# RELATIONSHIPS BETWEEN MACROFUNGI AND VEGETATION IN THE BURREN

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ABSTRACT

The relationships among macrofungi, vegetation and soil variables were assessed in a three-year study of sporocarp abundance in ten permanent plots in *Dryas* heath vegetation in the Burren. Ectomycorrhizal fungi associated primarily with *Dryas octopetala* constituted 83% of the sporocarp biomass but only 35% of the species number. One ectomycorrhizal species, *Craterellus lutescens*, constituted almost 50% of the total sporocarp biomass. Diversity of ectomycorrhizal sporocarps in the plots was positively correlated with the extent of *Dryas* cover, while diversity of saprotrophic species was positively correlated with extractable soil phosphorus. Differences in distribution patterns of saprotrophic and ectomycorrhizal species were evident between the plots. The distribution of sporocarps of the ectomycorrhizal species was dictated largely by the distribution of *Dryas*, but soil depth and organic matter also influenced the distribution of some *Cortinarius* species. Soil depth and soil type also influenced distribution patterns of sporocarps of saprotrophic species. Relationships between the plots based on macrofungal composition were very similar to relationships based on vegetation.

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## INTRODUCTION

Large areas of the Burren are covered by grassy, heath-like vegetation that contains a number of arctic–alpine elements. Mountain avens (*Dryas octopetala*) is the most abundant of these. These *Dryas* heaths harbour an unusual macrofungal biota, which was first described by Harrington (1996). The largest component, comprising 30 species, was of forest fungi in the strict sense. Many of these are normally ectomycorrhizal with forest trees (Trappe 1962) and had not previously been found in association with *Dryas*. Most surprising was the occurrence of *Cortinarius* species (subgenus *Phlegmacium*), i.e. *C. atrovirens*, *C. caesiocanescens*, *C. calochrous*, *C. infractus*, *C. odorifer* and *C. mussivus*. These have not been previously recorded growing in *Dryas*-dominated communities nor have they been recorded from any other Irish habitat, with the exception of *C. calochrous* and *C. atrovirens*, which have been observed in mixed woodland of beech and yew on limestone in Limerick (Harrington 1994). They are usually found as ectomycorrhizal symbionts of conifers (*Abies* spp, *Picea* spp, *Pinus* spp) on calcareous soils in boreal and montane regions of Europe (Brandrud *et al.* 1990–8). Also abundant is the chanterelle-like *Craterellus lutescens*. In northern Europe *C. lutescens* is normally found under pine and spruce, often at high elevations on acid and alkaline soils. While *C. lutescens* is regarded normally as an ectomycorrhizal associate of spruce and pine in northern Europe, its host range appears to be wider than this and may also include a number of broadleaf tree species. In arctic–alpine habitats, *Dryas* is associated with a relatively large number of macrofungi (Kühner and Lamoure 1986), including many specialised arctic–alpine associates such as *Lactarius dryadophilus*, *Hydropus dryadicola* and *Marasmius epidryas*. Some of these are saprotrophs but many others are presumed to be mycorrhizal species that form ectomycorrhizae on the roots of *Dryas*. No arctic–alpine fungi or any of the specialised *Dryas* associates have been found in the Burren *Dryas* heaths so far.

Based on these observations, a three-year survey of the occurrence of macrofungi in the *Dryas* heaths was initiated in 1996, involving the routine sampling of macrofungal sporocarps in ten permanent plots in different locations in the Burren. The survey addressed a number of issues including taxonomic considerations, the relationship between the occurrence of sporocarps and mycorrhizae, the relationship between the distribution of the macrofungi and vegetation differences within the *Dryas* heaths and the influence of vegetation and other site factors on the distribution of the macrofungi. This paper reports on the last two issues.

## MATERIALS AND METHODS

### SAMPLE PLOTS

Ten permanent plots were marked out in the

Burren in summer 1997. Each plot was square, measuring 10m × 10m. Five of the plots (3–7) were located on the western side of the Burren, with one plot at Slieve Elva (M102032), two near Black Head (M165095 and M166103), one at Ballyryan (M090019) and one at Gleninagh Mountain (M178103). The remaining five (1, 2, 8–10) were located on the eastern side of the Burren at Ballybornagh (M349042), Clab (M295023), Mullagh More (R329955), Slieve Roe (R335965) and Bouleevin (M343030). The presence of *Dryas* in the vegetation was the main criterion for selecting sites for the plots. In addition, each plot represented, by subjective assessment, an example of one of the recognised *Dryas* communities or their major variants described from the Burren (Ivimey-Cook and Proctor 1966). Altitude, aspect and accessibility, given time constraints, were also taken into account in the siting of the plots. The vegetation cover of each plot was surveyed in summer 1998 using three randomly-placed quadrats (0.5m × 0.5m), and an index of percentage *Dryas* cover was obtained by measuring intercept lengths on two line transects stretched across the diagonals of each plot. The average soil depth was determined for each plot from 50 measurements per plot. Percentage organic matter was determined as loss on ignition at 400°C. Extractable phosphorus was determined using Morgan's extractant following the method of Byrne (1979). Soil pH was determined using a glass electrode (1:1 soil:water paste). The averages of these parameters were estimated from analysis of 4–5 separate samples per plot.

## MACROFUNGAL SAMPLING

Commencing in August 1997, sporocarps of each species were collected at selected sampling intervals from each of the ten plots described in the previous section. From mid-September to mid-November in 1997, 1998 and 1999, sampling was carried out at roughly two-week intervals, with longer intervals at other times of the year, when very little fruiting took place. Each of the plots was sampled six times during the main fruiting season, i.e. between the last week of August and the first week of October. The plots were sampled six times in 1997, nine times in 1998 and ten times in 1999, giving a total of 250 samples. All visible sporocarps were collected from the plots and returned to the laboratory in sealed plastic containers. The sporocarps of each species were counted and weighed on the same day. Sporocarp biomasses were determined by drying at 75°C for 48h. To assess the relative importance of each species based on its sporocarps, and for comparison with other studies, the following parameters were determined:

1. Total sporocarp biomass of species$_x$ ($tBS_x$) = $BS_x^{1997} + BS_x^{1998} + BS_x^{1999}$ where $BS_x$ = biomass of sporocarps of species$_x$ in all 10 plots (g/1000m$^2$). Average sporocarp biomass per year of species$_x$ ($aBS_x$) = $tBS_x/3$. Relative biomass of sporocarps of species$_x$ ($rBS_x$) = $(tBS_x/tBS_{Total}) \times 100$.
2. Total sporocarp density of species$_x$ ($tDS_x$) = $DS_x^{1997} + DS_x^{1998} + DS_x^{1999}$ where $DS_x$ = density of sporocaps of species$_x$ in all 10 plots (numbers/1000 m$^2$). Average sporocarp density per year of species$_x$ ($aDS_x$) = $tDS_x/3$. Relative density of sporocarps of species$_x$ ($rDS_x$) = $(tDS_x/tDS_{Total}) \times 100$.
3. Plot frequency of species$_x$ over the three-year sampling period ($PF_x$) = $\left(\frac{\text{Number of plots containing species}_x}{\text{Number of plots (10)}}\right) \times 100.$
4. Sample frequency of species$_x$ over the three-year sampling period ($SF_x$) = $\left(\frac{\text{Number of samples containing species}_x}{\text{Number of samples (250)}}\right) \times 100.$
5. The *importance percentage* (*IP*) of each species (Greig-Smith 1983) was calculated from its relative biomass (*rBS*), relative density (*rDS*) and sample frequency (*SF*). Importance percentage of species$_x$ ($IP_x$) = $(rBS_x + rDS_x + SF_x)/3$.

## STATISTICAL ANALYSES

The relationship between the macrofungi, the vegetation and the soil variables was assessed by canonical correspondence analysis (CCA) using CANOCO 4 (Software for Canonical Community Ordination version 4) (ter Braak and Šmilauer 1998). The analyses were carried out using sporocarp biomass data that was $\log_{10}$-transformed to take account of the large range of variation in sporocarp biomass between the different species. Descriptive statistics and Spearman's rank correlation coefficients were calculated using SPSS.

# RESULTS

## MACROFUNGAL DIVERSITY

Eighty-eight taxa were recorded from the 10 permanent plots over the sampling period August 1997–December 1999 (Table 1). Thirty-one, or 35%, belong to the ectomycorrhizal genera *Boletus*, *Cortinarius*, *Hebeloma*, *Hydnum*, *Inocybe*, *Lactarius*, *Ramaria*, *Russula*, *Suillus* and *Tricholoma*. *Cortinarius* was the largest genus represented (19 species), followed by *Entoloma* (17) and *Hygrocybe* (10).

