



Summary volume 1-3

Hoofdstuk 15

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The Ecological Atlas of fungi in Drenthe presents the results of mycofloristic and myco-ecological research in the period 1800-2014 in Drenthe. This province occupies an area of 2626 km² in the northeastern part of the Netherlands. The publication concentrates on records in the period 1999-2010, when systematic mapping of fungi was carried out by a group of volunteers, united in the Paddestoelen Werkgroep Drenthe ('Fungi Studygroup Drenthe'). It is based on over 400,000 records on 2350 species of fungi.

This work is divided into three volumes. Volume 1 is the introductory part, including chapters on e.g. regional history of mycology, methodology, presentation of the results, changes in the regional mycoflora, general distribution patterns of fungi, threatened species, mycological hotspots, species newly described from Drenthe in the past and species discovered in Drenthe since 2010. It contains also a general index of species, treated in volumes 1-3, and a complete list of references to literature. Fungal species are treated in an ecological context. Each species has been assigned to a certain ecological group. Each chapter is devoted to an ecological group and its characteristic species. Volume 2 treats the fungi growing in grasslands, heathlands, moorlands, marshy forests and urban environments. Volume 3 treats the fungi growing in forests on mesic to dry soils, as well as fungi from burnt places. The content of each chapter is summarized below.

Ecological Atlas of fungi in Drenthe, volume 1

Chapter 1. Introduction

An introduction is given to the systematic position, biology and ecology of fungi, meant for readers who are not familiar with these organisms. The characteristics of mycelia and sporocarps are described, including features such as fairy rings and demarcation lines in colonized substrates (photographs p. 10,12). Periodicity and annual fluctuations are explained, illustrated with graphs of periodicity of some species in Drenthe (Fig. 1.1.). The artificial division into macrofungi and microfungi is evaluated. In this Atlas mainly macrofungi are covered, comprising all basidiomycetes, with the exception of rust fungi (*Pucciniomycotina*) and smut fungi (*Ustilagomycotina*), and in addition a minority of ascomycetes with larger sporocarps. Also part of the microfungi are included, viz. some ascomycetes with sporocarps smaller than 1 mm. Data on microfungi are incomplete, however. The Myxomycota are not treated in this Atlas. It is explained that distribution patterns of species, presented in this work, may be influenced by the visibility of sporocarps in the field, the possibilities to identify them in the field and the presence

or absence of regional knowledge of some taxonomic groups.

Modern taxonomy of fungi, based on molecular relationships, does often no longer reflect traditional morphological groups. However, the latter classification is still frequently used in practice. Each of the species in this Atlas is assigned to one of ten taxonomic-morphological groups, based on a combination of morphological and taxonomic characteristics (representative photographs on p. 10). The numbers of species of different taxonomic-morphological groups in Drenthe are presented in Table 1.1 and Fig. 1.3.

Different life strategies of fungi are concisely treated. Three main functional groups are distinguished: saprotrophic, parasitic and symbiotic fungi. The saprotrophs are subdivided into species mainly colonizing herbaceous parts of plants (leaves, stems), and those growing on litter and humus, wood or dung. Parasites are subdivided into biotrophic and necrotrophic species. Symbiotic fungi mainly include ectomycorrhizal species, but also fungi associated with mosses and a few basidiolichens (representative photographs on p. 17). The shares of species of different functional groups in Drenthe are presented in Fig. 1.4.

Chapter 2. A concise history of mycology in Drenthe

An outline is given of the development of mycology in the province of Drenthe. Until recently the mycoflora of this province was much less intensively investigated than of the western, central and southern parts of the Netherlands, due to its relatively remote position, the absence of universities or other centres of biological research, the low number of amateur mycologists and the absence of mycological hotspots. In the 19th century only five records of fungi are known. Around 1930 the situation improved somewhat with the establishment of a Biological Field Station in Wijster by the naturalist Willem Beijerinck. He started to collect and depict fungi. Some of his water colour paintings are reproduced in this book. He invited well-known mycologists to carry out fieldwork in Drenthe, e.g. A.F.M. Reijnders, which resulted in some publications on macrofungi in Drenthe.

Later on the Biological Field Station was taken over by Wageningen Agricultural University and in 1957 Jan Barkman was appointed as the new director. His main interest was phytosociology, with the focus on cryptogams like bryophytes and lichens, soon also larger fungi. For many years he analysed mycocoenoses in juniper communities throughout Northwestern Europe, since 1966 assisted by Bernhard de Vries, who developed a special interest in corticioid fungi. Barkman initiated a series of mycosociological studies by undergraduate and PhD students and in this way he laid the foundation for the mycological exploration of Drenthe. For that reason the first volume of this work is dedicated to Jan Barkman. The position of mycology improved by the appointment of Eef Arnolds and Thom Kuyper. In the 1980's the Biological Station at Wijster developed to a well-known mycological centre in the Netherlands and abroad. Main subjects of research were geographical distribution, field ecology, decline and conservation of fungi. Also taxonomic publications were produced. Later on field and laboratory experiments were carried out on the effects of air pollution and soil properties on fungi and on the ecology of ectomycorrhizas. These professional activities came to an end with the closing of the Biological Station in 1998.

In 1999 Eef Arnolds, Bernhard de Vries and Rob Chrispijn established the foundation 'Paddestoelen Werkgroep Drenthe (PWD)', uniting a group of volunteers with as main purpose to carry out systematic mapping of fungi in the province of Drenthe and to publish the results in a book. The PWD organises field excursions, as well as meetings to exchange knowledge and to present and discuss the results of the mapping programme. Each year a newsletter is published and spread, supported by a grant of the provincial government. An anthology of excursion reports of these newsletters is given on p. 34 and 35. The activities of the PWD led to a strong increase of records of fungi in Drenthe, in particular after the introduction of specific criteria for each square kilometre in 2004 (Fig. 2.2; see summary chapter 3). In 2010 the systematic mapping programme was finished. Over 200 individuals have contributed to the collection of over 400,000 distributional data on fungi (supplement 2.1). About 85% of the data were recorded by a 'hard core' of nine observers (Fig. 2.3).

After the fieldwork in 2010 data processing started under supervision of Roeland Enzlin, manager of the database. Writing of the texts for this Atlas started by a collective of seven authors under supervision of the editor in chief, Eef Arnolds. Rob Chrispijn was responsible for the collecting and selection of photographs.

Chapter 3. Methods: Fieldwork and data processing

Mapping of fungi in Drenthe is part of a national mapping programme, co-ordinated by the Netherlands Mycological Society. The programme in Drenthe is unique by the systematic approach of the fieldwork. In order to facilitate fieldwork and data processing a shortlist with abbreviations of all regularly encountered species was produced (Fig.

3.4). It was intended to obtain representative lists of fungi in all 2844 kilometre squares in the province, as defined on national geographical maps. For this purpose conditions were set on the minimum number of species, expected to occur in each square. The required minimum number of species was determined on forehand on the basis of landscape structure in each kilometre square. The numbers varied from less than 10 species in open agricultural areas without trees up to over 100 species in forests (Fig. 3.5, 3.6). This approach has been chosen for several reasons: (1) to reach complete covering of the area and all habitats present; (2) avoidance of artificial distribution patterns, caused by focusing on some well-known, interesting areas and neglecting less promising areas (almost all mycological mapping projects suffer from selective sampling), (3) stimulation of fieldwork by formulation of realistic, quantitative goals. In 2010 the complete province had been investigated according to the agreed minimum demands. The progress of the mapping process is illustrated in Fig. 3.8.

Some advantages of this approach are illustrated in Fig. 3.3.b and 3.3.c, showing for two species denser, more even and more realistic distribution patterns in Drenthe than in other parts of the country. Nevertheless also in Drenthe some areas have been more intensively investigated than others (Fig. 3.10 and 3.11). In particular the southeastern part of the province, mainly consisting of intensive farmland, has been less intensively studied than the western part. After the field-season the collected data were entered into the database of the Netherlands Mycological Society (NMV), but for quick handling of the data also in a provincial data base ('Drenthe file'). This file was kept up to date and at the end provided the basic information for this Atlas. A special computer programme, entitled 'ZWAM', has been developed by Marien van Westen to enable easy handling of the data, making various calculations, and editing maps and graphs in a user-friendly way (Fig. 3.9).

Chapter 4. Presentation of data in the Atlas

In this Atlas the species are treated within an ecological context. All species are assigned to one of 13 chapters and 32 subchapters, devoted to a certain type of habitat. A survey of (sub)chapters and the treated habitat types is presented in Table 4.1, together with the numbers of species treated in each chapter. Each chapter begins with a general introduction on the characteristics of the vegetation, soil conditions and mycoflora in the habitat concerned. Properties of the characteristic fungi are presented in five graphs, presenting the numbers of species belonging to (1) taxonomic-morphological groups, (2) functional groups, (3) frequency classes in Drenthe, (4) trend classes in Drenthe and (5) categories in the national Red Data list. As an example such graphs are presented for all 2304 treated species in Fig. 4.1. In addition, in each (sub)chapter maps are presented with total numbers of species and Red Data list species only per kilometre square, in order to show regional patterns in species diversity (examples in Fig. 4.2). The distinguished classes and groups are defined and discussed in this chapter.

