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Ecological differences between *Calluna*- and *Empetrum*-dominated dry heath communities in Drenthe, The Netherlands

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SUMMARY

In dry heaths of the north Netherlands, both *Calluna vulgaris* and *Empetrum nigrum* may be the dominant dwarf shrub. The differences in growth form, vegetative and generative reproduction, leaf size and leaf inclination are discussed here, as well as differences in behaviour of the two species in and around shrubs of *Juniperus communis*. It is suggested that the horizontal leaves enable *E. nigrum* to endure more shade than *C. vulgaris*. *E. nigrum* also differs ecologically by not being attacked by the heather beetle or other insects, not being eaten by sheep, but being affected adversely by mowing, burning and sod cutting. It is more tolerant to burial by drift sand, but less tolerant to trampling. It prefers somewhat richer soils. The occurrence and even dominance of *E. nigrum* on very poor, heavily podzolized sand is probably due to either the former presence of a pine wood or to a combination of a heather beetle plague and overgrazing. The present threat to *C. vulgaris* by *Deschampsia flexuosa* does not seem to affect *E. nigrum*. *E. nigrum* heath differs in structure from *C. vulgaris* by being both lower and denser, without a hollow structure, with a better developed moss layer and an even, smooth canopy. The microclimate is therefore moister and milder, with much lower temperature maxima and higher minima, particularly when there is a snow cover. Dry *E. nigrum* heath in Drenthe, The Netherlands differs from *C. vulgaris* heath by 17 differential species; *C. vulgaris* heath differs from *E. nigrum* heath by 26 differential species. In *E. nigrum* heath, hepatics and tree seedlings are more numerous, in *C. vulgaris* heath herbs and lichens are more numerous. The latter has been described as Genisto–Callunetum. The former is described here as a new association, the Orthocaulio–Empetretum. It is slightly more allied to coniferous scrub and forest associations than the Genisto–Callunetum. The same applies to its mycoflora, which is slightly richer than that of the Genisto–Callunetum and resembles in particular juniper scrub and conifer forests.

Key-words: Calluna vulgaris, Empetrum nigrum, microclimate, mycoflora, vegetation structure.

INTRODUCTION

In The Netherlands dry heath is as a rule dominated by *Calluna vulgaris* and wet heath by *Erica tetralix*. In the northern part of the country *Empetrum nigrum* is also present. It can dominate both dry and wet heath. The first question that arises, therefore, is: what factors determine whether *E. nigrum* or one of the other ericoid plants is dominant? The second question is: do these species differ in their modification of the environment and does this affect the flora and fauna of their communities?

Both questions will be discussed here, but neither can fully be answered at present. This paper deals only with dry heath and consequently with the differences between *C. vulgaris* and *E. nigrum*.

In order to answer the first question it is useful to first consider all the differences between these species' adaptive morphological characters and complete habitat range within and outside heathland.

MATERIALS AND METHODS

All observations were made in inland heath and bog communities in the province of Drenthe (NE Netherlands). *Calluna vulgaris* and *Empetrum nigrum* were analysed with regard to growth form (Barkman 1988b), height, leaf size and leaf inclination (Barkman 1979) and frost resistance (as the percentage of survival). Microdistribution of the two species within heathland was studied in relation to soil type, exposition, inclination and shading by trees; microdistribution within bogs in relation to the ground water table and pH.

The vertical and horizontal structures of *Calluna*- and *Empetrum*-dominated heathland were studied using the method described by Barkman (1988a).

Microclimatic research included weekly measurements of minimum and maximum temperatures at soil level and in the soil (at a depth of 10 cm) beneath *C. vulgaris* and *E. nigrum* over several years (1961–1964), with ordinary minimum and maximum thermometers. Air humidity at 3 cm above the soil was measured with an Ultrakust aspiration psychrometer. Measurements were carried out from 1000 to 1600 hours, local time, once a week from 1 April to 1 October 1963. Potential evaporation was measured with Piche evaporimeters, also at 3 cm and during the same period, with weekly readings. Throughfall was measured with buried glass bottles provided with funnels a few centimetres above the soil surface. Readings were done weekly over 10 months (1963–1964).

Vegetation analysis was carried out during the years 1958–1972, mainly over the period 1963–1968. For *E. nigrum* heath the analyses were repeated in 1976. Wherever possible, *C. vulgaris* and *E. nigrum* stands were chosen in pairs, close together. Sample plot size varied from 20 to 50 m^2. Analyses included vascular plants and terrestrial bryophytes and lichens, with cover-abundance estimations following the scale of Barkman, Doing & Segal (1964).

R.N.A. Kramer (unpublished data) investigated the macrofungi of both *C. vulgaris* and *E. nigrum* heath in Drenthe and Friesland during two successive years (1967 and 1968). Within each stand much care was taken to choose homogeneous plots of 100 m^2 without any trees or tree seedlings in or nearby the plots, in order to avoid contamination with mycorrhizal fungi. Each plot was visited two to four times a year in high season. All carpophores of every species were counted at each visit. Abundance values of carpophores were classified in an eight-part scale, as shown in Table 1. The numbers of fruit bodies refer

Table 1. The eight-part scale used for classification of abundance of carpophores

Numbers of carpophores	Symbol	Converted value
1–5	r	1
6–15	r–o	2
16–30	o	3
31–50	o–f	4
51–100	f	5
101–250	f–a	6
251–500	a	7
>500	va	8

Abbreviations: r, rare; o, occasional; f, frequent; a, abundant; va, very abundant.

to the number within a surface of 100 m^2. For each species and plot the highest abundance reached during the 2 years (converted values, 1–8) was taken as the basis for the calculation of the AMAC value (average maximum abundance of carpophores) of a species in all plots of one vegetation type, converted to 100 relevés.

Nomenclature of vascular plants follows Heukels-Van der Meijden (1983) and, with a few exceptions, nomenclature of bryophytes follows Margadant-During (1982), nomenclature of lichens Wirth (1980) and nomenclature of fungi Arnolds (1984). The nomenclature of syntaxa follows Westhoff & Den Held (1969) and De Smidt (1977).

RESULTS AND DISCUSSION

Morphology of the species

Both *C. vulgaris* and *E. nigrum* are ericoid, long-lived, perennial dwarf shrubs with small, sclerophyllous, evergreen leaves. *C. vulgaris*, however, is normally an erect shrub without vegetative propagation. *E. nigrum* is a creeping shrub with ascending branches; the creeping stems may make abundant adventitious roots and new vegetative plants. The difference in growth form between *C. vulgaris* and *E. nigrum* was noticed as early as 1918 by Warming (1918), but his observation was largely ignored by later authors. The difference applies to heathland. In *Sphagnum* bogs *C. vulgaris* can form large polycorms (up to 7 m across) with adventitious roots due to massive clonal growth, whereas *E. nigrum* does not spread vegetatively except where *Sphagnum* growth is poor (Backéus 1985).