**Table 1—Macrofungal diversity data recorded in ten permanent plots in the Burren, 1997–1999, arranged according to importance percentage of each species.**

| *Species* | | *tBS* (*g 1000m*$^{-2}$) | *% tBS* | *aBS* (*g 1000m*$^{-2}$ *y*$^{-1}$) | *tDS (numbers 1000m*$^{-2}$) | *aDS (numbers 1000m*$^{-2}$ *y*$^{-1}$) | *PF* | *SF* | *IP (%)* |
|---|---|---|---|---|---|---|---|---|---|
| *Craterellus lutescens* | m | 3089.9 | 43.4 | 1030.0 | 2954 | 984.67 | 80 | 29.6 | 0.379 |
| *Collybia dryophila* | s | 311.9 | 4.4 | 104.0 | 225 | 75 | 90 | 25.2 | 0.059 |
| *Cortinarius odorifer* | m | 641.7 | 9.0 | 213.9 | 52 | 17.33 | 70 | 10 | 0.045 |
| *Entoloma serrulatum* | s | 136.9 | 1.9 | 45.6 | 188 | 62.67 | 100 | 14 | 0.035 |
| *Boletus luridus* | m | 646.4 | 9.1 | 215.5 | 9 | 3 | 50 | 2.4 | 0.034 |
| *Cortinarius cinnamomeus* | m | 108.7 | 1.5 | 36.2 | 203 | 67.67 | 50 | 12.4 | 0.033 |
| *Stropharia semiglobata* | s | 151.71 | 2.1 | 50.6 | 145 | 48.33 | 80 | 12.4 | 0.031 |
| *Mycena pura* | s | 79.3 | 1.1 | 26.4 | 106 | 35.33 | 80 | 16.8 | 0.031 |
| *Cortinarius calochrous* | m | 250.1 | 3.5 | 83.4 | 60 | 20 | 70 | 11.2 | 0.029 |
| *Entoloma sericeum* | s | 96.1 | 1.4 | 32.0 | 150 | 50 | 90 | 10 | 0.026 |
| *Paneolus sphinctrinus* | s | 32.21 | 0.5 | 10.7 | 88 | 29.33 | 100 | 13.6 | 0.023 |
| *Cortinarius infractus* | m | 218.5 | 3.1 | 72.8 | 53 | 17.67 | 70 | 6.8 | 0.022 |
| *Cortinarius brunneus* | m | 211 | 3.0 | 70.3 | 71 | 23.67 | 40 | 6 | 0.017 |
| *Cortinarius caesiocanescens* | m | 163.3 | 2.3 | 54.4 | 11 | 3.67 | 70 | 6 | 0.017 |
| *Cortinarius anomalus* | m | 160.9 | 2.3 | 53.6 | 44 | 14.67 | 30 | 4 | 0.015 |
| *Entoloma* sp. 1 | s | 23 | 0.3 | 7.7 | 41 | 13.67 | 100 | 8 | 0.013 |
| *Cortinarius mussivus* | m | 67.2 | 0.9 | 22.4 | 29 | 9.67 | 40 | 4.4 | 0.010 |
| *Ramaria* sp. | m | 40.9 | 0.6 | 13.6 | 21 | 7 | 40 | 4 | 0.008 |
| *Clitocybe costata* | s | 32.8 | 0.5 | 10.9 | 17 | 5.67 | 50 | 4.4 | 0.008 |
| *Hygrocybe conica* | s | 14.5 | 0.2 | 4.8 | 20 | 6.67 | 40 | 4.4 | 0.007 |
| *Melanoleuca grammopodia* | s | 44.5 | 0.6 | 14.8 | 14 | 4.67 | 30 | 2.8 | 0.006 |
| *Mycena leptocephala* | s | 2.1 | 0.0 | 0.7 | 14 | 4.67 | 70 | 4.4 | 0.006 |
| *Hebeloma sinapizans* | m | 58 | 0.8 | 19.3 | 8 | 2.67 | 20 | 2.4 | 0.006 |
| *Hygrocybe* sp. | s | 7.7 | 0.1 | 2.6 | 17 | 5.67 | 50 | 3.2 | 0.005 |
| *Telamonia* sp. 3 | m | 5.4 | 0.1 | 1.8 | 11 | 3.67 | 50 | 3.6 | 0.005 |
| *Cortinarius uraceus* | m | 21.3 | 0.3 | 7.1 | 40 | 13.33 | 20 | 1.2 | 0.005 |
| *Cortinarius atrovirens* | m | 27.8 | 0.4 | 9.3 | 5 | 1.67 | 20 | 2 | 0.005 |
| *Hygrocybe nitrata* | s | 28 | 0.4 | 9.3 | 7 | 2.3 | 40 | 2.4 | 0.005 |
| *Agaricus porphyrizon* | s | 63.4 | 0.9 | 21.1 | 5 | 1.67 | 10 | 1.2 | 0.005 |
| *Hygrocybe virginea* | s | 13 | 0.2 | 4.3 | 21 | 7 | 20 | 2 | 0.004 |
| *Hygrocybe miniata* | s | 4.1 | 0.1 | 1.4 | 10 | 3.33 | 20 | 2.8 | 0.004 |
| *Entoloma* sp. 2 | s | 16 | 0.2 | 5.3 | 20 | 6.67 | 40 | 1.6 | 0.004 |
| *Cortinarius* sp. | m | 7.2 | 0.1 | 2.4 | 10 | 3.33 | 50 | 2.4 | 0.004 |
| *Entoloma* sp. 3 | s | 6.2 | 0.1 | 2.1 | 10 | 3.33 | 40 | 2.4 | 0.004 |
| *Hebeloma circinans* | m | 5.4 | 0.1 | 1.8 | 6 | 2 | 40 | 2.4 | 0.003 |
| *Unidentified* 1 | s | 3.4 | 0.0 | 1.1 | 7 | 2.33 | 40 | 2.4 | 0.003 |
| *Telamonia* sp. 1 | m | 16.4 | 0.2 | 5.5 | 25 | 8.33 | 10 | 0.8 | 0.003 |
| *Entoloma sarcitulum* | s | 2.1 | 0.0 | 0.7 | 14 | 4.67 | 40 | 2 | 0.003 |
| *Cortinarius bivelus* | m | 33.3 | 0.5 | 11.1 | 3 | 1 | 30 | 1.2 | 0.003 |
| *Mycena aetites* | s | 0.51 | 0.0 | 0.2 | 6 | 2 | 50 | 2.4 | 0.003 |
| *Microglossum viride* | s | 3 | 0.0 | 1.0 | 8 | 2.67 | 30 | 2 | 0.003 |
| *Entoloma mougeotti* | s | 3.5 | 0.0 | 1.2 | 7 | 2.33 | 40 | 2 | 0.003 |
| *Entoloma* sp. 4 | s | 4.7 | 0.1 | 1.6 | 20 | 6.67 | 20 | 1.2 | 0.003 |
| *Tricholoma myomyces* | m | 18.8 | 0.3 | 6.3 | 5 | 1.67 | 10 | 1.2 | 0.003 |
| *Unidentified* 2 | s | 4 | 0.1 | 1.3 | 5 | 1.67 | 40 | 1.6 | 0.002 |
| *Psathyrella* sp. | s | 1 | 0.0 | 0.3 | 7 | 2.33 | 30 | 1.6 | 0.002 |
| *Mycena* sp. | s | 0.7 | 0.0 | 0.2 | 7 | 2.33 | 30 | 1.6 | 0.002 |
| *Galerina* sp. | s | 0.4 | 0.0 | 0.1 | 4 | 1.33 | 30 | 1.6 | 0.002 |
| *Hebeloma* sp. | m | 8.4 | 0.1 | 2.8 | 5 | 1.67 | 30 | 1.2 | 0.002 |

