A vegetation analysis of the transition between subalpine heathlands and their surroundings in the Monts du Forez (Massif Central, France)

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SUMMARY

The spatial distribution of species in boundary situations between heathland communities and adjacent vegetation types in the subalpine zone of the Monts du Forez was studied. Ten transects were analysed, four dealing with the transition between heathland and ombrotrophic peatland, and six dealing with the transition between heathland and communities characterized by tall forbs. Species cover and the composition of vascular plants in each square metre were studied in detail. The distribution pattern of the species along the transects is interpreted ecologically and discussed phytosociologically. The similarity between the heathland and adjacent vegetation was calculated and a number of quantitative characteristics of the boundary situations (species diversity, floristic fall, dissimilarity) were analysed. The four methods applied for measurement of alteration in the floristic composition were compared with each other, and their usefulness is discussed here.

Key-words: Massif Central, subalpine heathlands, transect analysis, vegetation boundaries.

INTRODUCTION

Since 1984, investigations, including synecological and classification aspects, have been carried out in the subalpine heathlands of the Monts du Forez and the adjacent communities. This study was done in close co-operation with the Laboratory of Palaeobotany and Palynology of the University of Utrecht and the Department of Botany of the University of Clermont-Ferrand (see Thébaud 1988). Very little botanical research has been carried out in this area before, and no information was available to put it in a European context. Information however, is urgently needed. The Monts du Forez has proved itself to be one of the best intact low-mountain ranges in Europe but the preservation of the plant communities is by no means guaranteed. As a consequence of social and economic developments, the traditional agricultural system, which strongly influenced the present vegetation, has collapsed. Part of the research concerns transitional situations, both temporal and spatial. The study of spatial relationships, carried out in 1987, included analysis of the behaviour of species (populations) as well as the shifts within communities.

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This is the topic of the present paper dealing, with boundaries between adjacent vegetation stands analysed along transects. The temporal relationship between heathlands and other communities was investigated using broad enquiries into former and present land use. The results will be discussed in a publication concerning the influence of human activities.

The analysis of transects, both spatial and temporal, is a useful method of obtaining an insight into the characteristics of boundary situations in vegetation. As the research on the distribution of species in boundary situations between subalpine heathlands and their surroundings in the Monts du Forez was carried out within one vegetation season, only patterns in vegetation ('variety-in-space') are dealt with.

The study of transects can enhance the knowledge obtained from relevés collected according to the Braun-Blanquet approach to phytosociology. The latter makes use of a large number of sample plots to obtain an outline of the variation in vegetation within a certain area. The former method starts from a relatively small number of sites, the internal variation of which will be analysed in detail. As transects include a sequence of adjacent stands within a short distance, the ecological behaviour of species can be studied without the need to account for major factors within each transect, namely the parameters of altitude, exposition and meso- and macroclimate for any separate stand of the transect. The sequential stands of any transect may however, vary considerably in soil character- istics, inclination and vegetation structure as well as the microclimate resulting from the latter.

Generally, the study of gradient situations is concerned with the variation in vegetation and its relationship to the variation in other environmental factors (Whittaker 1967), whether or not the analysis is direct or indirect (Fresco 1972). In the present study, the relationship between vegetation and environmental factors is not emphasized. Several aspects of the vegetation itself have however been examined with regard to the distribution patterns of species and the variation in species cover.

Prior to the description of the methods and transects, some attention was paid to the area of investigation and the heathland types present. Furthermore, the similarity between heathland and adjacent communities is discussed, followed by an analysis of the changes in species diversity and alterations in floristic composition. Finally, the distribution pattern of the species along the transects is interpreted ecologically and discussed phytosociologically. The number of participating orophytes, the rate of occurrence of species indicating a high atmospheric humidity, and the distribution of dwarf-shrub species are considered.

AREA OF INVESTIGATION

The Mont du Forez include a low-mountain range of Hercynical origin, situated in the northeastern part of the Massif Central (France). The mountain range roughly runs from north to south and measures 60×20 km approximately; the summit reaches to 1642 m. The Forez massif consists of granitic igneous rock. Generally, the slopes have been cultivated or afforested up to 1300 m; to a large extent, the area above the forest boundary, usually referred to as 'hautes-chaumes', consists of dwarf-shrub heathlands. Furthermore, grasslands, peatlands, and communities dominated by tall forbs are present. The overall surface of the hautes-chaumes measures 8000 ha.

The area above the forest boundary includes a north–south oriented ridge with relatively steep slopes and strongly wind-exposed tops, and a number of extensive plateaus at lower altitude. The local climate is characterized by a high annual precipitation

(1800 mm), a long period of frost (100 days/year), a prolonged snow-cover in spring and early summer, and the frequent occurrence of fog (Suchel 1985; Thébaud 1988). This environmental setting is reflected in the vegetation pattern.

The heathland communities of the hautes-chaumes are classified here within the order Vaccinio-Genistetalia (class Nardo-Callunetea). Since the syntaxonomy of the subalpine heathlands of France is not yet fully understood, we will deal here with a provisional classification. The syntaxonomical discussion will be the subject of a forthcoming paper.

Some stands on the west-facing slopes and the larger part of the vegetation of the plateaus belong to the Genistion and have been described as Vaccinio-Genistetum pilosae (Thébaud 1988). This community is relatively poor in species and is co-dominated by *Calluna vulgaris* and *Genista pilosa; Vaccinium myrtillus* is frequent but not abundant. A number of species characteristic of the higher altitudes are rare or lacking, namely *Trifolium alpinum, Alchemilla alpina, Allium victorialis, Veratrum albrum*, and *Vaccinium uliginosum; Gentiana lutea* occurs occasionally.

The vegetation of the ridge, as well as a small part of the vegetation of the plateaus (at relatively high altitude, slightly inclined), belong to the Genisto-Vaccinion (Braun-Blanguet 1926), and comprise two associations. The communities present on the plateaus and slopes (particularly on those with an eastern exposure, where influences of snow-cover are preponderant; see hereafter) have been described as Stachyo-Vaccinietum (Thébaud 1988). In our opinion however, this community should be considered as a subassociation of a broader association which is as yet undescribed, but which we provisionally refer to as Allio-Vaccinietum. The stands are co-dominated by *Vaccinium myrtillus* and *Vaccinium uliginosum; Calluna vulgaris* occurs with relatively low cover-abundance values. The subalpine character of the vegetation is apparent, not only from the occurrence of orophytes, but also from the presence of species restricted to a relatively high atmospheric humidity. At lower altitude, these species are more or less confined to forests, e.g. *Anemone nemorosa, Convallaria majalis, Maianthemum bifolium, Melampyrum pratense*, and *Polygonatum verticillatum*. As such, this is an example of the 'Law of the relative habitat constancy' (Walter & Straka 1970). The Allio-Vaccinietum includes four sub-associations, namely (1) typicum, (2) vaccinietosum uliginosi at high altitude, (3) veratretosum at places with scattered rocks, and (4) stachyetosum on steep and relatively warm slopes.

The wind-exposed tops carry a community which has provisionally been named Alchemillo saxatilis-Vaccinietum uliginosi (Thébaud 1988). The vegetation is low; it is dominated by *Calluna vulgaris* and (to a lesser extent) *Vaccinium uliginosum;* character-istic species are *Trifolium alpinum, Alchemilla alpina, Viola lutea*, and *Antennaria dioica*. Where the vegetation cover is relatively open, a number of lichens stand out, e.g. *Cetraria islandica, Cladonia chlorophaea, Cladonia pyxidata*, and *Cladonia furcata*.

METHODS

Transects

The transects were plotted out perpendicularly to the zonation of vegetation, comprising the dwarf-shrub heathland, the transition zone, and the adjacent community. Their surface varies between $12 \times 4 \text{ m}^2$ and $20 \times 4 \text{ m}^2$. In order to record the distribution pattern of the species in detail, the cover of each species in each square metre of the transect has been estimated, using a scale based on that of Hult–Sernander (Hult 1881, revised by Sernander 1898; see also Du Rietz 1921, and Braun-Blanquet 1951). Detailed analysis was
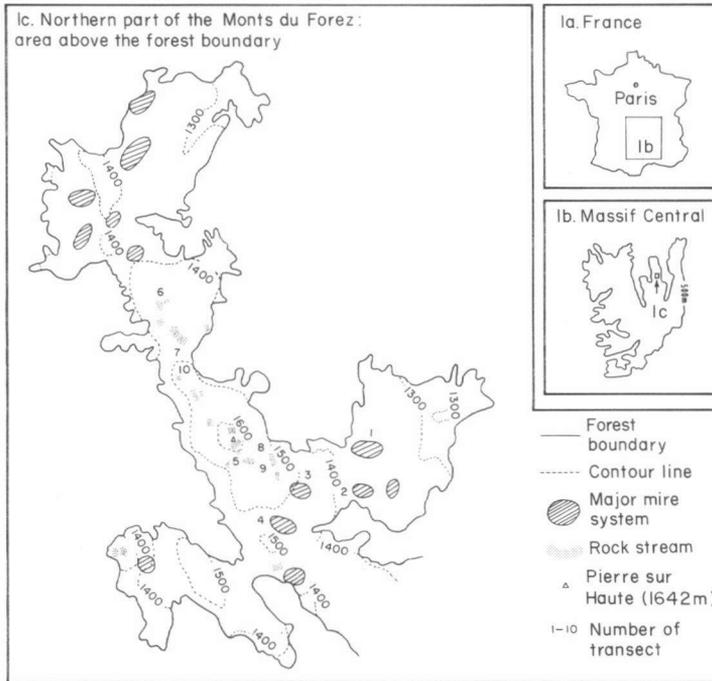
Fig. 1. Situation of study area, within France and the Massif Central. The location of the transects is indicated in Fig. 1(c). 1. Gourds des Aillères, 2. Jasseries de Colleigne, 3. Pré Mouray, 4. Source de Lignon, 5. Rocher de la Chaize, 6. Peyre Mayou, 7. Procher, 8. Corniche-en-Coeur I, 9. Corniche-en-Coeur II, 10. Col de la Chamboite.

carried out on vascular plants only. Species nomenclature follows *Flora Europaea* (Tutin *et al.* 1964, 1968, 1972, 1976, 1980).