Adult plants of *C. vulgaris* are taller than those of *E. nigrum*, but in The Netherlands the former have decreased in height during the last 50 years whereas the latter have increased. Beijerinck (1940) mentioned 1·85 m as the maximum height of *C. vulgaris* ever observed in The Netherlands. In 1937 a dense, healthy *C. vulgaris* heath near Uffelte (Drenthe) was seen by the present author, in which all shrubs were about 1 m tall. G. Heil (1984, personal communication) has not observed any *C. vulgaris* taller than 80 cm in the last 10 years. Normally the species is now 30–50 cm high. An exceptional situation is the heath on a rich, heavy glacial loam (boulder clay) at the sand excavation site of Smilde (Drenthe). Most *C. vulgaris* shrubs are thriving here and are 30–50 cm high, but many less healthy shrubs reach 60–90 cm, and an almost dead heather shrub 98 cm. *E. nigrum* is normally 10–30 cm high. Beijerinck (1935) described an *E. nigrum* stem with 32 year rings at a height of 10 cm. According to the published photograph, this plant measured only 45 cm in height. Nowadays crowberry shrubs often reach 50–60 cm, forming hummocks, for instance in the Lheebroeker Zand (Dwingeloo, Drenthe). The highest free-standing shrub there measures 77 cm. These shrubs are still healthy and are at least 60 years old.

C. vulgaris is unable to climb scattered trees, but *E. nigrum* may do so wherever it meets a trunk. No attention has ever been paid to this climbing faculty, although it was noticed by Du Rietz in 1931. *E. nigrum* may climb oak and pine trees up to 60 cm, but juniper shrubs as high as 1·8 m. Young junipers can be overgrown completely and killed by *E. nigrum*, whereas *C. vulgaris* avoids the zone around any juniper shrub.

The behaviour of *E. nigrum* in juniper is likely to be due to the enrichment of the upper humus layers by *Juniperus communis* litter. It has been found (M. J. H. A. Van der Linden, unpublished data) that juniper litter is fairly rich in potassium and soluble phosphate. Also, the nitrification rate is much higher than in *C. vulgaris* or *E. nigrum* heathland without juniper. A better nutrient supply may enable a plant to change the root/shoot ratio to more above-ground biomass and change its life form from a ground dweller to a climber (cf. the behaviour of *Hedera helix* and *Lonicera periclymenum*).

The leaves of *C. vulgaris* measure only 0·6–0·8 mm^2 (one-sided), i.e. they are bryophyllous, while those of *E. nigrum* are 6–8 mm^2, being leptophyllous. But according to Backéus (1985) the difference in dry leaf weight is much less, averaging 0·1 mg in *C. vulgaris* and 0·3 mg in *E. nigrum*. This means that the degree of sclerophylly (dry weight/leaf surface) is more than three times as high in *C. vulgaris*. The leaves of *C. vulgaris* are spherical, i.e. with all inclinations from $+90°$ to $-90°$ (Barkman 1979). The leaves of *E. nigrum* are mainly horizontal.

The net primary production/above-ground biomass ratio is higher in *C. vulgaris* (about 0·3) than in *E. nigrum* (about 0·2), according to data given by Backéus (1985).

C. vulgaris is monoecious. It flowers in August and September and is pollinated by insects. Its extremely light, dry seeds ripen in October and are dispersed by wind. *E. nigrum* is dioecious. It flowers in March and is pollinated by wind. Its heavy berries ripen in midsummer and are dispersed by birds. By vegetative growth, large unisexual polycorms of *E. nigrum* can be formed, sometimes making perfectly circular patches some 5 m or more across.

Ecology of the species

E. nigrum is more shade tolerant and occurs in juniper scrub and in moderately dense pine woods, whereas *C. vulgaris* does not, at least not in The Netherlands. This may be connected with the horizontally positioned leaf of the former, which is more efficient at intercepting sunlight than spherical leaves. No attention has been paid in the literature to the different leaf inclinations of *C. vulgaris* and *E. nigrum* and their possible bearing on the shade tolerance of the latter. Hagerup (1946) discussed the leaf arrangement of *E. nigrum* in whorls or spirals, which is much less informative from an ecological point of view. Schroeter *et al.* (1987) observed that in the shade a large proportion of the older leaves of *E. nigrum* have no revolute margins. This could be an adaptation to low light intensity, as the light-absorbing leaf area is thus increased.

Since *C. vulgaris* is a suboceanic species and *E. nigrum* a more boreal species, it is to be expected that the former is less frost tolerant and might be replaced by the latter after a severe winter. This actually occurred not infrequently in Denmark and south Sweden in the 1940s and 1950s (T. W. Böcher, personal communication). In The Netherlands, where winters are milder, the phenomenon was unknown until recently, but after two very cold winters (1985–1986 and 1986–1987) severe frost damage was observed in *C. vulgaris* in Drenthe (between 50 and 90% of the above-ground parts were killed), whereas in *E. nigrum* only 10–30% were killed. Unlike *E. nigrum*, *C. vulgaris* is in decline nowadays. This is due to the attacks of the heather beetle, *Lochmaea suturalis* Thomson, which has become more and more frequent over the last 10–20 years. According to Heil (1984) this is due to the increased nitrogen input from the atmosphere, which makes the *C. vulgaris* leaves a more attractive food for the beetles. It seems likely that the reduced vitality of *C. vulgaris* makes it more sensitive to frost. Actually the greatest damage was done in the second cold winter (1986–1987), particularly in February and March, when there was strong insulation and the soil was still frozen. The real damage therefore seems to have been due to desiccation, as reported earlier from Scotland, UK (Watson *et al.* 1966). This fits in very well with the beetle damage theory. It has been demonstrated that, as a consequence of the damage to the photosynthetic apparatus by the heather beetle in summer, carbohydrate production and storage as well as root development are much reduced and the shrubs therefore suffer most from drought in the following winter and spring (Berdowski 1987). Also, the frost resistance of *C. vulgaris* is much lower in early spring than in early winter (Larcher 1977). Germination of *C. vulgaris* is stimulated by sod cutting and burning, rejuvenation from old stocks by superficial burning, mowing and sheep grazing. Burning and mowing are detrimental to *E. nigrum*; grazing does not affect it, since crowberry is rarely eaten by sheep. Grant *et al.* (1987) stated that in Scottish moorland *E. nigrum* is grazed less readily than *C. vulgaris*, not only by sheep but also by cattle. Overgrazing may even favour *E. nigrum*, as it kills *C. vulgaris*. Trampling by 'flat feet' (man) soon destroys *E. nigrum*, more readily than *C. vulgaris* (Dalby 1961; observations by the present author).