Each species description begins with the scientific and popular name according to the current checklist of fungi in the Netherlands (Arnolds & Van den Berg, 2013). A periodicity table provides the number of records in each month of the year. Under the heading 'Status' quantitative data on the species are summarized: total number of occupied kilometre squares in Drenthe; number of occupied kilometre squares before and since 1999; trend class; category in the national Red Data list; first year of recording; quantitative data on the frequency of a species in different types of habitat, on different substrates and in association with different organisms, according to ecological codes used in the national mapping programme (Tables 4.7-4.9). Each

species description provides a short morphological characteristic and details on regional distribution patterns and ecology, also compared with data from other areas. When a species is known from seven or more kilometre squares a distribution map is provided. Records from before 1999 are indicated with open black squares, since 1999 with solid red dots. When a species is known from less than seven kilometre squares, the known localities are mentioned in the text.

Many species are illustrated with photographs or drawings, most of them made by members of the regional mycological study group. Some photographs have been selected for their aesthetic qualities, others because they represent rare species or species that have been rarely depicted.

Chapter 5. Drenthe as an environment for fungi

An introduction is given on topography, soils, water, climate and human expansion in the province of Drenthe. The province covers an area of 2626 km² in the northeastern part of the Netherlands and does not border the seacoast. It consists mainly of a low, sedimentary plateau of sandy and loamy soils, intersected by some brook valleys (Fig. 5.1). The altitude ranges between 1 m below up to 25 m above sea level (Fig. 5.4). The central part of Drenthe is mainly covered by acidic, oligotrophic, sandy soils of Pleistocene glacial origin. In some places more base-rich loamy deposits and old clay soils occur. In the brook valleys and along the borders peaty soils are widespread. Solid rock is completely absent at the surface (Fig. 5.5). In brook valleys base-rich seepage water is reaching the ground level in many places (Fig. 5.6). The climate is moderate maritime. In comparison with other parts of the country, winters are relatively cold (Fig. 5.2) and humidity is fairly high (Fig. 5.3). The landscape has been strongly influenced by man since c. 5000 years, when clearing of the original pristine deciduous forest started. Around 1850 very few forests were left, whereas heathlands and peat bogs were dominating the landscape (Fig. 5.7). Nowadays most of these areas have been converted into agricultural land and plantation forest.

The occurrence of fungi not only depends on abiotic conditions, but also on biotic conditions, in particular the presence of appropriate host plants. Distribution patterns are compared between some important host plants and fungi that are dependent on them (Fig. 5.9-5.19).

Chapter 6. The changing mycoflora in Drenthe

Various methods used to study changes in the mycoflora are described and evaluated. The study of long-term changes in Drenthe is complicated by lack of old distributional data on fungi. A theoretical reconstruction is made on changes in frequency of some species since 1900, based on documented changes in vegetation and environmental conditions (Fig. 6.1). On the basis of our database only conclusions can be drawn on changes during the latest decades. For each species the trend in Drenthe has been determined by comparison of the number of occupied kilometre squares in the periods 1800-1998 and 1999-2010 (Table 6.1). Interpretation of the results is complicated due to methodological factors, that are discussed. Examples are given of 30 species that have not been seen in Drenthe since 1990 and are regarded as regionally extinct (Table 6.2); of 25 species with a very strong negative trend in Drenthe (Table 6.3); of 25 species with a very strong positive trend in Drenthe (Table 6.4) and of the 25 most frequent species that have been found only since 1999 (Table 6.5). The proportions of various categories of decreasing and increasing species in some habitat types are presented in graphs (Fig. 6.3). Since 1999 110 fungal species are monitored throughout the Netherlands in permanent plots in forests and roadsides with trees, including 97 plots in Drenthe. Some results of this monitoring project are presented and trends of some species are depicted in Fig. 6.4.

Chapter 7. The mycoflora of Drenthe in a national context

The results of fungal mapping in Drenthe are compared with data from the national database, owned by the Netherlands Mycological Society. For each habitat group, distinguished in this Atlas, the number of species found in Drenthe is compared with the number of species present in the Netherlands (Table 7.1). In some habitat groups over 80% of the characteristic species in the Netherlands occur in Drenthe, e.g. heathlands and wet hay-meadows. In other groups this proportion is less than 30%, e.g. characteristic species from coastal dunes and limestone grasslands. The frequency of some species is much higher in Drenthe than in other parts of the country, as is demonstrated for 82 species in Table 7.2. The distribution in The Netherlands for four species of this group is shown in Fig. 7.1. On the other hand, some species are less frequent in Drenthe than in other parts of the country, as is demonstrated for 72 species in Table 7.3. The distribution in The Netherlands for four species of that group is shown in Fig. 7.2.

Within the Netherlands, Drenthe and its direct surroundings are recognized as a phytogeographic district (Drenthe district), characterized by the occurrence of some boreal plant species (Fig. 7.3). It is discussed whether the Drenthe district can also be recognized by distribution patterns of fungi. In particular species of moist heathlands and spruce forests seem to favour this district. Within the province four phytogeographical subdistricts are distinguished (Fig. 7.4). A selection of species with preference for one or several of these subdistricts is listed in Table 7.4. Distribution patterns of eight species are presented in Fig. 7.5 and 7.6.

Chapter 8. Conservation of fungi and their significance as indicators for environmental quality

The conservation status of fungi in Drenthe is based on the Red Data list of threatened fungi in the Netherlands (Arnolds & Veerkamp, 2008). The proportions of species in different categories of the Red Data list in the Netherlands and in Drenthe are indicated in Fig. 8.1. Figure 8.2 presents proportions of characteristic species in each of the habitat types, distinguished in this Atlas, that are on the Red Data list. In general low shares of Red Data list species are found in eutrophic habitats (indicated with green in the graph). The proportions are generally higher in mesotrophic environments (yellow bars) and highest in oligotrophic habitats (red bars). Ten major threats for the regional mycoflora are indicated and discussed: nitrogen deposition, acidification, artificial drainage, cutting down of old coniferous forests, inappropriate management of roadside-verges, disappearance of shell-paved paths, loss of veteran trees and dead logs, inappropriate processing of trimmings, widespread soil disturbance and inappropriate grassland management.

Fungi have proved to be very useful as indicators of environmental quality, in particular for eutrophication (nitrogen deposition), acidification, drainage and forest development (presence of veteran trees and large dead wood). Maps with numbers of indicator species in kilometre squares for these conditions are presented in Fig. 8.3. Fungi are especially useful as indicator organisms in habitats where other indicator organisms, such as vascular plants, are less diverse. The numbers of characteristic plants and fungi in various habitat types are compared in Table 8.1. Numbers of plants outnumber numbers of fungi in eutrophic marshes and dynamic environments. Fungi are much more diverse in all forest communities, with a maximum difference in coniferous forests. In Figure 8.4 species numbers of fungi and vascular plants are compared for all kilometre squares in Drenthe. The patterns are very different. Species diversity of fungi is highest in large forested areas, where diversity of plants is low. Legal protection of fungi and the role of fungi in nature conservation

are discussed. It is concluded that fungi receive less attention than they deserve. None of the species is protected by law in the Netherlands or the European Community. Other problems are a lack of interest in and knowledge of fungi within nature conservation agencies and inadequate communication between mycologists and people, involved in nature management.

Chapter 9. Important mycological areas in Drenthe

Characteristics are given of twelve areas in Drenthe with outstanding mycological qualities, in the Netherlands entitled 'mycological crown jewels' (Jalink, 1999). The crown jewels in Drenthe have been designated on the basis of the number of Red Data list species, with a weight for different categories in this list, ranging from 1 point for species of the category 'sensitive' to 5 points for species that have not been recorded in the last 30 years. Addition of these points for all Red Data list species produces the Mycological Value of an area (Jalink, 1999; example in Table 9.1).

The geographic position of the most valuable areas in Drenthe is indicated in Fig. 9.1. The size ranges between 5,3 ha and 500 ha. The areas include small-scale landscapes with deciduous forest, heathland and grassland (9.1, 9.2), forest plantations on former wind-blown sand dunes (9.3), grasslands and heathlands on calcareous loam (9.4, 9.8), old deciduous forests on heavy, base-rich clay (9.5, 9.6.), forest plantations with poor roadside-verges with old trees (9.7), estates and town parks (9.8, 9.12), oak forests on poor, sandy soils with calcareous verges of shell-paved paths (9.9) and old, unimproved hay-meadows in a brook valley (9.11). The description of each area begins with data on the name, size and owner of the area. In addition quantitative data are given on the numbers of species and Red Data list species and the resulting Mycological Value (MW). Some of the most interesting species are listed. A description of the area is provided with details on the mycoflora, landscape, plant communities, environmental conditions and human influence.

