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The Macromycete flora in roadside verges planted with trees in comparison with related forest types

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Summary. – The results of mycocoenological research in different types of roadside verges with planted *Quercus robur* and *Fagus sylvatica* in Drenthe, northeastern Netherlands, are compared with studies in forest types of the same tree species in the same area. The roadside verges were investigated in the years 1986–1988. Three types of roadside verges with *Quercus* and two with *Fagus* were distinguished on the basis of their communities of green plants. Three types of oak forests were studied in the period 1972–1979 by Jansen and IJpelaar (Jansen, 1984). Two types of beech forest were studied by Van Steenis (1991) and Opdam (1991). Forests and roadside verges that were included in this study are situated on sandy soils. A comparison is made between the presence-degrees of macromycete species in these types. The differences between roadside verges with trees and forest communities are described and discussed, emphasizing the different patterns for ectomycorrhizal and saprotrophic fungi. Differences between *Quercus* and *Fagus* plots are outlined and discussed. In addition, the data are compared with results of mycocoenological research from other parts of Europe. Efforts are made to explain the occurrence of many characteristic ectomycorrhizal species in roadside verges. The significance of different types of roadside verges and forests for threatened macrofungi is evaluated.

Zusammenfassung. – Die Ergebnisse der mykozönologischen Untersuchungen in verschiedenen mit *Quercus rubur* oder *Fagus sylvatica* bepflanzten Straßenrändern in Drenthe, nordöstliche Niederlande, werden verglichen mit Wäldern mit den selben Baumarten. Die Arbeiten über die Straßenränder erfolgten von 1986 bis 1988. Dabei wurden bezüglich ihrer Vegetation drei Typen mit *Quercus* und zwei mit *Fagus* unterschieden. Zwischen 1972 und 1979 wurden von Jansen und IJpelaar (Jansen 1984) drei Eichenwaldtypen untersucht. Van Steenis und Opdam (van Steenis, 1991; Opdam, 1991) erforschten von 1989 bis 1990 zwei Buchenwaldtypen. Sowohl die Eichen- und die Buchenwaldtypen als auch die Straßenrandflächen befinden sich auf sandigem Boden. Die Stetigkeit der Großpilze in den verschiedenen Typen wird ver-

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glichen. Die Unterschiede zwischen Alleen und Waldgesellschaften werden beschrieben für saprotrophe und Ektomykorrhizapilze. Die Unterschiede zwischen Untersuchungsflächen mit *Quercus* und jenen mit *Fagus* werden dargestellt und diskutiert. Außerdem werden die Daten verglichen mit mykologischen Untersuchungen aus anderen Teilen von Europa. Es ist versucht worden, das Vorkommen von vielen charakteristischen Arten an Straßenrändern zu erklären. Die Bedeutung von verschiedenen Straßenrand- und Waldgesellschaften für gefährdete Pilze wird bewertet.

1. Introduction

Comparative mycocoenological studies were carried out by Keizer in the years 1986–1988 in roadside verges planted with Common Oak (*Quercus robur* L.) or Beech (*Fagus sylvatica* L.). All plots were situated on sandy soils in Drenthe in the north-eastern part of the Netherlands. Detailed results of these studies have been published elsewhere (Keizer, 1993a) including classifications of mycocoenoses and phytocoenoses, and their relation to various environmental variables.

The main aim of this research was to determine the characteristics of mycocoenoses of roadside verges planted with trees as compared with those of forests with the same tree species. Factors which may reduce the mycoflora in roadside verges are: 1. their openness, making them subject to increased drought stress and 2. pollution and soil compaction, as caused by traffic. On the other hand, factors which may increase the mycoflora are: 1. the heterogeneity of the habitat caused by a gradient perpendicular to the road and 2. the annual mowing regime with eventual removal of the herb layer.

In this paper, a quantitative comparison is made with mycocoenological studies previously carried out by different researchers in *Quercus* and *Fagus* forests in Drenthe. It is also tried to determine which fungal species are characteristic for either roadside verges or forests dominated by the mentioned trees.

In addition, more qualitative comparisons are made with some mycocoenological studies from other areas in Europe.

Roadside verges planted with trees are a very important habitat for rare and decreasing macromycetes (section 4.7; Keizer, 1993a). This importance is evaluated with the aid of the Red Data List for macrofungi in the Netherlands (Arnolds, 1989), also in comparison with data of related forest types.

After the observation that the mycoflora of roadside verges differs widely from forests, five hypotheses were formulated in order to explain the striking differences in mycorrhizal flora between these two habitats, in particular the occurrence of so many species characteristic for this man-made habitat:

(1) The differences in mycoflora are mainly caused by differences in microclimate, exposed roadside verges being warmer and drier than forests.

(2) The differential species of roadside verges do not occur optimally in the forest types with which a comparison was made, but are more frequent in different, sympatric forest communities, for instance on richer and/or disturbed soils.

(3) The differential species of roadside verges are indigenous in forest types, which do not occur in the region.

(4) The differential species of roadside verges are relict, which have disappeared from comparable forest types in recent years.

(5) Roadside verges are a man-made habitat with unique ecological characteristics, so that some ectomycorrhizal fungi are regularly found in roadside verges which are very rare in more natural forest types.

The above-mentioned explanatory hypotheses are discussed on the base of research, carried out in the Netherlands. Additional support will be given, using data from other countries.

2. Material and methods

2.1. Selection of plots

A total of 76 plots were selected in Drente in the northeastern Netherlands in 1986. The area is situated about 10–20 metres above sea-level and has a cool-temperate climate (average precipitation 781 mm/year, mean temperature in January 1.2 °C and in July 15.9 °C). All plots are situated on more or less acid, pleistocene sands with a variable organic matter content. The organic soil profiles are disturbed due to road (re)construction. Fifty-three plots, planted with *Quercus robur* and 23 with *Fagus sylvatica* were selected. In addition, plots were selected based on: (1) exposition (a. exposed roads in open landscapes; b. roads along forest margins and c. roads inside forests), (2) composition of the herb layer, ranging from oligotraphent to eutraphent as an expression of soil conditions and (3) the age of the trees (only for *Quercus*), in three age-classes: young: <20 years; middle-aged: 21–50 years and old: >51 years old.

Within the plots with mature oak trees a subset of 9 plots was selected in order to investigate the influence of the microclimate by selecting roadside verges with different exposure. Four plots were selected along roads bordering the southern edges of forest stands ("south-exposed plots"), five plots bordering the northern or northwestern edges of forests ("north-exposed plots"). The structure of the herb layer and soil fertility were similar in the two groups.

All plots were 100 metres long and the width varied between 1.5 and 6.5 metres with a number of trees per plot between 9 and 35. All sporocarps of

macromycetes were counted and identified with intervals of 3 to 4 weeks in the period August–November during the years 1986–1988. Soil profiles and soil-chemical characteristics were determined in all plots and published in Keizer (1993a). In addition, the communities of green plants were described and classified according to the Braun-Blanquet method (e.g. Westhoff & Van der Maarel, 1973).

On the basis of vegetation relevés, phytocoenological classifications were carried out, for the roadside verges with *Fagus* and *Quercus* separately, using the computer program TWINSPAN (Hill, 1979). The roadside verges with *Fagus* were divided into two types and each of them into two subtypes. The roadside verges with *Quercus* were divided into three types and two of them were subdivided. A summary of the most important phytocoenological and environmental characteristics of these types is presented in Table 1.

In addition, a mycocoenological classification was made on the basis of the mycological data. This classification in some respects gives different results (Keizer, 1993a). In this publication we will compare mycological characteristics on the basis of the phytocoenological types because (1) these types are based on primary producers and therefore are more relevant for a biocoenological classification; (2) they are more generally used in ecological studies than mycocoenological classifications; (3) they are more easily recognized in the field, and (4) the comparable data on forests in principle are also based on phytocoenological classifications. In spite of some discrepancies, the phytocoenological typology of roadside verge communities has a high predictive value concerning composition and development of the macromycete flora.

2.2. Forests of *Quercus* and *Fagus*

The mycocoenological data on roadside verges are compared with data on *Quercus* and *Fagus* forests on acidic sandy soils in Drenthe. These forests were studied in homogeneous rectangular plots of 30×35 m (c. 1000 m²), visited with intervals of 3 to 4 weeks, consequently about 3 to 4 times during the main fruiting season (September–November).

Three types of native forests dominated by *Quercus robur* were investigated by Jansen (1984) in the period 1976–1979: (1) the Dicrano-Quercetum (3 plots) on very nutrient-poor windblown sand dunes without developed soil profile and with thin litter layer, the undergrowth with very few herbs but rich in bryophytes such as *Dicranum scoparium* Hedw. and *Leucobryum glaucum* (Hedw.) Angstr., (2) the Querco-Betuletum (8 plots) on poor, in general podzolic soils, with a understorey of e.g. *Vaccinium myrtillus* L. and *Melampyrum pratense* L. and (3) the Violo-Quercetum (18 plots) on slightly richer soils with a thick litter layer and herbs such as *Maianthemum bifolium* (L.) Schm. and *Oxalis*

Table 1. Characteristics of vegetation types in roadside verges planted with *Fagus sylvatica* or *Quercus robur* in Drente, the Netherlands, compared with characteristics in forests of these tree species in the same area.

Landscape type	Roadside verges									Forests					
	Vegetation type	FFe	FFf	MFp	MFd	HQh	HQI	AQi	AQt	DfQ	LF	RF	DQ	QB	VQ
Dominant tree	<i>Fagus sylvatica</i>					<i>Quercus robur</i>					<i>F. sylvatica</i>				
Number of plots		5	7	5	6	5	21	6	17	4	10	9	11	8	18
Nr. trees/1000 m ²	34	55	58	64	41	43	38	50	65	— ⁷⁾	—	—	—	—	—
Av. age of trees (yr in 1988)	58	52	77	69	54	55	95	106	116	—	—	—	—	—	—
Av. vitality (class 1–4) ¹⁾	2.3	3.1	2.0	2.4	—	2.1	1.8	1.9	1.8	—	—	—	—	—	—
Av. cover herb layer (%)	74	59	29	9	69	76	63	75	35	2	1	4 ⁶⁾	60	33	
Av. cover moss layer (%)	3	17	4	13	26	11	0	0	6	2	6	27	3	1	
Av. traffic intensity (class 1–4) ²⁾	3.0	2.4	1.8	1.0	1.6	2.0	2.3	2.2	1.0	—	—	—	—	—	—
Av. potential sun (hr/day Oct.) ³⁾	5.7	6.0	0.7	0	6.9	6.8	3.6	2.7	0	0	0	0	0	0	0
Av. Ellenberg N value ⁴⁾	6.6	5.3	6.0	3.3	3.8	5.4	6.2	6.9	4.0	4.6	6.2	2.7	3.3	4.1	
Av. thickness organic layer (mm)	0	30	24	52	0	20	7	12	55	47	60	50	70	60	
Av. pH-CaCl ₂	4.4	4.0	4.2	3.5	4.2	3.9	4.0	3.3	3.0	3.1	—	—	—	—	—
Av. pH-H ₂ O	—	—	—	—	—	—	—	—	—	—	—	3.9 ⁶⁾	3.8	3.8	
Av. NO ₃ (mg.kg ⁻¹ soil)	3.6	1.0	0.4	1.3	0.8	1.0	0.17	1.5	0.8	0.9	4.8	—	—	—	
Av. NH ₄ (mg.kg ⁻¹ soil)	6.4	7.1	5.2	9.3	6.2	9.7	8.8	9.1	12.3	7.3	10.4	—	—	—	
Av. N total (%)	.19	.16	.13	.17	.14	.17	.17	.19	.24	.37	.43	—	—	—	
Av. C total (%)	3.0	2.8	2.6	3.9	2.4	3.2	3.3	2.8	3.7	12.2	10.7	—	—	—	
Av. C/N ratio	16	18	20	22	18	19	20	17	16	33	25	24	23	22	
Av. P soluble (mg.kg ⁻¹ soil)	1.0	0.1	0	0.7	0	0.5	0.2	0.4	3.0	1.0	4.2	—	—	—	
Av. P total (mg.kg ⁻¹ soil)	346	224	254	179	213	281	200	296	146	183	368	—	—	—	

