten waren). Dit suggereert dat de veel besproken '*hump-shaped*' relaties hun oorsprong ook zouden kunnen hebben in een algemeen aanwezige covariatie tussen biomassa en/of productiveit en andere factoren zoals bodem en/of beheer. Dit spreekt het bestaan van een unimodale relatie met biomassa of productiviteit niet tegen, maar plaatst deze wel in een ander daglicht. Bovendien bleek dat het beheer een beduidend groter gedeelte van de variatie in soortenrijkdom verklaart dan de unimodale biomassa relaties. Dit wijst er op dat het effect van beheer op soortenrijkdom niet alleen loopt via het beïnvloeden van de maximale staande biomassa, maar suggereert dat er ook meer directe effecten van het beheer op soortenrijkdom bestaan.

Wanneer rekening gehouden wordt met de positieve invloed van zowel het maaien als het afvoeren (additieve effecten) blijft er een zwak maar significant verband herkenbaar tussen soortenrijkdom en de maximale staande biomassa. Dit verband is niet langer unimodaal, maar positief (lineair). Blijkbaar zijn locaties met een hoge staande biomassa niet noodzakelijkerwijs soortenarm (hetgeen vaak verondersteld wordt).

De *evenness* van de soorten bleek hoger te zijn (de mate van dominantie lager) bij een hogere maaifrequentie (onderzochte bereik: 0 tot 2) en bij een lage staande biomassa. Dit doet vermoeden dat in deze situaties de intensiteit van concurrentie tussen soorten afneemt en het domineren van enkele soorten voorkomen wordt.

Aangezien het vóórkomen van zeldzame en rode-lijst soorten vooral sterk begrensd wordt door een hoge bovengrondse biomassa, maar positief beïnvloed wordt door het beheer, wordt de conclusie getrokken dat dergelijke soorten gevoeliger zijn voor inter-specifieke concurrentie dan andere. Via directe zowel als indirecte (biomassa) effecten, moet vegetatiebeheer als een belangrijk hulpmiddel gezien worden bij het creëren of in stand houden van een hoge diversiteit in het algemeen, en van mogelijkheden voor zeldzame of bedreigde soorten in het bijzonder.

Ellenberg indicatie getallen

In hoofdstuk 6 werd het karakter onderzocht van de Ellenberg indicatie getallen voor vocht, stikstof, en zuurgraad (*'Bodenreaktion'*, *'soil reaction'*). Hierbij werd gebruik gemaakt van de brede reeks aan onderzochte standplaatsen en het grote aantal gemeten variabelen dat beschikbaar was.

De Ellenberg vochtgetallen correleerden het beste met het laagste vochtgehalte van de bodem in de zomer, maar met een aantal grondwaterstands variabelen (met name het jaargemiddelde en de gemiddelde voorjaarsstand) was de correlatie ook goed.

Ellenberg N-getallen bleken slechts zwak gecorreleerd te zijn met de gemeten bodem variabelen, waaronder de jaarlijkse netto N mineralisatie in het veld en de concentratie beschikbaar N. De correlatie met de bovengrondse biomassaproductie was echter sterk. Blijkbaar vatten de N indicatie getallen een complex van factoren samen die regulerend zijn voor de biomassaproductie. Hierbij kan gedacht worden aan een complex van nutriënten-beschikbaarheidsfactoren, vochtvoorziening, zuurgraad, en dergelijke. Op die manier is het Ellenberg N-getal representatief voor de vruchtbaarheid zoals 'ervaren' door de vegetatie, en niet zoals uitgedrukt door één enkele meetbare bodemfactor. Op grond van dit resultaat wordt voorgesteld de term stikstofgetal te vervangen door 'productiviteitsgetal'.