Chapter 10. Made in Drenthe

A survey is given of 53 taxa of fungi that have been originally described from Drenthe, comprising 39 new species and 14 new varieties. In addition four taxa were included that have been provisionally described. Among the 57 newly proposed taxa, 55 belong to the agarics, including 28 taxa of the genus *Entoloma* and 7 taxa of *Psathyrella*. For each species information is provided on the source of the original description, the type collection and type locality, the present condition of the type locality and the present taxonomic status. It appears that over half of the type localities have been destroyed or severely disturbed. 34 species and 11 varieties are still maintained as 'good' taxa by at least some authors. The remaining taxa are nowadays regarded as synonyms of other taxa.

Chapter 11. New records of fungi in Drenthe in the years 2011-2014.

After intensive mapping for this Atlas in the years 1999-2010 fieldwork in Drenthe has been continued, although in a less intensive way. The collected data since 2011 could not be considered for this Atlas anymore during data processing and writing. An exception has been made for 54 species, that were observed for the first time in Drenthe during this period. These species are treated in this chapter in the same way as in other descriptive chapters (see summary chapter 4). Thirty species are depicted with photographs, including rare or little-known species, such as *Boletus junquilleus* (= *B. pseudosulphureus*), *Clavulinopsis subtilis*, *Cortinarius sphagnophilus*, *Entoloma leochromus*, *Lepista martiorum*, *Phaeohelotium italicum* and *Rhizopogon villosulus*.

Chapter 12. Uncertain and incorrect records of fungal species in Drenthe

In this chapter 34 species are briefly discussed that have been reported from Drenthe, but without sufficient evidence to accept the records. The occurrence of most of them is unlikely unlikely in view of their distribution or ecology in the Netherlands. Five species are illustrated with photographs from outside Drenthe.

Chapter 13. Glossary

Some technical terms and abbreviations, used in this Atlas, are explained.

Chapter 14. Literature

A list of references is provided, mentioned in the three volumes of this atlas. Part 2 and 3 do not contain a separate list of references.

Addendum. In the addendum descriptions are given in English of four species and one variety, new to science. All of them have been recorded in Drenthe.

Ecological Atlas of fungi in Drenthe, volume 2

Chapter 16. Grasslands

In Drenthe 219 species of fungi have a preference for grasslands. The chapter is divided into three subchapters: Fungi with an optimum in dry, poor, unimproved grassland (16a); fungi of moist to wet, poor, unimproved grasslands (16b) and fungi of grasslands on nutrient-rich soils (16c). In the 1970's an extensive mycosociological study has been carried out in Drenthe in various types of grasslands by Arnolds (1981, 1983). The results are summarized in Table 16.1.

In Drenthe 110 species are mainly found in mesic to dry, poor, unimproved grasslands (chapter 16a). Characteristic species are predominantly agarics, including 32 species of *Entoloma* (e.g. *E. sericellum*, *E. chalybaeum*, *E. papillatum*), 13 species of waxcaps (e.g. *Hygrocybe conica*, *H. virginea*, *H. psittacina*) and 7 species of *Omphalina* (e.g. *O. obscurata*). Well-represented are also clavarioid fungi with 11 species, e.g. *Clavaria fragilis* and *Clavulinopsis helvola*, and earth-tongues with 5 species, e.g. *Geoglossum umbratile* and *Trichoglossum hirsutum*. The majority of characteristic species are assigned to the saprotrophic soil fungi, but the life strategy of many of them is not yet understood, e.g. of waxcaps (see p. 17). In this habitat type 90% of the characteristic fungi are rather to extremely rare and 71% of them are included in the national Red Data list (graphs on p. 16). In Drenthe very few kilometre squares count over 20 species of this group (maps on p. 21) and they are restricted to small patches in nature reserves, roadside-verges and along canal banks. Such grasslands usually have a short, low productive sward of various grasses and herbs, with species as *Agrostis capillaris*, *Luzula campestris*, *Hieracium pilosella* and *Campanula rotundifolia*, and a well-developed moss-layer. The mycoflora can be very diverse, averaging 45 species in plots of about 200 m², with maxima over 70 species. Essential factors for the development of grasslands with a rich mycoflora are: absence of soil disturbance during decades, no fertilizer application, and continued grassland management, producing a short sward in autumn by mowing or grazing. Without doubt dry, unimproved grasslands with a rich mycoflora have been widespread in Drenthe in the first half of the 20th century, but data on grassland fungi from that period are not available. Nowadays the few remains of these grasslands are still threatened by soil disturbance, nitrogen deposition and inappropriate management.

Until recently moist to wet, nutrient-poor grasslands were widespread

in the brook valleys in Drenthe. In traditional farming they were used as unfertilized hay-meadows. Nowadays such grasslands have become rare and almost restricted to nature reserves. The mycoflora in wet grasslands is much poorer in species and sporocarps than in grasslands on dry soils. Nevertheless 41 species are considered characteristic of wet hayfields, mainly agarics, including ten species of the genus *Entoloma*, e.g. *Entoloma infula* and *E. porphyrophaeum*. Other characteristic species are e.g. *Agrocybe elatella*, *Galerina jaapii* and *Mycena bulbosa*. Almost all characteristic species of this group are rare to extremely rare and included in the Red Data list, if evaluated. The few remaining areas of this habitat type are threatened by nitrogen deposition, acidification, deep drainage and lack of management. Sometimes also restoration of the hydrology in brook valleys has a negative impact when this leads to long-lasting inundations.

In chapter 16c 68 species of fungi are treated with an optimum in nutrient-rich, in most cases fertilized grasslands. In this chapter also species are included with a broad range in grassland communities, inhabiting both poor and rich soils. Almost all characteristic species are agarics, living as saprotrophs on litter and humus (graphs on p. 10), including well-known species, such as *Agaricus campestris*, *Clitocybe rivulosa*, *Entoloma sericeum*, *Marasmius oreades* and *Mycena olivaceomarginata*. With 37% of the characteristic species on the Red Data list this ecological group contains considerably less rare and threatened species than the groups of poor grasslands. Species diversity in nutrient-rich grasslands is quite variable. It can be high in old, permanent grasslands on mesic and dry soils, supplied with moderate quantities of straw-rich stable dung. Here also some waxcaps and other characteristic species of poor grasslands (chapter 16a) may occur in considerable numbers. Grasslands treated with liquid manure or artificial fertilizers are much poorer in soil inhabiting fungi. Also permanently wet and periodically inundated meadows are an unfavourable habitat for this group. At present most agricultural grasslands are frequently ploughed and resown with grass seeds. Such grasslands possess a fragmentary mycoflora, resembling the poor mycoflora of arable fields.

Chapter 17. Fungi on dung

Coprophytic fungi can be found in all kinds of habitats where grazing animals live or where dung is deposited by man, consequently not only in grasslands, but also in e.g. heathlands, marshes, forests, roadside-verges and gardens. In Drenthe 88 species are assigned to this ecological group. Most of them are exclusively found on dung, others also occasionally on compost, very rich soils and rotting vegetable materials, such as decomposing heaps of hay or straw. Most species grow on excrements, some species only on dung heaps where the inside temperature is much higher because of microbial processes.

In Drenthe a majority of this group (70%) belong to the agarics, e.g. *Conocybe pubescens*, *Coprinopsis stercorea*, *Deconica coprophila*, *Panaeolus papilionaceus* and *Stropharia semiglobata*. Ascomycetes are also well-represented with 24 species, mainly small cup-fungi (Pezizales), such as *Ascobolus crenulatus*, *Cheilymenia granulata* and *Saccobolus glaber* (graphs on p. 142). In reality the share of ascomycetes is much higher, but fieldwork for this Atlas has paid little attention to the numerous small pyrenomycetes occurring on dung. Although dung is a widespread substrate, 93% of the coprophytic fungi in Drenthe are classified as more or less rare. It is remarkable that 38% of the species decreased or even disappeared since 1999. A similar proportion of coprophytic fungi is included in the national Red Data list. Our fieldwork has revealed that coprophytic fungi have mainly decreased in intensively used, agricultural pastures. This is

attributed in the first place to the altered consistency of cow dung, which is nowadays very soft and without straw-like components. Such dung is decomposing too fast to enable sporocarp formation in many species. Possibly also the use of antibiotics in cattle feed has a negative impact, as has been demonstrated for *Poronia punctata*. On the other hand, coprophytic fungi have strongly increased in nature areas, such as heathlands and forests, as a result of increased grazing as part of nature management. In such areas slowly decomposing, straw-rich dung is still available. This is also clear in distribution patterns of species in Drenthe, with highest diversity in grazed nature reserves (maps on p. 141). Since the area occupied by intensive cattle breeding is much larger than the area of grazed nature areas, the balance for coprophytic fungi is negative in the end.