**Table 1—(Continued).**

| *Species* | | *tBS* (*g 1000m*$^{-2}$) | *% tBS* | *aBS* (*g 1000m*$^{-2}$ *y*$^{-1}$) | *tDS (numbers 1000m*$^{-2}$) | *aDS (numbers 1000m*$^{-2}$ *y*$^{-1}$) | *PF* | *SF* | *IP* (*%*) |
|---|---|---|---|---|---|---|---|---|---|
| *Inocybe bongardii* | m | 1.6 | 0.0 | 0.5 | 4 | 1.33 | 20 | 0.8 | 0.002 |
| *Inocybe flocculosa* | m | 5.7 | 0.1 | 1.9 | 7 | 2.33 | 20 | 0.8 | 0.002 |
| *Entoloma* sp. 5 | s | 3.5 | 0.0 | 1.2 | 6 | 2 | 10 | 0.8 | 0.002 |
| *Lepista nuda* | s | 19 | 0.3 | 6.3 | 2 | 0.67 | 10 | 0.4 | 0.001 |
| *Clitopilus prunulus* | s | 4.6 | 0.1 | 1.5 | 4 | 1.33 | 10 | 0.8 | 0.001 |
| *Telamonia* sp. 2 | m | 5 | 0.1 | 1.7 | 10 | 3.33 | 10 | 0.4 | 0.001 |
| *Hygrocybe virginea var. fusc.* | s | 2.2 | 0.0 | 0.7 | 5 | 1.67 | 20 | 0.8 | 0.001 |
| *Entoloma bloxami* | s | 4.8 | 0.1 | 1.6 | 2 | 0.67 | 10 | 0.8 | 0.001 |
| *Inocybe* sp. 1 | m | 3.2 | 0.0 | 1.1 | 3 | 1 | 30 | 1.2 | 0.001 |
| *Marasmius androsaceus* | s | 0.02 | 0.0 | 0.0 | 2 | 0.67 | 20 | 0.8 | 0.001 |
| *Boletus erythropus* | m | 15.2 | 0.2 | 5.1 | 1 | 0.33 | 10 | 0.4 | 0.001 |
| *Hygrocybe flavescens* | s | 3.5 | 0.0 | 1.2 | 2 | 0.67 | 20 | 0.8 | 0.001 |
| *Hygrocybe* sp. 2 | s | 0.7 | 0.0 | 0.2 | 3 | 1 | 10 | 0.8 | 0.001 |
| *Cortinarius venetus* | m | 1.8 | 0.0 | 0.6 | 2 | 0.67 | 20 | 0.8 | 0.001 |
| *Entoloma scabiosum* | s | 7.5 | 0.1 | 2.5 | 4 | 1.33 | 10 | 0.4 | 0.001 |
| *Leotia lubrica* | s | 3.7 | 0.1 | 1.2 | 6 | 2 | 10 | 0.4 | 0.001 |
| *Melanoleuca exscissa* | s | 6.4 | 0.1 | 2.1 | 2 | 0.67 | 10 | 0.4 | 0.001 |
| *Entoloma griseocyaneum* | s | 4 | 0.1 | 1.3 | 3 | 1 | 10 | 0.4 | 0.001 |
| *Entoloma* sp. 6 | s | 2.3 | 0.0 | 0.8 | 4 | 1.33 | 10 | 0.4 | 0.001 |
| *Cortinarius croceocaeruleus* | m | 4.7 | 0.1 | 1.6 | 2 | 0.67 | 10 | 0.4 | 0.001 |
| *Tricholoma scalpturatum* | m | 6.1 | 0.1 | 2.0 | 1 | 0.33 | 10 | 0.4 | 0.001 |
| *Entoloma turci* | s | 2.4 | 0.0 | 0.8 | 3 | 1 | 10 | 0.4 | 0.001 |
| *Hygrocybe russocoriacea* | s | 1.4 | 0.0 | 0.5 | 3 | 1 | 10 | 0.4 | 0.001 |
| *Entoloma porphyrophaeum* | s | 3.3 | 0.0 | 1.1 | 1 | 0.33 | 10 | 0.4 | 0.001 |
| *Lyophyllum ozes* | s | 0.1 | 0.0 | 0.0 | 3 | 1 | 10 | 0.4 | 0.001 |
| *Collybia obscura* | s | 1.2 | 0.0 | 0.4 | 2 | 0.67 | 10 | 0.4 | 0.001 |
| *Geoglossum* sp. | s | 1 | 0.0 | 0.3 | 2 | 0.67 | 10 | 0.4 | 0.001 |
| *Entoloma chalybaeum* | s | 2.4 | 0.0 | 0.8 | 1 | 0.33 | 10 | 0.4 | 0.001 |
| *Trichoglossum hirsutum* | s | 0.3 | 0.0 | 0.1 | 2 | 0.67 | 10 | 0.4 | 0.001 |
| *Telamonia* sp. 4 | m | 1.7 | 0.0 | 0.6 | 1 | 0.33 | 10 | 0.4 | 0.001 |
| *Entomoma incana* | s | 1 | 0.0 | 0.3 | 1 | 0.33 | 10 | 0.4 | 0.001 |
| *Dermoloma cuneifolium* | s | 0.5 | 0.0 | 0.2 | 1 | 0.33 | 10 | 0.4 | 0.001 |
| *Hygrocybe laeta* | s | 0.4 | 0.0 | 0.1 | 1 | 0.33 | 10 | 0.4 | 0.001 |
| *Clavulina rugosa* | s | 0.3 | 0.0 | 0.1 | 1 | 0.33 | 10 | 0.4 | 0.001 |
| *Cortinarius spilomeus* | m | 0.3 | 0.0 | 0.1 | 1 | 0.33 | 10 | 0.4 | 0.001 |
| *Gerronema* sp. | s | 0.2 | 0.0 | 0.1 | 1 | 0.33 | 10 | 0.4 | 0.001 |
| *Conocybe* sp. | s | 0.1 | 0.0 | 0.0 | 1 | 0.33 | 10 | 0.4 | 0.001 |
| *Lepiota* sp. | s | 0.1 | 0.0 | 0.0 | 1 | 0.33 | 10 | 0.4 | 0.001 |
| *Clavaria vermicularis* | s | 0.03 | 0.0 | 0.0 | 1 | 0.33 | 10 | 0.4 | 0.001 |

*IP* = importance percentage; *tBS* = total biomass of sporocarps; *%tBS* = the percentage of the total biomass; *aBS* = the average sporocarp biomass produced per year; *tDS* = the total number of sporocarps; *aDS* = the average density of sporocarps per year; *PF* = the plot frequency of each species; *SF* = the sample frequency of each species; m = mycorrhizal spp; s = saprotrophic spp.

Thirty-five species (40%) are primarily woodland species, and virtually all of the 31 mycorrhizal species most commonly occur as ectomycorrhizae on trees and possibly other woody hosts. The range of species recorded was consistently greater in some plots (Plots 1 and 2) than others (Fig. 1). The number of species recorded per plot over the three-year period ranged between 21 in Plot 5 to 41 in Plot 8 (mean = 26.9), although in individual years the numbers were much less than this and subject to year-to-year variations. Diversity was much less in 1998 compared to 1997 or 1996. The

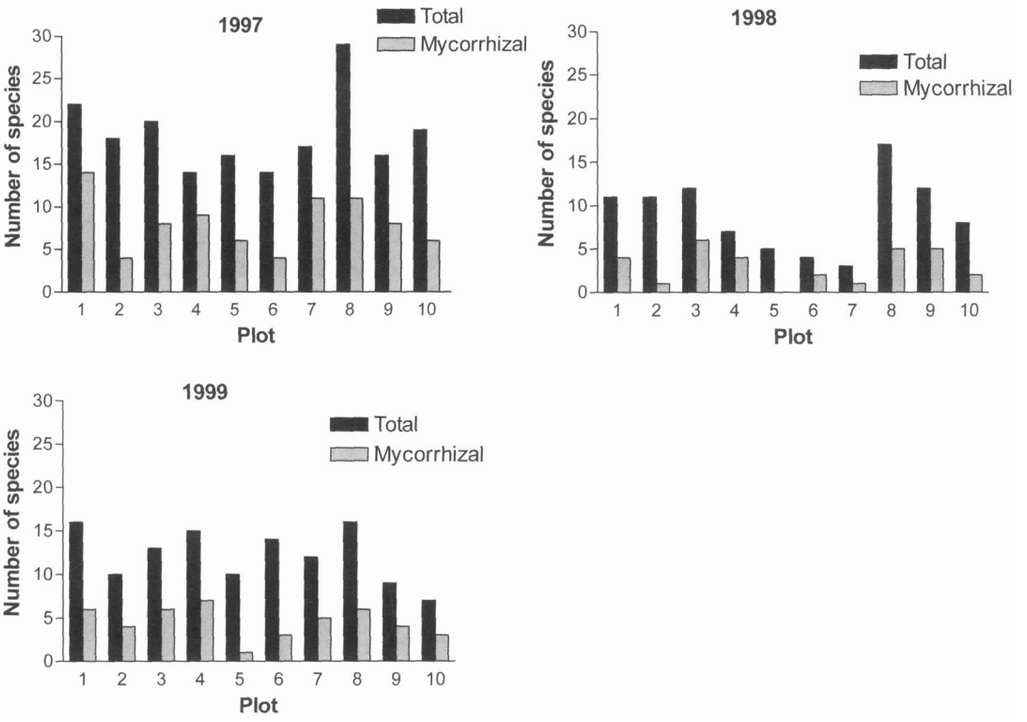


**Fig. 1—Variation in numbers of macrofungal species (all species and mycorrhizal species) in ten 100m$^2$ plots in the Burren in 1997, 1998 and 1999.**

proportion of mycorrhizal species in each plot ranged from 0% (Plot 5, 1998) to 68% (Plot 7, 1997) of the total, and on average 38% of the species per plot were ectomycorrhizal (marked 'm' in Table 1). Thirty-nine species occurred in only one year: 26 were found only in 1997, 6 only in 1998 and 7 only in 1999. Only two species, *Panaeolus sphinctrinus* and *Entoloma serrulatum*, occurred in all plots.