Van de drie onderzochte indicatiegetallen bleek het Ellenberg 'zuurgraad'-getal het meest problematisch. Hoewel er in het algemeen van uit wordt gegaan dat bodem-pH de geïndiceerde factor is, was het verband met de gemeten pH zeer onbevredigend. De indicatiewaarden (proefvlakgemiddelden) waren ongeveer gelijk voor alle proefvlakken met een pH-$CaCl_2$ groter dan 4.75. Een effectieve indicatie was alleen mogelijk voor proefvlakken met lagere pH-waarden. Als belangrijkste oorzaak werd aangemerkt de zeer brede pH tolerantie van veel van de soorten met een intermediair pH optimum. Een dergelijk systematisch verschil in tolerantie vormt een conflict met één van de meest kritieke voorwaarden waaraan voldaan moet zijn wil het berekenen van gewogen gemiddelden gebruikt kunnen worden als een effectieve methode voor 'kalibratie'. In tegenstelling tot de problemen met pH, bleken de indicatiegetallen goed gecorreleerd te zijn aan de hoeveelheid totaal calcium (gedefinieerd als uitwisselbaar Ca^{2+} plus de Ca in de vorm van carbonaten). Ten dele is dit het gevolg van het feit dat een systematische verschil in de tolerantie van soorten veel minder uitgesproken is voor totaal calcium dan voor pH. Daarnaast kan totaal calcium ook opgevat worden als een integratie van de factoren pH en kalkgehalte. Waar er geen of vrijwel geen kalk aanwezig is bestaat totaal calcium vrijwel geheel uit uitwisselbaar Ca^{2+} en is als zodanig sterk gerelateerd aan de pH. Naarmate er meer kalk in de bodem aanwezig is wordt totaal calcium meer en meer bepaald door calcium afkomstig uit de carbonaten, terwijl in deze situaties de (hoge) pH in het algemeen weinig of niet meer varieert. Het gecombineerde belang van zowel pH als $CaCO_3$ gehalte bleek ook in hoofdstuk 2, waar beide variabelen (in aanvulling op elkaar) naar voren kwamen als discriminerende factoren. Ze geven beide informatie in verschillende gedeelten van het totale gradiënt. Er wordt voorgesteld om de term zuurgraad-getal te vervangen door 'calcium-getal'.

Voor diverse soorten bleek het nodig om de indicatiewaarde aan te passen aan de Nederlandse situatie, met name voor het calcium-getal ('zuurgraad-getal'). Verschillende soorten met een hoge indicatiewaarde komen in noord-west Europa niet meer voor, en de soorten die in deze streken karakteristiek zijn voor kalkrijke situaties hebben veelal indicatiegetallen (gebaseerd op centraal Europa) die voor deze streken te laag zijn. Dit bemoeilijkt vooral de indicatie van kalk. Mogelijke verschuivingen in de oecologische 'preferentie' (optima) van soorten dienen serieus in overweging te worden genomen voordat Ellenberg calcium-getallen toegepast worden buiten centraal Europa.

Een aspect dat tot nog toe weinig aandacht heeft gekregen is de ongelijkmatige verdeling van de indicatorwaarden binnen de flora van een bepaalde regio. In het algemeen zijn soorten met een intermediair indicatiegetal veel talrijker dan die met meer extreme waarden. Dit heeft een onmiskenbare invloed op het gemiddelde indicatiegetal van een bepaalde vegetatie, omdat de soortensamenstelling mede afhangt van het regionale 'reservoir' aan beschikbare soorten. Een vegetatie die voorkomt onder condities die het best weerspiegeld wordt door indicatiegetal 3, heeft een veel hogere kans op het mede aanwezig zijn van soorten met de meer algemene indicatorwaarden 4 en 5 dan op het ook aanwezig zijn van soorten met de zeldzamere indicatorwaarden 1 en 2. Gemiddelde indicatiegetallen neigen hierdoor naar het indicatiegetal dat het meest algemeen is in de regionale flora (in het algemeen de meer intermediaire waarden). Dit komt boven op een grens-effect dat de gemiddelde waarden weg houdt van de uiteinden van de schaal. In de studie werd daarom voor het mogelijke effect van de ongelijkmatige distributie van indicatiegetallen gecompenseerd. Hoewel het positieve effect van deze correctie op de correlaties met de gemeten waarden gering was, bleken de relaties in het algemeen een meer lineair karakter te krijgen. Ook bleek dat de gemiddelde indicatiewaarde van de proefvlakken waar een soort haar optimum bereikte, minder afweek van het eigenlijke indicatiegetal van de betreffende soort. De correctie werd om deze redenen als een verbetering aangemerkt.

De indicatorwaarden voor mossen bleken goed aan te sluiten bij die voor hogere planten, en beide kunnen dan ook in combinatie gebruikt worden. Het gebruik van abundanties als weegfactor bij het berekenen van het proefvlak-gemiddelde gaf in het algemeen iets betere resultaten dan het gebruik van aan- of afwezigheid, maar de verschillen waren (over de brede reeks van bestudeerde condities) klein.