Chapter 18. Heathlands and moors

In Drenthe 120 species of fungi are considered characteristic of heathlands and moors. Most species live saprotrophic on soil, litter and remains of herbs, some of them are associated with bryophytes. Characteristic wood inhabiting and ectomycorrhizal fungi are absent. This chapter is divided into four parts: heathlands and grass-heaths on dry soils (chapter 18a); heathlands and grass-heaths on moist and wet soils (chapter 18b); oligotrophic peat bogs (chapter 18c) and mesotrophic to eutrophic fens and marshes (chapter 18d).

Dry and mesic heathlands in Drenthe are dominated by *Calluna vulgaris* and *Empetrum nigrum*. On somewhat richer soils grass-heaths are found, dominated by grasses, such as *Festuca filiformis*, *Nardus stricta* and *Deschampsia flexuosa*. In Drenthe the area of dry heathlands has strongly decreased, but they are still fairly widespread, e.g. on windblown sand dunes and ridges of boulder-clay (maps on p. 194). Almost all remains are protected nature reserves nowadays. Since dry heathlands are semi-natural communities their conservation depends on continuation of traditional management: grazing, mowing, burning and cutting of sods. Twenty-four species of fungi are characteristic of this habitat type, e.g. *Clavaria argillacea*, *Entoloma fernandae*, *Galerina pumila* and *Hygrocybe miniata*. Most species are rare and included in the national Red Data list (graphs on p.193). The decrease of this group of fungi is mainly caused by habitat loss and the negative impact of nitrogen deposition. In the 1970's mycosociological research has been carried out in plots in dry grass-heaths. The results are summarized in Table 18.1.

Moist and wet heathlands are dominated by *Erica tetralix*. A century ago vast areas in Drenthe were covered by this community, mainly on sandy or peaty soils above semi-impermeable boulder-clay. The remaining areas, all nature-reserves, are still regarded as the largest and most important representatives of this plant community in Europe (maps on p. 209). By nitrogen input many *Erica* heathlands have become overgrown by *Molinia caerulea*. This grass is also an important component of moist grass-heaths, occurring on richer, loamy soils, and characterized by numerous herbs. In the 1970's mycosociological research has been carried-out in plots in moist grass-heaths and *Molinia*-dominated communities. The results are summarized in Table 18.1. In Drenthe 46 fungal species are characteristic of moist heathlands, including 13 species of *Entoloma*. Most of the characteristic species are rare and 69% are on the Red Data list (graphs on p. 210). Some well-known species are *Entoloma conferendum*, *Hygrocybe laeta*, *Hypholoma elongatum* and *Mycena adonis*. The maintenance of these vegetations depends on continued human management, including periodical removal of the organic top soil. After such a treatment a special fungus community develops on bare soil, with species such as *Gymnopilus fulgens*, *Omphalina chlorocyanea* and *O. mutila*.

Once oligotrophic peat bogs occupied large parts of Drenthe. These

communities are built up by various *Sphagnum* species and only fed by rain water. After massive peat digging only some relics remain, often suffering from desiccation and nitrogen pollution. In addition small peat bogs are still found in small depressions in heathlands and forests, scattered over the area (maps on p. 236). The mycoflora in peat bogs is poor, but highly specialized, including a high proportion (61%) of species associated with mosses, mainly *Sphagnum*. Eighteen species are listed as characteristic, most of them being rare. All evaluated species are on the Red Data list. The most widespread species of this ecological group are *Lyophyllum palustre* and *Galerina paludosa*. The mycoflora in peat bogs in Drenthe is poorly developed in comparison to Scandinavia and eastern Europe, probably because of the high nitrogen deposition, strongly exceeding the critical load for this community.

Mesotrophic to eutrophic marshes are influenced by groundwater or seepage water, rich in bases and nutrients. They are often dominated by large herbaceous plants, such as *Phragmites australis*, *Typha latifolia* and several *Carex* species. In Drenthe these communities cover relatively small areas in the lowest parts and in brook valleys (maps on p. 249). At least 32 species of fungi are regarded as characteristic of these communities, but this species list certainly will be incomplete, since marshes were not intensively investigated during the mapping project. The mycoflora is very poor in agarics and other larger fungi, and many small species have been neglected. Some characteristic species are *Marasmius limosus*, *Lachnum apalum* and *Belenopsis culmicola*. It is the only ecological group where according to our data disc fungi (*Helotiales*) are the largest group. Almost all characteristic species of eutrophic marshes are rare and the majority is not evaluated for the Red Data list (graphs on p. 247). Relations between the composition of the mycoflora and management, e.g. mowing of marshland, are poorly known.

Chapter 19. Marshy forests and scrub

The floristic composition of forests and scrub on wet, sometimes inundated soils is very different from forests on drier soils. Also the mycoflora is specialized with 206 characteristic species in Drenthe. This chapter is divided into four sections: scrub communities dominated by species of *Salix* (19a) or *Myrica gale* (19b) and forests dominated by *Betula pubescens* (16c) or *Alnus glutinosa* (19d). These plant communities have been subject to mycosociological studies in the 1980's. The results are summarized in Table 19.1.

Scrub dominated by *Salix* species (chapter 19a) can be subdivided into two communities: one dominated by *Salix cinerea* on rich soils under the influence of base-rich groundwater and one dominated by *Salix aurita* on mesotrophic soils, mainly fed by rain water. Both communities are fairly widespread in Drenthe (maps on p. 271), but the stands are usually small, at the most a few hectares. *Salix* scrub is a spontaneous, temporary stage in the succession from open water to forest. Especially old stands are interesting for fungi. In spite of different environmental conditions the two communities have many fungi in common, because many species are associated with *Salix*, without distinct preference for a certain species. A high number of 113 fungi have their optimum in *Salix*-scrub, including 50 wood decomposers, e.g. *Daedaleopsis confragosa*, *Diatrype bullata* and *Hymenoscyphus salicinus*, and 41 mycorrhizal fungi, e.g. *Alnicola salicis*, *Cortinarius uliginosus* and *Russula subrubens*. 36% of the characteristic species are listed in the Red Data list (graphs on p. 270). Important threats to sallow swamps and their mycoflora are desiccation and supply of nitrogen from surrounding land. These disturbances lead to a dense understorey of tall herbs. Dried-out *Salix* stands are much poorer in species, in particular in mycorrhizal fungi.

Stands of *Myrica gale* (chapter 19b) are found locally in Drenthe on

wet, acidic, often peaty soils with some influence of groundwater. They usually occur in gradients from heathlands to brook valleys. Often only small patches of this shrub are present, but occasionally *Myrica* forms extensive stands. The mycoflora is poor in species and mainly consists of saprotrophic litter fungi that are widespread in peat bogs and heathlands. *Myrica* does not form ectomycorrhiza. Most wood of this shrub is decomposed by widespread lignicolous fungi. Three small ascomycetes are characteristic of dead branches of *Myrica*, of which *Incrucipilum sulphurellum* can be numerous. One species is restricted to mummified catkins. The four characteristic species are rarely recorded, but their true distribution is unknown.

Marshy forests, dominated by *Betula pubescens* are rare in Drenthe. They are characterized by an open structure with a low canopy, a well-developed moss cover of various *Sphagnum* species and the presence of some plant species of peat bogs and wet heathlands. Such forests are mainly found along margins of peat bogs and in slightly enriched bogs. *Betula pubescens* is not restricted to this habitat, but also widespread in drier, oligotrophic forests. The mycoflora in swampy birch forests is fairly poor in species and mainly a mixture of species from peat bogs and mycorrhizal symbionts of *Betula*. Fifteen species are more or less characteristic of this habitat type, almost all of them mycorrhizal agarics, e.g. *Cortinarius armillatus*, *Lactarius vietus* and *Russula claroflava*. Except the last-named fungus all species are rare and 67% of them are included in the Red Data list (graphs on p. 334). Threats to this forest community and its fungi are drainage, nitrogen input and cutting by nature conservation agencies in attempts to restore open bogs.

Forests of *Alnus glutinosa* have been widespread in Drenthe in brook valleys and fens, in both cases on permanently wet, mesotrophic to eutrophic soils under the influence of base-rich ground or seepage water. In the past most alder forests have been cut and drained in favour of meadowland. Only a few, small areas were left (maps on p. 347), often devaluated by deep drainage in the surroundings. Wet alder stands can be rich in fungi with up to 120 species in plots of 1000 m². In Drenthe 74 species are considered characteristic of these forests, including 28 wood decomposers, e.g. *Mensularia radiata*, *Flammula alnicola* and *Pluteus salicinus*. In addition 22 ectomycorrhizal fungi are restricted to *Alnus*, e.g. *Alnicola escharoides*, *Cortinarius alnetorum*, *Lactarius obscuratus* and *Russula alnetorum*. Few species are common and 38% are on the Red Data list (graphs on p. 346). The most important threats to alder swamps and their mycoflora are desiccation and supply of nitrogen from surrounding land. These disturbances lead to an increase of *Urtica dioica* and other large herbs. The mycoflora in such stands is strongly impoverished and in particular mycorrhizal fungi are declining. In future new alder forests may develop in stretches of brook valleys, recently designated for nature development.