## SPOROCARP PRODUCTION

Sporocarp production varied considerably between years and between plots (Fig. 2). Average sporocarp production in the ten plots in 1997 was almost four times that of 1998 and over twice that of 1999, mirroring the differences in species diversity among years described above. Pooling the three yearly production totals for each plot and taking the range between the least productive and most productive plots as a yardstick, sporocarp production in the *Dryas* heaths ranged between a minimum of 0.45kg ha$^{-1}$ y$^{-1}$ and a maximum of 11.6kg ha$^{-1}$ y$^{-1}$ dry weight, with a plot average of 2.34kg ha$^{-1}$ y$^{-1}$. Plot 1 produced significantly more sporocarps than any of the other nine plots in all three years of the survey, and Plot 10 was the least productive plot in two of the three years.

Fig. 2 shows that in most plots in most years, mycorrhizal species produced the bulk of the sporocarp biomass. Over the three-year sampling period, 74% of the sporocarps and 83% of the sporocarp biomass were attributable to ectomycorrhizal macrofungi. The ectomycorrhizal *Craterellus lutescens* was the largest producer of sporocarps in Plot 1 and also in Plots 4, 5, 7 and 8, albeit in much smaller amounts (Table 1). This species alone was the largest producer of sporocarps in each year and contributed 43.5% of the total sporocarp biomass and 60% of the mycorrhizal sporocarp biomass over the three-year sampling period. *Boletus luridus* and *Cortinarius odorifer* each comprised approximately 9% of the total sporocarp biomass. *Cortinarius* as a group comprised 28% of the total sporocarp biomass over the sampling period.

Importance values were assigned to species on the basis of sporocarp biomass, sporocarp density and sample frequency. The species are arranged in order of decreasing importance percentages (*IP*) in Table 1. *Craterellus lutescens* was the most important species on the basis of most of these measures. Although it was not found in two plots (2 and 6), it was the most abundant species as measured by biomass in plots 1, 4, 7, 8 and 10. The distribution of sporocarps of this species was very uneven; 81% of the sporocarps were collected from one plot (Plot 1). Almost 50% of the total biomass of all fungi from all plots over the sampling period was

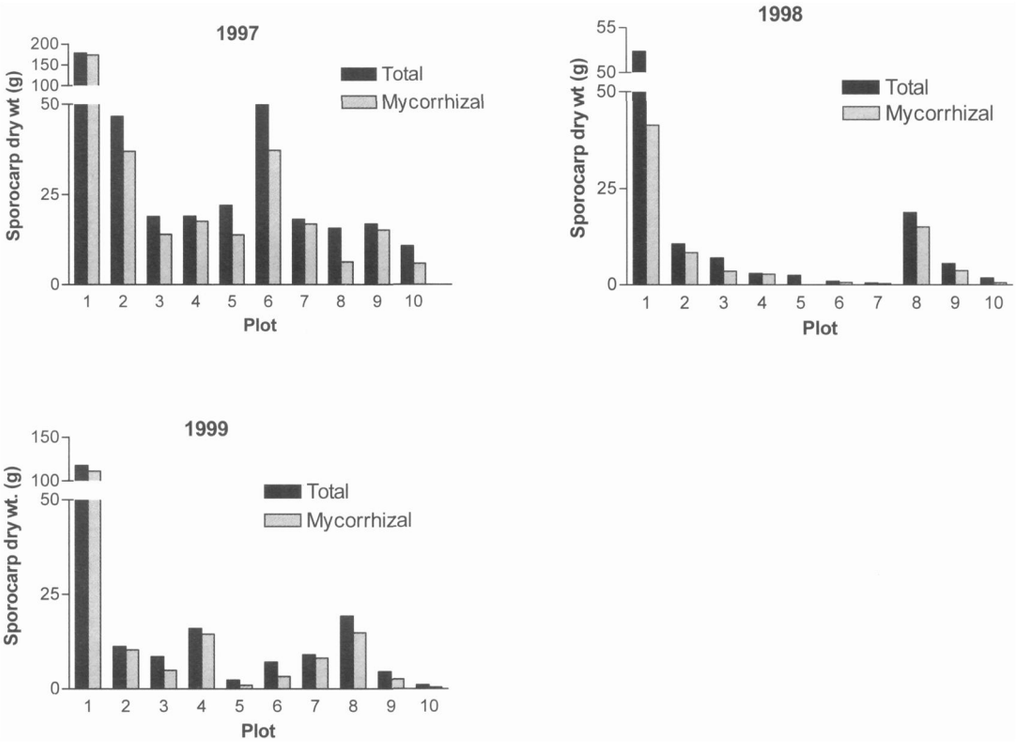


**Fig. 2—Variation in sporocarp production of macrofungal species (all species and mycorrhizal species) in ten 100m$^2$ plots in the Burren in 1997, 1998 and 1999.**

recorded from this one plot alone. If Plot 1 is omitted from the calculations, *C. lutescens* is still the most productive species (*rBS* = 16.7%). Fourteen other species constituted 89% of the sporocarp productivity in the 10 plots. In order of their calculated importance values (*IP*) these were *Collybia dryophila*, *Cortinarius odorifer*, *Entoloma serrulatum*, *Boletus luridus*, *Cortinarius cinnamomeus*, *Stropharia semiglobata*, *Mycena pura*, *Cortinarius calochrous*, *Entoloma sericeum*, *Cortinarius infractus*, *C. brunneus*, *C. caesiocanescens*, *C. anomalus* and *C. mussivus*. Omitting Plot 1 does not significantly alter this sequence. Ten of these are presumptive mycorrhizal species, two are common saprotrophs on leaf litter (*C. dryophila* and *M. pura*), two are regarded as humicolous (*E. serrulatum* and *E. sericeum*) and one (*S. semiglobata*) is, along with *Panaeolus sphinctrinus*, a common coprophilous species.

## RELATIONSHIP BETWEEN THE MACROFUNGI AND VEGETATION AND SOILS

The plant communities of the Burren have been described by Ivimey-Cook and Proctor (1966). They recognised three plant communities in which *Dryas* is found to varying extents that occur together in a complex intermingled pattern, particularly on higher ground in the Burren. White and Doyle (1982) reclassified the first two of these communities as heathlands rather than grasslands on account of the organic nature of the soils, and they also assigned them association status. The most common community is the *D. octopetala* – *Hypericum pulchrum* association (Hyperico–Dryadetum) in which *Dryas* is usually abundant. Where *Calluna vulgaris* is abundant in this association, for example on the more leached, organic soils, the vegetation has the appearance of a heath. The second community, the Arctostaphylo–Dryadetum association, is found on the upper slopes and summits of the hills where *Empetrum nigrum*, *Arctostaphylos uva-ursi* and *Juniperus communis* become common. There is a degree of confusion over what the third *Dryas* community should be called, although there is general agreement that it is a species-rich grassland community rather than a heath. This was described by Ivimey-Cook and Proctor (1966) as the *Antennaria dioica* – *Hieracium pilosella* community—a variant or 'nodum' of the Hyperico–Dryadetum found on the lower slopes of the hills on soils with increasing proportions of limestone drift. *Helianthemum canum*, *Sesleria albicans*, *Hieracium pilosella*, *Geranium sanguineum* and *Antennaria dioica* are frequently abundant in this community, with varying amounts of *Dryas* but usually less *Dryas* than in the other two

communities. This is probably the same community described by Shimwell (1971) as the Asperulo–Seslerietum association. These three communities are probably idealised points in a continuum or mosaic where the composition of the vegetation is determined mainly by drift content of the soil, altitude, exposure and possibly grazing. Plots were assigned subjectively to the different community types after inspection of the quadrat data from each plot. Plots 1, 2, 3 and 8 were assigned to the Hyperico–Dryadetum association. Plots 4 and 5, while similar in vegetation composition to Plots 1, 2, 3 and 8, contained significant amounts of *Arctostaphylos* and were therefore assigned to the Arctostaphylo–Dryadetum association. Plots 9 and 10, which had much more the appearance of grassland than the other plots, were assigned to the *Antennaria–Hieracium* community. Plots 6 and 7 were transitional (Tr.) between the Hyperico–Dryadetum community and the *Antennaria dioica – Hieracium pilosella* community on soils that have relatively high clay contents. Both plots have a vegetation cover that contains elements of these communities as well as species that were not found in the other plots, such as *Molinia caerulea* and *Schoenus nigricans*.