In the summer of 1987, 10 transects were selected within the area above the forest boundary (see Fig. 1c), according to the following criteria: (i) the transects should represent the diversity of heathland types in the area of investigation, (ii) the variation in vegetation types to which the heathlands form spatial transitions has to be reflected, (iii) each transect should comprise a well-developed transition zone (lacking local disturbances), flanked by more or less homogeneous stands of a heathland and adjacent community, respectively. Four transects deal with the transition towards ombrotrophic peatlands (all situated on plateaus, two at lower and two at higher altitude; Fig. 1c, 1–4), and six deal with the transition towards communities dominated by tall forbs (all situated on the slopes or the top of the ridge). Of the latter, three transects concern thermophilous communities on rock streams (Calamagrostion; Fig. 1c, 5–7), and three other ones concern hygrophilous communities just below the forest boundary as well as in shrubland above it (Adenostylion alliariae; Fig. 1c, 8–10). Calamagrostion and Adenostylion are attributed to the class Betulo-Adenostyletea. The heathland–peatland transect comprises three types of vegetation; apart from the heathland and peatland communities a grassland vegetation in between can be recognized. The peatland vegetation belongs to the Sphagnion magellanici (class Oxycocco-Sphagnetea).

Analyses

In this study we dealt with four types of vegetation (heathland, grassland, peatland, and communities dominated by tall forbs), each characterized by a specific horizontal arrange-
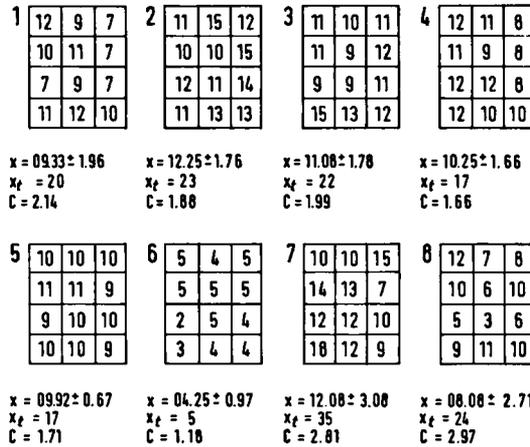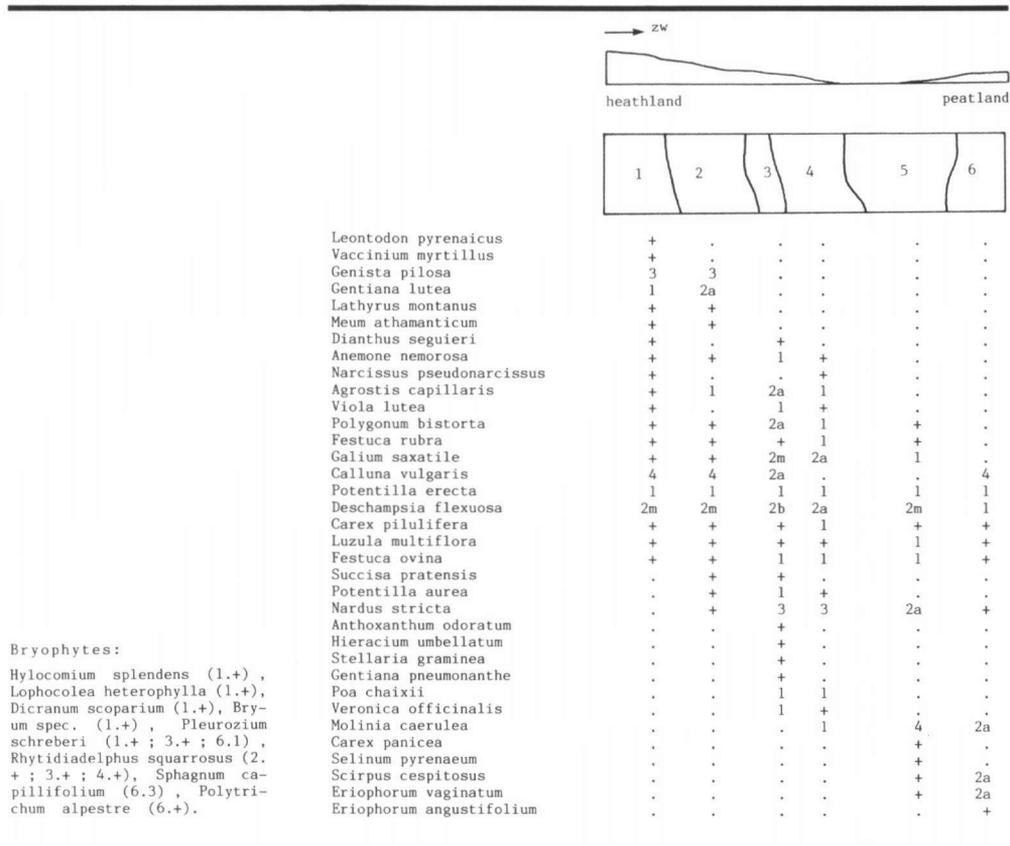
1

12	9	7
10	11	7
7	9	7
11	12	10

$x = 09.33 \pm 1.96$
$x_t = 20$
$c = 2.14$

2

11	15	12
10	10	15
12	11	14
11	13	13

$x = 12.25 \pm 1.76$
$x_t = 23$
$c = 1.88$

3

11	10	11
11	9	12
9	9	11
15	13	12

$x = 11.08 \pm 1.78$
$x_t = 22$
$c = 1.99$

4

12	11	8
11	9	8
12	12	8
12	10	10

$x = 10.25 \pm 1.66$
$x_t = 17$
$c = 1.66$

5

10	10	10
11	11	9
9	10	10
10	10	9

$x = 09.92 \pm 0.67$
$x_t = 17$
$c = 1.71$

6

5	4	5
5	5	5
2	5	4
3	4	4

$x = 04.25 \pm 0.97$
$x_t = 5$
$c = 1.18$

7

10	10	15
14	13	7
12	12	10
18	12	9

$x = 12.08 \pm 3.08$
$x_t = 35$
$c = 2.81$

8

12	7	8
10	6	10
5	3	6
9	11	10

$x = 08.08 \pm 2.71$
$x_t = 24$
$c = 2.97$

Fig. 2. Species diversity and variation in the various types of vegetation (Monts du Forez). Indicated are: species number/square metre, mean number of species with standard deviation (x), total number of species (x_t), and quotient between total number and mean number of species (c). 1 = Heathland community of the plateau, Gourds des Aillères, 1–3 m; 2 = Heathland community of the top of the ridge, Rocher de la Chaize 1–3 m; 3 = Heathland community of the slope of the ridge, Col de la Chamboi-te, 1–3 m; 4 = *Nardus* grassland, Gourdes des Aillères, 15–17 m; 5 = *Molinia* grassland, Gourds des Aillères, 10–12 m; 6 = Peatland, Jasseries de Colleigne, 18–20 m; 7 = Calamagrostion, Rocher de la Chaize, 12–14 m; 8 = Adenostylion, Corniche-en-Coeur I, 9–11 m.

ment of the participating species ('granularity'). The detailed analyses of the distribution patterns of the species however, must be carried out for each type of vegetation in one and the same way within each transect, to enable comparison.

We studied the distribution patterns of the species using a 1 × 1 square metre grid. This choice was based on field experience and literature (e.g. van der Maarel & Leertouwer 1967; Londo 1971; Thalen 1971; Sykora 1986). These references include various types of grassland vegetation. Since dwarf-shrub communities may be expected to present a coarser granulation than grassland, it may be concluded that the 1-metre scale will suffice. We used the following procedure to test the reliability of this scale. First, the number of species/square metre within each type of vegetation must be more or less constant. This however, does not guarantee a floristic homogeneity, as the individual sample plots within each type of vegetation can be colonized by different species. A second condition is that the quotient of the total number of species and the mean number of species/square metre has to be low; the value 'one' indicates absolute similarity. We calculated these parameters for each vegetation type by analysing three consecutive metres of the transect ($12 \, m^2$). Figure 2 shows that the peatland and grassland vegetation do have a (very) constant number of species/square metre, together with a low quotient. To a certain extent, this also applies to the heathland vegetation. The communities dominated by tall forbs, however, have a considerably higher quotient, whereas their number of species/square metre is much less constant.