De Smidt (1966) noticed near the sheep's pen at Ruinen (Drenthe) that after a *C. vulgaris* stand had been killed by heather beetles, followed by a fire, the combination of a hot and dry summer and excessive sheep grazing prevented the re-establishment of *C. vulgaris*. As the bare humus rapidly decayed by full exposure to sun and rain and was trampled down by sheep, bare sand was exposed. This substratum and the following wet years favoured the expansion of *E. nigrum*, turning the *Calluna* heath into an *Empetrum* heath. Probably the selective grazing was the main factor because drought and heat are not likely to affect healthy *C. vulgaris* any more than *E. nigrum*. The former is found in dry sunny sites, even in the lowlands of Poland, only in Russia it retreats to the shade of woods and to wet bogs. The latter, however, prefers a cool boreal climate. In The Netherlands it is most abundant on the wind-swept Frisian islands, with their very cool summers. The mainland area of *E. nigrum* coincides here with the region where the P/S quotient, in the sense of Meijer, for the most critical period (June–August inclusive) exceeds the value of 65. Within this region it is most abundant in the eastern part of Friesland and in Drenthe. The summers here are rainy and cloudy and the saturation deficit of the air is low (Barkman & Westhoff 1969). Here *E. nigrum* may dominate level ground and even slopes facing south, whereas more to the south (Veluwe, Central Netherlands) the species is restricted to shady sites and slopes facing north.

In most cases the balance between the two species in Drenthe in open, dry, sandy areas seems to be determined by the soil type. The Scotch heather prefers coarse and medium fine cover sands with a well-developed podsol profile, the crowberry prefers fine drift sand without podsol, or with a micropodsol. On very coarse, gravelly, pushed-up preglacial sands the latter species is not found at all. When there is a constant accumulation of wind-blown sand, *E. nigrum* can survive, *C. vulgaris* cannot. It thus seems that *E. nigrum* prefers slightly richer and less acid soils, which is confirmed by pH measurements in hummocks of these species in bogs and heath pools. [*E. nigrum* 4·6(3·5–6·8), *C. vulgaris* 3·6(3·0–4·2)]. In their common range competition might be important. In Swedish bogs Backéus (1985) considered *E. nigrum* to be a poor competitor in the struggle with *C. vulgaris*. However, J. T. De Smidt (personal communication), who has observed permanent plots in heaths for more than 30 years, has observed active overgrowing of *C. vulgaris* by *E. nigrum* but never noticed the reverse. Apparently the two species behave differently in Dutch heathlands and in Central Swedish bogs.

E. nigrum may be dominant on poor, heavily podsolized soils. This, however, seems to be restricted to the following two situations. (1) The exceptional coincidence of death of *C. vulgaris*, denudation of the humus layer and a series of wet years, as mentioned above. (2) The former presence of a pine wood. After cutting and storms that felled most or all of the trees in crowberry–pinewoods, *E. nigrum*, once established, maintained itself and was not replaced by *C. vulgaris*, at least not within 20 years of observation by the present author. Schroeter *et al.* (1987) found that revolute leaves of *E. nigrum* have a much lower transpiration rate than flat leaves. All young leaves are revolute, but in the shade many older leaves are flat. However, their drought tolerance is much higher than that of revolute leaves which more than compensates for their higher rate of water loss. It is therefore not surprising that after a sudden removal of the tree canopy *E. nigrum* can maintain itself; perhaps only the young leaves suffer some temporary damage, for they transpire much more than young sun leaves (in spite of being revolute) and have the same desiccation tolerance.

A very important difference, also from the point of view of nature conservation, has been observed recently (J. J. Barkman, personal observations). Many stands of *C. vulgaris*, especially those that are not extensively managed, turn nowadays into monotonous prairies of *Deschampsia flexuosa*. *E. nigrum* shows a remarkable resistance to invasion by this grass, however, so the mixed heaths now turn into prairies with scattered islands of *E. nigrum*. In the Mantinger and Balinger Zand (Drenthe) this process was completed within 10 years.

Structure and microclimate of the plant communities

E. nigrum heath is lower, but as a rule denser, than *C. vulgaris* heath. Figures 1 and 2 illustrate this. They refer to analyses, made on the same day (30 August 1979), of the vertical structure of two adjacent, representative heath stands, namely dense mature *Calluna* and dense mature *Empetrum*, both without a moss layer.

The structure has been analysed according to Barkman (1988a) (Table 2). The figures refer to the cover percentages of a 1-m long rod by the vegetation, as seen from aside or from above. The former is the horizontal cover (h_x) through a 10-cm broad vegetation layer at any height level, x. The latter is either measured per 10 cm : v_x (for instance v_{10} is the cover by the vegetation between 10 and 20 cm, all vegetation above having been removed), or cumulative: v'_x (for instance v'_{10} is the cover by all vegetation above 10 cm). From these data the degree of overlap o can be calculated, o_x^{x+10} being the overlap of the layer between x and $x+10$ cm with all other layers above it. (Barkman 1988a). Also the 'plant area index', PAI, and the 'green area index' GAI, can be calculated on the basis of all v_x and h_x values (PAI) and on the basis of these values for the green parts only (GAI).

In the investigated heath stands no green tissues were found below 25 cm (*C. vulgaris*) or 20 cm (*E. nigrum*), respectively. This is the borderline between the autotrophic and the heterotrophic zone of the stands, since neither of them had a moss layer.