De verkregen correlatiecoëfficiënten waren opvallend hoog, vooral gezien het feit dat de indicatorwaarden steeds aan individuele variabelen gecorreleerd werden terwijl zij naar alle werkelijkheid een integratie zijn van een complex van variabelen geassocieerd met de te indiceren factor. De conclusie is dat het systeem van Ellenberg indicatiegetallen een uiterst waardevol gereedschap voor habitat kalibratie is, er van uit gaande dat de juiste variabelen in ogenschouw worden genomen. De bruikbaarheid kan verder vergroot worden: door regionale aanpassingen van de indicatiegetallen (met name voor het calcium-getal), door de regionale verdeling van de indicatiewaarden te verdisconteren, en door de tolerantie van soorten als extra weegfactor te gebruiken (op het moment dat dergelijke gegevens beschikbaar komen).

Schatten van de jaarlijkse N mineralisatie

Hoofdstuk 7 had een tamelijk methodologisch karakter en onderzocht de N mineralisatie in de bodem. Een gebruikelijke methode om deze te bepalen is het uitvoeren van opeenvolgende veld-incubaties van ongestoorde bodemmonsters gedurende het hele jaar. Deze techniek is echter zeer arbeidsintensief en de studie richtte zich daarom op het vinden van een methode die minder arbeidsintensief is maar toch een betrouwbare schatting van deze belangrijke grootheid oplevert.

Het beperken van de reeks van opeenvolgende incubaties tot perioden korter dan een heel jaar liet nog steeds een hoge correlatie zien met de totale *jaarlijkse* mineralisatie wanneer de veld-incubaties uitgevoerd werden in de periode van begin maart tot half augustus. Kortere periodes voldeden ook nog redelijk, zo lang zij tenminste drie maanden omvatten en ergens in de periode begin maart tot half augustus lagen.

Het bleek ook mogelijk de gemiddelde jaarlijkse veld-mineralisatie met vrij hoge nauwkeurigheid te voorspellen met behulp van éénmalige (momentane) bodembepalingen, althans over de brede reeks van onderzochte bodemcondities. Drie grootheden van de bodem bleken hiervoor nodig: de aanwezige hoeveelheid mineraal N (N_{min}), het vochtgehalte van de bodem, en de pH. Deze dienen gemeten te worden in begin maart, net voor het begin van het groeiseizoen. Een hoger N_{min} gehalte (bij gelijke vocht en pH) wijst op een hogere jaarlijkse mineralisatie. Een hoger vocht gehalte indiceert een lagere jaarlijkse N mineralisatie (bij gelijke N_{min} en pH). Bodem pH liet een kwadratisch verband zien, met maximale jaarlijkse mineralisatie bij een pH-$CaCl_2$ waarde van 5.5 tot 5.6.

N_{min} bleek de belangrijkste voorspellende variabele te zijn. Zelfs wanneer alleen *binnen* plantengemeenschappen gekeken werd (dus over een veel beperktere reeks van bodemcondities), bleef de relatie met de jaarlijkse mineralisatie duidelijk bestaan. Factoren zoals totaal N, organisch stof gehalte, C:N ratio, oplosbaar organisch N, en de granulaire samenstelling lieten in het onderzoek slechts lage en niet significante correlaties zien, terwijl deze factoren in andere onderzoeken vaak als belangrijk aangemerkt worden. De discrepantie wordt waarschijnlijk veroorzaakt door de smallere reeks aan condities die normaal gesproken onderzocht wordt.

Er moet overigens benadrukt worden dat de resultaten gelden voor ongestoorde, onbemeste bodems, die (hoewel veelal onder een maaibeheer) toch het hele jaar een vegetatie dragen. Onder dergelijke condities zal N_{min} inderdaad grotendeels afhankelijk zijn van de netto N mineralisatie, en alleen gewijzigd worden door atmosferische depositie en door verliezen via uitspoeling en denitrificatie. Hoewel de hoeveelheid N die op een bepaald moment in de bodem aanwezig is (*N-pool*) in theorie niet gecorreleerd hoeft te zijn met de snelheid waarin deze N verdwijnt en weer door mineralisatie aangevuld wordt (*N-flux*), blijkt dit - in elk geval onder halfnatuurlijke omstandigheden - wel degelijk het geval te zijn.

Het beheer

Bodemverschraling is veelal een belangrijke doelstelling van het beheer. Het bleek echter (hoofdstuk 3) dat deze doelstelling niet gehaald wordt als het maaisel niet snel afgevoerd wordt, omdat de hoeveelheid afgevoerde nutriënten dan al snel daalt onder het niveau van de atmosferische aanvoer. Uit hoofdstuk 4 kan verder de conclusie getrokken worden dat 2x per jaar maaien en afvoeren in het algemeen een grotere verschraling tot gevolg zal hebben dan wanneer dit 1x per jaar aan het eind van het groeiseizoen gebeurt.

