Int. J. Speleol., 30 A (1/4) 2001: 27 - 37

THE DISTRIBUTION OF PLANTS IN SCOSKA CAVE, NORTH YORKSHIRE, AND THEIR RELATIONSHIP TO LIGHT INTENSITY

Allan PENTECOST and Zhang ZHAOHUI*

SUMMARY

The flora of a small limestone cave was investigated. A total of 59 species was recorded (4 algae, 3 lichens, 47 bryophytes, 4 ferns, 1 angiosperm) making it bryologically the richest cave in Britain and one of the richest in Europe. All but nine of the species had been recorded from other European caves. Species-richness declined irregularly from the entrance (relative irradiance with respect to open sky 12%) to 34m depth (rel. irradiance 0.004%). Bryophytes were found at 0-16m depth where relative irradiance declined to 0.2% and only algae were encountered at 34m depth. While irradiance, which declined exponentially, was the major factor controlling plant distribution, substratum characteristics and surface moisture were also important.

Keywords: caves, flora, bryophytes, light.

Introduction

Remarkably little has been published on the flora of British caves, despite the popularity of caving as a British sport. While cave surveys have been numerous, there has been little effort to systematically examine caves for their flora. This contrasts with continental Europe where the cave flora is much better known, e.g. Maheu (1906), Lammermayer (1916) and Dobat (1966 ;1970; 1998a,b). In Britain, Mason-Williams & Benson Evans (1958, 1967), Mason-Williams (1962; 1966) and Cubbon (1970; 1976) provide lists of bacteria, algae, bryophytes and angiosperms from several South Wales caves including some information on substratum pH, light and humidity. Dalby (1966) investigated the growth of a moss, *Eucladium verticillatum*

* Division of Life Sciences, King's College London, Franklin-Wilkins Building, 150 Stamford Street, London SE19 NN, UK.

in an English mine and found interesting adaptations to light, while Zhang & Pentecost (1999) published a short list of cave bryophytes from Yorkshire. Some British cave algae have also been noted by Claus (1967) and Carter (1971), but apart from this, there are only isolated references to the British cave flora in more general works such as Hill *et al.*, (1994).

The largest area of limestone caves in Britain is to be found in the Craven district of North Yorkshire. Surprisingly, this area is also one of the least well known for its cave flora. The senior author recognised Scoska Cave as a good site for the investigation of plant threshold communities some years ago. The entrance is 70m above the River Skirfare on a NE-facing steep scarp below Scoska Moor in Littondale (Nat. Grid Ref. 34/915724, alt. 285 m). It is the source of a small stream, Gildersbank Sike. Scoska is noted for its moderately wide (3-4m) and straight entrance passage which follows a horizontal bedding plane developed in Dinantian Great Scar Limestone. Light is able to visibly penetrate at least 40 m into the passage and is gradually attenuated by the simple geometry, an unusual occurrence in British caves. The roof is about 2m high following a higher bedding plane (Fig. la).

We report here on the flora of the cave and its relationships with light intensity, with particular reference to biodiversity (as species-richness).

Methods

We examined the cave on two dates: 1.4.2000 and 15.7.2000. In addition to collecting small samples of cave flora at regular intervals from the entrance, cave dimensions were measured together with microclimate; air temperature, relative and absolute humidity and irradiance. Humidity was measured with a hand-held psychrometer and irradiance with a Licor 185 B quantum meter, the sensor of which was placed directly toward the cave entrance. Absolute and relative photosythetically available radiation (PAR) measurements were obtained by comparison with the open, unobstructed sky. Critical plant groups were identified using standard British floras. Bryophytes were particularly conspicuous but we also examined lichens, ferns, spermatophytes and in less detail, the algae. Lichen, bryophyte and pteridophyte nomenclature follows Purvis *et al.*, (1992), Blockeel & Long (1998) and Stace (1991) respectively.