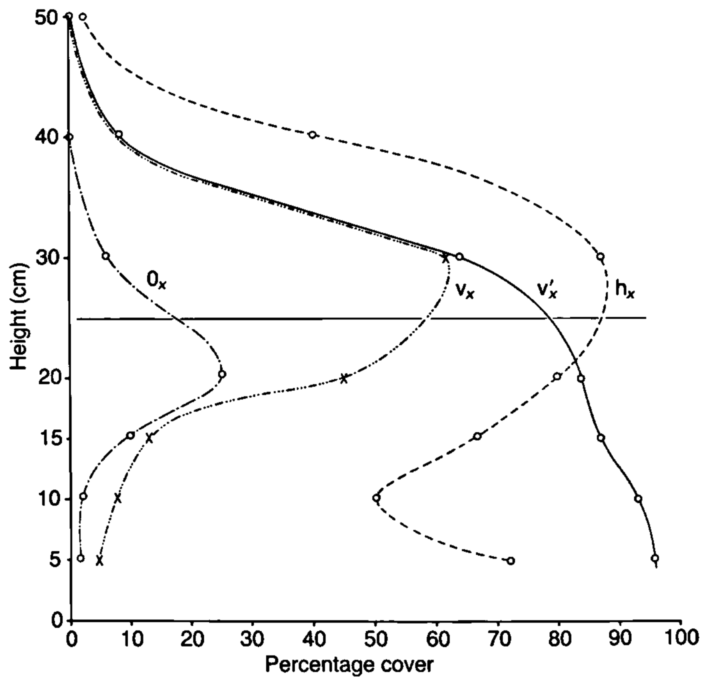

Fig. 1. Vertical structure of mature *Calluna* heath at Dwingeloo, The Netherlands, 30 August 1979. (——O——), v'_x; (—··—x—··—), v_x; (– – –O– – –), h_x; (–·–O–·–), o_x. For explanation of symbols see text. The horizontal line indicates the borderline between autotrophic and heterotrophic biomass.

Calluna heath has a more hollow structure than *Empetrum* heath: below the canopy h_x is much smaller than in *Empetrum* heath. The vertical biomass denseness (v_x) decreases even more in *Calluna* with decreasing height level compared with *Empetrum*. Accordingly, the degree of overlap (*o*) is much larger in *Empetrum*.

Although *E. nigrum* has horizontal leaves, thus taking away sunlight more efficiently in the upper layers, the GAI is higher than in *C. vulgaris*, but relative to the total above-ground plant area (GPR = GAI/PAI × 100) it is lower. *E. nigrum* has a greater mass of dead and living brown stems and branches than *C. vulgaris*, although they are concentrated in a smaller height interval.

GAI is a measure of the photosynthetic capacity of the vegetation as a whole, PAI and Σh its penetrability for animals, Σv of its effect on the microclimate. Owing to the larger biomass and the horizontal leaves, Σv is much higher under *E. nigrum* than under *C. vulgaris*. The microclimate is therefore likely to be much less extreme. Our measurements have confirmed this. Under crowberry, the maximum temperatures at soil level are much lower, minimum temperatures much higher. On one hot day (2 July 1961), for instance, the following temperatures were measured: air (2 m above the soil) 34·2°C, *C. vulgaris* (0 cm) 37·8°C, *E. nigrum* nearby (0 cm) 23·8°C. On 9 July 1959 at an air temperature of 34·4°C, the temperature at soil level was 26·2°C under *E. nigrum*, but in a small gap it amounted to 53·8°C. The maximum soil temperatures at 10 cm depth show a different picture. The highest value was found under *E. nigrum*, followed by dry *C. vulgaris* heath on level soil. The lowest maxima were observed under *Calluna* on wet, level soil and under *Calluna* on a north-facing slope. The higher value under *Empetrum* is most probably due

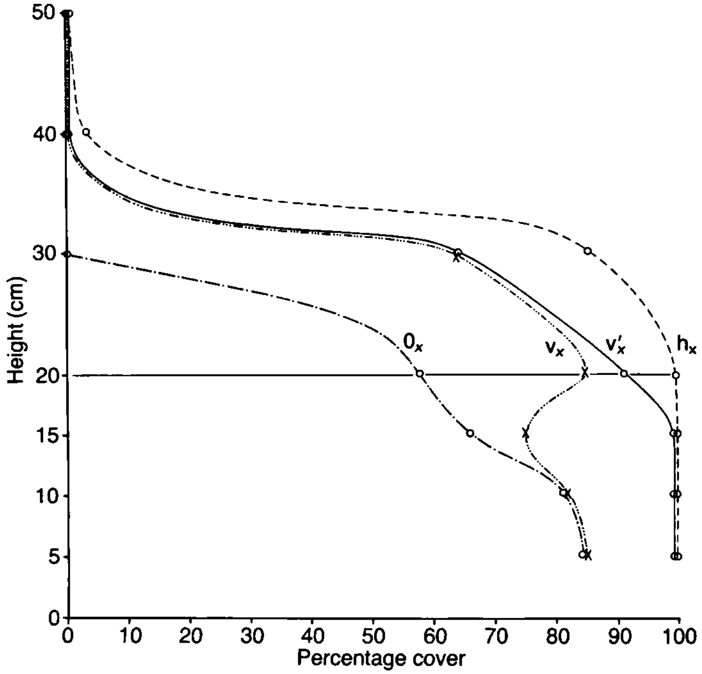

Fig. 2. Vertical structure of mature *Empetrum* heath at Dwingeloo, The Netherlands, 30 August 1979. For explanation see Fig. 1 and text.

Table 2. Vertical structure of dense *Calluna* and *Empetrum* stands

	Calluna vulgaris	*Empetrum nigrum*
Σ_v	145	391
Σ_h	398	488
Σ_o	45	291
PAI	422	625
GAI	192	240
GPR	45	38

Σ_v, sum of all 10-cm interval vertical cover values.

Σ_h, sum of all 10-cm interval horizontal cover values.

Σ_o, sum of all 10-cm interval vertical overlap values.

PAI, plant area index.

GAI, green area index.

GPR, green/plant area ratio (GAI/PAI × 100).

to the soil, being drift sand with little humus. Heat conductivity is much greater in this soil than in the thick humus layer normally found under *Calluna*.

On a cold winter night (air temperature −14·0°) the temperature under *Calluna* (0 cm) was −16·5°C, under *Empetrum* only −8·1°C (Barkman, 1965). These were measurements without snow cover. With snow the differences must be much larger because *Empetrum* has an even, smooth canopy and therefore supports a continuous snow cover. The air layer under it is completely isolated from the free atmosphere. *Calluna* has a loose uneven canopy and therefore a broken snow cover. The cold air that is formed during clear winter nights just above the snow is heavy and will flow through the gaps on to the soil. This air may have a temperature of −22°C at an air temperature (2 m high) of −14°C. At the same time a temperature of −0·6°C was measured at 0 cm under snow-covered *Empetrum* (21 cm of snow, 20 cm of air underneath) (Barkman & Stoutjesdijk 1987). This phenomenon is of the utmost importance for mosses and lichens and for small animals hibernating on or just below the soil surface. It will be of even greater importance in regions where snow cover lasts much longer than in The Netherlands. Even without snow cover it was observed that under dense *Empetrum* (night) frosts occurred only during 3½ months but under dense *Calluna* during 8½ months per year (observations in Drenthe in 1961–1962, when snow cover lasted less than 3 weeks).