Chapter 20. Built-up areas, orchards, arable land, roughs

The fungi, treated in this chapter, have their optimum in nutrient-rich, more or less dynamic habitats that are strongly influenced by man. The chapter is divided into four sections: urban green areas, such as parks, cemeteries, orchards, private yards and gardens (chapter 20a), arable land and roughs (chapter 20b), deposits of wood chips (chapter 20c) and buildings (chapter 20d).

In Drenthe 149 fungal species have a preference for parks and other green, man-influenced areas, mainly agarics (chapter 20a). Most characteristic species of this habitat are rare, but only few of them are decreasing or included in the Red Data list (graphs on p. 392). The ecology of fungi in this habitat type is quite varied. Many of them live saprotrophic on black, humus- and nutrient-rich soils, e.g. *Agaricus bitorquis* and *Coprinus comatus*. Other species grow on old trees in

parks, e.g. *Ganoderma adspersum* and *Hericium cirratum*, or on a variety of cultivated plants, e.g. *Trochila laurocerasi* and *Exobasidium japonicum*. Elsewhere most of the species of this ecological group are found in old deciduous forests on soils, rich in bases and nutrients, such as forests in river valleys. This forest type does not occur in Drenthe and parks and related man-made habitats may be regarded as artificial substitutes for this environment.

Fungi of arable land and ruderal plant communities are treated in chapter 20b. Arable land is characterized by regular soil disturbance and nutrient-rich conditions. Occasionally a few fungal species can be found in that habitat, sometimes in high densities of carpophores, but hardly any larger fungus can be considered as characteristic of arable fields. Also ruderal communities are characterized by a high nutrient status and dynamic conditions, but soil disturbance is often less intensive and more fungi can be seen, in particular in older stands. A total number of 25 species is regarded as characteristic of fields and roughs, mainly agarics and small ascomycetes (graphs on p. 472). Some well-known species are *Calvatia gigantea* and *Volvariella gloiocephala*. Many ascomycetes are living on dead stems of large herbaceous plants, such as *Urtica dioica*, e.g. *Leptosphaeria acuta* and *Trichopeziza sulphurea*.

It has become general practice to shred pruned branches mechanically, in particular in built-up areas. The produced wood chips are often spread in parks, roadside verges and on footpaths, or occasionally dumped on heaps. These microhabitats are colonized by many fungi. In Drenthe 34 species are considered as characteristic of wood chips (chapter 20c). Remarkable is massive fruiting of some species, e.g. *Coprinopsis lagopus*, *Psathyrella corrugis* and *P. conopilus*. Other characteristic species are e.g. *Agrocybe rivulosa*, *Clathrus archeri* and *Leratiomyces ceres*. Most of them belong to the agarics, living saprotrophic on wood or mixtures of fragmented wood and soil (graphs on p. 490). A majority of these species is rare because of the scattered availability of the specific substrate (maps on p. 491). Almost all fungi on wood chips have strongly increased or have been recently established. Very few species are on the Red Data list. However, in near future a decrease of this group is foreseen, because nowadays increasing quantities of wood chips are used as fuel in power stations.

Some fungi, often of (sub)tropical origin, are (almost) exclusively found inside buildings (chapter 20d). In Drenthe only six species of this group are known from very few localities. This habitat was not investigated during the mapping programme and therefore the data on fungi in buildings are very incomplete.

Chapter 21. Avenues and roadside verges with trees

Throughout Drenthe hundreds of kilometres of paved and unpaved roads are lined with trees, mainly with *Quercus robur*, also with *Fagus sylvatica*, *Quercus rubra* (introduced) and *Betula pendula*, more rarely with *Tilia*, *Populus*, *Acer*, *Aesculus* and *Fraxinus*. In Drenthe 237 species of fungi have their optimum in roadside verges with trees. The great majority of characteristic species belong to the agarics. Most of them are ectomycorrhizal (84%) and half of the species are included in the Red Data list (graphs on p. 516). Roadside verges with non-ectomycorrhizal trees, such as *Acer*, *Fraxinus* and *Aesculus*, are not interesting for species of this ecological group.

Mycorrhizal species in roadside verges with trees originate from two different sources. The majority of them occurred until 1960-1970 in native deciduous forests, but they have become rare or extinct in these habitats by the effects of acidification and nitrogen deposition. For these species roadside verges function as refuge. Environmental conditions are better there because the grass is mown and removed, dead leaves are blowing away in part, and the soil is locally richer

in bases by washing of minerals from the road, as a compensation for eutrophication and acidification by air pollution. Another group of roadside species has always been rare in undisturbed forests and probably originates from forest edges and open, grazed forests.

In the 1980's a mycosociological study has been carried out in Drenthe in roadside verges with *Fagus* and *Quercus* by Keizer (1993). Some results are summarized in Table 21.1. It appeared that species diversity of mycorrhizal fungi is strongly influenced by soil type, vegetation type and age of trees. Diversity is high under old trees on soils poor in nutrients, with a short grassy or moss-rich soil cover, managed by mowing and removal of the sward. It is low under young trees and on rich soils with a tall, dense grass cover and management by cutting without hay removal or no management at all. This chapter is divided into three parts: roadsides with trees on nutrient-rich soils (chapter 21a), on poor, acidic, sandy soils (chapter 21b) and on basic, loamy soils (chapter 21c).

Seventy species of fungi can be found in nutrient-rich roadside verges, but they are often also widespread on poorer soils. This ecological group is widespread in Drenthe (map on p. 526). Many common mycorrhizal species belong here, e.g. *Russula parazurea*, *R. amoenolens*, *Cortinarius vernus* and *Inocybe maculata*. On the average about ten mycorrhizal species occur in plots of 100 metres long. Also some parasites on trees are assigned to this group, e.g. *Grifola frondosa*, as well as some saprotrophic soil fungi, e.g. *Calvatia excipulliformis*. Most species have strongly increased in Drenthe because of increasing enrichment of the environment with nitrogen. Few species are on the Red Data list (graphs on p. 525).

Sixty species are characteristic of roadside verges on poor, sandy, acidic soil. Almost all of them are mycorrhizal symbionts that were found in the past in Drenthe mainly in oak- and beech forests on poor soils, e.g. *Boletus erythropus*, *Hydnellum conrescens*, *Lactifluus vellereus* and *Sarcodon scabrosus*. These fungi have decreased or disappeared there by acid and nitrogen deposition and have found a refuge in roadsides with oak and beech. Many species are rare and 62% of them are mentioned in the national Red Data list (graphs on p. 576). The refuges of these fungi in poor roadsides are threatened by continued nitrogen enrichment and lack of appropriate management. In Drenthe 107 species of fungi are characteristic of roadside verges on clayey or loamy, weakly acidic to basic soils. This ecological group has its main distribution in the Netherlands outside Drenthe, on heavy clay soils in the valley of the Rhine and his tributaries. Almost all characteristic species of this habitat type are ectomycorrhizal agarics, e.g. *Amanita phalloides*, *Boletus radicans* and *Russula pseudointegra*. Over 70% of the species are very rare in Drenthe and 60% of them are included in the Red Data list (graphs on p. 618). Their occurrence in Drenthe is very localized, mainly concentrated in a small area of heavy clay-soils in the north of the province (maps on p. 621). Species of this group tend to spread in sandy areas, presumably because of leaching of calcareous material from road pavement.

Chapter 22. Verges of shell-paved cycle tracks through forests

This is the most remarkable habitat type, treated in this Atlas in a chapter of its own. Within the Netherlands Drenthe is well-known as a favourite province for bicycle tourism, mainly because of the dense network of cycle tracks through beautiful scenery. A large proportion of these tracks, in particular in forests and heathlands, has been paved with shells (mainly cockles), obtained from the sea bottom. By washing of lime and other minerals from the shells into the verges of the tracks, gradually a steep gradient in acidity has developed from basic (pH 7,5) along the path to strongly acidic (pH 4) in the surrounding forest and heathland over a distance of only 5 metres. These narrow trips along cycle tracks form well-buffered, base-rich

microhabitats in a predominantly acidic environment.