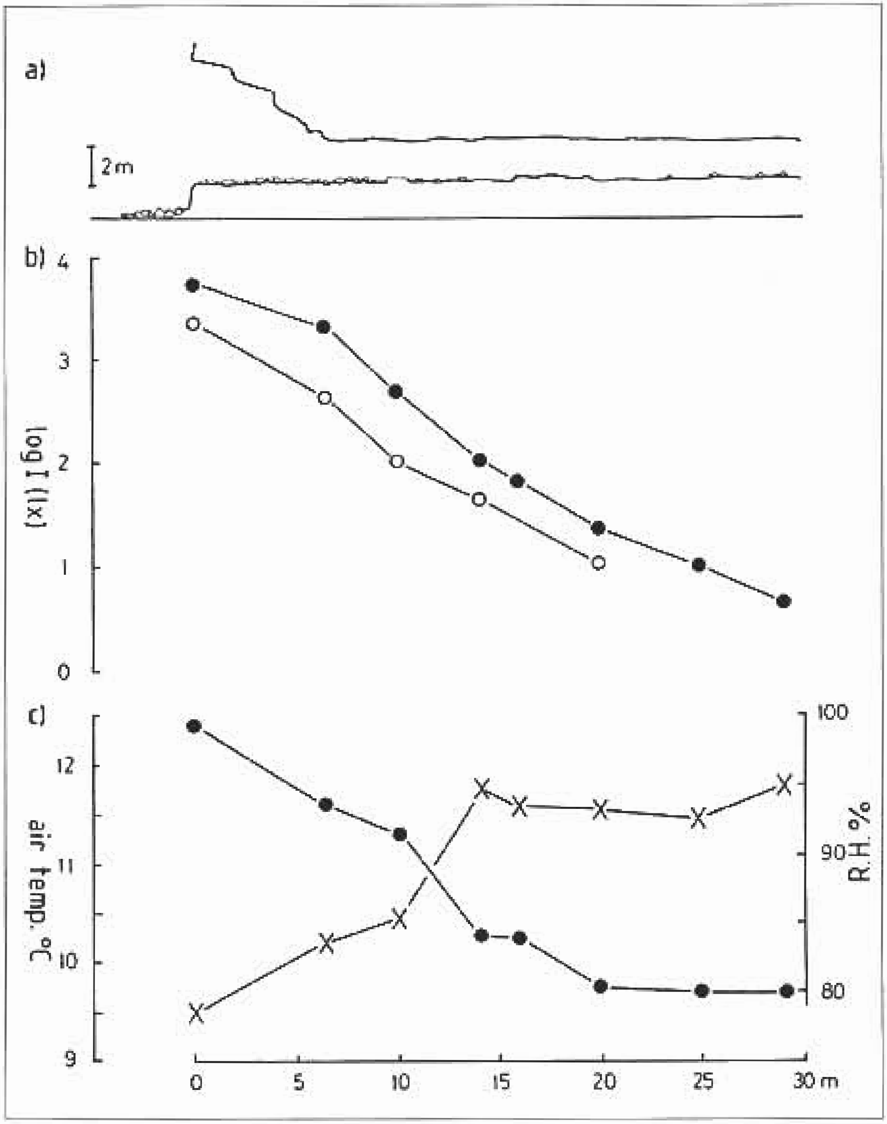

Fig. 1. Morphometric and climatic data for the entrance passage of Scoska Cave, North Yorkshire.
a) Cave profile showing rock-strewn passage and flat cave roof.
b) Photosynthetically available radiation (PAR) in Scoska Cave (lx). Closed circles April 2000 ; open circles July 2000. Note logarithmic scale for PAR.
c) Air temperature, °C (closed circles) and % relative humidity (crosses).

Result

1 *Cave substrata*

At the entrance, blocks of limestone cover the floor for a distance of about 10 m within (Fig. la). Thereafter a brown cave earth is exposed in places with scattered limestone blocks. The cave walls are steep, largely devoid of crevices and mostly dry with a little speleothem development about 30-40 m from the entrance. Sikes Beck breaks out from the floor 24 m within the cave but soon disappears under rocks, reappearing at the entrance. Its discharge was low and about 1 l/sec when visited. The water had pH 8.3, Ca 1.55 mM/l, Mg 0.02 mM/l, Na 0.11 mM/l, SO_4 0.09 mM/l and alkalinity 2.3 mEq/l.