No light or wind measurements were made under *Empetrum*, but air humidity and potential evaporation were measured. From 1 April to 1 October 1963, the mean saturation deficit at midday (1000–1600 hours local time) at 3 cm height amounted to 8·2 mbar under *Calluna* and 6·8 mbar under *Empetrum*. Extreme values, which are often more important for the survival of organisms than averages, differed more. On 2 July 1961, for instance, a maximum of 56·0 mbar was measured under *Calluna* and of 18·8 mbar under *Empetrum*. Potential evaporation (3 cm above the soil) in the period 1 May to 1 August 1963 averaged 2·18 mm per daily period of 6 h (1000–1600 hours) under *Calluna*, 1·42 mm under *Empetrum* (cf. Cladonietum mitis, 2·79 mm, and Spergulo–Corynephoretum, 3·30 mm, in the same period and same area). In September 1974 the average potential evaporation was 1·23 mm per day under *Calluna*, only 0·43 mm under *Empetrum*. No differences in throughfall rain was observed. This amounted to 33% under *Calluna*, and 34% under *Empetrum*. Both values are percentages of the free precipitation, only 2·4% of which fell as snow during the 10 months of observation.

Obviously dense *C. vulgaris* and *E. nigrum* create quite different microclimates. This must be of major importance for the undergrowth, although it should be realized that extremely dense *C. vulgaris* and *E. nigrum* have no undergrowth and loose canopies of the two species will differ less in the microclimate. Still greater must be the effect on fungi and animals, since they do occur under a very dense canopy.

The floristic composition of the communities

De Smidt (1977) has given a complete survey of the heath communities of The Netherlands. The results of this paper, (because in dealing only with Drenthe more attention was paid to the *C. vulgaris* and *E. nigrum* communities of that province and to their cryptogams), have added to the species lists of De Smidt. In Table 3, 36 relevés of dry *Calluna* heath are compared with 29 relevés of dry *Empetrum* heath. Species occurring with a presence of less than 15% in both communities were omitted, unless their presence exceeded 10% in one and was 0% in the other. Similarity indices were based, however, on all species present in either one or the other community type.

Table 3. Synoptic vegetation table of *Calluna vulgaris* and *Empetrum nigrum* heath in Drenthe, The Netherlands

		Calluna		*Empetrum*	
		P	TCV	P	TCV
Trees and shrubs (seedlings)					
E	*Amelanchier lamarckii*	6	2	21	14
C	*Betula pubescens*	31	22	7	7
*E	*Frangula alnus*	11	6	41	33
E	*Juniperus communis*	17	19	31	31
E	*Pinus sylvestris*	14	21	35	24
E	*Prunus serotina*	19	18	41	35
	Quercus robur	53	43	62	53
E	*Sorbus aucuparia*	14	18	41	40
Herbs and dwarf shrubs					
	Agrostis vinealis	53	87	52	90
C	*Arnica montana*	11	14	—	—
C	*Calluna vulgaris*	100	822	97	355
*C	*Carex pilulifera*	50	92	21	19
*C	*Corynephorus canescens*	17	18	—	—
*C	*Danthonia decumbens*	36	118	14	14
*C	*Deschampsia flexuosa*	50	131	17	41
*E	*Empetrum nigrum*	31	82	100	992
	Erica tetralix	42	117	55	112
	Festuca ovina spp. *tenuifolia*	72	257	86	164
	Galium saxatile	14	33	17	17
C	*Genista anglica*	17	15	3	7
*C	*Genista pilosa*	33	63	7	10
*C	*Hieracium pilosella*	14	15	—	—
*C	*Hieracium umbellatum*	29	32	7	3
C	*Hypochaeris radicata*	25	32	7	10
C	*Juncus squarrosus*	29	40	14	14
C	*Lycopodium clavatum*	11	39	—	—
	Molinia caerulea	39	54	31	47
	Nardus stricta	29	43	21	35
*E	*Polypodium vulgare*	—	—	10	9
	Potentilla erecta	22	38	24	38
C	*Rumex acetosella*	29	50	17	14
Bryophytes and lichens					
*E	*Aulacomnium androgynum*	—	—	14	16
E	*Barbilophozia barbata*	6	8	17	38
E	*Brachythecium rutabulum*	3	2	10	19
C	*Campylopus flexuosus*	33	111	31	41
	Campylopus pyriformis	36	76	52	62
	Cephaloziella divaricata	69	128	62	100
	Cetraria islandica	19	28	7	10
	Cladonia arbuscula	22	65	17	21
	Cladonia bacillaris	6	8	17	14
	Cladonia chlorophaea	86	165	86	204
C	*Cladonia fimbriata*	17	17	—	—
C	*Cladonia floerkeana*	42	51	24	19
C	*Cladonia furcata*	11	11	—	—
	Cladonia glauca	50	74	59	64

Table 3. (*Continued*)

		Calluna		*Empetrum*	
		P	TCV	P	TCV
*C	*Cladonia gracilis*	39	60	17	19
	Cladonia macilenta	33	33	17	31
	Cladonia pityrea	17	11	10	9
	Cladonia pleurota	42	39	24	29
	Cladonia portentosa	56	226	97	264
C	*Cladonia uncialis*	28	47	10	7
C	*Cornicularia aculeata*	22	25	3	1
*E	*Dicranum polysetum*	36	50	72	174
	Dicranum scoparium	78	276	100	280
	Dicranum spurium	14	17	17	12
	Gymnocolea inflata	25	50	17	22
*E	*Hylocomium splendens*	3	3	21	57
	Hypnum jutlandicum	86	418	100	407
C	*Hypogymnia physodes*	22	33	7	3
C	*Lecidea granulosa*	33	54	17	16
	Lecidea uliginosa	33	104	38	69
	Leucobryum glaucum	17	38	17	24
*E	*Lophocolea bidentata*	14	17	72	105
E	*Lophocolea heterophylla*	33	35	48	97
E	*Lophozia ventricosa*	17	15	28	52
*E	*Orthocaulis kunzeanus*	8	11	31	28
	Pleurozium schreberi	72	464	100	745
	Pohlia nutans	70	151	76	86
	Polytrichum commune	42	87	28	41
*C	*Polytrichum juniperinum*	19	28	—	—
*C	*Polytrichum piliferum*	29	43	3	1
	Pseudoscleropodium purum	6	10	10	21
	Ptilidium ciliare	39	78	48	141
	Scapania nemorosa	19	17	14	28

P refers to the presence percentage. TCV refers to the total cover value per 100 relevés, based on a more or less logarithmical transformation of the Braun–Blanquet cover–abundance values, slightly different from the one proposed by Barkman, Doing & Segal (1964): $r = 0{\cdot}5$, + = 1, 1 = 2, 2m = 3, 2a = 4, 2b = 6, 3 = 8, 4 and 5 = 10. Preferences have been indicated by the symbols C and E, significant preferences by *C and *E.