No less than 88 species of fungi are in Drenthe mainly found along paths and tracks, paved by shells or other base-rich materials, including Koersmix (a by-product of the production of sand-lime bricks) and grinded rubble of buildings. The characteristic mycoflora in this microhabitat is mainly originating from two sources. Some species are native to Drenthe, but have become rare or extinct on their original sites because of acidification by air pollution. For these species shell-paved paths are a refuge. Other species were originally absent or very rare in Drenthe and have spread from areas where natural calcareous soils are found, in the Netherlands for instance the coastal dunes, the valleys of the rivers Rhine and Meuse, and the limestone area in South-Limburg. Part of the species of this group are also less frequently found in other habitat types, e.g. in verges of paved roads, parks and forests on weakly acid to basic soils (Table 22.1).

The majority of the characteristic species of this ecological group belong to the agarics, including 14 species of *Inocybe*, 10 species of *Lepiota* and *Cystolepiota* and 8 species of *Pluteus*. Also the high number of 28 *Pezizales* is striking, including 10 species of *Helvella* and 8 species of *Peziza*. Representative species are e.g. *Helvella crispa*, *Cystolepiota seminuda*, *Geastrum triplex*, *Inocybe hirtella*, *Lepiota boudieri*, *Peziza michelii*, *Pluteus phlebephorus* and *Tarzetta catinus*. Saprotrophic fungi on litter make up 50% of the characteristic species, but ectomycorrhizal species are also well-represented with 44% of the species (graphs on p. 674). Only four species are more or less widespread in Drenthe. The remaining species are rare to some degree, including even 30 extremely rare species, known from 1-3 localities only. The high share of rarities is a consequence of the small, fragmented area occupied by this microhabitat. The maps on p. 676 show that clusters of species are mainly found in state forests, the areas where most cycle tracks occur in favourable habitats. The majority of species have increased in the last decades, due to the gradual development of the necessary weakly acidic to basic conditions. Most species are not threatened on a national scale. The prospects for this group of fungi are uncertain. The use of shells for pavement of cycle tracks is decreasing and many narrow, shell-paved cycle paths have been converted into broader asphalt or concrete tracks, usually with devastating effects on the verges and their mycoflora during construction.

Ecological Atlas of fungi in Drenthe, volume 3

Chapter 23. Fungi and forest management

As in the rest of northwestern Europe, forests are in Drenthe the most important habitat for fungi. About 75% of the species predominantly occur in forests and other habitats dominated by trees or shrubs. Species composition is strongly influenced by various kinds of human interference. Therefore a special chapter is devoted to this subject.

The current situation of forests and their fungi in Drenthe can only be understood in a historical context. Some millennia ago the entire province was covered with mixed deciduous woodland, except some border areas that were occupied by peat bogs. Forests on higher, sandy soils were dominated by *Quercus robur*, in brook valleys by *Alnus glutinosa*, and on rich loamy soils by *Fraxinus excelsior*, *Tilia*, *Ulmus* and *Corylus avellana*. Deforestation took mainly place from the early Middle ages onward by burning, cutting and subsequent grazing of cattle. Areas around settlements were reclaimed to arable fields and hay-meadows and extensive areas changed into heathland, grazed by sheep. In dry, sandy areas treeless, windblown sand dunes developed by overgrazing. About 1850 only 1.2% of the province

was covered with forest anymore (Fig. 23.1). In the remaining forests human influence was intensive by tree cutting, removal of litter and pasturing. Since 1850 the forested area expanded by the development of estates and in the 20th century by afforesting of large areas. Sand dunes were mainly planted with *Pinus sylvestris*, moist heathland also with introduced trees (see chapter 28). The area of forest in Drenthe increased to 8,5% in 1960 and 13% at present (Fig. 23.1). Most larger forest areas are owned and managed as state forests.

Consequently, most forests in Drenthe are first-generation plantations or young second-generation stands. Veteran trees and large, dead logs are rare, also because of intensive logging for timber production. The present composition of the mycoflora is still determined to a large degree by fertilizer application during planting of trees (see chapter 28). The most varied and interesting mycoflora, in particular concerning ectomycorrhizal fungi, is found in forests on poor, mineral soils without application of fertilisers. Also in such forests the original conditions have changed since 1960 by atmospheric pollution, causing acidification and N-deposition in the order of 50 kg N/ha/yr. Both lichen-rich pine forests and moss-rich oak forests have disappeared completely and many fungal species of these communities became extinct or very rare. At present acidification has been strongly reduced, but nitrogen deposition, about 30 kg N/ha/yr, is still a main problem in forest and naturemanagement.

At present most forests are explored from a multifunctional point of view, trying to find a balance between harvest of timber, creation of an attractive landscape, increase of biodiversity, conservation of certain (groups of) organisms, promotion of a natural forest structure and composition, and recreational activities. These different aims may lead to conflicting interests. Some aspects of forest management are reviewed here from a mycologist's point of view.

Clear cutting. Large scale clear cutting has been common practice for timber production. For forest fungi this is a devastating measure. At present clear cutting is generally considered an undesirable practice and therefore it is rarely applied.

Thinning and selective cutting. The effects of these measures vary in different forest types. In general they are harmful in mature spruce forests, but not so much in pine stands and deciduous forests. In the past branches often were taken away from the forest or burnt (see also chapter 29). Nowadays most small wood remains are left on the forest floor. On poor soils this practice may lead to eutrophication, also because more litter accumulates, and it is therefore unwanted in such areas. Pruned branches may also be chopped. Wood chips form a substrate for a specialized group of fungi (see chapter 20c), but application on poor soils should be avoided because of soil eutrophication.

Forest transformation. At present there is a strong tendency among foresters and nature conservationists to transform coniferous forests into forests of indigenous frondose trees by selective cutting and thinning of conifers. This development has a negative impact on the diversity of the mycoflora, since many forests of *Pinus sylvestris* and *Picea abies* have gradually become mature communities with a characteristic structure, microclimate and soil, inhabited by numerous specialised fungi and other organisms.

No management at all. From a mycological point of view in forests a management of non-interference is preferred in most cases. It enables in the long term the development of a natural forest structure, including old standing trees, dead large logs in various degrees of decay, wind throw of old trees and rejuvenation of trees in originated gaps. At present such forests do hardly exist in Drenthe.

Forest grazing. During the last decades cattle and sheep grazing has been introduced in some forests in order to enhance structural diversity. During fieldwork we did not notice positive effects on the

mycoflora, except for the appearance of some coprophytic fungi.

Sod cutting. In some experimental plots in oak and pine forests in Drenthe the nitrogen-rich organic top soil has been removed in order to study the possible regeneration of mycorrhizal fungi. The attempts had some positive, but short-lasting effects in pine stands only. The application of sod cutting as a management tool in forests is negligible.

Liming. In the Netherlands liming of forest soils has been mainly carried-out in an experimental context in order to study the possible effects on soil acidification, vegetation and fungi. Application of lime on litter layers appear to enhance the decomposition of nitrogen-saturated litter layers and has a strong, negative effect on the mycoflora, in particular on mycorrhizal species.

New forests on former agricultural land. In Drenthe recently new forests have been planted on former agricultural land. Young forests on heavily fertilized soils and soils with a high organic matter content are dominated by trivial saprotrophic fungi. Plantations on poorer soils with less humus are richer in mycorrhizal fungi and occasionally rich in interesting species, in particular young stands of *Picea abies* (see also chapter 28c). Some young forests with a rich mycoflora have developed spontaneously in new nature areas where the organic topsoil had been removed as deep as the mineral soil, which is very poor in nutrients.

Chapter 24. Fungi of deciduous and coniferous forests

In this chapter 143 species are treated with a broad ecological range in both deciduous and coniferous forests, including a number of rare species of which the ecology is incompletely known. In Drenthe the species of this ecological group do not show a distinct preference for deciduous or coniferous forests. Some common species are found in this group with a very wide range, growing also in habitats outside forests, such as heathlands and grasslands. This concerns mainly saprotrophic litter decomposers, such as *Mycena galopus* and *Gymnopus dryophilus*. The chapter is divided into two sections. Species inhabiting a wide variety of forests on various soil types or preferring rich soils are described in chapter 24a; species with a preference for oligotrophic soils in chapter 24b.

The group of fungi of deciduous and coniferous forests on various soils comprises 87 species. Agarics are represented with 27 species, including well-known fungi as *Agaricus silvaticus*, *Clitocybe metachroa*, *Hebeloma mesophaeum*, *Hypholoma fasciculare* and *Rickenella fibula* (see graphs on p. 27). It is the only ecological group where corticioid fungi have the largest share with 32 species, including e.g. *Hypochnicium punctulatum* and *Peniophorella praetermissa*. Also the high number of 18 tremelloid species is remarkable, e.g. *Dacrymyces stillatus*. Many rare species of these taxonomic-morphological groups are treated in this chapter because their ecological range is insufficiently known. Over half of the characteristic species grow on wood and only few species are ectomycorrhizal, e.g. *Hebeloma mesophaeum* and *Russula ochroleuca*. The share of Red Data list species (7%) is very low, but half of the species, mainly non-agarics, are not evaluated because of data deficiency. The species of this group are well-distributed in Drenthe, with the highest numbers in state forests on sandy soils, lower numbers in reclaimed moorlands and brook valleys (maps on p. 28).