Table 2 shows the variation between the ten plots with respect to *Dryas* cover, soil and vegetation type. The type of vegetation present is summarised in the last column. The percentage cover of *Dryas* in the plots ranged from 18% in Plot 6 to 80% in Plot 1. The plots represent a subjective profile from a continuum of vegetation in which *Dryas* ranges from being a dominant to a minor component.

The relationship between the plots was analysed based on macrofungal composition and environmental variables using CCA. Analyses were carried out separately for saprotrophic fungi and mycorrhizal fungi using standard settings on log-transformed sporocarp biomass data. Scaling based on interspecies distance was employed: i.e. plot points are located around the centroids of species distributions. The plot ordinations showed that there was a differentiation of the plots based on macrofungal composition. This was most marked for saprotrophic fungi. The first two canonical axes explained a higher proportion of the variance in the distributions of the saprotrophic than the mycorrhizal species (44% vs 32%). In the plot ordination based on saprotrophs, the first canonical axis was strongly correlated with soil depth. Seven plots (1, 2, 3, 4, 5, 7 and 8) were differentiated from the remainder on the basis of their saprotrophs (Fig. 3). Vegetation differences between the plots is reflected to some degree in the saprotroph and mycorrhiza plot ordinations, particularly in respect of Plots 1, 2 and 8, Plots 9 and 10, and Plot 6. In both ordinations Plot 6 is an outlier due to its soil characteristics and macrofungal species composition.

The patterns of species distribution underlying the plot ordinations can be seen in the species ordinations in Fig. 4. The most common saprotrophs, e.g. *Collybia dryophila*, *Entoloma sericeum*, *E. serrulatum*, *Mycena pura*, *M. aetites* and *Hygrocybe virginea*, attained maximum abundance in the Hyperico–Dryadetum plots (1, 2, 3 and 8) and the Arctostaphylo–Dryadetum plots (4 and 5) (Fig. 4a). All of these plots are characterised by extremely organic soils of varying depth. Plots 9

**Table 2—Vegetation and soil characteristics of the ten permanent plots.**

| *Plot* | *Dryas cover* % | *Organic matter* % | *Extractable phosphate (ppm)* | *Soil pH* | *Mean soil depth (cm)* | *Altitude (m)* | *Vegetation type* |
|---|---|---|---|---|---|---|---|
| 1 | 79 | 84.6 (±4.1) | 48.7 (±21.6) | 6.6 (±0.3) | 4.8 (±3.1) | 180 | Hyp.–Dry. |
| 2 | 54 | 85.8 (±4.4) | 51.0 (±9.8) | 6.3 (±0.2) | 3.8 (±3.3) | 250 | Hyp.–Dry. |
| 3 | 74 | 75.0 (±4.5) | 29.6 (±2.2) | 6.8 (±0.3) | 3.6 (±4.2) | 120 | Hyp.–Dry. |
| 4 | 47 | 74.1 (±4.2) | 23.3 (±9.4) | 6.7 (±0.4) | 2.7 (±1.6) | 240 | Arct.–Dry. |
| 5 | 31 | 79.6 (±16.2) | 39.6 (±21.5) | 6.5 (±0.6) | 5.2 (±3.9) | 310 | Arct.–Dry. |
| 6 | 18 | 27.7 (±3.2) | 9.5 (±0.3) | 6.7 (±0.4) | 7.6 (±4.0) | 20 | Tr. |
| 7 | 24 | 57.6 (±10.7) | 13.7 (±4.3) | 6.7 (±0.2) | 6.1 (±4.2) | 250 | Tr. |
| 8 | 69 | 87.4 (±1.2) | 54.1 (±3.2) | 6.4 (±0.1) | 5.8 (±4.1) | 180 | Hyp.–Dry. |
| 9 | 54 | 40.4 (±13.7) | 12.4 (±3.5) | 6.8 (±0.3) | 2.8 (±2.7) | 150 | Annt.–H. |
| 10 | 30 | 64.6 (±3.5) | 33.8 (±6.4) | 6.6 (±0.4) | 3.6 (±1.9) | 190 | Annt–H. |

Hyp.–Dry. = Hyperico–Dryadetum association; Arct.–Dry. = Arctostaphylo–Dryadetum association; Annt.–H. = *Antennaria dioica – Hieracium pilosella* community; Tr. = transitional community. Figures for organic matter, extractable phosphate and soil pH are means of 3–5 samples per plot (SD in parentheses).

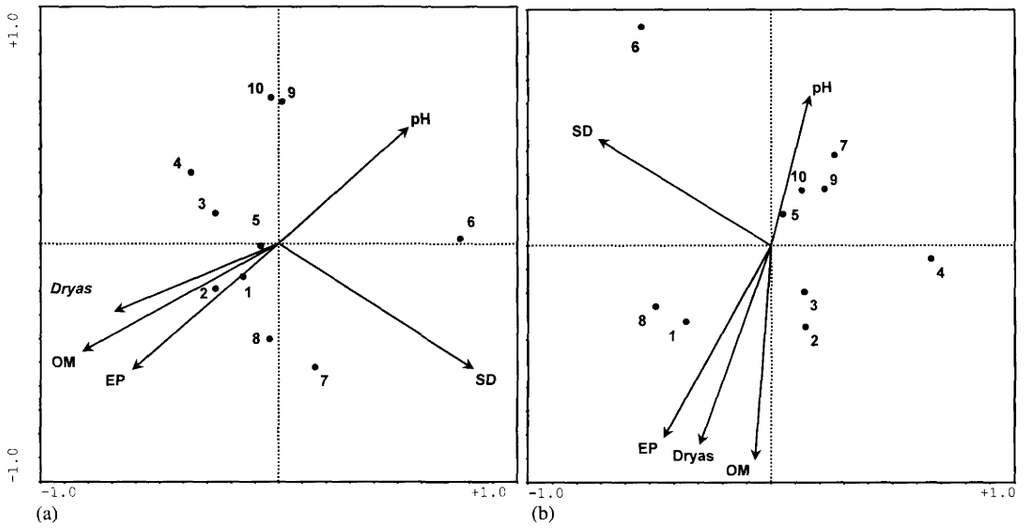


**Fig. 3—Plot ordination from CCA of macrofungal species found in ten permanent plots in the Burren based on sporocarp biomass. (a) saprotrophic macrofungi; (b) mycorrhizal macrofungi. OM = soil organic matter (%); EP = extractable soil phosphorus (ppm); SD = soil depth (cm); pH = soil pH; *Dryas* = *Dryas* cover (%).**

and 10 were distinguished by the presence of a number of species that are typical of poor grassland and were absent or uncommon elsewhere (*Clavaria rugosa*, *Lyophyllum ozes*, *Melanoleuca grammopodia* and *Trichoglossum hirsutum*). Similarly, Plot 6 harboured a number of grassland saprotrophs that were not found elsewhere (*Agaricus porphyrizon*, *Hygrocybe nitrata*, *Entoloma bloxami* and a number of other *Entoloma* species). Deeper mineral soils and *Dryas* and *Calluna* cover may be important factors influencing the distribution of these species. The coprophiles *Panaeolus sphinctrinus* and *Stropharia semiglobata* were also more abundant in Plot 6 than any other, possibly because of the heavier grazing pressure by cattle in this area.

The ordination of the mycorrhizal species showed differences in the distribution of a number of *Cortinarius* species, in particular between the Hyperico–Dryadetum plots and the rest (Fig. 4b). Axis 1 of the mycorrhizal ordination was negatively correlated with soil depth, and Axis 2 was negatively correlated with soil organic matter. Sporocarps of *Cortinarius odorifer*, *C. atrovirens*, *C. venetus*, *C. anomalus* and *Craterellus lutescens* attained maximum abundance in the Hyperico–Dryadetum plots (1, 2 and 8) on deeper organic soils, and a number of unidentified *Telamonia* species were confined to these as well. *Tricholoma myomyces* and *T. scalpturatum* were confined to Plot 1 in this group. In contrast, sporocarps *of Cortinarius calochrous*, *C. caesiocanescens*, *C. infractus* and *C. mussivus* were more strongly associated with the shallower and less organic soils (Plots 3, 4, 5 and 9). A number of species attained maximum abundance of sporocarps on plots with deeper, more mineral soils (6 and 7), e.g. *Boletus luridus*, *Hebeloma circinans*, *Ramaria* sp. and to a lesser extent *Cortinarius cinnamomeus*.