The average number of species per plot is 26·1 for *Calluna* heath, 25·2 for *Empetrum* heath. The ratio of vascular plants/bryophytes and lichens per stand is almost the same: 10·9/15·2 for *Calluna*, 9·8/15·4 for *Empetrum*, but the ratio of bryophytes/lichens is lower in *Calluna* (8·7/6·4) than in *Empetrum* (10·5/4·8). With the exception of very dense, old stands, a moss layer is always well-developed and often closed in *Empetrum* heath. *Pleurozium schreberi* is dominant (average cover 39%) and far more abundant than in *Calluna* heath (average cover 27%), where a moss layer is more discontinuous and confined to open spaces between shrubs, young *Calluna* and dying shrubs, opening in the centre. In the 1960s *Pl. schreberi* was fruiting in 17% of the *Empetrum* stands, in none of the *Calluna* stands.

In Drenthe *C. vulgaris* and *E. nigrum* heath differ by 43 differential species, 26 *Calluna* species and 17 *Empetrum* species. Many, however, have only a weak preference. A more marked preference is found in 10 *Calluna* and eight *Empetrum* species, indicated in Table 3 with an asterix. This seems sufficient to regard the *Empetrum* heath as distinct from the Genisto–Callunetum and consider it a separate association, the more so as it also differs markedly from the coastal dune *Empetrum* associations.

The floristic differences with the latter have already been pointed out by Barkman & Westhoff (1969). Recently, however, the coastal *E. nigrum*-heath communities have been revised by Barendregt (1982), who compared them with the unpublished relevés of J. J. Barkman (his Table 2). His conclusion, which follows from his two-dimensional diagram of dissimilarity values (his Fig. 7), is quite obvious: the inland *E. nigrum* heath is much more similar to the inland Genisto–Callunetum than to the coastal *Empetrum* heath types. Among the latter and dry types (Carici–Empetretum on various expositions and Polypodio–Empetretum on northern slopes) differ the least from the Drenthian *Empetrum* community. Both coastal types differ, however, by the presence of *Carex arenaria, Ammophila arenaria, Calamagrostis epigeios, Rosa pimpinellifolia* and *Orthodontium lineare* and by the absence or rarity of *Agrostis vinealis, Carex pilulifera, Molinia caerulea, Nardus stricta, Potentilla erecta,Barbilophozia barbata, Campylopus flexuosus, C. pyriformis, Cephaloziella divaricata, Cladonia macilenta, C. pleurota, Dicranum polysetum, Hylocomium splendens, Lecidea uliginosa, Lophocolea heterophylla, Lophozia ventricosa, Orthocaulis kunzeanus, Pohlia nutans, Polytrichum commune* and *Ptilidium ciliare.*

The differences between the inland *Empetrum* heath and the inland *Calluna* heath, although much smaller, are large enough to separate them as two associations. They are larger than that which appears from Barendregt's diagram because he included transitional stages (for instance De Smidt's Genisto–Callunetum lophozietosum) and because De Smidt's (1977) relevés of other types of the Genisto–Callunetum are somewhat incomplete: his average number of species per plot was 17, in this report it is 26. So our *E. nigrum* table is compared with our own *C. vulgaris* relevés from the same area.

The new association is called Orthocaulio–Empetretum, after the faithful species *Orthocaulis kunzeanus.* It is represented by the two right-hand columns of the synoptic Table 3. In accordance with the code of phyto-sociological nomenclature (Barkman, Moravec & Rauschert 1986), the type relevé is published here in detail. *Type relevé*: JJB no. 3141, 28 August 1965, The Netherlands province of Drenthe, municipality of Ruinen, Echtener Zand, area of windblown inland sand dunes. NNW slope, 10°–30°, 50 m^2.

Dwarf shrub layer (100%)
Empetrum nigrum 5·5 fr, *Quercus robur* +·1 juv, *Festuca ovina* ssp. *tenuifolia* 1·1 fr, *Hieracium laevigatum* 1·2 fr, *Polypodium vulgare* +·3 fr, *Agrostis vinealis* 1·2 fr, *Calluna vulgaris* +·2 fl, *Agrostis capillaris* +·2 v, *Rubus fruticosus* s·1. r·1 v, *Nardus stricta* 1·2 fr, *Sorbus aucuparia* +·1 s(eedling), *Frangula alnus* r·1 s.

Moss layer (70%)
Pleurozium schreberi 3·4, *Brachythecium rutabulum* 2a·3, *Drepanocladus uncinatus* +·2, *Lophocolea bidentata* 1·2, *L. heterophylla* +·2, *Hypnum jutlandicum* 3·4, *Pseudoscleropodium purum* +·3, *Dicranum scoparium* 1·2, *Polytrichum piliferum* r·2, *Pohlia nutans* r·2, *Aulacomnium androgynum* +·1, *Atrichum undulatum* r·1, *Palmogloea protuberans* 1·2, *Cladonia glauca* r·1, *C. chlorophaea* 1·2, *C. portentosa* +·1, *Cephaloziella divaricata* 1·2, *Campylopus pyriformis* r·2, *Plagiothecium laetum* r·1, *Lophozia ventricosa* +·3. Fungi: *Mycena sanguinolenta* and *Marasmius androsaceus.*

The Orthocaulio–Empetretum is partly synonymous with the Genisto–Callunetum lophozietosum ventricosae De Smidt 1977. For differences see De Smidt (1977), to which can be added *Dicranum polysetum* and *Lophocolea bidentata*.

The Orthocaulio–Empetretum (OE) differs from the Genisto–Callunetum (GC) typicum by the *Empetrum* species of Table 3 and the absence or rarity of the *Calluna* species. The latter are mainly herbs and lichens, the former mainly tree seedlings and hepatics. The ratios of differential species numbers, presented as C/E are: trees 1/6, herbs and dwarf shrubs 14/2, lichens 8/0, mosses 3/4, hepatics 0/5. This is interesting because in Britain *Empetrum* heath is generally rich in lichens (Bell & Tallis 1973). Apparently *Empetrum* heath, with its temperate, moist and shady microclimate, is more favourable for the germination of trees and for the delicate aerohygrophytic hepatics than *Calluna* heath, whereas the latter is preferred by the more xerophytic lichens. The ratio meso-hygrophytic/xerophytic species among the differential species is 5/13 for the G–C and 11/2 for the O–E (some species are indifferent). The number of species of trees and shrubs present as seedlings averages 1·7 per sample plot in the former, 2·8 in the latter.