Mathematically, the transects can be analysed in three ways.

1. The presence or absence of species is considered to be of central importance. For each linear metre of the transect ($4 \, m^2$) only the species presence is regarded.

2. The frequency of species is thought to be relevant. For each linear metre of the transect the number of square metres in which a species occurs is taken into consideration.

3. The cover of species is emphasized. Not only is the occurrence of the species in each square metre calculated but also the estimated quantity (cover) of each species.

	1	2	3	4	5	6
Leontodon pyrenaicus	+	.	.	.	.	.
Vaccinium myrtillus	+	.	.	.	.	.
Genista pilosa	3	3	.	.	.	.
Gentiana lutea	1	2a	.	.	.	.
Lathyrus montanus	+	+	.	.	.	.
Meum athamanticum	+	+	.	.	.	.
Dianthus seguieri	+	.	+	.	.	.
Anemone nemorosa	+	+	1	+	.	.
Narcissus pseudonarcissus	+	.	.	+	.	.
Agrostis capillaris	+	1	2a	1	.	.
Viola lutea	+	.	1	+	.	.
Polygonum bistorta	+	+	2a	1	+	.
Festuca rubra	+	+	+	1	+	.
Galium saxatile	+	+	2m	2a	1	.
Calluna vulgaris	4	4	2a	.	.	4
Potentilla erecta	1	1	1	1	1	1
Deschampsia flexuosa	2m	2m	2b	2a	2m	1
Carex pilulifera	+	+	+	1	+	+
Luzula multiflora	+	+	+	+	1	+
Festuca ovina	+	+	1	1	1	+
Succisa pratensis	.	+	+	.	.	.
Potentilla aurea	.	+	1	+	.	.
Nardus stricta	.	+	3	3	2a	+
Anthoxanthum odoratum	.	.	+	.	.	.
Hieracium umbellatum	.	.	+	.	.	.
Stellaria graminea	.	.	+	.	.	.
Gentiana pneumonanthe	.	.	+	.	.	.
Poa chaixii	.	.	1	1	.	.
Veronica officinalis	.	.	1	+	.	.
Molinia caerulea	.	.	.	1	4	2a
Carex panicea	.	.	.	.	+	.
Selinum pyrenaeum	.	.	.	.	+	.
Scirpus cespitosus	.	.	.	.	+	2a
Eriophorum vaginatum	.	.	.	.	+	2a
Eriophorum angustifolium	.	.	.	.	.	+

Bryophytes:

Hylocomium splendens (1.+), Lophocolea heterophylla (1.+), Dicranum scoparium (1.+), Bryum spec. (1.+), Pleurozium schreberi (1.+ ; 3.+ ; 6.1), Rhytidiadelphus squarrosus (2.+ ; 3.+ ; 4.+), Sphagnum capillifolium (6.3), Polytrichum alpestre (6.+).

Fig. 3. Transition between heathland community of the plateau (Vaccinio-Genistetum pilosae) and peatland community at Gourds des Aillères (Monts du Forez; transect 1). Signs and figures according to the Braun-Blanquet scale (Braun-Blanquet 1951), as refined by Barkman, Doing and Segal (1964).

In this paper, the methods for calculation of the various quantitative characteristics (species diversity, floristic fall, dissimilarity) will be mentioned and explained in the paragraphs dealing with these aspects.

RESULTS

Description of transects

As a treatment of all transects would require too much space, examples of the various boundary situations, namely heathland–peatland (transect 1), heathland-Calamagrostion (transect 5) and heathland-Adenostylion (transect 8), are presented. This selection comprises the overall variation in vegetation and serves to analyse quantitatively the characteristics examined. Figures 3–5 comprise the relief and vegetation maps, as well as the phytosociological tables. The vegetation of each transect has been described, using the Braun-Blanquet scale as refined by Barkman *et al.* (1964; see also Westhoff & Van der Maarel 1973). In Figure 6 the distribution patterns of the different elements are given: stones, growth forms (shrubs, dwarf-shrubs, graminoids and forbs), and a selection of the species.
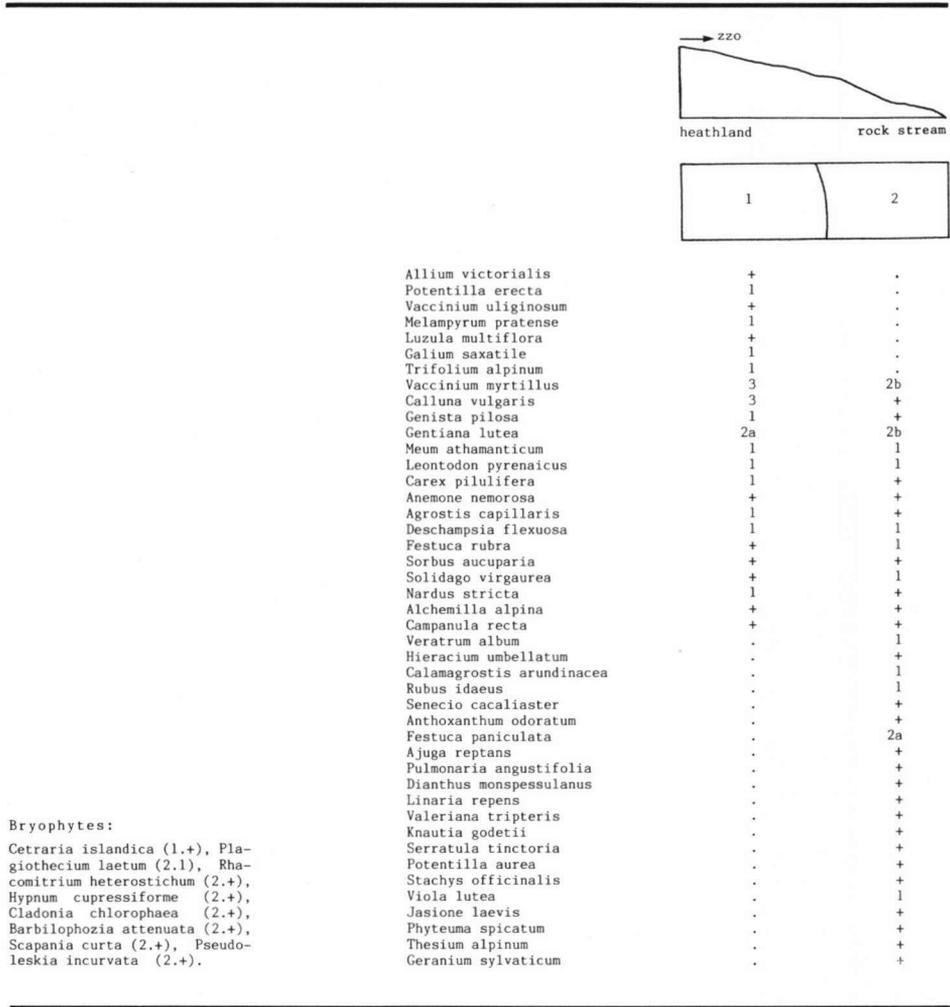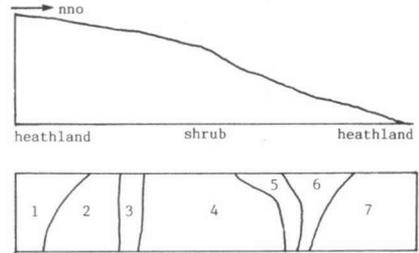
	1	2
Allium victorialis	+	.
Potentilla erecta	1	.
Vaccinium uliginosum	+	.
Melampyrum pratense	1	.
Luzula multiflora	+	.
Galium saxatile	1	.
Trifolium alpinum	1	.
Vaccinium myrtillus	3	2b
Calluna vulgaris	3	+
Genista pilosa	1	+
Gentiana lutea	2a	2b
Meum athamanticum	1	1
Leontodon pyrenaicus	1	1
Carex pilulifera	1	+
Anemone nemorosa	+	+
Agrostis capillaris	1	+
Deschampsia flexuosa	1	1
Festuca rubra	+	1
Sorbus aucuparia	+	+
Solidago virgaurea	+	1
Nardus stricta	1	+
Alchemilla alpina	+	+
Campanula recta	+	+
Veratrum album	.	1
Hieracium umbellatum	.	+
Calamagrostis arundinacea	.	1
Rubus idaeus	.	1
Senecio cacaliaster	.	+
Anthoxanthum odoratum	.	+
Festuca paniculata	.	2a
Ajuga reptans	.	+
Pulmonaria angustifolia	.	+
Dianthus monspessulanus	.	+
Linaria repens	.	+
Valeriana tripteris	.	+
Knautia godetii	.	+
Serratula tinctoria	.	+
Potentilla aurea	.	+
Stachys officinalis	.	+
Viola lutea	.	1
Jasione laevis	.	+
Phyteuma spicatum	.	+
Thesium alpinum	.	+
Geranium sylvaticum	.	+

Bryophytes:

Cetraria islandica (1.+), Plagiothecium laetum (2.1), Rhacomitrium heterostichum (2.+), Hypnum cupressiforme (2.+), Cladonia chlorophaea (2.+), Barbilophozia attenuata (2.+), Scapania curta (2.+), Pseudoleskia incurvata (2.+).