Explanations table 1:

- 1) Vitality classes: 1 = vital; 4 = not vital.
- 2) Traffic intensity classes: 1: < 625, 2: 625–1250, 3: 1250–2500, 4: 2500–5000, 5: 5000–10 000, 6: > 10 000 motorized vehicles day⁻¹.
- 3) Potential sunshine hours/day in October: determined with a horizontoscope (Barkman & Stoutjesdijk, 1987).
- 4) Ellenberg values: 1: characteristic for habitats poorest in Nitrogen 9: characteristic for habitats extremely rich in nitrogen (polluted). (Ellenberg, 1979).
- 5) Soil chemical analyses: standard methods in 0.01 N CaCl₂, according to Houba et al. (1988).
- 6) Average values based on 3 plots, only studied by Jansen (1984).
- 7) – = not determined

The following vegetation types are distinguished:

Roadside verges:

FFe: *Elytrigia* subtype of *Festuca rubra*-*Fagus* type,
FFf: Idem, *Festuca ovina* subtype,
MFp: *Poa trivialis* subtype of *Mnium hornum*-*Fagus* type,
MFd: Idem, *Dryopteris* subtype
HQh: *Hieracium pilosella* subtype of *Hypochaeris*-*Quercus* type,
HQI: Idem, *Lotus corniculatus* subtype,
AQi: Inops variant of *Anthriscus*-*Quercus* type,
AQt: Idem typical variant,
DFQ: *Deschampsia flexuosa*-*Quercus* type.

Forests:

LF: *Laccaria amethystea*-*Fagus* type,
RF: *Rickenella fibula*-*Fagus* type (after Opdam, 1991),
DQ: Dicrano-*Quercetum*,
QB: Querco-*Betuletum*,
VQ: Violo-*Quercetum* (after Jansen, 1984).

acetosella L. The data published by Jansen (1984) on the Dicrano-Quercetum comprised also data on 11 plots, studied by P. Ijpelaar, in the years 1972 and 1973.

In forests of *Fagus sylvatica* 19 plots were studied in 1989 and 1990 by Van Steenis (1991) and Opdam (1991). All of them are situated in planted stands since *Fagus* occurs only as scattered trees in hypothetical climax forest communities in Drenthe. A phytocoenological classification of *Fagus* stands was not well possible due to the very poor development of a herb and moss layer. The authors divided their plots therefore on the basis of the macromycete flora into two main types: the *Laccaria amethystea* type on nutrient-poor soils with a thin litter layer, corresponding with Dicrano-Quercetum and part of Querco-Betuletum, and the *Rickenella fibula* type on somewhat richer soils with a thicker litter layer, corresponding with the Fago-Quercetum and part of the Querco-Betuletum. Some important phytocoenological and environmental parameters of these forest types are included in Table 1.

2.3. Comparison between roadside verges and forests

In this paper the frequency of macromycete species in roadsides and forest types is compared on the basis of their presence-degree, i.e. the percentage of plots of a certain type in which a species has been found during the investigation (Tables 2, 3). A species is considered as differential when its presence-degree in a certain type is at least twice as high as in other types. Data on the abundance of sporocarps were in most cases not used since they are more sensitive for differences in methodology (Arnolds, 1981), e.g. different abundance values, different visit frequencies. In addition, the numbers of species of different niche-substrate groups (groups of species which inhabit a common microhabitat and substrate and which have a similar way of habitat exploitation; Arnolds, 1988a) in these types are compared (Figure 1).

For sake of surveyability the data on roadsides are only divided into two groups, those with *Quercus* and with *Fagus*, respectively. In fact nine types of roadside verge communities have been distinguished Keizer (1993a; Table 1). A synoptic table of macrofungi in these types has been published in Keizer (1993a). The data presented here allow the distinction of differential species for the entire variety of roadside habitats with regard to various forest communities and vice versa. However, some species may be differential for a certain type of roadside verges with regard to one certain forest type only. These data may also elucidate ecological differences in the mycoflora between roadside verges and forests. Therefore, Tables 2 and 3 also indicate the types of roadside verges where a species has its highest presence-degree.

Explanations table 2:

The values are presence-degrees in %. ? means presence-degree uncertain due to taxonomic confusion.

* followed by a number indicates the threatened status of a species according to the "Red List" (Arnolds, 1989): 1 = threatened with extinction; 2 = strongly threatened; 3 = threatened; 4 = potentially threatened.

Abbreviations of the forest types:

LF = *Laccaria amethystea* - *Fagus* forest (after Opdam, 1991),

RF = *Rickenella fibula* - *Fagus* forest (after Opdam, 1991),

DQ = Dicrano-Quercetum (after Jansen, 1984),

QB = Querco-Betuletum (after Jansen, 1984),

VQ = Violo-Quercetum (after Jansen, 1984).

In the last column vegetation types of roadside verges are mentioned for which a species is differential within roadside verge communities according to the following abbreviations (the figures are presence-degrees in %):

FFe: *Festuca-rubra-Fagus* type, subtype of *Elytrigia repens*.

FFF: *Festuca-rubra-Fagus* type, subtype of *Festuca ovina*.

MFp: *Mnium hornum-Fagus* type, subtype of *Poa trivialis*.

MFd: *Mnium hornum-Fagus* type, subtype of *Dryopteris carthusiana*.

HQh: *Hypochaeris-Quercus* type, subtype of *Hieracium pilosella*.

HQI: *Hypochaeris-Quercus* type, subtype of *Lotus corniculatus*.

AQi: *Anthriscus-Quercus* type, inops variant.

AQt: *Anthriscus-Quercus* type, typical variant.

DfQ: *Deschampsia flexuosa-Quercus* type.

Table 2. Synoptic table of ectomycorrhizal macromycetes in roadside verges planted with *Fagus sylvatica* or *Quercus robur* in Drente, the Netherlands, compared with forests of *Fagus* and *Quercus* in the same area.

Habitat type	ROADSIDE VERGES				FORESTS			presence degrees in vegetation types of roadside verges
	<i>Fag.</i>	<i>Que.</i>	<i>Fagus</i>	<i>Quercus</i>	<i>DQ</i>	<i>QB</i>	<i>VQ</i>	
Dominant tree	23	53	10	9	11	8	18	
Vegetation type								
Number of plots								

I. Differential species for roadsides with trees:

(A) For roadsides with *Fagus* and *Quercus*

<i>Russula parazurea</i>	78	68	30	44	—	—	17	MFp: 100, AQt:94
<i>Xerocomus chrysenteron</i>	57	45	—	33	—	25	22	MFp:80, AQt:76
<i>Scleroderma areolatum</i>	30	57	10	—	—	6	11	FFf:42, AQi:67
<i>Russula nigricans</i>	30	40	—	22	9	12	6	MFp:60, DfQ:75
<i>Hebeloma helodes</i>	39	28	—	—	—	—	—	FFt:42, HQ:40
<i>Clavulinina coralloides</i>	35	32	—	—	—	—	—	FFe:60, HQh:60
<i>Russula atropurpurea</i>	22	36	—	—	9	—	17	DfQ: 100
<i>Cortinarius striaepilus</i>	30	28	10	—	—	—	—	MFp:40, AQi:50
<i>Cortinarius saniosus</i>	30	23	—	—	—	—	—	FFf:57, HQh:60
<i>Cortinarius erythrinus</i>	26	21	—	—	—	—	—	FFf:42, HQh:60
<i>Naucoria bohemica</i>	22	23	—	11	—	—	—	HQl:60
<i>Inocybe umbrina</i>	17	19	—	—	—	—	—	MFp:40, AQi:50
<i>Cortinarius flexipes</i>	17	17	—	—	—	—	—	MFP:40, HQh:40
<i>Russula ionochlora</i>	13	11	—	—	—	—	—	AQi:29
<i>Inocybe maculata</i>	13	8	—	—	—	—	—	FFe:20, MFp:20
<i>Cortinarius lanatus</i>	9	9	—	—	—	—	—	MFp:20, AQi:33
<i>Russula grisea</i>	9	8	—	—	—	—	—	MFd:20, AQt:18
<i>Russula chamaeleontina</i>	9	4	—	—	—	—	—	MFp:20, HQh:20
<i>Inocybe albomarginata</i>	4	9	—	—	—	—	—	AQt: 18

(B) For roadsides with *Fagus*:

<i>Lactarius blennius</i>	61	—	20	—	—	—	—	FFf:71
<i>Tricholoma ustale</i> *3	39	—	—	—	—	—	—	FFf:71
<i>Inocybe petiginosa</i>	30	8	—	—	—	—	—	MFp:40, MFd:50
<i>Russula velenovskyi</i>	26	11	—	11	—	—	—	MFp:60
<i>Clitopilus prunulus</i> *3	26	11	—	—	—	—	—	FFt:57, HQh:60
<i>Amanita spissa</i>	26	6	—	—	—	—	—	MFp:40
<i>Amanita muscaria</i>	22	8	10	—	—	—	—	FFf:57
<i>Amanita pantherina</i>	22	4	—	—	—	—	—	FFf:42
<i>Inocybe sindonia</i>	22	2	10	11	—	—	—	MFd:33
<i>Inocybe fuscidula</i>	17	4	—	—	—	—	—	FFe:40
<i>Inocybe geophylla</i>	17	4	—	—	—	—	—	FFf:29
<i>Chalciporus piperatus</i>	17	6	—	—	—	—	—	FFf:29, HQh:20
<i>Inocybe flocculosa</i>	13	4	—	—	—	—	—	FFe:20
<i>Inocybe huysmanii</i>	13	—	—	—	—	—	—	FFe:40
<i>Inocybe ochroalba</i>	9	—	—	—	—	—	—	MFp:20