2 *Microclimate*

Climatic data are shown in Fig. 1. Irradiance (Fig. lb) becomes attenuated approximately logarithmically from the entrance to a depth of about 40m. Beyond this the passage turns to the left and light is abruptly diminished. No plants were observed beyond this point. The decline in intensity followed the exponential Bouguer-Lambert Law surprisingly well (regression Anova $p<0.001$) and provided a mean 'extinction coefficient' of 0.24 m^{-1}. Absolute light intensity was higher during April than July as the April measurements were made on a brighter day. Light levels at the entrance were 12% and 11% of the open sky during the April and July visits respectively. For the entrance measurements the sensor was directed horizontally out of the cave toward hillsides and trees and not the sky above. Absolute light levels in this cave would be expected to be maximum just before leaf expansion (April) since deciduous trees partly obstruct the entrance.

Temperature and humidity profiles were obtained in July and are shown in Fig. 1c. Air temperature underwent a linear decline from the entrance to a depth of 20m where it stabilised at around 9 °C. In contrast the relative humidity rose from about 80% at the entrance to 95% at 15 m depth. Deeper in the cave this high humidity was maintained. The air showed little movement and was probably stagnant as the cave system has only the one entrance. The water vapour pressure remained approximately constant, ranging from 11.3-11.9 mb (mean 11.4mb).

3 *Flora*

A total of 59 taxa were recorded consisting of four algae, three lichens, 47 bryophytes, four ferns and one flowering plant. The flora was dominated by bryophytes in terms of species-richness and cover (Table 1). Bryophytes grew only on the lower walls and floor of the cave and not the roof which was probably too dry.

TABLE 1 Cave flora

Cave flora												
Phylum/Genus	species	authority	0-2m	2-4m	4-6m	6-8m	8-10m	10-12m	12-15m	15-20m	20-40m	other caves[1]
Cyanobacteria												
Gloeocapsa	punctata	Naeg.									X	E
Phormidium	ambiguum	Gom.								X		E
Schizothrix	perforans	(Ercegovic) Geitler									X	B
Chlorophyta												
Gongrosira	sp.									X		E
Lichenes												
Lepraria	incana	(L.) Ach.	X	X	X	X	X	X	X	X		B
Lepraria	nivalis	Laundon	X	X								B
Leproplaca	chrysodeta	(Vain.ex Raes.) Laundon	X	X	X					X		B
Musci												
Amblystegium	serpens	(Hedw.)Br. Eur.						X				B,E
A.	tenax	(Hedw.) C. Jens				X						
Brachythecium	rutabulum	(Hedw.) Br. Eur.			X							E
Bryum	cf. pallens	Sw.			X	X						E
Bryum	pseudotriquetrum	(Hedw.) Schwaegr.		X								B
Cratoneuron	filicinum	(Hedw.) Spruce		X	X							B,E
Dichodontium	pellucidum	(Hedw.) Schimp.				X						
Didymodon	fallax	(Hedw.) R.H. Zander	X									E
Encalypta	streptocarpa	Hedw.			X							B,E
Eucladium	verticillatum	(Brid.) Br. Eur.	X	X								B,E
Eurhynchium	hians	(Hedw.) Sande Lac		X								B,E
E.	pumilum	(Wils.) Schimp.			X	X	X		X			E
E.	speciosum	(Brid.) Jur.				X						B,E
Fissidens	adianthoides	Hedw.					X					E
Fissidens	cristatus	Wils. Ex Mitt.		X						X		B,E
Fissidens	taxifolius ssp. pallidus	Hedw.		X	X							B,E
Gymnostomum	aeruginosum	Sm.	X	X								B
Heterocladium	heteropterum	(Bruch. Ex Schwaegr.) Br. Eur				X						B,E
Hymenostylium	recurvirostrum	(Hedw.) Dixon		X								E
Hypnum	resupinatum	Taylor							X			
Isopterygiopsis	pulchella	(Hedw.) Z. Iwats				X						E
Leptodontium	flexifolium	(With.) Hampe	X			X						
Mnium	stellare	Hedw.		X					X			E
Neckera	complanata	(Hedw.) Hub.					X					E
Orthothecium	intricatum	(Hartm.) Br. Eur.			X				X	X		
Palustriella	commutata var. commutata	(Hedw.) Ochyra	X	X								B,E