Fig. 4. Transition between heathland community of the top of the ridge (Alchemillo saxatilis-Vaccinietum uliginosi) and Calamagrostion community at Rocher de la Chaize (Monts du Forez; transect 5). Signs and figures according to the Brauns-Blanquet scale (Braun-Blanquet 1951), as refined by Barkman, Doing and Segal (1964).

Transect 1 (Fig. 3) shows a transition between a heathland community of the plateau (Vaccinio-Genistetum pilosae) and a peatland community. It is situated on the eastern side of Gourds des Aillères, at an altitude of 1340 m. The length of the transect is 20 m. The first 7 m are slightly inclined (5°) with a southwestern exposure and comprises heathland vegetation, co-dominated by *Calluna vulgaris* and *Genista pilosa*. The transition zone, rather broad (7–17 m) and more or less bowl-shaped, consists of two parts, one adjacent to the heathland and dominated by *Nardus stricta*, and one adjacent to the peatland and dominated by *Molinia caerulea*. The last 3 m of the transect are domed and include the peatland vegetation with *Sphagnum* hummocks, dominated by *Calluna vulgaris*.

Transect 5 (Fig. 4) represents a transition between a heathland community on the top of the ridge (Alchemillo saxatilis-Vaccinietum uliginosi) and a Calamagrostion community.

Bryophytes:

Dicranum scoparium (1.+; 3.+; 4.+; 5.+; 6.+; 7.+) , Plagiothecium succulentum (1.+; 2.+; 4.+; 5.+), Lophocolea heterophylla (1.+; 2.+; 3.+; 4.+) , Rhytidiadelphus triquetus (1.+ 6.+0 , Ditrichum heteromallum (1.+; 6.+; 7.+), Brachythecium starkei (1.+) , Drepanocladus uncinatus (2.+; 6.+; 7.+), Pogonatum nanum (2.+; 3.+), Brachythecium reflexum (2.+; 3.+) , Hypnum cupressiforme (3.+ ; 5.+), Rhytidiadelphus squarrosus (3.+), Pseudoleskia incurvata (3.+; 4.+) , Rhytidiadelphus loreus (3.+; 4.+; 5.+), Cetraria islandica (3.+; 4.+), Isobachus bicrenatus (3.+) , Barbilophozia lycopodioides (3 .+), Cladonia chlorophaea (3.+ ; 5.+), Isothecium alopecuroides (3.+; 4.+; 5.+) , Diplophyllum obtusifolium (3.+; 4. +), Polytrichum formosum (4.+) , Rhacomitrium heterostichum (4.+), Calypogeia neesiana (4. +), Cladonia squamosa (5.+), Paraleucobryum longifolium (5. +), Pleurozium schreberi (7.+)

	1	2	3	4	5	6	7
Solidago virgaurea	+	.	.	.	.	.	.
Alchemilla alpina	+	.	.	.	.	.	.
Genista pilosa	+	+	.	.	.	.	.
Sanguisorba officinalis	+	2a	.	.	.	.	.
Carex caryophyllea	.	.	.	.	.	.	+
Luzula multiflora	.	+	.	.	.	.	+
Nardus stricta	1	.	.	.	.	2a	2b
Trifolium alpinum	1	.	.	.	.	1	1
Carex pilulifera	1	+	.	.	.	+	+
Vaccinium uliginosum	2a	2a	.	.	.	+	2a
Calluna vulgaris	4	2a	+	.	.	.	2b
Melampyrum pratense	.	1	+	.	.	+	1
Thesium alpinum	.	+	.	.	.	+	.
Hieracium prenanthoides	.	.	+	.	+	.	.
Anthoxanthum odoratum	.	.	.	.	+	+	.
Knautia godetii	.	.	.	.	+	+	.
Viola sylvatica	.	.	.	.	+	+	.
Potentilla aurea	.	.	.	.	+	+	.
Linaria repens	.	.	.	.	+	.	.
Narcissus pseudonarcissus	.	.	.	.	.	.	1
Potentilla erecta	1	2a	.	.	+	+	1
Viola lutea	+	+	.	.	+	.	+
Leontodon pyrenaicus	+	1	.	.	+	1	1
Campanula recta	.	+	+	.	+	+	+
Festuca rubra	+	1	+	.	1	+	1
Agrostis capillaris	+	1	+	.	+	+	1
Anemone nemorosa	1	1	+	.	+	+	+
Gentiana lutea	2a	2b	+	.	+	2b	2b
Meum athamanticum	+	+	+	.	+	+	+
Vaccinium myrtillus	+	2b	2a	+	+	2b	2b
Deschampsia flexuosa	2m	2a	2b	1	1	1	1
Veratrum album	+	+	+	+	2a	2a	1
Polygonum bistorta	.	+	1	1	+	+	+
Galium saxatile	.	+	+	+	2a	2a	1
Senecio cacaliaster	.	.	.	+	.	.	+
Rubus idaeus	+	.	2a	2b	+	.	.
Sorbus aucuparia	.	.	2a	4	+	2a	.
Rumex arifolius	.	.	.	2b	+	+	.
Geranium sylvaticum	.	+	1	+	+	.	.
Oxalis acetosella	.	.	.	+	+	.	.
Calamagrostis arundinacea	.	.	2b	+	.	.	.
Athyrium distentifolium	.	.	.	+	.	.	.
Dryopteris filix-mas	.	.	.	2b	.	.	.
Athyrium filix-femina	.	.	.	2a	.	.	.
Hypericum maculatum	.	.	.	+	.	.	.
Epilobium angustifolium	.	.	.	1	.	.	.

Fig. 5. Transition between heathland community of the slope of the ridge (Allio-Vaccinietum) and Adenostylion community at Corniche-en-Coeur (Monts du Forez; transect 8). Signs and figures according to the Braun-Blanquet scale (Braun-Blanquet 1951); as refined by Barkman, *et al.* (1964).

It is situated on the upper-side of Rocher de la Chaize, some hundreds of metres to the south of Pierre-sur-Haute, at an altitude of 1600 m. The length of the south-facing transect (inclination 15°) measures 14 m. The first half comprises the heathland vegetation, co-dominated by *Calluna vulgaris* and *Vaccinium myrtillus*, and characterized by *Vaccinium uliginosum, Alchemilla alpina*, and *Trifolium alpinum*. The second half comprises the Calamagrostion stand. Here, the slope is studded with boulders, some of them with a diameter of more than 2 m. *Vaccinium myrtillus, Gentiana lutea, Calamagrostis arundinacea*, and *Festuca paniculata* are conspicuous.

Figure 6. Distribution patterns of different elements.
(Cover values: 0-1% ●, 1-3% ○, 3-6% ×, 6-13% ⊠, 13-25% ※, 25-50% ▧, 50-75% ▨, 75-100% ■)
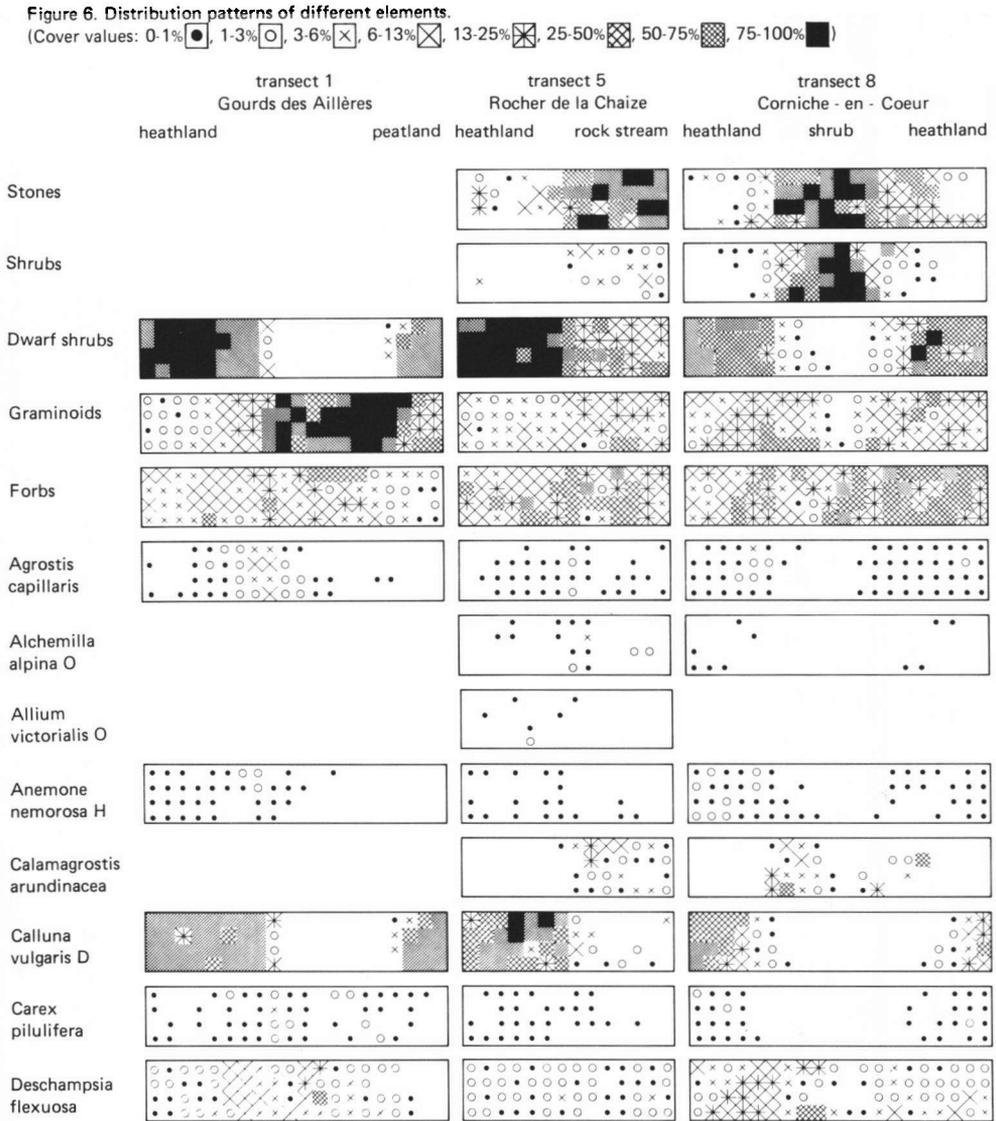
Fig. 6.