Habitat type	ROADSIDE VERGES				FORESTS			presence degrees in vegetation types of roadside verges
	<i>Fag.</i>	<i>Que.</i>	<i>Fagus</i>		<i>Quercus</i>	<i>DQ</i>	<i>QB</i>	<i>VQ</i>
Dominant tree	LF	RF						
Vegetation type								
(C) For roadsides with <i>Quercus</i>:								
<i>Russula amoenolens</i>	39	77	–	–	9	–	6	HQh:100, AQi:100
<i>Lactarius serifluus</i>	9	25	–	–	–	–	–	DfQ:50
<i>Russula pectinatoides</i>	–	28	–	11	–	–	–	AQi:50
<i>Russula odorata</i> *3	4	17	–	–	–	–	–	HQh:60
<i>Russula graveolens f. graveolens</i>	–	21	–	–	–	–	–	AQi:33
<i>Russula graveolens f. cicatricata</i>	–	11	–	–	–	–	–	HQh:40
<i>Russula graveolens f. purpurata</i>	–	9	–	–	–	–	–	AQi:33
<i>Xerocomus rubellus</i>	–	8	–	–	–	–	–	AQt: 18
<i>Xerocomus porosporus</i>	–	8	–	–	–	–	–	AQt:24
<i>Inocybe griseolilacina</i>	–	8	–	–	–	–	–	HQl: 15
II. Differential species for forests:								
(A) For forests of <i>Fagus</i> and <i>Quercus</i>:								
<i>Russula ochroleuca</i>	52	26	100	89	55	87	72	MFd: 100, DfQ: 100
<i>Lactarius theiogalus</i>	39	32	90	78	82	87	89	MFp:60, DfQ: 75
<i>Laccaria amethystea</i>	48	23	100	–	100	50	11	MFp:80, AQi: 50
<i>Xerocomus badius</i>	43	34	80	–	73	50	22	MFd:67, AQi: 50
<i>Cortinarius paleaceus</i>	30	26	70	–	82	12	–	MFp:40, HQl: 35
<i>Inocybe napipes</i>	26	11	80	44	55	37	17	MFd:83, DfQ: 50
<i>Amanita fulva</i>	13	21	80	–	100	25	–	MFd:33, DfQ: 50
<i>Thelephora terrestris</i>	22	11	30	–	55	–	–	MFp:60, DfQ: 50
<i>Russula emetica</i>	4	6	80	–	73	50	33	DfQ:50
<i>Xerocomus subtomentosus</i> *3	4	2	40	–	–	25	11	
<i>Cortinarius elatior</i> *3	–	4	20	–	36	25	–	
(B) For forests of <i>Fagus</i>:								
<i>Cortinarius paleiferus</i>	14	2	40	–	–?	–?	–?	MFp:40
<i>Laccaria bicolor</i>	4	13	60	22	–?	–?	–?	AQi:33
<i>Lactarius necator</i>	–	2	70	–	27	–	17	
(C) For forests of <i>Quercus</i>:								
<i>Lactarius proxima</i>	48	47	40	–	100	75	50	MFd: 100, AQi:83
<i>Russula fragilis</i>	13	40	20	–	100	25	–	Hqh:60
<i>Lactarius camphoratus</i> *3	13	15	–	–	64	62	11	MFp:40, AQi:50
<i>Lactarius chrysorrheus</i> *3	4	23	–	–	73	25	–	HQh:40
<i>Hebeloma longicaudum</i>	13	9	–	–	36	25	–	MFd:33
<i>Cantharellus cibarius</i> *3	9	11	20	–	10	–	–	AQi:50
<i>Boletus erythropus</i> *3	17	2	10	–	55	–	–	FFf:42
<i>Russula vesca</i>	4	13	–	11	36	12	–	AQi:50
<i>Cortinarius casimiri</i>	–	–	–	–	–	–	–	
(incl. <i>C. decipiens</i> s. Henry)	9	6	10	–	36	62	22	MFp:40
<i>Cortinarius obtusus</i>	9	6	–	–	62	–	–	DfQ:25

Habitat type	ROADSIDE VERGES				FORESTS			presence degrees in vegetation types of roadside verges
	<i>Fag.</i>	<i>Que.</i>	<i>Fagus</i> LF	<i>Fagus</i> RF	<i>Quercus</i> DQ	<i>Quercus</i> QB	VQ	
<i>Leotia lubrica</i> *3	4	8	10	—	64	—	—	
<i>Cortinarius umbrinolens</i>								
(incl. <i>C. glandicolor</i>)	—	6	10	—	45		—	
<i>Dermocybe cinnamomea</i> s. lat.	—	4	10	—	62	12	—	
<i>Cortinarius fusisporus</i> *2	4	—	10	—	62	12	—	
<i>Tylopilus felleus</i> *2	—	2	10	—	9	25	6	
<i>Hydnellum concrescens</i> *2	—	2	—	—	36	—	—	
<i>Hydnellum spongiosipes</i> *2	—	2	—	—	27	—	—	
<i>Tricholoma columbetta</i> *2	—	—	—	—	27	—	—	
<i>Tricholoma virgatum</i> *1	—	—	—	—	27	—	—	
<i>Tricholoma portentosum</i> *2	—	—	10	—	36	—	—	
<i>Sarcodon scabrosus</i> *2	—	—	—	—	27	—	—	
<i>Russula adusta</i>	—	—	—	—	36	—	—	
<i>Inocybe sambucina</i> *2	—	—	—	—	36	—	—	
<i>Hebeloma pumilum</i>	—	—	—	—	27	12	—	
<i>Cortinarius bolaris</i> *2	—	—	—	—	36	—	—	
<i>Cortinarius alboviolaceus</i> *2	—	—	—	—	27	—	—	

III. Indifferent species for roadsides and forests:

(A) For *Fagus* and *Quercus*:

<i>Laccaria laccata</i>	87	92	70	56	9	37	28	all types: 100
<i>Amanita rubescens</i>	87	57	90	33	82	75	50	MF:100, DfQ:100
<i>Scleroderma citrinum</i>	61	40	50	22	100	100	56	MFd:83, DfQ:50
<i>Paxillus involutus</i>	61	34	80	56	100	100	100	MFd:83, AQi:83
<i>Boletus edulis</i>	39	19	—	—	36	—	—	FFf:71, HQh:60
<i>Amanita citrina</i>	17	26	30	—	27	37	11	MFp:80
<i>Inocybe mixtilis</i>								
(incl. <i>I. xanthomelas</i>)	22	13	20	—	27	12	—	FfE:40
<i>Inocybe lacera</i>	13	17	20	—	—	—	—	HQh:40
<i>Cortinarius hinnuleus</i> *3	13	17	—	—	9	—	—	HQh:40
<i>Cortinarius anomalus</i>	4	8	10	11	—	—	—	AQt: 12

(B) For *Fagus*:

<i>Russula fellea</i>	70	—	70	44	—	—	—	FFf:86
<i>Russula mairei</i>	57	—	70	—	9	—	—	MFd:83
<i>Lactarius subdulcis</i>	35	—	50	22	—	—	—	MFd:50
<i>Hebeloma mesophaeum</i>	26	11	—	33	—	—	—	FfE:40

(C) For *Quercus*:

<i>Lactarius quietus</i>	4	89	—	—	100	100	100	AQi:100, DfQ:100
<i>Russula cyanoxantha</i>	9	25	—	—	36	12	—	AQi:50

Explanations table 3:

The figures are presence-degrees in %. “0” means present but rounded to 0; “–” means absent; “?” means unknown presence degree due to taxonomic confusion.

* followed by a number indicates the threatened status of a species according to the “Red List” (Arnolds, 1989): 1 = threatened with extinction; 2 = strongly threatened; 3 = threatened; 4 = potentially threatened.

Abbreviations of the forest types:

LF = *Laccaria amethystea* – *Fagus* forest (after Opdam, 1991),

RF = *Rickenella fibula* – *Fagus* forest (after Opdam, 1991),

DQ = Dicrano-Quercetum (after Jansen, 1984),

QB = Querco-Betuletum (after Jansen, 1984),

VQ = Violo-Quercetum (after Jansen, 1984).

In the last column vegetation types of roadside verges are mentioned for which a species is differential within roadside verge communities according to the following abbreviations (the figures are presence-degrees in %):

FFe: *Festuca-rubra*-*Fagus* type, subtype of *Elytrigia repens*.

FFf: *Festuca-rubra*-*Fagus* type, subtype of *Festuca ovina*.

MFp: *Mnium hornum*-*Fagus* type, subtype of *Poa trivialis*.

MFd: *Mnium hornum*-*Fagus* type, subtype of *Dryopteris carthusiana*.

HQh: *Hypochaeris*-*Quercus* type, subtype of *Hieracium pilosella*.

HQI: *Hypochaeris*-*Quercus* type, subtype of *Lotus corniculatus*.

AQi: *Anthriscus*-*Quercus* type, inops variant.

AQt: *Anthriscus*-*Quercus* type, typical variant.

DfQ: *Deschampsia flexuosa*-*Quercus* type.

Table 3. Synoptic table of saprotrophic and parasitic macromycetes in roadside verges planted with *Fagus sylvatica* or *Quercus robur* in Drente, the Netherlands, compared with forests of *Fagus* and *Quercus* in the same area.

Habitat type	ROADSIDE VERGES				FORESTS			presence degrees in vegetation types of roadside verges								
	<i>Fag.</i>	<i>Que.</i>	<i>Fagus</i> LF	<i>Quercus</i> DQ	<i>Quercus</i> QB	<i>Quercus</i> VQ										
Dominant tree	23	53	10	9	11	8	18									
Vegetation type																
Number of plots																
I. Differential species for roadsides verges																
IA. Without preference for <i>Fagus</i> and <i>Quercus</i>																
IA1. Saprotrrophic species on litter or humus of grassland plants																
<i>Mycena avenacea</i>	30	36	—	—	—	—	—	FFe: 60, FFf: 57, HQh: 60, HQl: 62								
<i>Mycena sepiaria</i>	26	30	—	—	—	—	—	FFf: 57, HQl: 51								
<i>Marasmius oreades</i>	13	28	—	—	—	—	—	FFe: 40, HQh: 40 HQl: 43								
<i>Mycena flavoalba</i>	17	17	—	—	—	—	—	FFe: 40, HQh: 40								
<i>Entoloma sericeum f. sericeum</i>	13	19	—	—	—	—	—	FQh: 40								
<i>Psilocybe semilanceata</i>	9	11	—	—	—	—	—									
<i>Marasmius graminum</i>	9	11	—	—	—	—	—									
<i>Calocybe carneola</i>	13	6	—	—	—	—	—	FFe: 20, FFf: 29								
IA2. Saprotrrophic species on litter or humus of forest plants																
<i>Mycena flavescens</i>	17	17	—	—	—	—	—									
<i>Helvella lacunosa</i>	17	11	—	—	—	—	—	FFe: 40								
<i>Tarzetta cupularis</i>	13	6	—	—	—	—	—									
IB. With preference for <i>Fagus</i>																
IB1. Saprotrrophic species on litter or humus of grassland plants																
<i>Psathyrella panaeoloides</i>	17	2	—	—	—	—	—									
IB2. Saprotrrophic species on litter or humus of forest plants																
<i>Agrocybe praecox</i>	17	6	—	—	—	—	—									
<i>Entoloma subradiatum</i>	17	2	—	—	—	—	—	FFe: 40								
IB3. Saprotrrophic species on wood																
<i>Tubaria furfuracea</i>	100	36	30	44	—	12	17									
<i>Psathyrella microrhiza</i>	17	6	—	—	—	—	—	MFp: 40, MFd: 33								
<i>Coprinus subimpatiens</i>	17	4	—	—	—	—	—	FFe: 40								
<i>Marasmius rotula</i>	13	2	—	—	—	—	—									
IC. With preference for <i>Quercus</i>																
IC2. Saprotrrophic species on litter of forest plants																
<i>Mycena polyadelpha</i>	4	26	—	—	—	—	6									
IC3. Saprotrrophic species on wood																
<i>Mycena adscendens</i>	4	17	—	—	—	—	—									
IC4. Saprotrrophic species on sporocarps of other macromycetes																
<i>Nyctalis asterophora</i> *3	—	15	—	—	—	—	—	AQi: 50								