Table 3 summarises the variation between the four vegetation types with respect to macrofungal diversity, *Dryas* cover and soil characteristics. The number of macrofungal species and the number of mycorrhizal species per plot were greater in the Hyperico–Dryadetum plots, significantly so when compared with the plots of the other three vegetation types collectively. The soils here were extremely organic, and the vegetation was characterised by extensive cover of *Dryas*, which was almost double that of the rest of the plots.

A significant correlation was found between the number of ectomycorrhizal species recorded from plots over the sampling period and the percentage of *Dryas* cover of plots, using Spearman's rank correlation ($r = 0.728$, $P \leq 0.01$) (Table 4; Fig. 5). The diversity of saprotrophic species was unrelated to the percentage cover of *Dryas* in the plots but was significantly correlated with extractable soil phosphorus. No relationship was found between the biomass of sporocarps and any of the environmental variables measured in the plots, but in the case of saprotrophic species the number of sporocarps produced per plot was positively correlated with soil organic matter and extractable soil phosphorus.

## DISCUSSION

The macrofungal biota of the Burren *Dryas* heaths comprises two principal ecological elements as distinguished by Harrington (1996). Saprotrophs

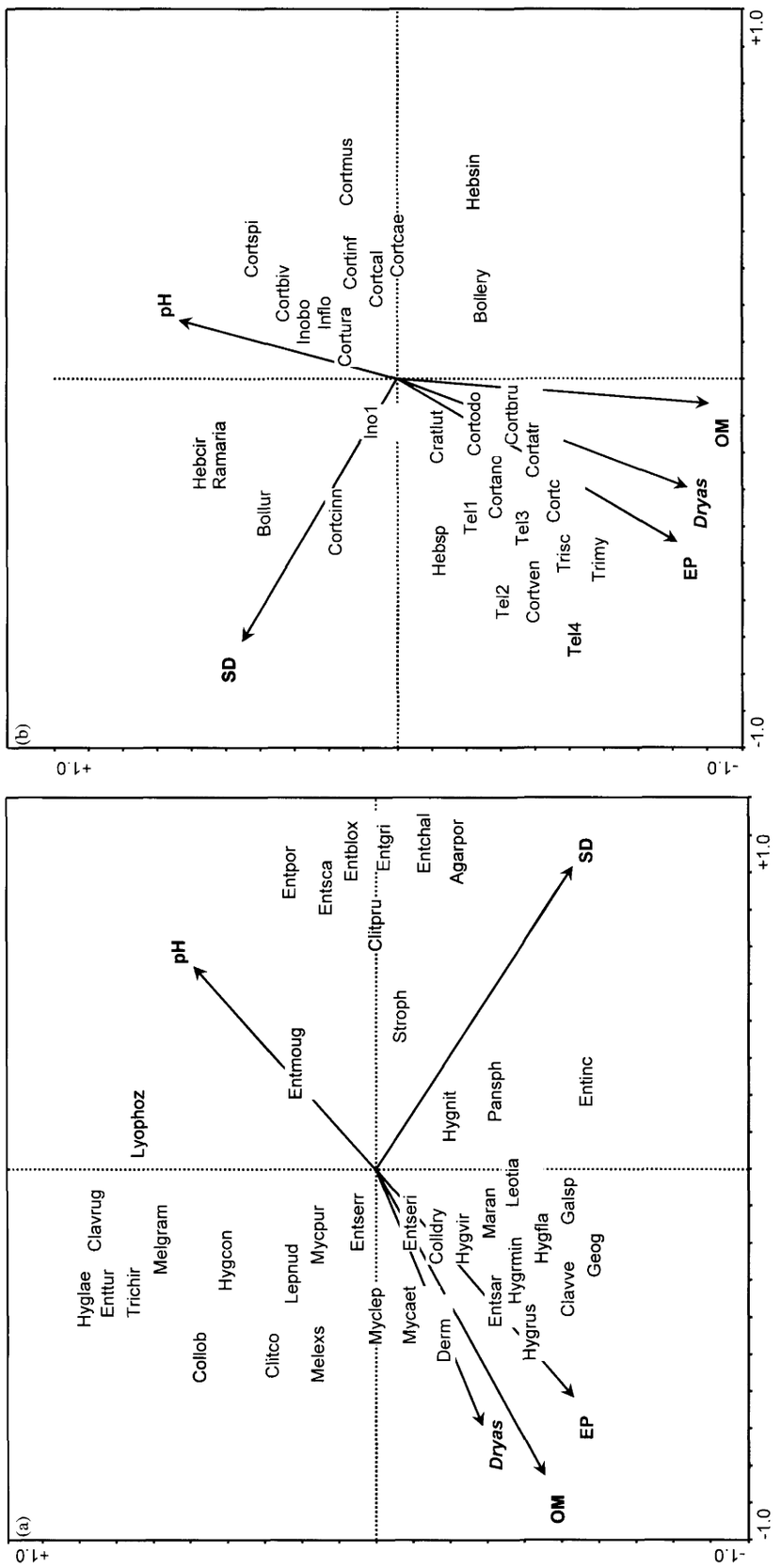


Fig. 4—Species ordination from CCA of macrofungi found in ten permanent plots in the Burren. (a) saprotrophic species (b) mycorrhizal species. Symbols as in Fig. 3.

**Agarpor** = *Agaricus porphyrizon*
**Bollery** = *Boletus erythropus*
**Bollur** = *B. luridus*
**Clavrug** = *Clavulina rugosa*
**Clavve** = *Clavaria vermicularis*
**Clitco** = *Cliticybe costata*
**Clitpru** = *Clitopilus prunulus*
**Colldry** = *Collybia dryophila*
**Collob** = *C. obscura*
**Cortano** = *Cortinarius anomalus*
**Cortatr** = *C. atrovirens*
**Cortbiv** = *C. hivelus*
**Cortbru** = *C. brunneus*
**Cortcae** = *C. caesiocanescens*
**Cortcal** = *C. calochrous*
**Cortcinn** = *C. cinnamomeus*
**Cortcro** = *C. crococaeruleus*
**Cortinf** = *C. infractus*
**Cortmus** = *C. mussivus*
**Cortodo** = *C. odorifer*
**Cortspi** = *C. spilomeus*
**Cortura** = *C. uracens*
**Cortven** = *C. venetus*
**Cratlut** = *C. lutescens*
**Derm** = *Dermoloma cuneifolium*
**Entblox** = *Entoloma bloxami*
**Entchal** = *E. chalybaeum*
**Entgri** = *E. griseum*
**Entinc** = *E. incana*
**Entmoug** = *E. mougeotii*
**Entpor** = *E. porphyrophaeum*
**Entsar** = *E. sarcitulum*
**Entsca** = *E. scabiosum*
**Entseri** = *E. sericeum*
**Entserr** = *E. serrulatum*
**Enttur** = *E. turci*
**Galsp** = *Galerina* sp.
**Geog** = *Geoglossum* sp.
**Hebcir** = *Hebeloma circinans*
**Hebsin** = *H. sinapizans*
**Hebsp** = *Hebeloma* sp.
**Hygcon** = *Hygrocybe conica*
**Hygfla** = *H. flavescens*
**Hyglae** = *H. laeta*
**Hygmin** = *H. miniata*
**Hygnit** = *H. nitrata*
**Hygrus** = *H. russocoriacea*
**Hygvir** = *H. virginea*
**Inflo** = *Inocybe flocculosa*
**Inobo** = *Inocybe bongardii*
**Ino1** = *Inocybe* sp. 1
**Leotia** = = *Leotia lubrica*
**Lepnud** = *Lepista nuda*
**Lyophoz** = *Lyophyllum oozes*
**Maran** = *Marasmius androsaceus*
**Melexs** = *Melanoleuca exscissa*
**Melgram** = *M. grammopodia*
**Mycaet** = *Mycena aetites*
**Myclep** = *M. leptocephala*
**Mycpur** = *M. pura*
**Pansph** = *Panaeolus sphinctrinus*
**Ramaria** = *Ramaria* sp.
**Stroph** = *Stropharia semiglobata*
**Tel1** = *Telamonia* sp. 1
**Tel2** = *Telamonia* sp. 2
**Tel3** = *Telamonia* sp. 3
**Tel4** = *Telamonia* sp. 4
**Trichir** = *Tricholossum hirsutum*
**Trimy** = *Tricholoma myomyces*
**Trisc** = *T. scalpturatum*