The properties of species of deciduous and coniferous forests on oligotrophic soils, treated in chapter 24b, are different. Among the 56 characteristic species, agarics are by far the largest group with some well-known species, such as *Amanita gemmata*, *Armillaria ostoyae*, *Clitocybe vibecina* and *Inocybe lacera*. Corticioid fungi have a much smaller share (12%), e.g. *Thelephora terrestris* and *Trechispora mollusca* (graphs on p. 74). About half of the species are ectomycorrhizal and 31% of the species are included in the Red

Data list. Many of them are sensitive to acidification and/or nitrogen input. Diversity of this ecological group is highest in sandy areas of the Drenthe plateau.

Chapter 25. Deciduous forests on various soil types

This chapter is dealing with 180 species of fungi that in Drenthe are mainly found in mesic to dry deciduous forests, without distinct preference for rich or poor soils. The environmental conditions for this group of fungi are similar to the conditions for the species, treated in chapter 24a. However, the characteristic species have a distinct preference for forests of deciduous trees and do not, or much less frequently, occur with coniferous trees. Agarics, corticioid fungi and polypores are well-represented (graphs on p. 110). Almost all characteristic species of this ecological group have a saprotrophic way of life, with a majority of them growing on woody substrates, e.g. *Bjerkandera adusta*, *Calocera cornea* and *Nectria cinnabarina*. Widespread saprotrophic litter decomposers are e.g. *Clitocybe nebularis* and *Rhodocollybia butyracea*. Only ten mycorrhizal species belong to this group, e.g. *Amanita muscaria* and *Laccaria laccata*. A large proportion of the characteristic species is common and widespread (maps on p. 111) and only 10% of them are mentioned in the Red Data list. Most species show an increase in recent years, caused by increasing soil eutrophication and the expansion of forests on former agricultural land.

Chapter 26. Deciduous forests on soils poor in nutrients

The mycoflora is described of deciduous forests on mesic to dry, acidic, sandy and loamy soils, originally poor in nutrients. It is one of the core-habitats in Drenthe, since such forests are the natural climax community in the higher parts of the province. Without human influence they would be the most widespread forest community. This pattern is still reflected in the distribution pattern of characteristic species of this group (maps on p. 211). Important trees in these forests are *Quercus robur*, *Betula pendula*, *B. pubescens*, *Fagus sylvatica*, *Sorbus aucuparia*, more locally *Populus tremula* and *Ilex europaeus*. A group of 136 species have their optimum in these forests. In ecological respect this group of fungi is comparable with the species treated in chapter 24b, but the characteristic species have a distinct preference for deciduous trees and do not, or much less frequently, occur with coniferous trees. In the past this ecological group comprised a larger number of species, but many species have almost disappeared from forests by environmental pollution. These fungi have found a refuge in roadside verges with trees on poor soils and are therefore treated in chapter 21b. The majority of the characteristic species of oligotrophic, deciduous forests are agarics, with ascomycetes in second position (graphs on p. 210). Both ectomycorrhizal fungi, saprotrophs on wood and saprotrophs on litter are well-represented. Numbers of rare and common species are rather similar. The share of Red Data list species is moderate with 25% of the total number. Well-known species of this ecological group are e.g. *Amanita muscaria*, *Cantharellus cibarius*, *Gymnopus dryophilus*, *Leotia lubrica*, *Fomes fomentarius* and *Pycnoporus cinnabarinus*.

Deciduous forests on poor soils have been subject of several mycosociological studies in the 1970's and 1980's: oak-dominated forests were investigated by Jansen (1984), birch-dominated forests by Jalink & Nauta (1984) and beech-dominated forests by Arnolds et al. (1994). The numbers of fungal species in these communities range between 70 and 130 in plots of 1000 m². Species composition varies strongly with the composition of the tree layer and with soil conditions. A special type of oak and beech forests was locally found on windblown sand dunes with a thin litter layer and a groundcover of mainly mosses and lichens (*Betulo-Quercetum cladonietosum*).

These communities were rather poor in litter saprotrophs and wood inhabiting fungi, but quite rich in ectomycorrhizal fungi, including several hydroid species and e.g. *Tricholoma saponaceum* and *Cortinarius lividochraceus*. Since about 1975 this forest type has become practically extinct due to nitrogen deposition in combination with natural soil development. At present most characteristic species of this forest type are almost exclusively found in roadside verges with planted oak and beech. Some less critical species show partial recovery in forests since the beginning of this century as a result of a considerable reduction of atmospheric nitrogen, e.g. *Cantharellus cibarius*, *Cortinarius bolaris* and *Elaphocordyceps ophioglossoides*.

Chapter 27. Deciduous forests on rich soils

This chapter is devoted to 312 species of fungi with a preference for deciduous forests on soils that are relatively rich in nutrients and/or bases. The effects of a high content of nutrients (nitrogen and phosphorus) on forest communities and their mycoflora are different from the effects of a high base content (mainly lime and potassium). However, these soil properties often occur combined, e.g. in forests on former agricultural soils. Therefore it may be difficult to estimate the importance of these factors for a certain fungal species. In many publications authors refer to 'preference for rich soils', leaving aside whether the soils are base-rich and/or nutrient-rich. Characteristic fungi of 'rich soils' are treated in chapter 27a, species characteristic of base-rich, loamy soils in chapter 27b and species of nutrient-rich, recently disturbed soils in chapter 27c.

The group of characteristic fungi of forests on rich soils comprises 118 species (chapter 27a), e.g. *Armillaria lutea*, *Coprinellus disseminatus*, *Crepidotus cesatii*, *Diatrype stigma* and *Macrotyphula juncea*. Agarics form the largest group, but also polypores, corticioid fungi and discomycetes are well-represented (graphs on p. 299). Most fungi are wood decomposers and very few are mycorrhizal. Most species are rare, but also some common fungi belong here. Only 14% of the species is on the Red Data list and a large majority is expanding its range in Drenthe, taking advantage of the increasing eutrophication of soils and the expansion of forestland on agricultural soils.

Fungi with a preference for deciduous forests on moist, loamy and clayey, more or less base-rich soils are treated in chapter 27b. Important trees and shrubs in these forests are *Fraxinus excelsior*, *Corylus avellana* and *Prunus padus*, intermixed with *Quercus robur* and *Alnus glutinosa*. Characteristic herbs are e.g. *Anemone nemorosa* and *Ficaria verna*. Such rich forests are very rare in Drenthe. The stands are small and almost restricted to old clay-soils in the north of the province (maps on p. 363). The mycoflora in older stands of this forest type is very rich in species, up to 200 species in plots of 1000 m² (Table 27.1). Most of the 85 characteristic species belong to the agarics, e.g. *Amanita olivaceo-grisea*, *Entoloma euchroum* and *Lactarius pyrogalus*. Examples from other taxonomic groups are *Mycoacia uda*, *Ramariopsis crocea* and *Steccherinum fimbriatum*. The numbers of characteristic soil inhabiting, wood decomposing and ectomycorrhizal fungi are almost equal (graphs on p. 362). All characteristic species are rare and almost half of them are included in the Red Data list. The few old forests on base-rich, loamy soils in Drenthe are protected nature reserves. Nevertheless some of them are threatened by drainage in the surroundings, eutrophication and urban development.

In Drenthe recent expansion of forests has mainly taken place by forestation of former agricultural soils. Such plantations are rich in nutrients and bases because of fertilizer application in the past, and soil profiles have been disturbed by repeated ploughing. The ground cover is mainly composed of tall herbaceous plants, characteristic of ruderal communities, e.g. *Elytrigia repens*, *Urtica dioica* and *Galium*

aparine. Characteristic fungi of such deciduous woods are treated in chapter 27c. Species from young coniferous plantations are described in chapter 28. Many characteristic species are also found in related habitats with similar conditions, such as forest edges along fields, strips of woodland in agricultural landscapes, intensively managed gardens and parks. In Drenthe 111 fungal species are characteristic of this habitat type, mainly agarics, e.g. *Agaricus brunneolus*, *Clitocybe fragrans* and *Lepista flaccida*. Species from other taxonomic groups are e.g. *Auricularia auricula-judae*, *Datronia mollis* and *Hyphodontia sambuci*. Both saprotrophs on soil and wood are well-represented, but characteristic mycorrhizal species are almost absent (graphs on p. 402). Almost all species have strongly increased and the proportion of Red Data list species is very low. Species of this group occur in the entire province (maps on p. 403).