Habitat type	ROADSIDE VERGES				FORESTS				presence degrees in vegetation types of roadside verges
	<i>Fag.</i>	<i>Que.</i>	<i>Fagus</i>	<i>Quercus</i>	LF	RF	DQ	QB	VQ
Dominant tree									
Vegetation type									

II. DIFFERENTIAL SPECIES FOR FORESTS

IIA. For forests of *Fagus* and *Quercus*

IIA1. Soil-inhabiting fungi on litter, humus and bryophytes

<i>Mycena sanguinolenta</i>	35	40	100	67	64	100	89	MFp:60, MFd:50, DfQ:75
<i>Clitocybe metachroa</i>	17	49	70	78	18	100	78	MFp:40, DfQ: 100
<i>Galerina hypnorum</i>	26	23	100	89	64	100	89	MFp:40, MFd:50
<i>Stropharia aeruginosa</i> s. lato	22	15	10	33	–	25	50	FFe:40, FFf:43, DfQ:50
<i>Clitocybe vibecina</i>	13	17	70	22	82	100	83	MFd:50, DfQ:75
<i>Collybia peronata</i>	22	4	20	33	9	37	72	MFp:60, DfQ:25
<i>Mutinus caninus</i>	13	6	10	22	–	25	33	MFd:33, DfQ:25
<i>Entoloma rhodocylix</i>	13	4	40	22	36	25	6	MFd:33, DfQ:25
<i>Phallus impudicus</i>	9	4	40	11	9	50	94	MFd:33, DfQ:25
<i>Cystoderma amianthinum</i> s. lato	9	4	50	–	100	62	33	
<i>Clitocybe clavipes</i>	4	6	30	33	55	25	6	
<i>Marasmius androsaceus</i>	4	4	50	–	82	50	22	
<i>Entoloma turbidum</i> *3	4	4	40	–	36	–	–	
<i>Mycena epipterygia</i>	–	2	80	22	–	50	33	
<i>Galerina luteofulva</i>	0	2	60	11	27	50	44	

IIA2. Wood-inhabiting fungi (selection)

<i>Armillaria obscura</i>	43	25	60	89	45	87	67	MFp:80, MFd:83, DfQ:50
<i>Psathyrella artemisiae</i>	26	20	90	67	36	100	78	MFd:67. DfQ:95
<i>Polyporus brumalis</i>	13	28	50	22	9	91	50	MFp:40. HQh:60
<i>Hypholoma fasciculare</i>	9	32	100	89	82	100	94	
<i>Psathyrella piluliformis</i>	13	20	50	44	27	62	44	AQi:50
<i>Pluteus atricapillus</i>	13	8	50	89	45	100	94	
<i>Oudemansiella platyphylla</i>	13	9	80	89	36	100	100	MFd:33, DfQ:50
<i>Trametes versicolor</i>	9	8	50	56	36	87	39	
<i>Mycena haematopus</i>	4	8	50	44	–	62	50	DfQ:50
<i>Gymnopilus penetrans</i>	4	4	100	56	64	87	44	DfQ:50
<i>Hypholoma sublateritium</i>	4	2	60	44	36	62	61	
<i>Calocera cornea</i>	4	2	70	44	64	75	94	
<i>Bjerkandera adusta</i>	0	2	50	33	9	62	56	
<i>Kuehneromyces mutabilis</i>	–	–	50	11	–	25	28	

IIA3. Species growing on sporocarps of other macromycetes

<i>Collybia cirrhata</i>	30	15	80	11	36	62	28	FFf:57
<i>Collybia cookei</i>	13	6	80	44	18	87	50	

Habitat type	ROADSIDE VERGES				FORESTS			presence degrees in vegetation types of roadside verges	
	<i>Fag.</i>	<i>Que.</i>	<i>Fagus</i>	<i>Quercus</i>	LF	RF	DQ	QB	VQ
Dominant tree									
Vegetation type									
IIB. For forests with <i>Fagus</i>									
IIB1. Soil-inhabiting fungi on litter and humus									
<i>Mycena capillaris</i>	17	—	40	44	—	25	6	MFp:60	
<i>Flammulaster subincarnatus</i>	17	—	70	67	—	—	—	MFd:50	
<i>Collybia maculata</i>	9	—	40	33	18	—	6	MFd:33	
<i>Hygrophoropsis aurantiaca</i>	—	4	50	—	—	—	—	—	
<i>Collybia konradiana</i>	—	—	70	22	—	—	—	—	
IIb2. Wood-inhabiting fungi									
<i>Oudemansiella radicata</i>	9	—	30	44	—	—	—	—	
<i>Mycena oortiana</i>	4	6	50	22	—	—	6	MFp: 20, MFd:17	
<i>Pholiota lenta</i>	4	—	—	44	—	—	—	—	
IIC. For forests with <i>Quercus</i>									
IIC1. Soil-inhabiting fungi on litter, humus and bryophytes									
<i>Tephrocybe tesquorum</i>	9	19	10	—	27	87	56	MFd:33, DfQ:50	
<i>Mycena stylobates</i>	—	20	—	11	—	75	56	—	
<i>Galerina atkinsoniana</i>	4	15	10	—	55	62	17	—	
<i>Clitocybe candicans</i>	—	9	10	—	27	75	22	—	
<i>Psathyrella dicrani</i>	—	4	—	—	36	—	—	—	
<i>Tephrocybe ambusta</i>	—	2	—	—	27	37	28	—	
<i>Mycena rorida</i>	—	2	10	—	27	100	50	—	
<i>Galerina cinctula</i>	—	2	—	—	9	37	50	—	
<i>Galerina calyptata</i>	—	—	30	—	73	50	6	—	
<i>Galerina ampullaceocystis</i>	—	—	10	—	18	25	56	—	
<i>Clitocybe phyllophila</i>	—	—	—	11	9	37	22	—	
IIC2. Wood-inhabiting fungi with preference for <i>Quercus</i> (selection)									
<i>Psilocybe crotula</i>	4	6	10	—	—	25	44	—	
<i>Panellus stypticus</i>	4	2	20	—	18	50	22	MFd:17, DfQ:25	
<i>Panellus serotinus</i>	—	4	20	11	18	50	56	DfQ:50	
<i>Hapalopilus rutilans</i>	—	4	—	—	—	50	33	—	
<i>Tyromyces chioneus</i>	—	—	—	—	—	62	33	—	
<i>Pluteus salicinus</i>	—	—	—	—	—	36	39	—	
<i>Mycena inclinata</i>	—	—	—	—	—	12	56	—	
<i>Marasmiellus ramealis</i>	—	—	—	—	—	50	39	—	
<i>Hohenbuehelia atrocaerulea</i>	—	—	—	—	—	25	28	—	
IIC3. Species growing on sporocarps of other macromycetes									
<i>Cordyceps ophioglossoides</i> *3	4	4	10	—	100	12	—	—	
<i>Cordyceps canadensis</i> *3	—	2	10	—	73	12	—	—	

Habitat type	ROADSIDE VERGES				FORESTS			
	<i>Fag.</i>	<i>Que.</i>	<i>Fagus</i>	<i>Quercus</i>	presence degrees in vegetation types of roadside verges			
Dominant tree	LF	RF	DQ	QB	VQ			
Vegetation type								

III. SPECIES WITHOUT PREFERENCE FOR ROADSIDE VERGES OR FORESTS

IIIA. Without preference for *Quercus* or *Fagus*

IIIA1. Soil-inhabiting fungi on litter, humus and bryophytes

<i>Mycena galopus</i>	95	75	100	89	100	100	100
<i>Mycena filopes</i> var. <i>filipes</i>	56	77	70	56	9?	50?	78?
<i>Mycena leptocephala</i>	69	62	20	44	?	?	?
<i>Collybia dryophila</i>	43	77	80	56	100	100	61
<i>Psathyrella fulvescens</i>	56	55	50	44	36	75	72
<i>Mycena cinerella</i>	39	57	100	89	64	87	50
<i>Collybia butyracea</i>	52	40	80	44	45	87	67
<i>Rickenella fibula</i>	43	43	40	56	–	37	28
<i>Mycena filopes</i> var. <i>metata</i>	26	36	20	44	–?	–?	–?
<i>Mycena pura</i>	21	25	30	44	–	50	22
<i>Psathyrella spadiceogrisea</i>	26	6	–	–	9	12	22
<i>Rickenella setipes</i>	13	17	10	22	–	12	–
<i>Lepista nuda</i>	9	19	–	–	9	12	28
<i>Marasmiellus vaillantii</i>	9	17	–	11	–	20	6
<i>Lycoperdon foetidum</i>	–	11	10	–	36	12	17

IIIA2. Wood-inhabiting fungi

<i>Mycena vitilis</i>	74	96	100	89	36	100	100
<i>Mycena galericulata</i>	48	72	100	100	100	100	100
<i>Psathyrella frustulenta</i>	9	13	–	11	–	–	17

IIIA3. Species growing on sporocarps of other macromycetes or on pupae of insects

<i>Collybia tuberosa</i> *3	13	8	10	–	18	12	–
<i>Cordyceps militaris</i>	13	20	–	–	–	12	–

IIIB. With preference for *Fagus*

IIIB1. Wood-inhabiting fungi

<i>Crepidotus variabilis</i>	43	17	80	78	9	25	22
<i>Psathyrella candolleana</i>	22	11	–	22	–	–	–

IIIC. With preference for *Quercus*

IIIC 1. Wood-inhabiting fungi

<i>Mycena polygramma</i>	4	26	30	33	55	87	61
<i>Mycena speirea</i>	–	15	–	–	18	25	22