Transect 8 (Fig. 5) represents a transition between a heathland community on the slope of the ridge (Allio-Vaccinietum vaccinietosum uliginosi) and an Adenostylion community. It is situated near Corniche-en-Coeur, on the eastern slope at an altitude of 1540 m, where snow is accumulating during winter (exposition NNE, inclination 10–40°). The length of the transect measures 20 m. The central part (7–13 m) is bouldery and covered by *Sorbus* shrub with species like *Rubus idaeus*, *Rumex arifolius*, *Dryopteris filix-mas*, and *Athyrium filix-femina*. The heathland vegetation is present on both sides of the shrubland; *Vaccinium uliginosum*, *Vaccinium myrtillus*, *Calluna vulgaris*, and *Gentiana lutea* are the most conspicuous species.
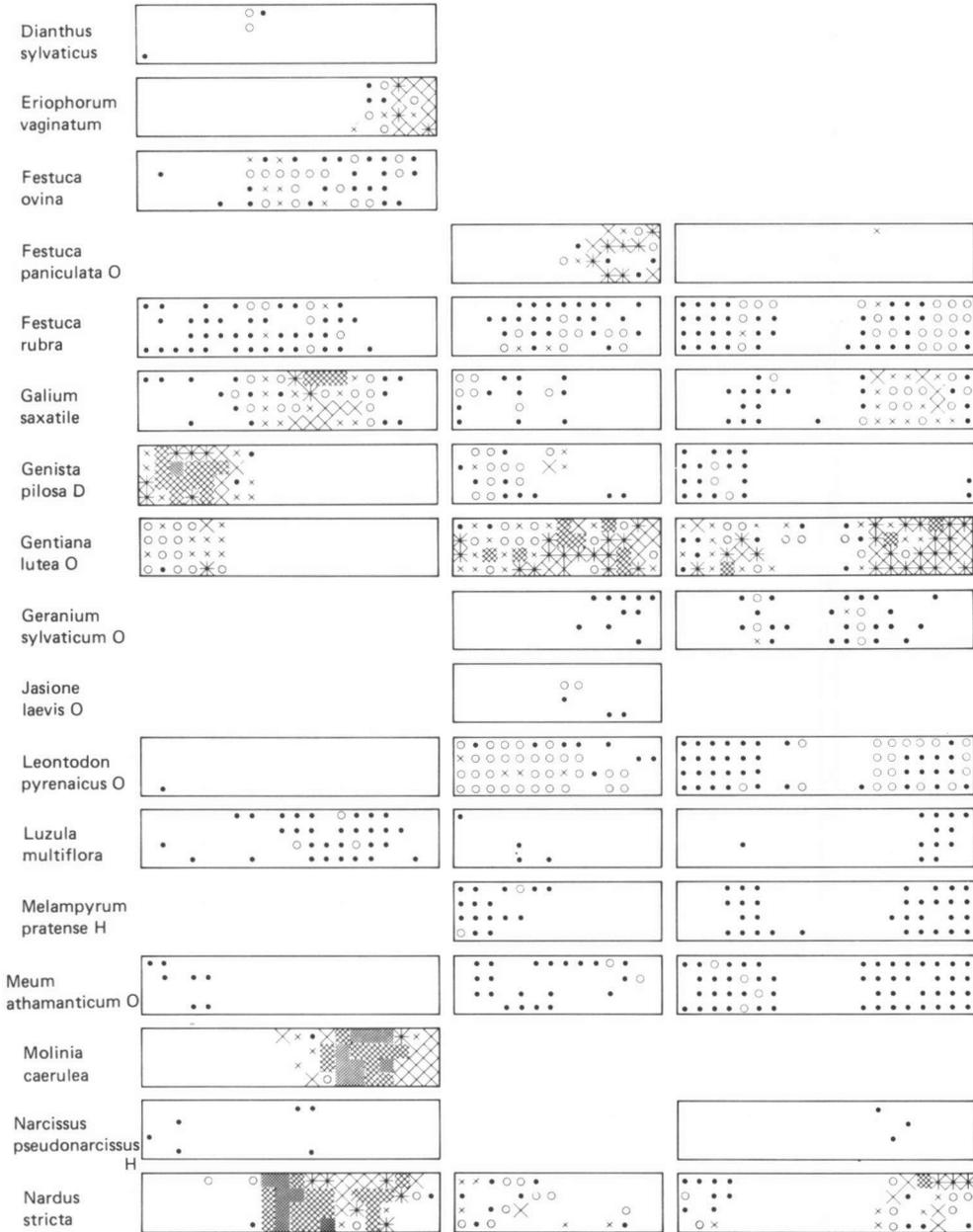
Fig. 6. Continued

Similarity between heathlands and adjacent communities

The similarity between heathland and adjacent communities was analysed by comparing the floristic composition of the first 3 linear metres of the heathland stand (12 quadrats) with 3 linear metres of the adjacent community across. The similarity index (Sørensen 1948) of these two parts of the transect was calculated: $S = 2c/(a+b)$, where a and b are
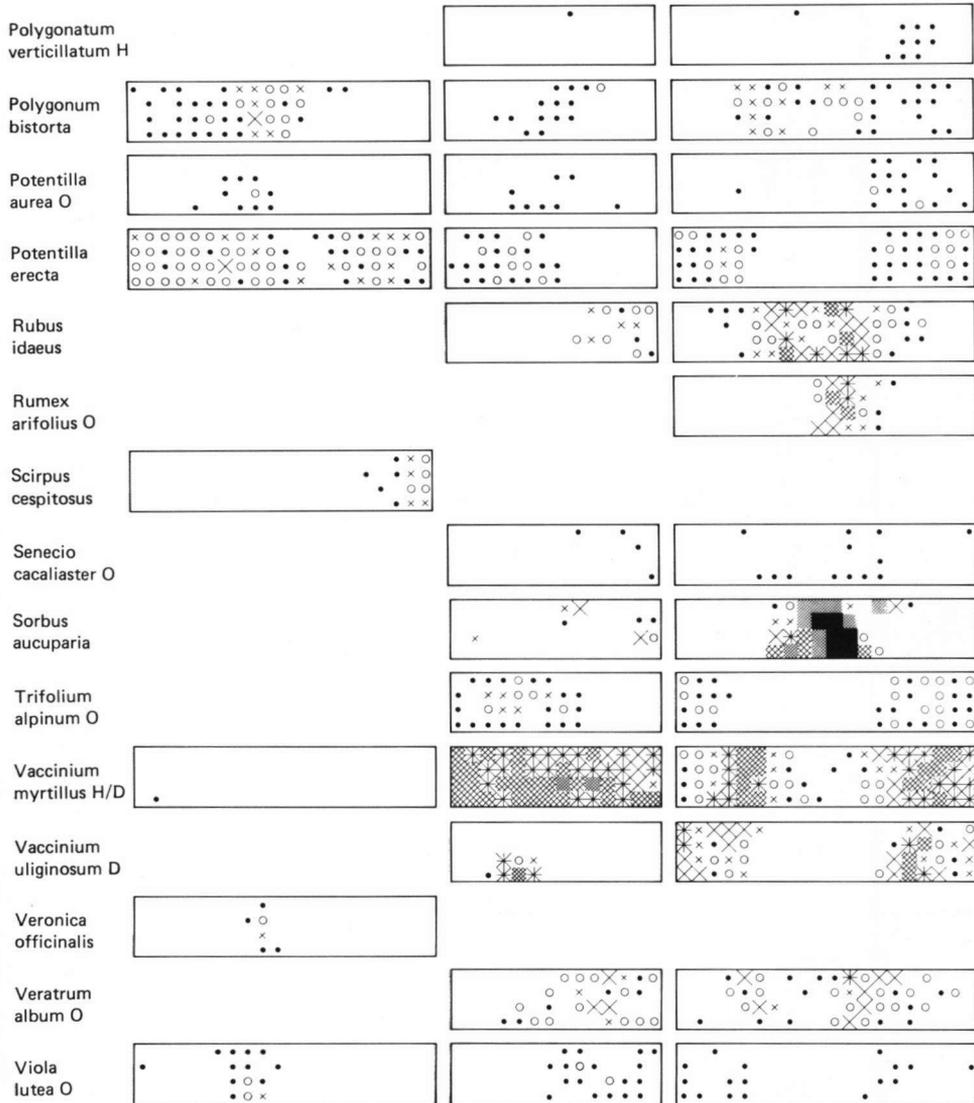
Fig. 6. Distribution patterns of different plant species, life forms and stones. 'Orophytes', 'humidity indicators', and 'dwarfshrub species' are indicated with the symbols O, H, and D.

numbers of species in each of the two parts of the transect and c is the number of species these parts have in common. Furthermore, the distribution of the species in the heathland part and in the opposite part, respectively, was investigated for each (linear) metre of the transect. A distinction was made between species that are exclusive for one of the two homogeneous stands and species that also occur in the rest of the transect. The second group can be divided into species that are present or absent in the other two homogeneous stands. The results are presented in Fig. 7.