It was shown that the microclimate under *E. nigrum* resembles more of a wood climate than that under *C. vulgaris*. It is interesting to notice that the ratio of wood plants/non-sylvatic species is only 2/24 for *Calluna* species, 10/7 for *Empetrum* species. It is therefore not surprising that the OE has a more floristic resemblance to the juniper scrub community Dicrano–Juniperetum (DJ) than the GC. For the degrees of similarity of the three combinations, based on the formula

$$\frac{\Sigma\gamma}{\sqrt{\Sigma\alpha \times \Sigma\beta}}$$

(Barkman 1958), only the 42 Drenthian relevés of the DJ were used. Species occurring only in the DJ were omitted from the calculations, so the similarity indices GC–OE cannot be compared with the indices GC–DJ and OE–DJ. Two diagrams were constructed, one with A_1 values (A = affinity = similarity) in which α, β, and γ refer to differences and common values of presence degrees, and one with A_2 values, in which α, β and γ refer to TCV as used in Table 3 (Fig. 3). The stronger similarity between OE and DJ compared with GC and DJ is therefore most evident when only presence values are compared.

Most curious is the occurrence on the soil in the OE of species normally growing on rotten wood in forests, such as *Aulacomnium androgynum* and *Lophocolea heterophylla*. On poor soils *Brachythecium rutabulum* is also normally restricted to rotten wood.

C. vulgaris and *E. nigrum* also seem to differ in the phytogeographical elements of their companion species. The GC in Drenthe has one boreal and five Atlantic species, the OE has five boreal and no Atlantic species among its differentials. The latter fact is not surprising, but under *Calluna* with its rather extreme and dry microclimate one would expect continental rather than Atlantic species to occur.

It was also shown that *Empetrum* probably grows on richer soil. Yet this is not evident from Table 3: five out of the 26 *Calluna* species (19%) are meso-eutraphent compared with four out of the 17 *Empetrum* species (24%).

Changes in floristic composition

Heathlands on The Netherlands have become drastically impoverished over the last 50 years. Species that have disappeared from or became extremely rare in dry *Calluna* heath are: *Dicranum spurium, Lycopodium clavatum, L. tristachyum, Antennaria dioica* and *Cuscuta epithymum*. The species *Hieracium umbellatum, Genista anglica, G. pilosa* and

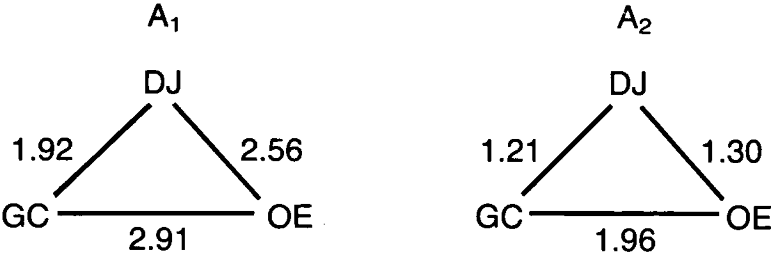

Fig. 3. Similarity values between stands in Drenthe of dry heath and juniper scrub communities, based on green plants. GC = *Genisto-Callunetum*; OE = *Orthocaulio-Empetretum*; DJ = *Dicrano-Juniperetum*. For further explanation see text.

Ptilidium ciliare have become less frequent and abundant in that heath type. *Rubus fruticosus* and *Campylopus introflexus*, on the other hand, have become much more abundant. These changes have taken place in communities still dominated by *Calluna vulgaris*. However, most *Calluna* heaths have turned into monotonous *Deschampsia flexuosa* steppes. The loss of species is much more drastic in that situation.

E. nigrum has effectively resisted this grass plaque. This does not mean, however, that nothing has changed in the OE. Ten years after the analyses that served as the basis for Table 3, an approximately equal number of relevés was again made in the OE in Drenthe. This research was carried out in 1976 and yielded some remarkable results. The number of tree seedlings had diminished considerably, from 2·8 to 1·3 species per plot. This applied to all trees and shrubs except *Sorbus aucuparia*, which had become slightly more frequent. *Frangula alnus* showed the strongest decline: present in 41% of the plots in 1963–1968, it was not seen in a single plot in 1976. The presence of *Quercus robur* dropped from 62 to 22%, that of juniper seedlings from 31 to 11%. For herbs and cryptogams, the following species had disappeared or become less frequent (in parentheses are the degrees of presence in 1963–1968/1976): *Agrostis vinealis* (52/11), *Carex pilulifera* (21/0), *Potentilla erecta* (24/0), *Aulacomnium androgynum* (14/0), *Brachythecium rutabulum* (10/0), *Cladonia glauca* (59/11), *Cl. chlorophaea* (86/67) (decrease mainly in cover/abundance), *Dicranum spurium* (17/0), *Hylocomium splendens* (21/0), *Lophocolea bidentata* (72/22), *Pseudoscleropodium purum* (10/0), *Ptilidium ciliare* (48/11). The following species had increased: *Deschampsia flexuosa* (17/33), *Campylopus pyriformis* (52/89), *Cladonia floerkeana* (24/56), *C. pleurota* (24/56), *C. squamosa* (7/33), *Lophocolea heterophylla* (48/89), *Lophozia ventricosa* (28/56) and *Scapania nemorosa* (14/33). For three species the decline in average cover (TCV) was even greater than in degree of presence: *Agrostis vinealis* (TCV 90/11), *Cladonia chlorophaea* (204/78) and *Lophocolea bidentata* (105/22). It would certainly be interesting to analyse the situation as it is now.

The causes of the declines and increases are completely unknown. There are three possibilities: (i) fluctuations as a result of weather conditions, (ii) normal autogenic succession, and (iii) allogenic succession as a result of human interference. In the case of Dutch heathlands, human interference can be classified as drainage, management, eutrophication and air pollution. Drainage is certainly responsible for the disappearance of many wet heathland species, but not for those of dry *Empetrum* heath. Contrary to *Calluna* heath, *Empetrum* heath is not being actively managed. Most *Empetrum* heaths are far from cultivated land and not under the influence of enriched ground water or wind-blown fertilizers (solid particles). Which leaves air pollution by ammonia and sulphur dioxide. However, fluctuations and normal succession cannot be excluded.