TABLE 1 Cave flora												
Plagiomnium	undulatum	(Hedw.) Kop.	X									B,E
Platydictya	confervoides	(Brid.) Crum.					X		X	X		E
Pseudotaxiphyllum	elegans	(Brid.) Ž. Iwats				X		X		X		E
Rhynchostegiella	teesdalei	(Br. Eur.) Limpr.							X	X		E
Rhynchostegiella	tenella	(Dicks.) Limpr.						X		X		E
Rhynchostegium	riparioides	(Hedw.) C. Jens			X							B,E
Thamnobryum	alopecurum	(Hedw.) Nieuwl.	X	X						X		B,E
Thuidium	tamariscinum	(Hedw.) Br. Eur.	X									E
Tortella	tortuosa	(Hedw.) Limpr.		X	X		X		X			E
Weissia	cf perssonii	Kindb.							X			
Hepaticae												
Conocephalum	conicum	(L.) Underw.	X						X			B,E
Jungermannia	atrovirens	Dum.				X						E
Jungermannia	exsertifolia	Steph.				X						E
Leiocolea	badensis	(Gott.) Joerg.				X						
Leiocolea	bantriensis	(Hook.) Joerg.	X			X						
Lophocolea	bidentata	(L.) Dum.	X			X						E
Metzgeria	conjugata	Lindb.							X			E
Pellia	endiviifolia	(Dicks.) Dum.	X					X				B,E
Plagiochila	britannica	Paton	X	X								
Plagiochila	porelloides	(Torr. Ex Nees) Lindenb.			X							B,E
Preissia	quadrata	(Scop.) Nees			X							E
Pteridophyta												
Asplenium	adiantum-nigrum	L.							X			E
Asplenium	trichomanes	L.							X			B,E
Asplenium	trichomanes-ramosum	L.							X			B,E
Dryopteris	filix-mas	(L.) Schott							X			B,E
Spermatophyta												
Chrysosplenium	oppositifolium	L.					X	X				B,E
Mid-point relative irradiance %			8.24	5.03	3.08	1.88	1.15	0.71	0.38	0.15	0.007	
Species-richness			18	18	13	15	7	6	15	11	2	
[1]B : Recorded from other British caves; E, other European caves.												

The total species richness peaked at 0-4m and 10-15m from the entrance where 16 species were recorded. Beyond 15m species richness declined rapidly and beyond 20m only two plant species, both algae, were recorded. Common threshold bryophytes which were absent from the interior included *Eucladium verticillatum*, *Gymnostomum aeruginosum* and *Palustriella commutata* var. *commutata*. These grew on moist walls of the cave where there was a small seepage, depositing small amounts of travertine. At the threshold, 0-4m from the entrance, irradiance was *5-10%* of the open sky (hereafter defined as the relative irradiance or RI). Many species penetrated further. For example, frequent bryophytes in the region 6-10m with RI 1-2% were *Eurhynchium pumilum*, *Fissidens adianthoides* and *Pseudotaxiphyllum (Isopterygium) elegans*. Deeper still were *Amblystegium serpens*, *Fissidens cristatus* and *Thamnobryum alopecurum*. The last species was the most frequently encountered bryophyte in the cave and also occurred at the threshold. Progressing further into the cave we found *Orthothecium infricatum*, *Pseudotaxiphyllum elegans*, *Rhynchostegiella teesdalei* and *Platydictya confervoides* (15.9m, RI 0.23%). Bryophytes penetrating to the greatest depth were *Fissidens cristatus* and *Thamnium alopecurum* (both to 16.2m with RI 0.20%). Liverworts were much less common with large thallose species abundant only at the moist threshold. Within the cave conditions were probably too dry to support luxuriant liverwort growth, but a few species such as *Conocephalum conicum* and *Metzgeria conjugata* penetrated to 12m. Four ferns were noted only 12m from the entrance but none was common. Three species of leprose lichens were conspicuous on threshold walls where they formed diffuse yellow and white patches. *Lepraria incana* was the commonest and found to a depth of 17m.

Only a few algae were collected. Sparse populations of the cyanobacteria *Gloeocapsa* and *Schizothrix* were recovered from damp speleothem at depths of 34m and 27m respectively and no algae were visually evident beyond 34m. Light levels were extremely low at these points, with RI values of approximately 0.004% and 0.014% respectively. An unidentified coccoid green alga was associated with the *Gloeocapsa*.