The various communities all have a notable number of species in common. The similarity between heathland and Calamagrostion ($S = 0.56$) proves to be the most
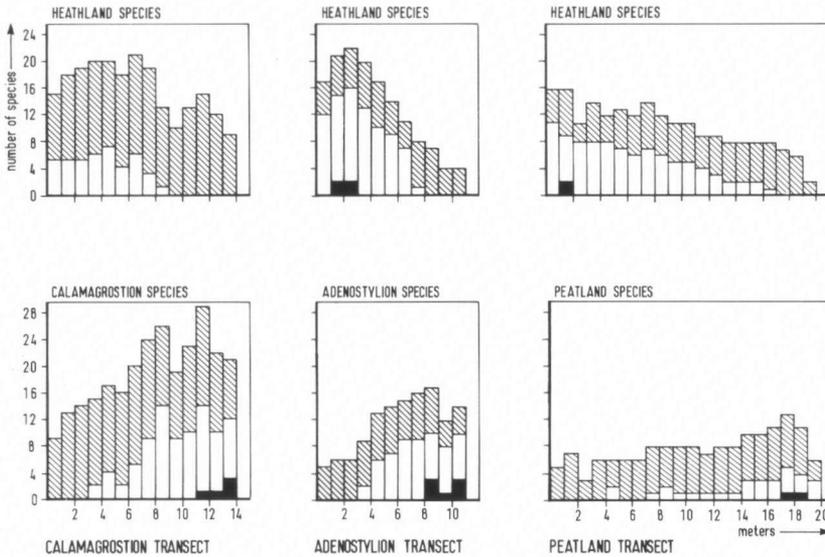
Fig. 7. Similarity (after Sørensen 1948) between heathlands and adjacent communities, respectively Calamagrostion (Rocher de la Chaize), Adenostylion (Corniche-en-Coeur I) and peatland (Gourds des Aillères; Monts du Forez). Exclusive species are indicated in black; species that also occur in the rest of the transect are divided in species that are (white) and species that are not (shaded) present in the other of the two homogeneous stands.
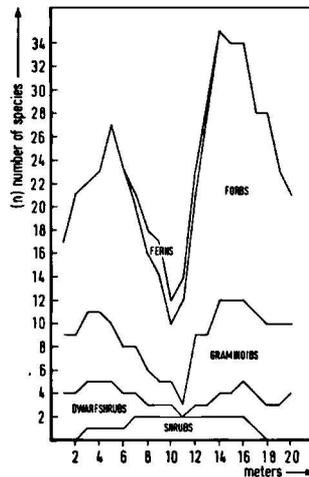
Fig. 8. Spatial variation in species diversity in a transition between heathland and Adenostylion (Corniche-en-Coeur I, Monts du Forez).

pronounced, whereas heathland and Adenostylion show the greatest differences ($S = 0.29$). The similarity index of the heathland–peatland transect is 0.42. In the heathland–Calamagrostion-transect, the heathland vegetation has no characteristic species and the mean number of mutual species (per linear metre of transect) here is larger than in the other transects (10, six, and six respectively). The boundary situation between heathland and Adenostylion is marked by many species that occur in either heathland and transition
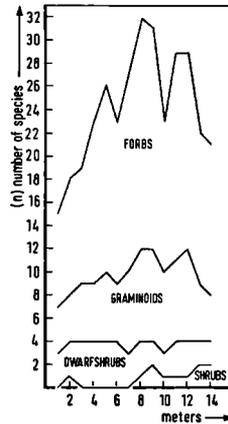
Fig. 9. Spatial variation in species diversity in a transition between heathlands and Calamagrostion (Rocher de la Chaize, Monts du Forez).
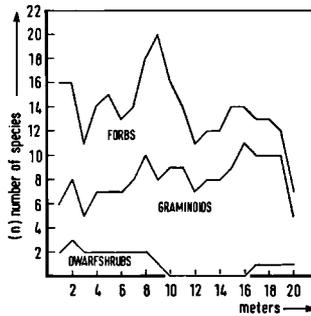
Fig. 10. Spatial variation in species diversity in a transition between heathland and peatland (Gourds des Aillères, Monts du Forez).

or Adenostylion and transition, but that are missing in the other part of the transect; the transition shows conspicuous changes.

Spatial variation in species diversity and alterations in floristic composition

In a study on the variation in some saltmarsh and dune vegetation in The Netherlands, Thalen (1971) compared a number of methods that analyse species diversity, namely number of species/area, the diversity index proposed by Williams (Williams 1964), the formula of Margalef (Margalef 1958), and the formula of Shannon (Shannon & Weaver 1964). The last two methods are based on the numbers of individuals of each species and are labour-intensive. In the present research, changes in species diversity were determined by calculating the number of species/linear metre of transect. The results are given in Figs 8–10.

In the figures, distinction has been made for a number of growth forms: shrubs, dwarf-shrubs, graminoids, forbs, and ferns. The diagrams show some distinct peaks. Comparison with Figs 2–4 demonstrates that these peaks correspond to vegetation boundaries; comparison with Fig. 5 shows their correspondence, more specifically, with

important changes in the dominance of species or growth forms (shrubs, dwarf-shrubs, graminoids). Some striking exceptions however, have been noted.

The heathland–Adenostylion transect (Corniche-en-Coeur I, Fig. 8) can be interpreted easily. The transitions between heathland and shrub are marked by two sharp peaks ($n = 27, 35$), that correspond well with changes in the dominant species. The mean number of species in the heathland is 21, that in the Adenostylion is 14. The other heathland–Adenostylion transects (Corniche-en-Coeur II, Col de la Chamboite) show the same tendencies.

In the heathland–Calamagrostion transect (Rocher de la Chaize, Fig. 9), the patterns in dominancy are less conspicuous, but here too some peaks are visible ($n_{max} = 32$). The differences in mean number of species between heathland and Calamagrostion, 17 and 24 respectively, are comparable with those between heathland and Adenostylion. As far as the Calamagrostion stand is concerned, the separate metres of the transect show great differences in the number of species, phenomenon which can also be seen in the heathland–Calamagrostion transects at Procher and Peyre Mayou. The probable explanation is the disproportionate distribution of underlying and outcropping stones.

The diagrams of the heathland–peatland transects are less easy to understand. Although clear changes in dominant species are present, they are not always marked by distinct peaks in species number. In the heathland–peatland transect of Gourds des Aillères (Fig. 10), two peaks can be seen, the first one at 9 m, the second one (less conspicuous) at 15–16 m. The transition between the heathland and grassland ($n = 20$) is more accentuated than the transition between grassland and peatland ($n = 14$). In other heathland–peatland transects however, the transition between grassland and peatland (Pré Mouray and particularly Source de Lignon) is more clear and determined by a larger number of (graminoid) species. The mean number of species in the different communities is relatively low and decreases still more in the peatland zone.

In the present study, alterations in floristic composition along the transects were determined using four approaches. In the first the prime question is whether a species is present or not ('qualitative'): $I = (a + b) - 2c$, where a and b are the numbers of species in each of two adjacent metres of a transect and c is the number of species these metres have in common (see Thalen 1971). In the second approach, the number of square metres for each linear metre of the transect in which a species occurs is taken into account ('quantitative'). In the third, instead of single metres, couples of metres were compared. Floristic differences are recognized only when a species is absent in one of the two couples; if so, the number of square metres in which the species occurs is counted (semi-quantitative'). This approach was followed in order to study the effects caused by the granularity of the vegetation and the isolated occurrence of species. The fourth approach (dissimilarity) gives information on changes in species composition in relation to the number of species present: $d = 1 - 2c/(a + b)$. In communities poor in species, small differences in floristic-fall may cause a considerable dissimilarity. The results are presented in Figs 11–13.

In the upper diagrams, the floristic-fall (qualitative) is further divided in the number of species that have increased and decreased. The mirror symmetry shows that, often, the 'loss' of a species is compensated for by the establishment of a new one. This phenomenon is probably connected with the availability of a limited amount of space. In the bar diagrams the data are transformed; for each transect, the highest value is set at 10, to which all other values are (linear) referred.