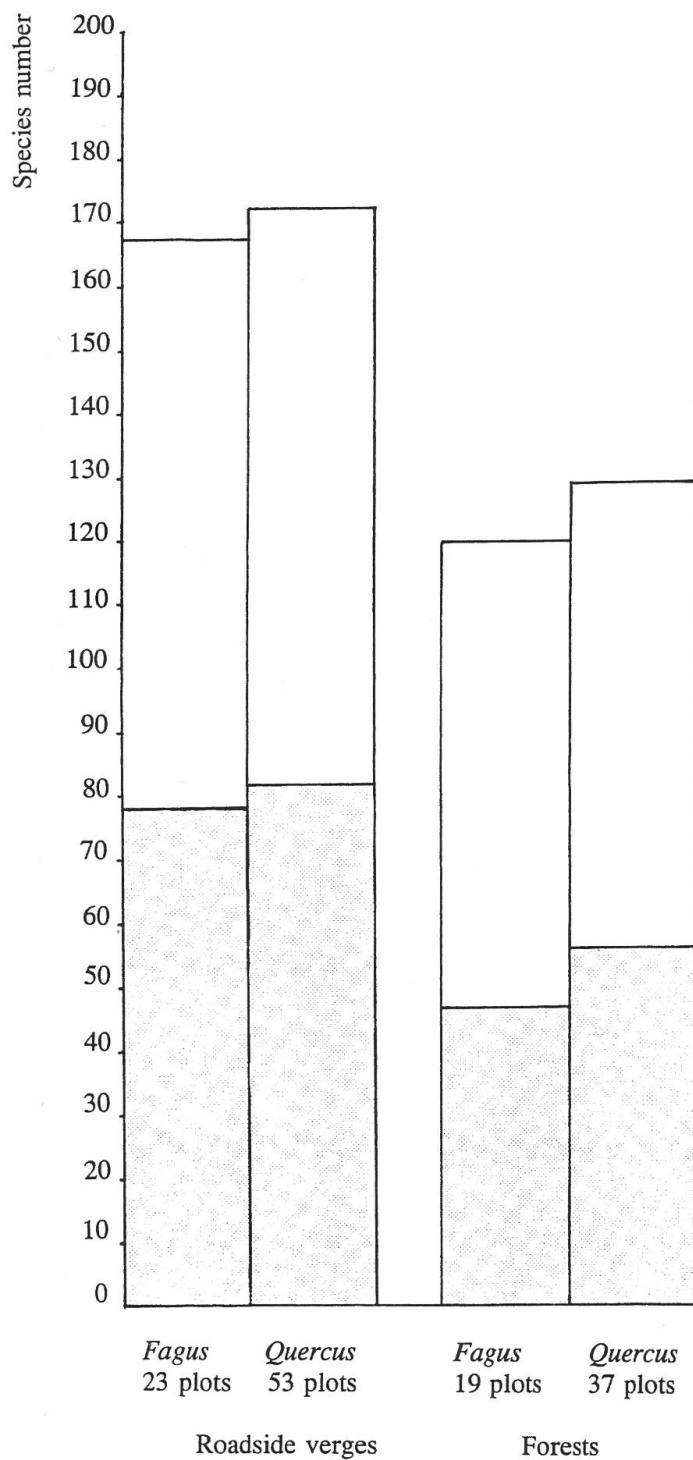


Figure 1. Comparison of species numbers of ectomycorrhizal (grey) and saprotrophic (white) fungi in roadside verges and forests with Oaks and Beech trees. For the species the same selection criteria were used as for Tables 2 and 3. Data of roadside verges are based on the present study; data of forests are based on various literature sources (see text).

On the base of these tables we have expressed the value for nature conservation of the roadside verges and the comparable forest types, using the Red Data List of macrofungi in the Netherlands (Arnolds, 1989). In this list five categories of threatened macrofungi are distinguished, ranging from probably extinct (no species of this category encountered) to potentially threatened (see also Table 4). For each category two values are calculated: (1) the total number of threatened species found in a type, (2) the average number of threatened species per plot.

2.4. Nomenclature

Nomenclature of phanerogams is after Heukels & Van der Meijden (1983), of bryophytes after Margadant & During (1982), of fungi mainly after Kreisel (1987). Taxonomic notes on critical and rare species are published in Keizer, (1993a). The names of forest syntaxa are after Westhoff & Den Held (1969). The other phyto- and mycocoena are indicated with -type or -subtype in order to stress their preliminary and unofficial status.

3. Results

The numbers of species belonging to various “niche-substrate groups” in roadside verges, Oak forests and Beech forests are presented in Figure 1. From this figure it appears that the number of ectomycorrhizal species found in roadside verges is higher than in any of the forest communities. In contrast with roadside verges, forests are extremely poor in saprotrophic grassland-fungi. The numbers of species associated with bryophytes and with other substrates (dung, burnt wood, feathers, sporocarps of fungi, insects) are similar in all studied communities. The macromycetes in roadside verges and forests are divided into two main groups on the basis of their functional relationship with green plants, the ectomycorrhizal fungi and the saprotrophic and parasitic fungi. This classification is based on various sources (Trappe, 1962; Arnolds, 1984; Kreisel, 1987) including our own field-experience. However, of a few species no functional group can be established with certainty (see discussion).

3.1. Ectomycorrhizal species

The presence-degrees of the more important ectomycorrhizal macromycetes in roadside verges with *Quercus* and *Fagus* and in corresponding forest types in Drenthe are presented in Table 2. Only species with a presence-degree of > 8 % in at least one of the types are included. The species are divided into three differential groups on the basis of their preference for either roadside

verges (group I), forest communities (group II) or the lack of preference (group III). For some frequent species a slightly less-pronounced difference in presence-degree is allowed when they show also a large difference in abundance of sporocarps (if this was clear from the data; data not presented here, see Keizer, 1993a). Within these groups subgroups are distinguished on the basis of preference for *Fagus* (B), *Quercus* (C) or the lack of preference (A).

Among the 99 treated species, 44 are differential for roadside verges, 39 for related forests and only 15 are indifferent to these habitats. Twenty-one species prefer roadsides and/or forests with *Fagus*, 37 are differential for vegetation types with *Quercus* and 41 do not show a distinct preference for the tree species.

3.2. Saprotrrophic and parasitic species

The presence-degrees of the more important saprotrophic and parasitic macrofungi in roadside verges and corresponding forest types are presented in Table 3. They are divided into groups and subgroups using the same criteria as for the mycorrhizal fungi (see above). This group is much more heterogeneous as to its microhabitats and substrates. Therefore a subdivision is made within each subgroup into species mainly occurring on (a) litter and humus of grassland plants, (b) litter and humus of forest plants, (c) dead wood and (d) sporocarps of other macromycetes.

A total of 107 species are included in Table 3. Only 21 of them (20%) have a preference for roadside verges, 62 (58%) occur mainly in forests and the remaining 24 species (22%) are indifferent in this respect. Seventeen species (16%) have a preference for *Fagus* vegetation, 17 other species (16%) for *Quercus* vegetation whereas the remaining 73 species (68%) are indifferent.

3.3. Threatened macromycete species

The total and average numbers of threatened species in the studied vegetation types are presented in Table 4, also differentiated for ectomycorrhizal and saprotrophic macromycetes. The species are classified according to the preliminary red data list of threatened species by Arnolds (1989) into 5 classes:

- class 0: species, (probably) extinct in the Netherlands, i.e. not recorded since 1970 (not present in the studied plots);
- class 1: species threatened with extinction, i.e. very rare species restricted to strongly threatened habitats;
- class 2: strongly threatened species, i.e. rare species, restricted to threatened habitats, or species with strong decline;
- class 3: uncommon species, mainly found in threatened habitats or distinctly declining;

Explanations table 4:

The numbers of threatened species include the species with very low frequencies, which are therefore not included in Tables 2 and 3.

Vegetation types distinguished according to Keizer (1993a; see also Table 1). ECM = Ectomycorrhizal; SA = Saprotrrophic; TOT = Total.

The following categories of threatened species are distinguished after Arnolds (1989): 1: threatened with extinction, 2: strongly threatened, 3: threatened, 4: potentially threatened.

The following vegetation types are distinguished:

Roadside verges:

FFe: *Festuca rubra*-*Fagus* type, *Elytrigia* subtype

FFf: *Festuca rubra*-*Fagus* type, *Festuca ovina* subtype

MFp: *Mnium hornum*-*Fagus* type, *Poa trivialis* subtype

MFd: *Mnium hornum*-*Fagus* type, *Dryopteris* subtype

HQh: *Hypochaeris*-*Quercus* type, *Hieracium pilosella* subtype

HQl: *Lotus corniculatus* subtype, *Hieracium pilosella* subtype

AQi: *Anthriscus*-*Quercus* type, inops variant

AQt: *Anthriscus*-*Quercus* type, typical variant

DFQ: *Deschampsia flexuosa*-*Quercus* type

Forests:

LF: *Laccaria amethystea*-*Fagus* type

RF: *Rickenella fibula*-*Fagus* type (after Opdam, 1991)

DQ: Dicrano-Quercetum

QB: Querco-Betuletum

VQ: Violo-Quercetum (after Jansen, 1984)

TABLE 4. Numbers of threatened species of macrofungi in different types of roadsides planted with trees in Drente, the Netherlands.

A. Total number of species per type

Functional group of fungi			ECM				SA				TOT				
Category of threat			1	2	3	4	1	2	3	4	1	2	3	4	1-4
Vegetation types, number of plots															
FFe 5	ROAD SIDE VERGES	FAGUS	1	-	2	-	-	-	-	-	1	-	2	-	3
FFf 7			-	-	6	-	-	-	4	1	-	-	10	1	11
MFp 5			-	1	8	1	-	-	1	-	-	1	9	1	11
MFd 6			-	6	-	-	-	1	-	-	-	7	-	7	14
HQh 5		QUERCUS	-	-	7	1	-	-	4	-	-	-	11	1	12
HQl 21			3	7	18	2	1	-	14	-	4	7	32	2	45
AQi 6			-	1	7	-	-	-	1	-	-	1	8	-	9
AQt 17			-	4	12	1	-	-	3	3	-	4	15	4	23
DfQ 4			1	-	4	-	-	-	-	-	1	-	4	-	5
LF 10	FORESTS	FAGUS	-	3	7	-	-	-	3	1	-	3	10	1	14
RF 9			-	1	-	-	-	-	2	1	-	1	2	1	4
DQ 11		QUERCUS	5	12	10	-	-	-	5	-	5	12	15	-	32
QB 8			-	3	8	-	-	-	-	-	-	3	8	-	5
VQ 18			1	-	2	-	-	-	2	-	1	-	4	-	5

Table 4 (suite)**B. Average number of species per plot**

Functional group of fungi			ECM				SA				TOT				
Category of threat			1	2	3	4	1	2	3	4	1	2	3	4	1–4
Vegetation types, number of plots															
FFe 5	ROAD	<i>FAGUS</i>	.2	–	.4	–	–	–	–	–	.2	–	.4	–	.6
FFf 7			–	–	2.1	–	–	–	.7	.1	–	–	2.8	.1	2.9
MFp 5			–	.2	1.6	.2	–	–	.2	–	–	.2	1.8	.2	2.2
MFd 6			–	–	1.5	–	–	–	.3	–	–	–	1.8	–	1.8
HQh 5		<i>QUERCUS</i>	–	–	2.0	.2	–	–	.8	–	–	–	2.8	.2	3.0
HQl 21			.2	.4	1.8	.1	.1	–	1.0	–	.3	.4	2.8	.1	3.6
AQi 6			–	.3	2.3	–	–	–	.3	–	–	.3	2.6	–	2.9
AQt 17			–	.2	.7	.1	–	–	.2	.1	–	.2	.9	.2	1.3
DfQ 4			.2	–	1.5	–	–	–	–	–	.2	–	1.5	–	1.7
LF 10	FORESTS	<i>FAGUS</i>	–	.3	1.2	–	–	–	.6	.3	–	.3	1.8	.3	2.4
RF 9			–	.1	–	–	–	–	.2	.1	–	.1	.2	.1	1.4
DQ 11		<i>QUERCUS</i>	.6	2.5	5.0	–	–	–	2.7	–	.6	2.5	7.7	–	10.8
QB 8			–	.4	1.7	–	–	–	–	–	–	–	.4	–	.5
VQ 18			.1	–	.2	–	–	–	.2	–	.1	–	.4	–	.5

– class 4: potentially threatened species: rare and very rare species without tendency to decrease.