Table 4. Mycoflora of inland *Calluna vulgaris* and *Empetrum nigrum* heath

		Calluna		*Empetrum*	
		P	AMAC	P	AMAC
C	*Clavaria argillacea*	38	115	—	—
E	*Clitocybe clavipes*	—	—	19	19
(C)	*Clitocybe vibecina*	100	290	100	137
	Collybia dryophila	31	31	13	13
(C)	*Cystoderma amianthinum* s.l.*	69	108	56	56
	Entoloma cetratum s.l.†	85	85	100	113
C	*Entoloma fernandae* s.l.‡	38	62	13	13
	Entoloma helodes	61	69	56	56
	Entoloma inutile	15	15	6	6
C	*Entoloma lampropus*	23	23	6	6
	Entoloma turbidum	8	8	19	19
C	*Entoloma vinaceum*	23	23	—	—
(E)	*Galerina allospora*	31	46	63	63
(E)	*Galerina atkinsoniana*	77	115	95	193
	Galerina calyptrata	100	285	100	232
E	*Galerina heterocystis*	8	8	63	125
E	*Galerina mniophila*	8	8	44	44
E	*Galerina pumila*	23	23	100	257
(C)	*Marasmius androsaceus*	100	615	100	213
	Mycena cinerella	100	465	100	314
E	*Mycena epipterygia*	8	8	100	450
E	*Mycena filopes*§	23	54	75	163
	Mycena galopoda	100	550	100	444
	Mycena leptocephala	15	15	13	13
E	*Mycena metata*¶	8	8	44	69
	Mycena sanguinolenta	92	378	100	563
E	*Mycena vulgaris*	—	—	13	13
	Omphaliaster asterosporus	15	15	19	19
	Psathyrella fulvescens	8	8	19	19
C	*Rickenella fibula*	15	15	—	—
	Tephrocybe ambusta	15	15	13	13
C	*Tephrocybe tylicolor*	38	77	6	6

*Includes *C. jasonis* (= *longisporum*).
†Includes *E. farinogustum*.
‡*vide* Arnolds (1984).
§ss. Kummer = *M. iodiolens* ss. Kühner & Romagnesi.
¶*M. vitrea* var. *tenella* ss. Kühner & Romagnesi.
P refers to presence degree in percentage.
AMAC refers to average maximum abundance of carpophores. See Materials and methods.

Three of the above-mentioned species have also become rare in other communities, namely *Dicranum spurium, Hylocomium splendens* and *Lophocolea bidentata.* Here air pollution, and in particular sulphur dioxide, is likely to be cause of the decline. In the last 15 years this source of pollution has drastically diminished in The Netherlands, because power stations, industry and house heating have changed from the use of oil and coal to natural gas. There has been a come-back of *Hylocomium splendens* and *Lophocolea*

Table 5. Distribution of differential species of macrofungi over ecological groups (groups mainly according to Arnolds, 1984)

	GC species	OE species
Heathland species	3	—
Juniper scrub species	3	4
Coniferous forest species	1	4
Deciduous forest species	—	2
Grassland species	2	—

bidentata in juniper scrub (J. J. Barkman, personal observation). Sulphur dioxide has been replaced as the main pollutant by ammonia and nitrogen oxides. It seems that these substances do not harm the bryophyte species in question. In any case *Lophocolea bidentata* is rather indifferent to soluble nitrogen compounds in the soil and *Hylocomium splendens* prefers soils that are moderately rich in nitrogen (Stapelveld 1955).

The macrofungi of the communities

R. N. A. Kramer (unpublished data) investigated the macrofungi of the GC and the OE heath in Drenthe and Friesland. Thirteen stands of dense *Calluna* heath and 16 stands of dense *Empetrum* heath were studied during two successive years (1967 and 1968). The main results are summarized in Table 4. The criteria for omission of species are the same as in Table 3. A total of 46 species of macrofungi was found in the 29 plots, all of them saprophytes of litter and humus. The average number of carpophores is the same for *Calluna vulgaris* and *Empetrum nigrum*, and so is the total number of species (*Calluna* 37 spp., *Empetrum* 36 spp.). The average number of species per plot is somewhat higher in *Empetrum* heath (*Calluna* 13·4, *Empetrum* 16·2). These numbers are low if compared with grassland (22–37 species per plot) and even with *Erica tetralix* heath (average 23·6) (Arnolds 1981). Only very dry (Spergulo–Corynephoretum: 8·2 species) and very wet grassland (e.g. *Caricetum elatae*: four spp.) are much poorer than these heath communities. However, juniper scrub on the same poor pleistocene sands, often adjacent to the above heath plots, has an average of 93·5 species, although juniper has no ectomycorrhiza fungi. The differences in species numbers of the heath communities are not directly related to the dominant heather species because in raised bogs and heath pools the healthy *E. tetralix* low hummocks (Erico–Sphagnetum magellanici) have an average of 7·7 macrofungi per stand, the healthy *E. nigrum* high hummocks (Empetro–Sphagnetum rubelli) of 12·0 species (Barkman, 1990).

Among the differential species of the GC (C and perhaps (C) in Table 4), three are exclusive, three have a much higher degree of presence and only three a higher abundance than in the OE. For the OE (E and perhaps (E) in Table 4) these figures are 1, 7 and 2. The distribution of these species over ecological groups is as in Table 5. Apparently the mycoflora of *Empetrum* heath resembles that of juniper scrub and woods more than *Calluna* heath does. Again, this might be associated with the cooler, moister and more equal microclimate of *Empetrum* heath.

The floristic similarity values between the two heath associations and the juniper scrub, based on the mycoflora, have been calculated in the same way as was done for the

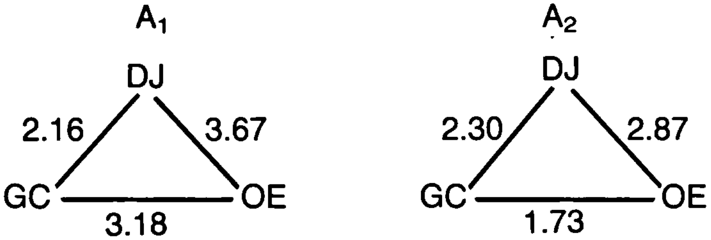

Fig. 4. Similarity values between stands in Drenthe of dry heath and juniper scrub communities, based on macrofungi. For explanation of abbreviations see Fig. 3 and text.

autotrophic plants. A_1 values refer to presence degree, A_2 values to AMAC. The result is shown in Fig. 4. Again the A_1 values show more clearly the similarity between *Empetrum* heath and juniper scrub than the A_2 values.

In this connection it is interesting to observe that the resemblance of *Empetrum* heath to juniper scrub and coniferous woods applies not only to fungi and microclimate, but also to the fauna of carabid beetles, albeit in a negative sense: they are all very poor in carabids (*Empetrum* heath 19 species, juniper scrub six spp., conifer woods 7–10 spp., *Calluna* heath 33 species). The number of individuals caught per stand per year are: 84, 29, 46–260 and 1018, respectively (Den Boer, 1968; and personal communication).

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