The various approaches give an insight into the floristic variation within the transects. The transition between heathland and Adenostylion (Fig. 11) shows two clear boundaries
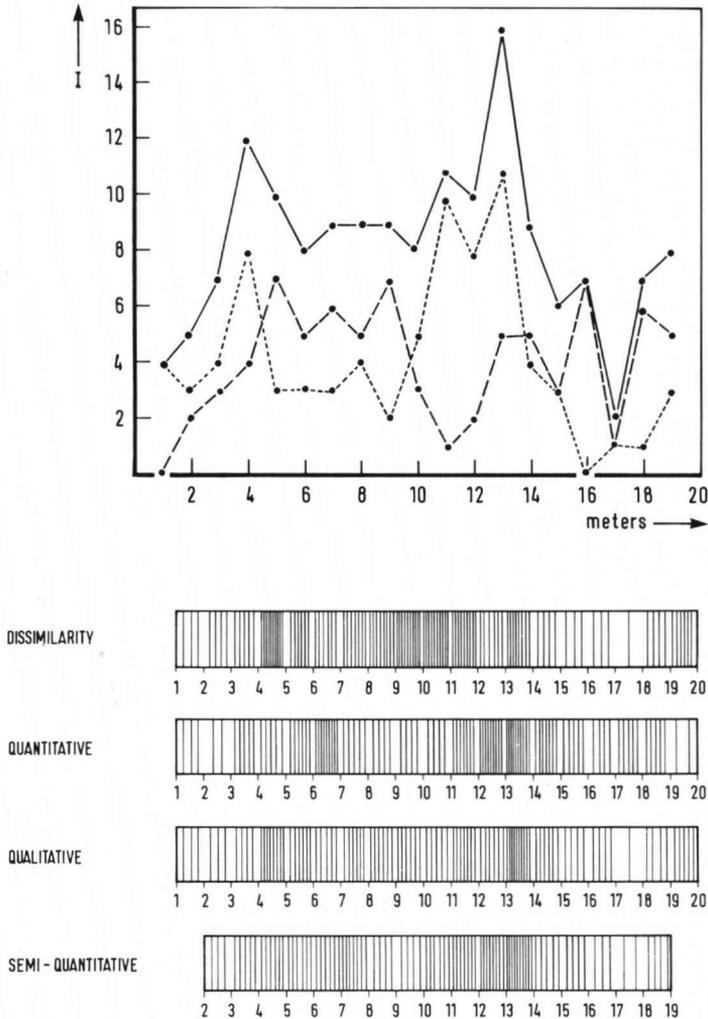
Fig. 11. Floristic fall and dissimilarity in a transition between heathland and Adenostylion (Corniche-en-Coeur I, Monts du Forez). In the upper diagram, the floristic fall (qualitative) is divided into the number of species that increased (. . .) and decreased (– – –). For calculations and transformation, see text.

with a high floristic-fall. The dissimilarity within the Adenostylion part of the transect (internal variation) is great. This also applies to the peatland part in the heathland–peatland transect. In this transect (Fig. 13), distinct boundaries are absent; the various approaches lead to different pictures. The transition between heathland and Calamagrostion (Fig. 12) shows one boundary and a continuing high floristic-fall in the Calamagrostion part of the transect, not necessarily dependent on changes in the total number of species (Fig. 7).

Communities that seem to be homogeneous may demonstrate a high floristic-fall, as can be seen in the dwarf-shrub heathland at Gourds des Aillères. It all depends on the granularity of the various components of the vegetation and the method of vegetation sampling. The heathland is characterized by a dense canopy of dwarf-shrubs, with other species (graminoids, forbs) scattered among them. In the 'semi-quantitative' approach, this
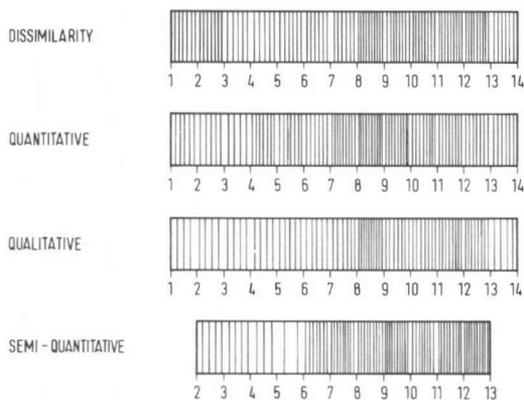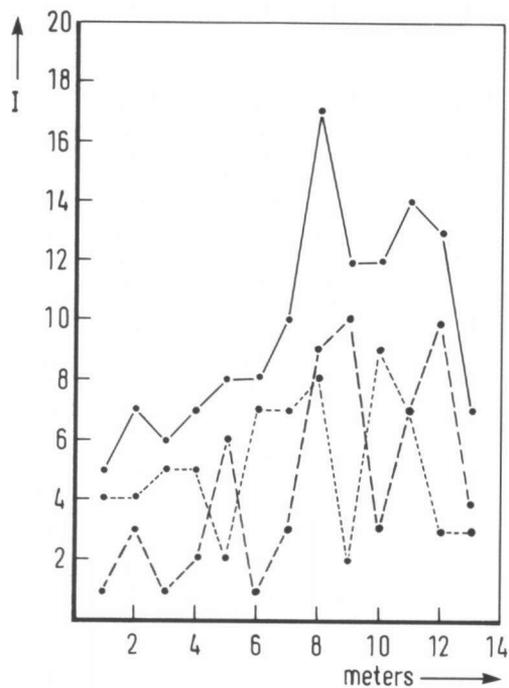
Fig. 12. Floristic fall and dissimilarity in a transition between heathland and Calamagrostion (Rocher de la Chaize, Monts du Forez). In the upper diagram, the floristic fall (qualitative) is divided into the number of species that increased (. . .) and decreased (– – –). For calculations and transformations, see text.

'heterogeneity' is eliminated, in contrast to the internal variation of the Calamagrostion stand. Using the $1 \times 1 \, \text{m}^2$ grid, the Calamagrostion vegetation appears to be a mosaic.

DISCUSSION

In the Monts du Forez, the variation in heathland types is expressed by the number of participating orophytes, the rate of occurrence of species indicating a high atmospheric
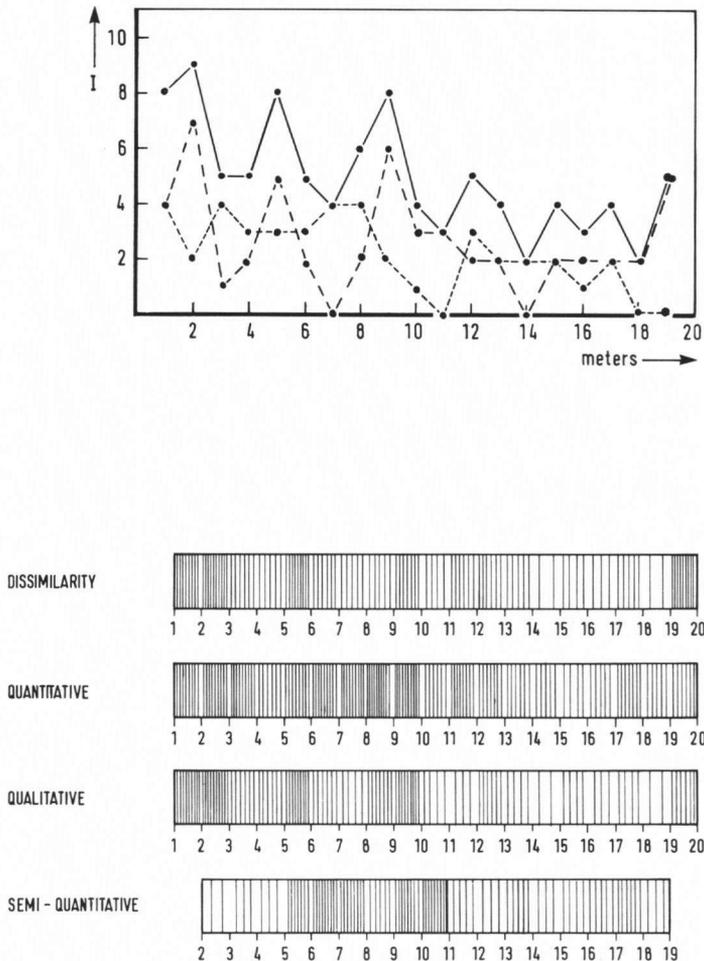
Fig. 13. Floristic fall and dissimilarity in a transition between heathland and peatland (Gourds des Aillères, Monts du Forez). In the upper diagram, the floristic fall (qualitative) is divided into the number of species that increased (. . .) and decreased (– – –). For calculations and transformations, see text.

humidity, and the distribution of the dwarf-shrub species. These parameters are used as a starting point for the discussion.

With respect to the orophytes, distinction can be made between species with a main distribution in the montane–subalpine zone for which we use the denomination 'katorophytes' (altitudinal optimum 700–1500 m) and species that are more or less confined to the alpine zone ('anorophytes'; optimum 1500–3000 m). *Meum athamanticum, Viola lutea, Campanula recta, Arnica montana*, and *Pseudorchis albida* are examples of the first ones; concerning the second group, *Leontodon pyrenaicus, Trifolium alpinum, Alchemilla alpina, Allium victorialis*, and *Veratrum album* can be mentioned (Fournier 1961; Guinochet & De Vilmorin 1973, 1975, 1978, 1982, 1984).