The average number of threatened species per plot varies in forests from 0.4 in the *Rickenella-Fagus* type to 10.8 in the Dicrano-Quercetum, in roadside verges between 0.6 in the *Elytrigia* subtype of the *Festuca-Fagus* type and 3.6 in the *Lotus* subtype of the *Hypochaeris-Quercus* type.

4. Discussion

4.1. Differential ectomycorrhizal species for the studied vegetation types

44% of all species appear to be differential for roadside verges with regard to forests (Table 2, group I). This group comprises both widespread species with a distinct preference for this habitat, such as *Russula nigricans*, *R. parazurea* and *Xerocomus chrysenteron*, and less common species which are restricted to roadside verges, e.g. *Tricholoma ustale*, *Lactarius serifluus* and *Cortinarius erythrinus*. The latter group includes also many rare species, which were observed in one or two plots only, but which are also (almost) exclusively found in roadsides in other areas, e.g. *Cortinarius subbalaustinus*, *C. valgus*, *C. velenovskyi*, *Inocybe amethystina*, *Lactarius vellereus*, *Russula brunneoviolacea*, *R. chloroides* and *R. decipiens*.

Within the roadside verges most species have their highest presence-degree in the nutrient-poor types of open landscapes (*Fagus* plots: *Festuca ovina* subtype of the *Festuca rubra* type (FFf): 11 species; *Quercus* plots: *Hieracium pilosella* subtype of the *Hypochaeris* type (HQh): 11 species), or in the slightly richer and more shady *Mnium hornum* – *Fagus* type, subtype of *Poa trivialis* (11 species). Environmental conditions in these types show the most pronounced differences with the forest communities under comparison concerning both microclimate and soil-factors (Table 1).

On the other hand, only five species of group I have their highest frequency in shady forest roads with *Fagus* (*Dryopteris* subtype of the *Mnium hornum* type: 2 species) and/or *Quercus* (*Deschampsia flexuosa* (DfQ) type: 3 species). These types show the largest resemblance to corresponding forest types, in particular with respect to the shady, relatively cool microclimate and the accumulation of litter. Considering the forest communities, the mycorrhizal floras of the Dicrano-Quercetum and the *Laccaria* – *Fagus* type have the largest affinity to roadsides in general. The essential ecological variables in common seem to be the thin litter layer, at least in places, and the strongly oligotrophic soil conditions.

Thirty-nine species are more frequent in (part of) the studied forest types than in roadside verges. Only seven species are exclusively found in forests,

all of them being characteristic species of the Dicrano-Quercetum on very nutrient-poor sand dunes, e.g. *Tricholoma portentosum*, *T. columbetta*, *Inocybe sambucina* and *Cortinarius alboviolaceus*.

However, the data on the Dicrano-Quercetum were mainly collected in the period 1972–1973. It has been demonstrated that the mycorrhizal flora in this association has become strongly impoverished during the last twenty years (Arnolds, 1991) and almost all characteristic species have nowadays disappeared completely, even a species such as *Cantharellus cibarius*, which was found in the early seventies in all plots in great abundance. A number of these species were probably equally widespread in the poorest types of *Fagus* forests and of roadside verges (FFf and HQh), but have now also become very rare in these habitats. In fact, the few remaining localities of former characteristic species of the Dicrano-Quercetum are now mainly situated in roadsides planted with *Quercus*. Consequently, it is questionable whether exclusive species for forest communities do really exist or do not.

It is striking that among the differential species of forests, only few species within roadside verges have their optimum in open, exposed types (1 species in *Festuca ovina* subtype of the *Festuca rubra*-*Fagus* type, 1 species in HQh). Highest presence-degree values are most often reached along shady forest roads with litter accumulation (*Fagus* plots: the *Poa trivialis* subtype (MFp) and the *Dryopteris* subtype (MFd) of the *Mnium hornum* type: 7 and 6 times respectively; *Quercus* plots: DfQ: 7 times). This habitat type comes closest to the forest communities. Their frequency in these types is often comparable to that in forests. Only 16 species do not show a distinct preference for either roadside verges or forests. None of them has an optimum in one of the roadside verge types.

4.2. Preference of ectomycorrhizal species for *Quercus* or *Fagus*

The majority of the studied species (58 species, 59%) have a distinct preference for either *Fagus* or *Quercus*. This preference is the same in both roadside verges and forests, with the following exceptions:

1. *Russula pectinatoides* in roadsides was only found with *Quercus*, but in one *Fagus* forest plot;
2. *Laccaria bicolor* had a weak preference for roadside verges with *Quercus*, but was only reported from *Fagus* forests. However, both species occur only in one or a few plots. *L. bicolor* may have been included in *L. proxima* in the study of *Quercus* forests (Jansen, 1984) and is known to occur with many tree species, also coniferous trees (Kreisel, 1987; Jansen, 1991).
3. *Lactarius camphoratus* was found in rather few roadside verges with both *Quercus* and *Fagus*, but in forests it was restricted to *Quercus*. It is usually

regarded as an aspecific symbiont of these tree species as well as coniferous trees (Neuhoff, 1956; Kreisel, 1987).

4. *Boletus erythropus* had in the investigated roadsides a preference for *Fagus*, in forests for *Quercus*. It is reported as a mycorrhizal symbiont of both trees in literature (e.g. Kreisel, 1987) and has been observed by us in roadside verges with *Quercus* outside the plots.

Mycorrhizal fungi show different host ranges which may vary from broad, intermediate or narrow (Molina & Trappe, 1982). Examples from this study are *Russula ochroleuca* and *R. parazurea* and *Laccaria proxima* with a broad, and *Lactarius quietus* and *L. chrysorrheus* with a narrow host range (with *Quercus*). Host ranges are caused by physiological interactions involving recognition and/or defence mechanisms. The exact mechanisms of such host specific relations are largely unknown, but depend possibly on the excretion of substances (elicitors) by the host, which prevent a successful symbiosis in incompatible combinations, but are masked or not produced in compatible combinations (Duddridge, 1987).

More indirectly, the host preference may be influenced by environmental variables such as climate or soil properties (fertility, pH, etc.), or properties of the host itself such as vitality or age (Mason, 1987; Termorshuizen, 1990). Environmental variables may either affect the predisposition of the host to infection, or determine the suitability for the mycorrhizal fungus to establish and survive in the soil.

Thus, physiological interactions may play a role in the exclusive occurrence of *Lactarius quietus* and *L. chrysorrheus* with *Quercus* and *Russula fellea*, *R. mai-rei* and *Tricholoma ustale* with *Fagus*. Environmental variables may "explain" the preference of *Inocybe* spp. for the *Fagus* group IB and of *Cantharellus cibarius* for the *Quercus* group IIc. The occurrence of *Hebeloma mesophaeum* in group IIIB may be connected with the age of the host.

However, many species showing a preference in this study for either *Fagus* or *Quercus* are reported in literature having a broader host range (Arnolds, 1984; Kreisel, 1987). In addition, differences between the studies concerning the years of observations may influence the observed preferences. The oak forests were studied in the period 1972–1979, beech forests in 1989–1990. The lower presence degree of, for instance, *Cantharellus cibarius* in *Fagus* forests compared to *Quercus* forests, is probably mainly caused by the strong impoverishment of the mycoflora that started in the sixties (Arnolds, 1988b, 1991). This species has probably been equally common in *Fagus* forests of the *Laccaria amethystea* type.

4.3. Differences in ectomycorrhizal fungi between roadside verges and forests

No arguments to support the microclimate-hypothesis (1) can be found. The microclimate was supposed to be relatively warm and dry in the south-exposed plots due to a large quantity of direct solar radiation, and relatively cool and wet in the north-exposed plots (Barkman & Stoutjesdijk, 1987). On the basis of the above hypothesis, it should be expected that differential species of roadside verges were more frequent in south-exposed plots. However, there was no significant difference: the average number of such species were 24 and 36 in north- and south-exposed plots respectively. Moreover, all plots of this subset were classified on the basis of their mycorrhizal fungi in a single type, the *Russula ochroleuca* type (Keizer, 1993a), another indication that microclimatological factors play a minor role for the explanation of differences in the mycorrhizal flora, in comparison with other environmental variables. In addition, there is no indication that the observed differential species of roadside verges have a more southern or continental distribution in Europe, which would be expected for thermo- or xerophilous species. Microclimatological conditions on the mycorrhizal fungi along roads on clay or calcareous soils may possibly be more important (Reijnders, 1968).

Hypothesis 2 ("roadside-species" are more common in different indigenous forest types) is supported by data for a few species, such as *Amanita muscaria*, which is more often found in forests dominated by *Betula* in Drenthe (Jalink & Nauta, 1984). *Clavulina coralloides*, *Inocybe geophylla* and *Scleroderma areolatum* are regularly found in mixed deciduous forests on weakly acid soils, rather rich in nutrients, for instance in the Alno-Padion on loamy soil in Drenthe (Arnolds, unpublished mycocoenological data). These species are not characteristic for road sides. Their occurrence in roadside verges can be explained by the higher pH and higher nutrient contents in this habitat than the compared forest communities. However, the vast majority of species of group I (Table 2) are also characteristic of roadsides in other parts of the Netherlands and only rarely found in forests (unpubl. data Netherlands Mycological Society).

Hypothesis 3 is probably valid for the majority of differential species of roadside verges, viz. that these species are characteristic of forest types, not indigenous in the Netherlands at the moment. In this connection we think for instance of open, natural woodlands, grazed by large herbivores, with a herb-rich understorey or the anthropogenic equivalent: so-called "tree-meadows", i.e. very open cattle-grazed "forests" with a grassland undergrowth (Ryman & Holmåsen, 1984:23), or old, small-scaled agricultural landscapes consisting of a mosaic of small, extensively grazed woodlands and grasslands (Jahn &

Jahn, 1986). In the Netherlands, many differential species of roadside verges indeed are also found in meadows with scattered trees on old estates. Some species might have their optimal, natural habitat in foreign forest communities on steep slopes, with a permanent natural removal of litter and nutrients (Jahn, 1986). Additional support is found in some data from forests in other countries (see section 4.4.). Examples of this group are *Lactarius serifluus*, *Russula odorata*, *Clitopilus prunulus* and *Lactarius vellereus*.

Hypothesis 4, postulating that roadside verge fungi may be relicts, which were once widespread in forests, is probable for part of the species. It was noticed before that presently many former characteristic species of the Dicran-Quercetum are confined to roadside verges on poor soils (mainly the *Hieracium pilosella* subtype of the *Hypochaeris-Quercus* type, also the typical variant of the *Anthriscus-Quercus* type). The resemblance of the environmental conditions is striking: in the two vegetation types the herb layer is open, the moss layer is well-developed, the soil is acid, dry, very poor in nutrients, the soil profile is poorly developed and little litter accumulation occurs (Table 1). Probably, the roadside verges of the *Festuca rubra-Fagus* type (mainly *Festuca ovina* subtype) have a similar relationship to *Fagus* forests on very poor soils, but unfortunately accurate old data on the mycoflora in these forests are lacking. Examples of this group are *Boletus erythropus*, *Cantharellus cibarius* and *Lactarius blennius*, which are nowadays more frequent in roadside verges than in forests on poor sand.