constitute the largest element, and these can be subdivided into grassland/heathland species (especially *Entoloma* and *Hygrocybe*) and a smaller group of woodland litter fungi (e.g. *Mycena* spp, *Lepista nuda*). Thirty-one mycorrhizal species constitute the second element, and these are considered to be normally ectomycorrhizal species of trees (Trappe 1962). It has been shown that fifteen of these form ectomycorrhizae on *Dryas* roots (Harrington and Mitchell 2002a). Further work will show in all likelihood that *Dryas* forms mycorrhizae with most of the other putative mycorrhizal fungi, although one important exception to this—*C. cinnamomeus*—forms ectomycorrhiza-like structures exclusively with *Carex* spp in the Burren (Harrington and Mitchell 2002b) and other species may be associated with *Arctostaphylos* and *Helianthemum*. *Boletus luridus*, *B. erythropus* and an indeterminate *Ramaria* were found in plots with less organic soils and with less *Dryas* cover. *Helianthemum canum*, which is more common in these areas, may be a host for these species. *B. luridus* has been observed fruiting in association with the common rock rose *H. nummularium* in Britain (Henrici 2000), and Wilkins and Patrick (1939) noted an association between *B. erythropus*, *Cortinarius anomalus* and *H. nummularium* in chalk grassland in Oxfordshire.

The primary determinant for the presence of most of the ectomycorrhizal woodland fungi in the *Dryas* vegetation is their ability to form ectomycorrhizae with *Dryas*, a phenomenon that has not been reported from other *Dryas* habitats. The diversity and distribution of the ectomycorrhizal species is therefore determined principally by the distribution of *Dryas*. Diversity

**Table 3—Macrofungal diversity, *Dryas* cover and soil characteristics of plots representing four vegetation types in the Burren.**

| | *Hyperico–Dryadetum* | *Arctostaphyo–Dryadetum* | *Antennaria–Hieracium* | *Transitional* |
|---|---|---|---|---|
| Mean number of macro fungal species/plot | 31.8 (±7.3) | 22.0 (±1.4) | 27.5 (±2.1) | 23.0 (±1.4) |
| Mean number of mycorrhizal species/plot | 12.5 (±4.8) | 8.0 (±2.8) | 10.5 (±2.1) | 8.5 (±3.5) |
| Mean percentage *Dryas* cover | 69.0 (±9.8) | 39.0 (±8.8) | 42.0 (±13.2) | 24.0 (±6.6) |
| Mean percentage organic matter | 83.2 (±5.1) | 76.9 (±3.0) | 52.5 (±13.3) | 42.7 (±16.4) |
| Mean extractable soil phosphorus (ppm) | 45.9 (±10.0) | 31.5 (±8.9) | 23.1 (±11.7) | 11.6 (±2.3) |
| Mean soil pH | 6.5 (±0.2) | 6.6 (±0.1) | 5.1 (±0.1) | 6.8 (±0.1) |
| Mean soil depth (cm) | 4.5 (±0.9) | 4.0 (±1.4) | 3.2 (±0.4) | 6.8 (±0.9) |
| Number of quadrats | 12 | 6 | 6 | 6 |
| Plots | 1, 2, 3, 8 | 4, 5 | 9, 10 | 6, 7 |

**Table 4—Relationship between number of macrofungal species per plot, number of sporocarps produced per plot and site variables in ten plots in the Burren estimated using Spearman's correlation coefficient *r*. The analysis was carried out on the total numbers of species and numbers of sporocarps recorded per plot over the three-year sampling period.**

| | *Number of species* | | | *Number of sporocarps* | | |
|---|---|---|---|---|---|---|
| | *A* | *m* | *s* | *A* | *m* | *s* |
| *Dryas* cover % | 0.629 | 0.728* | 0.251 | 0.573 | 0.525 | 0.528 |
| Soil organic matter % | 0.405 | 0.302 | 0.319 | 0.408 | 0.345 | 0.818** |
| Extractable soil P (ppm) | 0.609 | 0.260 | 0.644* | 0.471 | 0.387 | 0.842** |
| Soil pH | −0.099 | −0.009 | −0.132 | 0.208 | 0.382 | 0.070 |
| Mean soil depth (cm) | 0.097 | −0.129 | 0.247 | 0.111 | 0.092 | 0.173 |

* significant at $P \leq 0.05$; ** significant at $P \leq 0.01$; A = all species; m = mycorrhizal species only; s = saprotrophic species only.

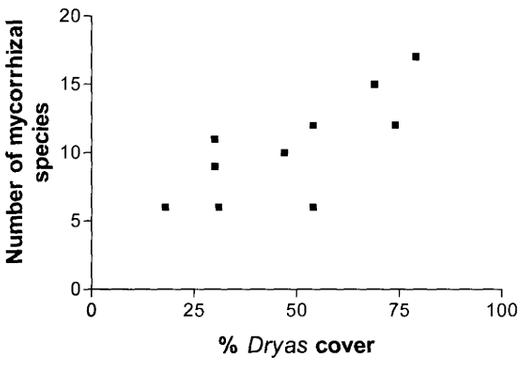


**Fig. 5—Relationship between the numbers of mycorrhizal macrofungal species recorded from the ten plots over the sampling period and the percentage *Dryas* cover in the plots.**

of ectomycorrhizal species in the permanent plots, for instance, was strongly correlated with the degree of *Dryas* cover. A similar relationship was found between diversity of ectomycorrhizal fungi and the cover of host trees in a study by Villeneuve *et al.* (1988) in forests in the Laurentide Mountains of Quebec. Other factors, however, appear to have a secondary but nonetheless important influence on the distribution of these fungi. The majority of ectomycorrhizal species fruited most abundantly on the highly organic soils of varying depth as distinct from the mineral soils. Positive relationships of this kind between diversity and productivity of ectomycorrhizal sporocarps and soil organic matter have been frequently observed in studies of macrofungi in forests (Tyler 1985; 1989). It can, however, be misleading to draw inferences about fungal distributions from the presence or absence of sporocarps since for most species the relationship between the fungal mycelium and the extent of fruiting in the field is unknown. However, work on ectomycorrhiza distribution in different soil types in the Burren indicates that most of the ectomycorrhizal macrofungi are poorly represented as mycorrhizae on *Dryas* in the more mineral soils compared to the organic soils (Harrington 2001). Thus, differences in sporocarp abundance between the plots probably reflect real differences in ectomycorrhizal distributions, at least for some species. It appears, therefore, that most of the ectomycorrhizal species associated with *Dryas* do not accompany *Dryas* over its entire edaphic range within the Burren but are restricted to part of it. Nantel and Neumann (1992) noted this phenomenon in respect of sporocarp distribution in forest ecosystems in southern Quebec. Soil depth also appears to have an effect on sporocarp distribution. *Craterellus lutescens* was the most abundant ectomycorrhizal species on the deeper organic soils (Hyperico–Dryadetum plots), whereas a number of *Cortinarius* subgenus *Phlegmacium* species fruited more abundantly on the shallower organic soils where *Dryas* formed low, spreading cushions. Members of the subgenus *Phlegmacium* are normally found on highly calcareous forest soils in Europe (Brandrud *et al.* 1990–8) so it is not surprising that they are more common on the shallower soils where the influence of the limestone substratum is greatest.

Soil organic matter and soil depth also appear to be important factors in the distribution of individual saprotrophic species, if sporocarps can be regarded as quantitative indicators of physiological activity. This is illustrated by the marked differences in species composition between the heathy Hyperico–Dryadetum plots on very organic soils and Plots 6, 7 and 9, which in contrast, had grassland vegetation on clay soil. In plots 6, 7 and 9, a number of *Entoloma* and *Hygrocybe* species were recorded that were absent from, or rare in the Hyperico–Dryadetum plots. Density of sporocarps (numbers of sporocarps per plot) was strongly correlated with soil organic matter. This was most marked for woodland/heathland species such as *Collybia dryophila* and *Mycena* spp, and the large amounts of leaf litter produced by *Dryas* and *Calluna* in the Hyperico–Dryadetum plots probably explains the abundance of these species in these areas. Wilkins and Patrick (1939) noted similar differences in species diversity and sporocarp production between organic chalk soils and mineral clay soils in Oxford. Arnolds (1981) found no relationship, however, between species diversity or sporocarp production and soil organic matter in grasslands and moist heathlands in the Netherlands. In the Burren, *Entoloma* and *Hygrocybe* dominated the saprotrophic assemblage, which contained many species typical of old unfertilised grassland or grass–heath such as *Entoloma bloxami*, *Hygrocybe nitrata* and *Dermoloma cuneifolium*. Saprotrophic fungi were more diverse in areas that had less *Dryas* and *Calluna* cover and more graminaceous cover. *Entoloma* is much more diverse in the Burren *Dryas* vegetation than *Hygrocybe*, and this may reflect the preference of most *Hygrocybe* species for grassland over mixed vegetation of grasses and dwarf shrubs.