Effecten van vegetatiebeheer op de soortsdiversiteit kunnen gedeeltelijk veroorzaakt worden door de effecten van bodemverschraling, maar er zijn diverse andere aspecten verbonden met het maaien en het afvoeren (hoofdstuk 5). Het handhaven van een relatief lage maximale staande biomassa bleek belangrijk voor de algemene diversiteit aan soorten, maar cruciaal voor het voorkomen van zeldzame soorten of rode-lijst soorten. Er waren echter sterke aanwijzingen voor het bestaan van meer directe positieve effecten van het beheer. Hierbij kan vooral gedacht worden aan een toename van de kleinschalige heterogeniteit en de preventie van strooisel-accumulatie. Dit laatste heeft een negatieve invloed op de kieming en vestiging van veel soorten. Vooral niet of slecht afgevoerd maaisel en de grote hoeveelheden strooisel van onbeheerde vegetaties, hebben een verstikkend effect dat slecht is voor de soortenrijkdom.

De meeste plantengemeenschappen hebben één of andere vorm van beheer nodig. In laagproductieve gemeenschappen kan 1x per jaar maaien voldoende zijn, maar in de meeste andere gemeenschappen (met name wanneer deze soortenrijk of anderszins waardevol zijn) is een beheer van 2x maaien per jaar nodig. Na maaien moet worden afgevoerd, en dit dient zonder veel vertraging (binnen een week of hooguit 10 dagen) gebeurd te zijn. Een vertraagde afvoer (of helemaal geen afvoer) is door praktische of financiële overwegingen in wegbermen niet ongebruikelijk. Dit moet echter beschouwd worden als een verspilling van eerdere investeringen (waaronder het maaien zelf) omdat het slechts negatieve consequenties voor de vegetatie heeft. Zelfs een onzorgvuldige afvoer kan de positieve kanten van beheer ten dele ongedaan maken, met name in de meer waardevolle gemeenschappen. Wanneer oecologisch bermbeheer echter serieus ter hand genomen wordt, liggen er grote mogelijkheden voor soortenrijke of anderszins waardevolle plantengemeenschappen, niet alleen in bermen, maar ook in andere infrastructuur-gerelateerde habitats.

Acknowledgements

Finally the work is done, and I can sit back and look back. Although a PhD thesis is considered to be an independent piece of work performed all by oneself, the acknowledgements usually suggest otherwise. This thesis is no exception to the rule.

The first person that should be mentioned here is Karlè Sýkora. He was the one who envisioned a study on the synecology of roadside plant communities long ago, and I am very grateful that he trusted me to perform it when this study was finally initiated. Although our combined enthusiasm may have resulted in an underestimation of the time needed, he never doubted the completion of this work (or at least he never showed it). He was also very helpful in structuring the thesis. Karlè, I much valued your enthusiastic comments on the manuscripts. When I wasn't very sure, your comments were always supportive and heartwarming. Thanks for all your trust, support and friendship during these past years. And don't worry, you will soon be able to find your missing books and articles again when I have returned all the material I borrowed from your bookshelves.

Secondly I would like to thank Frank Berendse. Without him this thesis would not yet have been finished, and would probably have appeared one or two years later. Although I did not always appreciate the pressure put upon me, I cannot deny that I am relieved to be free of the unease of a thesis not yet finished. Frank, I prize the swiftness with which you usually returned my manuscripts, and I am very grateful for your comments which were invariably of great value to me. They always improved the manuscripts, both directly and by helping me to focus my mind.

The person who has probably read all manuscripts at least two or three times is Aad Termorshuizen. That he was always encouraging me to give him a newer version almost made it seem as if he was hopelessly looking for something to keep him occupied, even though I know how pressed for time he really was. Aad has an almost uncanny quality for text length reduction, being able to take an entire paragraph and cross out large parts of different sentences, leaving (without adding or redirecting a single word) a perfectly sound and relatively short statement nearly as informative as the old paragraph. Aad, thanks to you, large parts of the text reductions almost ritually requested by reviewers of scientific journals could actually be realised.

Dad, you deserve a prominent position in this acknowledgement. You were, as you rightfully labelled yourself: "fieldwork assistant first class". No one has accompanied me more often on the approximately 200 fieldwork days than you. You usually had to take the 06:15 train in order to meet me in some far-away corner of the country for another day of what you called "gathering scientific dust". But, although you often made fun of this activity, you really liked to be out working together. Dad, I enjoyed your company equally much, and I am happy to have a father with whom I can share more than a childhood period 'only'. I hope there will be many more fieldwork days with you in the future.