Hypothesis 5 seems to apply to a fairly large group of species, which in most areas are mainly known from roadside verges with trees and only rarely are found in natural forest communities, for instance *Russula amoenolens*, *R. pectinatoides*, *Inocybe maculata* and several other *Inocybe* species. The unique combination of environmental conditions along roads – disturbance of the soil profile, removal of litter, mowing of grass, irregular water supply, local soil compaction and local soil enrichment is very rare in forest communities, but may have been selective for some ectomycorrhizal species, which could extend their distribution area after the appearance of man-made roadside verges with trees. Naturally, there is a connection with the human-influenced landscapes described above.

At present it is not possible to determine per species which is the most probable hypothesis to explain its preference for road sides because reliable data on the frequency of such species in many other forest communities are still lacking.

4.4. Mycorrhizal fungi in forests built by *Quercus* species outside the Netherlands

Mycocoenological studies in European oak forests have been carried out, by Wilkins et al. (1937) in England, Bohus & Babos (1960, 1967) in Hungary and Darimont (1973) in Belgium.

The oak forests studied by Wilkins et al. (l.c.) comprised 26 plots, distributed over three types; on rather dry, weakly loamy sand soil (comparable to *Violo-Quercetum*), moist loamy soil (comparable to *Querco-Carpinetum*) and on wet clay (comparable to *Alno-Quercetum*). None of the communities showed much resemblance concerning its mycoflora to roadsides and/or oak forests in the Netherlands, presumably owing to considerable differences in soil conditions. Constant species in all types, such as *Amanita phalloides* and *Hydnus repandum* were hardly or not found at all in our plots. Some species, characteristic of roadsides in the Netherlands, were mentioned from forests in England, for instance *Clitopilus prunulus*, *Cortinarius hinnuleus*, *Lactarius serifluus*, *L. velutinus* (in 17 out of 20 plots!), *Russula atropurpurea*, *R. lutea*.

Several grassland species were reported from oak forests by Wilkins et al. (1937), e.g. *Hygrocybe coccinea* and *Camarophyllum niveus* (as *Hygrophorus virginicus*), which might suggest an open structure of the canopy and possibly grazing by cattle. Unfortunately no details on management of the stands are presented by the authors. These data support the validity of hypothesis 4, postulated in the previous section.

Bohus & Babos (1960) studied several forest associations dominated by *Quercus* in the Hungarian mountains. Only the community called "Luzulo-Quercetum subcarpaticum, *Dicranum* facies" shows considerable similarities with oak forests in Drenthe, in particular the Dicrano-Quercetum, and with the roadside verges with Oak on very poor soils (*Hypochaeris-Quercus* type). The environmental conditions are also comparable: on slopes with acid soils without well-developed profile, at most a micropodzol. Some species reported by Bohus & Babos (1960) from forests have an optimum in roadside verges in Drenthe, e.g. *Amanita pantherina*, *Lactarius serifluus*, *Russula chamaeleontina* (as *R. lutea*), *R. nigricans* and *R. graveolens* (as *R. xerampelina*).

Darimont (1973) investigated in the period 1940–1945 four communities in Belgium where *Quercus* was dominant, three of them on neutral to basic, calcareous soils and consequently with a mycoflora strongly different from the oak communities in Drente. The "Quercetum sessiliflorae medioeuropaeum" occurs on weakly acid brown earth and is more or less comparable with the *Violo-Quercetum* in the Netherlands. However, the Belgian community is much richer in mycorrhizal species, which may indicate that the stands in the

Netherlands are strongly impoverished in this respect. A repeated inventory of Darimont's plots might throw light on this question.

Interestingly, several species which are nowadays regarded as differential of roadside verges were found by Darimont in acid oak forests, e.g. *Amanita spissa*, *Chalciporus piperatus*, *Clitopilus prunulus*, *Helvella lacunosa* (in this study arranged among the saprotrophs), *Inocybe petiginosa*, *Lactarius vellereus*, *Russula atropurpurea*, *R. nigricans* and *R. graveolens* (as *R. xerampelina*).

Darimont (1973) was one of the very few mycocoenologists who paid attention to verges of forest roads and main roads, considered by him as two microcommunities ("synmycies") inside the *Quercetum sessiliflorae*. He was among the first researchers who noticed that the mycoflora along roads with trees is a combination of grassland- and forest elements. The microcommunity along main roads was characterized by a great variety of 14 *Inocybe* species, including *I. maculata*, *I. griseolilacina* and *I. flocculosa*, which are regarded as differential for roadside verges in Drenthe as well. Differences in methodology prevent a more accurate, quantitative comparison, because Darimont counted groups of sporocarps which he supposed to represent mycelia.

In conclusion, the data by Bohus & Babos (1960) and Darimont (1973) support hypotheses 3 and 5 for a number of species.

4.5. Mycorrhizal fungi in forests of *Fagus* outside the Netherlands

Mycocoenological studies of *Fagus* dominated forests were carried out by Jahn (1986) and Jahn et al. (1967), Haas (1932) and Runge (1989) in Germany, Wilkins et al. (1937, 1938) in England, Smarda (1972) in Czechoslovakia, Guminska (1962) and Lisiewska (1963, 1974) in Poland and Darimont (1973) in Belgium. Data on roadsides with planted *Fagus* are lacking. Most of the studies concern beech forests on rich, loamy and/or calcareous soils, for instance belonging to the associations *Carici-Fagetum* and *Melico-Fagetum*. The communities of green plants and fungi are widely different from the acidophytic communities in Drenthe and are not further considered here.

Wilkins et al. (1937) mentioned six fungi with highest frequency in *Fagus* forests on acid (pH 4.0–4.5) sand or clay with raw humus in England: (*Amanita citrina*, *Boletus edulis*, *Cortinarius elatior*, *Russula fellea*, *Russula rosea* Pers. (as *R. lepida*) and *Xerocomus chrysenteron*. Most of them have been found in both forests and roadside verges in the Netherlands, except *R. rosea*, which was not recorded at all.

Jahn et al. (1967) studied the mycoflora in plots in various beech communities in the Weser mountains. The stands of the *Luzulo-Fagetum* on acid, loamy soil show most affinity to the roadsides with *Fagus* of the *Festuca rubra* type and the *Laccaria-Fagus* forest in Drente. Typical roadside species, such as

Inocybe petiginosa, *Lactarius blennius*, *Russula lutea*, *R. nigricans*, *Tricholoma ustale* were observed with rather high presence degrees in Luzulo-Fagetum forests, mainly in the subassociation Leucobryetosum on very poor soils. This confirms the hypotheses in which the mycorrhizal flora in roadside verges is considered to be a fragment of a community not present in the Netherlands (hypothesis 3) or a relict of formerly richer forest types (hypothesis 4).

Similar conclusions can be drawn from a comparison with the mycocoenoses in Hungarian Luzulo-Fagetum, investigated by Bohus & Babos (1960), where *Lactarius vellereus* and *Russula delica* were the most abundant macrofungi. In the Netherlands they are almost confined to roadside verges, at least at present. Likewise, characteristic roadside fungi, such as *Amanita spissa*, *Corticarius elatior*, *Inocybe umbrina*, *Lactarius blennius* and *Xerocomus chrysenteron* were reported by Darimont (1973) from acidophytic beech forests in the Belgian Ardennes.

However, several differential species of roadsides were not or only rarely reported during mycocoenological studies in forests elsewhere in Europe, for instance *Naucoria bohemica*, *Russula amoenolens*, *R. pectinatoides*, *R. odorata* and various *Inocybe* species. These species probably belong to the group of truly characteristic roadside verge fungi, which are rare in natural forest communities (hypothesis 5).

4.6. Differential saprotrophic species

The communities of saprotrophic fungi in roadside verges and corresponding forests are much more different from each other than those of ectomycorrhizal fungi: only 24 species (22%) occur with comparable frequencies in the two groups of habitats (Table 3, group III). Most of them are very common saprotrophs on leaf litter and humus without distinct preference for a certain kind of substrate (ubiquists, group II A1). It should be noticed that the abundance of sporocarps is often considerably larger in forests than in road sides. *Rickenella fibula* and *R. setipes* are associated with living bryophytes, which are growing in both roadside verges and forests. Only seven wood-inhabiting species are equally common in roadside verges and forests. They are able to grow on small wood remains, such as twigs and wood chips, a substrate widespread in the two habitat types.

The number of saprotrophic species, differential for roadside verges, is considerably smaller than the number of differential ectomycorrhizal species (Table 3, group I). Among the twenty differential species nine are characteristic for litter or humus in grassland communities (Arnolds, 1981, 1984). Eight of them are equally common in roadside verges with *Quercus* and *Fagus*, but *Psathyrella panaeoloides* has an unexplained preference for *Fagus*.

The remaining species of differential group I are more heterogeneous in ecological respect. *Entoloma subradiatum*, which has a preference for *Fagus*, is a terrestrial forest species (Noordeloos, 1988:103) and may possibly be a mycorrhizal symbiont. The nutritional status of many *Entoloma* species is still unclear.

Nyctalis asterophora is a saprophyte on dead sporocarps of *Russula nigricans* (Kreisel, 1987). This ectomycorrhizal species occurs in large quantities only in some roadsides with old *Quercus* trees and is much rarer in forest communities (Table 2 group Ia). It is striking that *Nyctalis* is almost confined to areas with high densities of sporocarps of *Russula nigricans*.

Agrocybe praecox, *Helvella lacunosa*, *Mycena flavescens* and *Tarzetta cupularis* are mainly found outside roadside verges on leaf litter and humus in nutrient-enriched, disturbed places in forests, for instance along foot paths and forest edges among *Urtica dioica* L.. Such microhabitats were excluded from the plots in *Fagus* and *Quercus* forests, which explains the absence of these species from these forests.

Mycena polyadelpha is a very small agaric on intact, dead leaves of *Quercus* and may be either overlooked in the study of *Quercus* forests or possibly be characteristic of forests on richer soils.

Coprinus subimpatiens, *Marasmius rotula*, *Mycena adscendens*, and *Tubaria furfuracea*, inhabit small twigs and wood chips and have their optima in forests on richer soils, such as the Alno-Padion (Arnolds, unpublished data). Within the plots, *Mycena adscendens* has a preference for *Quercus*, the other species of *Fagus* twigs.

The occurrence of many indicator species of nutrient-rich soils in roadside verges can be explained by eutrophication by traffic, blown-in fertilizers, deposition of waste, wood chips and excrements (dogs, horses). In addition, decomposition rates may be higher in some roadside verges than in forests.