Sporocarp production was unevenly distributed between the plots, with the four plots of the Hyperico–Dryadetum producing almost 70% of the sporocarp biomass. This is due to the fact that the most productive ectomycorrhizal species, (*Craterellus lutescens* and *Cortinarius odorifer*), and other *Cortinarius* species with large sporocarps fruited abundantly in Plots 1, 2, 3 and 8. Data from ectomycorrhiza surveys (Harrington 2001) suggest that the fruiting patterns of these species reflect their higher frequency of occurrence as ectomycorrhizae on *Dryas* roots in these plots

compared to the other plots. Average annual sporocarp production in the Burren ranged between 0.5kg $ha^{-1}y^{-1}$ and 11kg $ha^{-1}$ $y^{-1}$ dry weight depending on the productivity of the plots. Production is much lower in true arctic–alpine *Dryas* vegetation (Senn-Irlet 1988). Figures for heathlands (0.1–0.7kg $ha^{-1}$ $y^{-1}$ dry weight) and grasslands (0.3–5.1 kg $ha^{-1}$ $y^{-1}$ dry weight) produced by Arnolds (1981) in the Netherlands are considerably lower because of the absence of ectomycorrhizal macrofungi in these habitats. Since the Burren *Dryas* vegetation harbours so many woodland macrofungi, it is interesting to compare its sporocarp production with that of woodlands (see Vogt *et al.* (1992) for a summary of these figures). In temperate deciduous woodlands and boreal coniferous forests, sporocarp production ranges between 3kg $ha^{-1}y^{-1}$ and 40kg $ha^{-1}$ $y^{-1}$ dry weight. While a number of plots in the Burren are inside this range, the plot average (2.34kg $ha^{-1}$ $y^{-1}$ dry weight) is just outside. Over the three-year sampling period ectomycorrhizal fungi constituted 83% of the sporocarp biomass, and the bulk of this was contributed by the fifteen species known to be ectomycorrhizal on *Dryas* roots. The high production of *Cortinarius* sporocarps, while secondary to *Craterellus*, is a feature shared by boreal coniferous woodlands in particular (Dahlberg *et al.* 1997).

Given the huge difference in net primary productivity between forest trees and *Dryas*, levels of sporocarp production in the Burren *Dryas* heaths are extraordinarily high, suggesting that a large amount of the carbon assimilated by *Dryas* may be appropriated by its ectomycorrhizal macrofungi. Estimates of carbon allocation to ectomycorrhizal fungi in forests range from 10% to 15% of net primary production (Vogt *et al.* 1982; Smith and Read 1997), and it is probable that the comparable figure for the Burren *Dryas* heaths is in excess of this. Although no studies have yet been carried out on the carbon economy of *Dryas* in the Burren, it is possible that the mild climate and extended growing season of the Burren may promote a high level of $CO_2$ assimilation by *Dryas*, which is exploited by its ectomycorrhizal fungi.

## REFERENCES


Arnolds, E. 1981 Ecology and coenology of macrofungi in grasslands and moist heathlands in Drenthe, the Netherlands: Part 1. *Introduction and synecology. Bibliotheca Mycologica* **83**. Vaduz, Liechtenstein. J. Cramer.

Brandrud, T.-E., Lindstrøm, H., Marklund, H., Melot, J. and Muskos, S. 1990–8 *Cortinarius Flora Photographica* 1–4. Matfors, Sweden. Cortinarius HB.

Byrne, E. 1979 *Chemical analysis of agricultural materials*. Dublin. An Foras Taluntais.

Dahlberg, A., Jonsson, L and Nylund, J.-E. 1997 Species diversity and distribution of biomass above and below ground among ectomycorrhizal fungi in an old-growth Norway spruce in south Sweden. *Canadian Journal of Botany* **75**, 1323–35.

Greig-Smith, P. 1983 *Quantitative plant ecology*. London. Blackwell.

Harrington, T. 1994 New Irish fungal records. *Irish Naturalists' Journal* **24**, 413–4.

Harrington, T. 1996 Observations on the macrofungi of *Dryas* communities in the Burren, western Ireland. *Irish Naturalists' Journal* **25**, 157–92.

Harrington, T.J. 2001 Macromycete diversity and ectomycorrhizal associations in *Dryas* heaths in the Burren. Unpublished PhD thesis, University College Dublin, National University of Ireland, Dublin.

Harrington, T. and Mitchell, D.T. 2002a Characterization of *Dryas octopetala* ectomycorrhizas from limestone karst vegetation, western Ireland. *Canadian Journal of Botany* **80**, 970–82.

Harrington, T. and Mitchell, D.T. 2002b Colonization of root systems of *Carex flacca* and *C. pilulifera* by *Cortinarius* (*Dermocybe*) *cinnamomeus*. *Mycological Research* **106**, 452–9.

Henrici, A. 2000 Notes and records. *Field Mycology* **1**, 87–9.

Ivimey-Cook, R.B. and Proctor, M.C.F. 1966 The plant communities of the Burren, Co. Clare. *Proceedings of the Royal Irish Academy* **64**B, 211–301.

Kühner, R. and Lamoure, D. 1986 Catalogue des agaricales (basidiomycètes) de la zone alpine du parc national de la vanoise et des régions limitrophes. *Travaux scientifiques du Parc national Vanoise* **15**, 103–87.

Nantel, P. and Neumann, P. 1992 Ecology of ectomycorrhizal basidiomycete communities on a local vegetation gradient. *Ecology* **73**, 99–117.

Senn-Irlet, B. 1988 Macromycetes in alpine snow-bed communities—mycocoenological investigations. *Acta Botanica Neerlandica* **37**, 251–63.

Shimwell, D.W. 1971 Festuca–Brometea Br.-Bl. et R. Tx. 1943 in the British Isles: the phytogeography and phytosociology of limestone grasslands. *Vegetatio* **23**, 1–27, 29–60.

Smith, S.E. and Read, D.J. 1997 *Mycorrhizal symbiosis*, 2nd edn. London. Academic Press Ltd.

ter Braak, C.J.F. and Šmilauer, P. 1998 *CANOCO Reference Manual and User's Guide to Canoco for Windows*. Software for Canonical Community Ordination (version 4). Centre for Biometry Wageningen (Wageningen, Netherlands) and Microcomputer Power (Ithaca, New York).

Trappe, J.M. 1962 Fungus associates of ectotrophic mycorrhizae. *The Botanical Review* **28**, 538–606.

Tyler, G. 1985 Macrofungal flora of Swedish beech forest related to soil organic matter and acidity characteristics. *Forest Ecology and Management* **10**, 13.

Tyler, G. 1989 Edaphical distribution patterns of macrofungal species in deciduous forest of south Sweden. *Acta Oecologia/Oecologia Generalis* **10**, 309–26.

Villeneuve, N., Grandtner, M.M. and Fortin, J.A. 1988 Frequency and diversity of ectomycorrhizal and saprophytic macrofungi in the Laurentide Mountains of Quebec. *Canadian Journal of Botany* **67**, 2616–29.

Vogt, K.A., Grier, C.C., Meier, C.E. and Edmonds, R.L. 1982 Mycorrhizal role in net primary production and nutrient cycling in *Abies amabilis* ecosystems in western Washington. *Ecology* **63**, 170–80.

Vogt, K.A., Bloomfield, J., Ammirati, J.F. and Ammirati, S.R. 1992 Sporocarp production by basidiomycetes, with emphasis on forest ecosystems. In C. Carrol and D.T. Wicklow (eds), *The fungal community, its organization and role in the ecosystem*, 563–81. New York. Marcel Dekker.

White, J. and Doyle, G. 1982 The vegetation of Ireland: a catalogue raisonné. *Journal of Life Sciences, Royal Dublin Society* **3**, 289–368.

Wilkins, W.H. and Patrick, S.H.M. 1939 The ecology of larger fungi III. Constancy and frequency of grassland species with special reference to soil types. *Annals of Applied Biology* **26**, 25–46.