Chapter 28. Coniferous forests

In this chapter 324 fungal species are treated that in Drenthe are mainly or exclusively found in coniferous forests. Forests dominated by coniferous trees are not native to Drenthe, with the exception of juniper scrub. However, several conifers have been planted on a large scale in the past. Many of them have become gradually naturalized. In the 1980's a mycosociological study has been carried out in order to compare mature stands of *Pinus sylvestris*, *Picea abies*, *Larix kaempferi* and *Pseudotsuga menziesii*. Some results are presented in Table 28.1, 28.2 and the box on p. 469. This chapter is divided into four parts: coniferous forests in general (chapter 28a), pine forests (28b), forests of spruce, larch, douglas fir and other introduced trees (28c), and juniper scrub (28d).

Many fungi are mainly known of coniferous forests, but without distinct preference for one of the dominant tree genera. The 132 species of this group are treated in chapter 28a, e.g. *Baeospora myosura*, *Cortinarius croceus*, *Entoloma cetratum*, *Fomitopsis pinicola*, *Gymnopilus sapineus*, *Gymnopus androsaceus* and *Lactarius hepaticus*. Most species belong to the agarics and corticioid fungi. Wood inhabiting fungi dominate with 63 % of the species. The characteristic species of this ecological group are equally divided over common and rare species and the contingent of Red Data list species is relatively small with 28% (graphs on p. 476). The distribution of this group reflects the distribution of coniferous plantations in the province, with the highest numbers in state forests.

The most widespread coniferous tree in Drenthe is Scots pine (*Pinus sylvestris*). This tree may be native to Drenthe, but in that case during the last centuries only as scattered trees on sand dunes or in peat bogs. Scots pine has been planted on a large scale on poor, dry, sandy soils. It has become naturalized and in some places spontaneous pine stands are found, originating from established seedlings in dry heathlands and on sand dunes. In Drenthe 72 fungal species are mainly or exclusively found in pine forests, including 40 agarics and boletes, e.g. *Coltricia perennis*, *Lactarius deliciosus*, *Russula paludosa* and *Suillus bovinus*. Also hydroid fungi are relatively well-represented with seven species. Besides *Pinus sylvestris* also *Pinus nigra* and *P. strobus* have been planted locally. The latter species is accompanied by two extremely rare mycorrhizal boletes: *Suillus placidus* and *S. pictus*. A majority of characteristic species in this group are ectomycorrhizal. Also wood decomposers are well-represented (graphs on p. 554). About half of the species are included in the Red Data list. The large proportion of extinct species is remarkable, including all six mycorrhizal hydroid fungi in this group. Only 20% of the species in pine forests are considered as not threatened.

Forests of Scots pine in Drenthe have been subject to various mycosociological studies, in mature forests with a different understorey (Table 28.3) and in stands of different age-classes in order to

study the succession of mycorrhizal fungi (Table 28.4, 28.5, 28.6). Species diversity and composition of the mycoflora in pine forests vary strongly in relation to soil conditions. The most interesting pine forests are found very localized on dry, wind-blown sand dunes with a thin litter-layer. They are inhabited by many mycorrhizal fungi, such as *Tricholoma equestre*, *T. portentosum* and *Russula adusta*. Also some pine-heaths on loamy soils are rich in rare mycorrhizal fungi, e.g. *Cortinarius scaurus* and *Lactarius hysginus*. Older pine forests often have a ground cover of *Empetrum nigrum*, a characteristic forest type for Drenthe with boreal tendencies. Here the mycoflora is less varied, with *Russula paludosa* as a characteristic species. The most widespread type of pine forests has a dense groundcover of *Deschampsia flexuosa* and *Dryopteris* spp. as a result of fertiliser application during planting and nitrogen deposition from air pollution. In such forests mycorrhizal fungi are very scarce, with dominance of *Lactarius hepaticus*. Pine forests in Drenthe are decreasing because of natural succession to deciduous woodland, cutting of stands and the effects of air pollution.

Fungi associated with introduced coniferous trees are treated in chapter 28c. In the 20th century many moist heathlands on somewhat richer, loamy soils have been planted with several exotic trees, mainly *Picea abies* from North and Central-Europe, *Larix kaempferi* from Japan and *Pseudotsuga menziesii* from North-America, less frequently also *Picea sitchensis*, *Abies alba*, *A. grandis* and some others. At present these stands have developed to mature forests and most introduced tree species are naturalized, producing viable offspring. In spite of the foreign origin of the trees 88 species of fungi are mainly found in these forests, mainly agarics, less polypores and corticioid fungi. Examples of characteristic species are *Cortinarius cinnamomeus*, *Gloeophyllum sepiarium*, *Lactarius deterrimus*, *L. trivialis*, *Phaeolus schweinitzii* and *Suillus grevillei*. Most of them are ectomycorrhizal symbionts, but also wood and soil inhabiting fungi are well-represented (graphs on p. 605). A majority of species are increasing or have become recently established in Drenthe, but nevertheless half of the characteristic species are still on the national Red Data list.

The mycological significance of these forests is largely correlated with soil fertility. Young plantations were usually supplied with various fertilizers, ranging from lime and other minerals to compost and green fertilizers, such as *Lupinus*. Today the effects are still visible in the mycoflora. Stands where many organic fertilizers have been applied half a century ago are still characterized by a semi-ruderal mycoflora, very poor in mycorrhizal fungi. On the other hand, some less intensively treated stands of *Picea abies* on former moist heathlands have developed to impressive, almost natural forests with an increasingly rich mycoflora, resembling natural spruce forests in Scandinavia. Recently established and spreading species are e.g. *Cortinarius camphoratus*, *C. malachus* and *C. tortuosus*. Unfortunately many old spruce forests have recently been cut or severely damaged because forestry policy aims at a reduction of introduced trees.

Another recent phenomenon is the development of an interesting mycoflora in some young spruce plantations on former sandy, base-rich, agricultural soils, with characteristic species such as *Cortinarius caninus*, *C. pluvius*, *Calocybe chrysenteron*, *Hygrophorus agathosmus*, *H. pustulatus* and *Lyophyllum boudieri*.

Juniper has been widespread in Drenthe, but the species has strongly decreased by reclamation and afforesting of heathlands. It mostly occurs as solitary scrub or low tree, but localized junipers form extensive bushes in dry heathlands and on sand dunes. The mycoflora of juniper scrub is described in chapter 28d. Dark dots in the maps on p. 660 indicate the position of these areas, at present all of them protected nature reserves. The composition of mycocoenoses in these bushes is well-known by extensive mycosociological research by Barkman and De Vries between 1960 and 1980. The mycoflora is fairly rich in species because of the large variation in microhabitats within juniper scrub. The frequency of some species in different microhabitats is presented in Table 28.7. The mycoflora is widely different from other coniferous forests because ectomycorrhizal species are lacking (graphs on p. 659). Almost half of the 32 characteristic species belong to the corticioid fungi, growing on juniper wood, e.g. *Amylostereum laevigatum*, *Gloiothete citrina* and *Kavinia alboviridis*. Agarics come second, mainly saprotrophic soil fungi, e.g. *Clitopilus caelatus*, *Lyophyllum ambustum* and *Omphaliaster asterosporus*. All characteristic fungi of juniper scrub are rare and all evaluated species are on the Red Data list. The future of these fungi is at risk because all juniper stands are old and degrading, whereas rejuvenation of juniper is severely inhibited by partially unknown reasons.

Chapter 29. Burnt forests and bonfire sites

Burnt forests and bonfire sites form an ephemeral habitat for a group of specialized fungi. In Drenthe 37 species are mainly or exclusively found in this microhabitat, including burnt soil, burnt wood, charcoal and mosses growing in burnt places. It is the only ecological group in which the majority of species (57%) belongs to the cup-fungi (*Pezizales*), e.g. *Anthracobia melanoma*, *Plicaria trachycarpa* and *Rhizina undulata* (graphs on p. 680). The second important group are agarics, with e.g. *Coprinellus angulatus*, *Myxomphalia maura* and *Pholiota highlandensis*. Nowadays fungi from burnt areas are rare and occur very local, illustrated in the maps on page 681. Not a single species is more or less common; only two species are classified as rather rare, the remaining as rare to regionally extinct. Among the characteristic fungi of burnt areas 33 species are on the Red Data list, four are not considered and only two species are regarded as not threatened at present.

Until the 1970's concentrated burning of trimmings and other smaller wood remains was common practice in the Netherlands. Many species must have been widespread in those years. The earlier distribution in Drenthe of fungi of burnt areas is practically unknown. However, a detailed study on succession of fungus communities on fire sites by Geesink (1972) revealed the occurrence of 14 species in a single area. The dramatic decline of this ecological group is mainly caused by regulations, prohibiting burning of wood in the open air. Also the numbers of spontaneous (by lightning) and accidental forest fires have decreased. It has been demonstrated by experimental small-scale burning in a young nature area without forest history that suited substrates are still easily colonised by a number of specialized species. Therefore it is likely that this ecological group of fungi can be easily recovered by reintroduction of concentrated burning of wood remains.