The list of differential saprotrophic species for forests (Table 3, group II) is considerably longer, which is likely the result of the much larger quantities of available substrates, mainly leaf litter and wood. In exposed roadside verges most of the leaf litter is blown away in the course of the autumn. Fallen boughs and branches are always removed and most wood remains in roadside verges are small twigs and occasionally stumps of died trees. Exceptions to this rule are the verges of forest paths, where normal litter accumulation occurs and dead wood is often left. Such roadside verges mainly belong to the *Mnium hornum-Fagus* type (F3, F4) and the *Deschampsia flexuosa-Quercus* type (Q5) (Keizer, 1993a). Many species of group II in Table 3 are within the roadside verges differential for these types, where they often have a presence degree comparable to the corresponding forest types.

4.7. Mycological evaluation of roadside verges and forests with *Fagus* and *Quercus* in the scope of nature conservation

The numbers of threatened species per vegetation type are presented in Table 4. The highest number of threatened species (45) is found in the *Lotus* subtype of the *Hypochaeris-Quercus* roadside verges, but the highest average number per plot is found in forests of the Dicrano-Quercetum. The categories of strongly threatened species (classes 1 and 2) are also best represented in this type. However, these values are not well comparable with the other data in Table 4 since the Dicrano-Quercetum was mainly investigated in the period 1972–1973 (only 3 plots also in 1976–1979) and it has been demonstrated that a strong decline of mycorrhizal fungi has taken place since 1960–70 (Arnolds, 1989; 1991). The entire fungal community of the Dicrano-Quercetum has become practically extinct in the Netherlands, partially due to natural succession of the community, but mainly caused by atmospheric deposition of nitrogen compounds (Arnolds, 1991), and the mycological value is nowadays comparable to the levels of the Querco-Betuletum and the *Laccaria amethystea*-*Fagus* type. The occurrence of threatened fungi in the most widespread, more eutrophic forest types of *Rickenella-Fagus* and the *Violo-Quercetum* is very limited.

A considerable number of threatened fungi occur in roadside verges planted with trees. In the investigated plots a total of 69 species, reported in the "Red List" of threatened macromycetes in the Netherlands (Arnolds, 1989), were recorded, including six species which are considered to be threatened with extinction, viz. *Boletopsis leucomelaena*, *Cortinarius causticus*, *Dermocybe cinnabrina*, *Leucopaxillus giganteus*, *Lyophyllum semitale*, and *Phellodon confluens*. In addition, twelve strongly threatened species were found, viz. *Amanita porphyria*, *Cortinarius fusisporus*, *C. subbalaustinus*, *C. torvus*, *Entoloma solstitiale*, *Inocybe calospora*, *Hydnellum concrescens*, *H. spongiosipes*, *Pseudocraterellus sinuosus*, *Tricholoma saponaceum*, *T. sculpturatum* and *Tylopilus felleus*.

The average numbers of threatened species are highest in the *Festuca ovina* subtype of the *Festuca rubra-Fagus* community, the two subtypes of the *Hypochaeris-Quercus* community and the *inops* subtype of the *Anthriscus-Quercus* community. These numbers (approx. 3 species per plot) are much lower than in the former Dicrano-Quercetum, but, on the other hand, they are higher than in the actual relics of this forest type (Arnolds, 1991) and the *Laccaria-Fagus* type. The roadside verges contain more different threatened species than the forests, for instance, in the 11 plots of the Dicrano-Quercetum a total of 32 Red List species have been found with an average number of 10.8 species per plot; in the 21 plots of the *Lotus* subtype of the *Hypochaeris-Quercus* type, 45 species with an average of 3.6 species per plot. Consequently, roadside verges offer a

potential habitat to a large number of threatened fungi, which enhance their value from a nature conservation point of view.

All four types of roadsides being rich in threatened fungi, have a number of environmental characteristics in common (Table 1): they are situated in open landscapes, the organic layers ($A_0 + A_{00}$) are relatively thin, a moss layer is usually well-developed (with exception of the *inops* variant of the *Anthriscus-Quercus* type, the AQi), the herb layer is usually short and the soluble phosphor content and nitrogen availability (expressed as Ellenberg N-value) are low (except Ellenberg N-value in AQi). These ecological conditions in the forest types studied are most similar to the situation in the Dicrano-Quercetum and the *Laccaria-Fagus* forest type, in particular concerning the occurrence of a thin litter layer. In these forest types a patchy pattern occurs of places where litter is blown away and where it accumulates. The places with a thin litter layer have a high moss cover and here concentrations of threatened and rare mycorrhizal species are found (Jansen, 1984). Important differences are the higher pH and lower C/N ratio in roadside verges.

The majority of threatened species in the investigated types of roadside verges and forests belong to the ectomycorrhizal fungi. The relatively high number of threatened saprotrophic and parasitic fungi in the Dicrano-Quercetum is mainly caused by the high frequency of two *Cordyceps* species, growing as parasites on ectomycorrhizal *Elaphomyces* species, consequently in fact caused by ectomycorrhizal fungi in an indirect way. The relative high numbers of threatened saprotrophs in some types of roadside verges (FFf, HQh, HQl) are mainly caused by the occurrence of decreasing species of poor, unfertilized grasslands.

The occurrence of strongly threatened ectomycorrhizal species (classes 1 and 2) is usually correlated with the occurrence of a large number of less threatened species (classes 3 and 4). High numbers of threatened species are concentrated in only very few plots, viz. plot Q2 (23 threatened species), Q83 (16), Q32 (8) and F43 (4). Plots Q2, Q83 and Q32 are roadside verges with old *Quercus* trees on nutrient-poor soil. Roadside verges with Beech are less rich in threatened fungi; the richest is plot F43 with 4 Red List species. These localities certainly deserve special attention concerning planological protection and management (Keizer 1993a and b).

The knowledge about the ecology of mycologically rich roadside verges can be used in favour of nature management measures which can be carried out in forests that are mycologically impoverished. In forests where a thick organic layer has accumulated, sod removal can cause a regeneration of the mycoflora (Baar & Kuyper, 1993). In other forests, repeated litter collection may create a decrease of the organic layer, together with a decrease of the nutrient content of the soil, which appear to coincide with a rich mycoflora. These measures are most promising

in areas with an originally nutrient-poor soil. In view of the experiences in roadside verges, most success is to be expected in ectomycorrhizal fungi.

Grazing with large grazers (horses, cattle) in combination with the development of an open forest structure will develop in the long run a landscape type approaching the “tree-meadows”, the old agricultural land use where a rich mycoflora can be present (see section 4.3).

There are some promising examples of these nature management types in the Netherlands (Baar & Kuyper, 1993; Keizer, 1993b).

5. Conclusions

In this paper we analyzed and discussed the differences between mycocoenoses in roadsides with planted *Quercus* and *Fagus* on the one hand and forests on sandy, acid soils dominated by these trees on the other. Both are strongly different, for ectomycorrhizal as well as saprotrophic fungi. In both groups only a minority of species are equally frequent in roadsides and forests.

The differential saprotrophic fungi of roadside verges are in part characteristic for grasslands, which is understandable since the herb layer in open, exposed roadsides (*Hypochaeris-Quercus* type, *Festuca rubra-Fagus* type) is comparable with some grassland communities and is treated in the same way, i.e. it is usually mown once or twice a year. Some differential species of roadside verges are characteristic of forest types on richer soils which were not considered in this study. Their occurrence is determined by local enrichment of roadside verges. Differential fungi of forests are many saprotrophs on leaf litter and wood-remains, in particular those on larger branches, trunks and stumps. This can be explained by the much larger frequency of these substrates in forest stands. Shady roadside verges, situated in forests (*Mnium hornum-Fagus* type, *Deschampsia flexuosa-Quercus* type), are in these respects intermediate: differential grassland species are lacking and forest saprophytes are much more frequent than in other types of roadsides, but less frequent than in forests.

The explanation of the differences in ectomycorrhizal fungi is more complicated. Many species have their optimum in roadside verges with planted trees and most of them occur mainly in open, exposed roadside types. The mycocoenoses in such roadside verges mostly resemble forest types on very poor, acid, sandy soils without distinct soil profile development and a thin litter layer, i.e. in the Netherlands the Dicrano-Quercetum and *Laccaria amethystea-Fagus* community. The differential species of roadside verges may in part be considered as species which have disappeared from these forest communities in recent years (Arnolds, 1988b, 1991). This phenomenon is ascribed to natural forest succession in combination with high nitrogen deposition. It is beyond the scope of this paper to treat this subject in detail.

The characteristic ectomycorrhizal flora along roads is made up of four elements:

- (1) species which have become rare or extinct in forests on poor, sandy soils;
- (2) species which have their optimum in indigenous forest associations on richer soils;
- (3) species which have their optimum in forest associations, not or hardly occurring in the Netherlands, e.g. the Luzulo-Fagetum;
- (4) species which occur sporadically in natural forest communities, and are stimulated by the prevalent environmental conditions in roadside verges.

On the other hand, a number of mycorrhizal species have their optimum in forest communities. Many of them are known as differential species for the Dicrano-Quercetum, but all of these species have strongly decreased in the forests themselves since the early seventies, when this forest association was studied. At present their frequency in such forests is very low and many of them have become differential for roadside verges, although with a lower presence-degree than in formerly well-developed stands of the Dicrano-Quercetum, for instance *Boletus erythropus*, *Cantharellus cibarius*, *Lactarius chrysorrheus*. The corresponding *Fagus* forests on very poor soils, belonging to the *Laccaria-Fagus* community, were only recently studied and therefore no long list of differential species is available with respect to roadside verges with beech. Part of the differential species of forests are found with comparable frequency along shady forest roads.

At present, roadside verges with trees are extremely valuable as habitat for rare and threatened macrofungi, in particular ectomycorrhizal species, but also for some grassland fungi. The richest plots, rating urgent protection, are all exposed roadside verges with medium-old to old trees on very poor, acid soil with a low, grassy or moss-rich understorey, usually mown with regular intervals. They contain the last localities of some species in the Netherlands, which can be regarded as relics which have become extinct in forest communities. It should be emphasized that the valuable roadside verges make up a very small proportion (less than approx. 1%) of all roadsides planted with trees. Therefore their protection, adequate management and extension of their area is necessary. Most roadside verges are situated on primarily nutrient-rich soils, often supplied from elsewhere, or strongly influenced by fertilizers and dung from adjacent agricultural land. Such roadside verges have a poorly developed mycoflora.

We consider as key factors for a well-developed mycorrhizal flora with rare species an extremely low availability of nitrogen (and phosphorus?), absence of litter accumulation and a short, low productive herb layer. These conditions were fulfilled in the past in many forest stands, but the increased acidification and atmospheric deposition of nitrogen have disturbed these ecosystems (Ter-

morshuizen, 1990) and have lead to a virtual extinction of the communities of Dicrano-Quercetum and Cladonio-Pinetum in the Netherlands, with the exception of some relics along the coast (Arnolds, 1991; Van der Werf, 1991). Although nitrogen deposition is at least equally high in roadside verges with trees, the influence on the soil conditions is considerably less in well-managed, exposed roadsides due to the transport of nitrogen from the system by the removal of litter by the wind and the removal of part of the sward by mowing practices.

Management measures in forests, directed towards a reduction of the organic matter and nutrient content of the soil, combined with an open forest structure (wind influence) can regenerate a rich ectomycorrhizal mycoflora.

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