In the heathland communities, the contribution of the anorophytes is low. None are specific to heathland vegetation; most are characteristic of vegetation units of the class Betulo-Adenostyletea (J. H. J. Schaminée *et al.*, unpublished observations). The transects

confirm this phenomenon. It must be mentioned that the specific habitat where Betulo-Adenostyletea stands can be found in Western and Central Europe, is bound to mountain areas, and, unlike peatlands and heathlands, does not occur at lower altitudes. Of greater importance however, is the fact that Betulo-Adenostyletea communities, at least above the forest boundary, must be considered as a natural climax-vegetation. Carbiener (1969), for instance, refers to the Calamagrostion as 'primäre Hochgrasprärien' and 'Urwiesen'. Several of the anorophytes avoid the heathland vegetation almost completely. This concerns Adenostylion species (e.g. *Adenostyles alliariae, Athyrium distentifolium, Rumex arifolius*; see transect 8) as well as Calamagrostion species (e.g. *Festuca paniculata, Knautia godetii, Valeriana tripteris;* see transect 5). Some are almost exclusive of fringe situations. The best example is *Rosa pendulina; Geranium sylvaticum* and *Senecio cacaliaster* behave more or less similarly (see Fig. 6).

The orophytes, characteristic of the Calamagrostion and Adenostylion, that do occur in heathland vegetation are almost restricted to the Allio-Vaccinietum veratretosum. The transects show that the Calamagrostion and Adenostylion communities are rather isolated; usually, within a distance of 1–2 m of the shrubland or rock stream the distinctive species have disappeared. The floristic assemblage of such small fringes is not identical to that of the typical Allio-Vaccinietum veratretosum. Apparently, the Allio-Vaccinietum veratretosum is not merely a transitional type that can be found at the edges of well-developed stands dominated by tall forbs.

Leontodon pyrenaicus is a constant companion of all heathland types in the Monts du Forez, but its presence and cover-abundance are greatest in grasslands (see Hennekens *et al.* 1986; Thébaud 1988). The differential orophytes of the Alchemillo-Vaccinietum (*Trifolium alpinum* and *Alchemilla alpina*) are just as inexclusive. They also occur along paths and in snowbeds. The transects situated in Corniche-en-Coeur illustrate the affinity of *Alchemilla alpina* and *Trifolium alpinum* for areas with prolonged snow cover during spring and early summer. An open site is a prerequisite: the Sorbus shrubland in the middle of the transect is avoided completely. *Alchemilla alpina* can also grow on top of boulders with only a thin soil layer, as illustrated in transect 5 (Rocher de la Chaize; see Fig. 6).

In the Monts du Forez, many species can be found that are bound to a relatively high atmospheric humidity (*Anemone nemorosa, Convallaria majalis, Maianthemum bifolium, Melampyrum pratense, Narcissus pseudonarcissus, Polygonatum verticillatum* and *Stellaria holostea*). As mentioned before, they are generally characteristic of forest vegetation (Oberdorfer 1957; Ellenberg 1978). If we consider their ecological indication value, most are shade-tolerant and anatomically hygro- to mesomorphic (Ellenberg, 1974). Their distribution seems to be more determined within the Monts du Forez by microclimatic than by macroclimatic factors. Those species do not have their main distribution on the rainy west side of the ridge (as might be expected), but on the relatively warm and dry east-facing slopes. Which dwarf-shrub species dominates the vegetation is of crucial importance. The dense foliage of *Vaccinium myrtillus* and *Vaccinium uliginosum* protects the aforementioned species from desiccation, unlike the small leaflets of *Calluna vulgaris* and *Genista pilosa*. The ultimate explanation can be found in the disproportionate distribution of snow during spring and early summer. Snow accumulates on the slopes with an eastern exposure, which has a major impact on the rate of dominance of the dwarf-shrub species. *Vaccinium myrtillus* and *Vaccinium uliginosum* are strongly favoured, whereas *Calluna vulgaris* and *Genista pilosa* cannot endure much snow (J. H. J. Schaminée *et al.*, unpublished observations).

The preference of the 'humidity indicators' for communities dominated by *Vaccinium* (Allio-Vaccinietum) can be seen from phytosociological tables (Hennekens *et al.* 1986; Thébaud 1988). *Convallaria majalis* and *Polygonatum verticillatum* seem to be most sensitive to desiccation; they have their optimum in the Allio-Vaccinietum veratretosum. The transects emphasize that both species prefer the protection of the *Vaccinium* species to the shelter of the shrubland (transect 8) or the 'Krummholz' brushwood just below the forest boundary (transect 10). Apparently, *Vaccinium myrtillus* and *Vaccinium uliginosum* may be better sun and wind screens that *Sorbus aucuparia* and *Fagus sylvatica*, but it is also possible that litter quality, especially that of *Fagus*, is a limiting factor. As far as the other species are concerned, the transects that deal with the transition between heathland and peatland provide the best information because of their variation in vegetation structure. *Maianthemum bifolium, Melampyrum pratense*, and *Stellaria holostea* only occur in transect 3 and 4, the transition between *Vaccinium* heathland and peatland (altitude 1450–1500 m). *Anemone nemorosa* and *Narcissus pseudonarcissus* also occur in transects 1 and 2, the transition between *Calluna/Genista* heathland and peatland (altitude 1350 m). Both species are not typical of the dwarf-shrub heathland. They also grow in the open grassland vegetation dominated by *Nardus stricta* and *Anemone*, even with higher cover-abundance values. Because of their early development in spring, these species do not suffer from summer drought. Of the trio *Maianthemum, Melampyrum*, and *Stellaria*, only the second is able to survive outside the dense cover of *Vaccinium*, as it grows in the open grassland strip between heathland and peatland at Source de Lignon (transect 4). In fact, Source de Lignon is situated in a valley where cold air accumulates, which greatly affects the vapour pressure of water required to saturate air. *Maianthemum bifolium* gives evidence of the strongest dependence of *Vaccinium*; it disappears some 3–5 m before *Vaccinium*. An example of the preference of a 'humidity indicator' to a certain dwarf-shrub species within one transect can be seen in transect 8, where *Melampyrum pratense* is closely linked to the presence of *Vaccinium myrtillus*; conversely, *Melampyrum* does not occur in association with *Calluna vulgaris* (see Fig. 6).

The behaviour of the dwarf-shrub species (*Calluna vulgaris, Genista pilosa, Vaccinium myrtillus*, and *Vaccinium uliginosum*) can be studied in detail, where mixed populations encounter transitions between plant communities or types of vegetation structure. As stated before, the rate of dominance of the dwarf-shrub species is mainly determined by the disproportionate distribution of snow during spring and early summer; the small-scale patterns within the dwarf-shrub populations, however, make clear that more factors and processes are involved.

The specific reaction of each dwarf-shrub species is correlated with its cover-abundance value. In the transects that deal with the transition between heathland and peatland on the plateaus at lower altitude, where the heathland (Vaccinio-Genistetum pilosae) is co-dominated by *Calluna vulgaris* and *Genista pilosa*, the sharp boundary between the heathland and the adjacent grassland strip is determined completely by *Calluna*. *Genista* diminishes gradually, and disappears some metres before *Calluna; Vaccinium myrtillus* is absent even earlier. In the peatland, *Calluna vulgaris* and *Vaccinium myrtillus* are the only dwarf-shrubs present, provided that *Calluna* occurs with higher cover-abundance values than *Vaccinium* (see transect 1). At variance is the behaviour of the dwarf-shrub species in the transects that deal with the transition between heathland and peatland on the plateaus at higher altitude, particularly where the heathland is exposed to eastern short or faint slopes, and the heathland (Allio-Vaccinietum typicum) is co-dominated by *Calluna vulgaris* and *Vaccinium myrtillus*. Here, the transition towards the grassland strip is

marked by *Vaccinium myrtillus; Calluna* and *Genista* disappear earlier. Where the relief is more pronounced, the differences are clearer. The peatland again is dominated by *Calluna vulgaris*, but *Vaccinium myrtillus* and *Vaccinium uliginosum* are also more or less abundant (see Fig. 6).

The boundary situations between heathlands and communities dominated by tall forbs are mainly characterized by *Vaccinium myrtillus; Calluna vulgaris, Genista pilosa*, and *Vaccinium uliginosum* are less abundant. The only exception concerns the transition between Alchemilo-Vaccinietum and Calamagrostion (Rocher de la Chaize, transect 5), where *Calluna vulgaris* exists with the highest cover-abundance values. Here again, *Calluna* ceases abruptly. The transects that deal with the transition towards Calamagrostion show that *Vaccinium myrtillus* can penetrate Calamagrostion communities fairly well, even when a dense shrubland is present. The latter situation occurs at Procher (transect 6), where *Cytisus purgans* dominates the Calamagrostion stand. The Adenostylion communities are much more resistant to dwarf-shrub species (Fig. 6).

The occurrence of the various dwarf-shrub species is closely related to the distribution pattern of stones. Small stone groups can be covered by *Vaccinium myrtillus* and, to a lesser extent, *Vaccinium uliginosum. Genista pilosa* may occur also, in open and scattered populations only. Rock streams are sometimes colonized by patches of *Vaccinium myrtillus* (see transects 5 and 8). *Calluna vulgaris* is extremely 'lithophobic' and avoids both the stone groups and rock streams almost completely (see Fig. 6).

ACKNOWLEDGEMENTS

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