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Of course, all the samples needed to be chemically analysed. Thanks to the guidance of Arie van den Berg (alias 'chief director') analysing the 2378 mineralization samples seldom was a boring task. His jokes, good humour and friendship changed what otherwise might have been a monotonous exercise, into a day ending with a smile. Arie, believe it or not, some of our discussions really changed my opinion on certain subjects. I wish more people had your attitude towards life and towards other people.

Joep Frissel performed a number of other soil analyses. Although this was not her most preferred type of work, she did a wonderful job and saved me precious time.

The actual chemical measurements were mostly performed by Erik Heij. I admire him for never fainting when I came around again. I know what a perfectionist and a nitpicker I can be, but still, he never objected when I asked for another round of measurements to be repeated again. For other measurements, Jan van Walsem and Yvonne Wilms had to put up with my perfectionism. Nevertheless, they always remained good-humoured. Jan, at last you can celebrate. The last remaining kilograms of the ca. 700 kg of air-dry soil initially stored in the containers will soon be gone for good.

Dr Houba was regularly consulted on matters of chemical analysis. His advice and comments are gratefully acknowledged. I have received perceptive support by Han Olff and Jacques Withagen on matters of data analysis. Margje Voeten showed me how to run discriminant analysis in SPSS.

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Ab Masselink checked the identification of most of the bryophyte and lichen species. He must have groaned inwardly when I filled his desk again with bags full of material, but he never protested. It grieves me that he did not live to see the completion of this thesis. He positively distinguished himself by always showing a genuine interest in my work and findings. Ab was the one who contributed most to my growing interest in vegetation science, with his field course on Terschelling almost 20 years ago. Without him, I probably would not stand where I am now. This thesis is dedicated to him in loving memory.

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Although Aira and Tirza are too young to have been helping me intentionally, their role should not remain unmentioned. Born during this project, they can both be considered a delay factor. But it is not a bad thing to be slowed down a little from time to time, as ideas and arguments often need time to ripen. Spending time with them, caring, playing and cuddling, not only prevented me from 'going off the rails' entirely, but also made life during this project ever more joyful.

Dear Loes. We have often made jokes during the past few years about how you should be mentioned in the acknowledgements. This already demonstrates that there is no simple way to thank you for all the things you have (sometimes forcedly) taken upon you. The general rule of PhD projects is that the partners usually suffer most, and again this project has been no exception. I will not suggest you never complained; at times you most rightfully did. I realize this shows your concern, and it often brought me back to earth for a while. Someone recently told me that anyone who manages to finish a PhD without ending up completely worn out, stressed or divorced, deserves a big cheer. But Loes, the cheer is on you!

Curriculum Vitae

André Schaffers was born on the 20th of July 1960 in Amsterdam, The Netherlands. He completed high school at the Bonhoeffer College (Atheneum-B) in Castricum in 1978. In the same year, he started to study Forestry at the Agricultural University in Wageningen. Throughout this study he took a strong emphasis on ecological and related subjects such as (among others) vegetation science, nature conservation, wildlife management, animal ecology, (micro-)climatology, soil science, geology and geomorphology. During his practical period he was involved in radio telemetry at the Institute of Terrestrial Ecology in Banchory, Scotland, focussing on the habitat selection of Red and Roe deer. After his graduation (*Cum Laude*) in 1986, he fulfilled his 'military' service as a conscientious objector at the Department of Fytopathology of the Wageningen Agricultural University until the end of 1988, studying the effects of air pollution and tree vitality on the occurrence of carpophores of mycorrhizal fungi in Scots Pine forests. The following years he was involved in various projects at the Department of Vegetation Science, Plant Ecology and Weed Science and he further developed his skills as a vegetation ecologist. In 1991 a PhD research proposal was granted by the Cornelis Lely Foundation and the Road and Hydraulic Engineering Division (Ministry of Transport, Public Works and Water Management). This study on the ecology of roadside plant communities provided him with much additional experience in soil sampling techniques, most notably field mineralization measurements. From 1991 until 1993 he also worked as freelance journalist for the VNU Business Publications discussing software and writing small computer programs. He furthermore developed the ecological software known as COCON and DENDRO. Since 1997 he is working as a scientist at the Nature Conservation and Plant Ecology Group of the Wageningen University and is involved in research on the importance of roadside plant communities for entomofauna. Here his main interests are the effects of both vegetation structure and species composition, and the role of the surrounding landscape. André currently lives in Wageningen with his partner Loes and his daughters Aira and Tirza.