Discussion

Our measurements of irradiance in Scoska Cave demonstrate an exponential decline in light with distance from the entrance. This is unusual and caused by the straight tube-like form of the passage and would also be expected in artificial excavations such as mine adits. Other caves show for part of their length a similar relationship (Dobat, 1998a) but presumably only where cave geometry permits. In

Skoska, air temperature fell to about 9.5 °C within the cave which is close, though slightly higher than the predicted mean air temperature at the site (8.5 °C). Ground air temperature is usually close to mean air temperature in Britain though minor differences often occur as discussed by Wigley & Brown (1976). Relative humidity was high which is to be expected for a cave with a moist floor and stream running through it. The humidity profile is remarkably similar to that of the Scheunenh6hle, Germany (Dobat, 1998a).

With a total of 59 plant species in five phyla the flora of this cave must be considered both rich and diverse. This is particularly surprising considering its small size. However, comparable species richness has been reported for several caves in Germany and France (Maheu, 1906; Lämmermeyer, 1912; Dobat, 1998b). In our site the richest area was at the threshold where 16 species were recorded over a length of 2m. Further into the cave species richness declined irregularly. This is partly the result of the rocky nature of the floor at the cave entrance, which gave way to clay within. The wet clay supported several species of fern, a flowering plant and several bryophytes. This must be one reason why the 6-8m and 10-12m sections had a species-richness approaching the threshold. Richness declined rapidly once the RI fell below 0.5% (Table 1). A similar decline has been found to occur at increasing distances from artificial cave lighting (Dobat, 1998b). Ainong bryophytes the moss *Thamnobryum alopecurum* penetrated the to greatest depth within Scoska Cave. In artificial 'Lampenfloras', Dobat (1998b) found that *Fissidens* species could tolerate an irradiance of 80-90 lux, which corresponds to the depth where *Thamnobryum* was found in Scoska. We also found *Thamnobryum* abundant in Sleets Cave nearby and it is one of the best-known cave mosses in Britain and Europe. In South Wales it has also found in low light regimes (Mason Williams & Benson-Evans, 1958) and it is common in shady British woodlands and ravines (Hill *et al.*, 1994). The fern flora of this cave according to Chapman (1993) is typical of British cave thresholds and the same species are encountered in caves of the adjacent continent. Only one flowering plant, *Chrysosplenium oppositifolium* was recorded. In South Wales, it was the most frequently recorded flowering plant in the caves investigated by Mason-Williams & Benson-Evans *(1958)*, where it occurred at light intensities of 18-24 lux, much lower than the intensities recorded at Scoska.

We did not pay much attention to the algae of Scoska but a thorough investigation would probably yield many species judging from previous studies (e.g. Claus 1962; Carter, 1971). It was clear that some algae tolerate lower irradiances than the bryophytes and vascular plants. Coccoid cyanobacteria such as *Gloeocapsa* are known to occur at low irradiances in other caves (Cox *et al.*, 1971). Some cyanobacteria can grow heterotrophically and their occurrence at such low levels may be explained by this. However their absence from the darkest recesses and a tendency for them to occur only on parts of speleothem facing the entrance of Scoska suggest they are in fact growing autotrophically. We know that algae occurred through most of the 35m section of cave investigated since lichens grew to a depth of 17m and contained the symbiotic green algae *Chlorella* and *Stichococcus*. Little is known of the ecology of lichens in caves but Jaros (1964) found that *Lepraria nivalis* occurred in relative light intensities ranging from *93-0.5%* in a Hungarian cave. In Scoska this species was only found close to the entrance and exposed to an RI of 5-10%.

Among the plants recorded at Scoska, nine have not been previously recorded from caves as far as we are aware, and all were bryophytes. Of these, six did not penetrate further than 8m from the entrance and the remaining three, *Hypnum resupinatum*, *Orthothecium intricatum*, and *Weissia* cf. *personnii* penetrated regions where the RI fell to about 0.4%. Most of the cave bryophytes are typical of limestone and base-rich waters such as those of Gildersbank Sike. Many of the species encountered grew on sheltered cliffs nearby. A few such as *Dichodontium pellucidum* grew only on clay soil demonstrating the importance of suitable substrata in caves for colonisation.

Light was clearly the most important factor controlling plant distribution as many other studies have demonstrated (see review of Dobat, 1998a). However, the irregular decline in species-richness points to other important factors, namely substratum type and moisture. Skoska Cave has few roof seepages in the illuminated zone and the bare limestone surface can only be weffed by condensation. While condensation undoubtedly occurs near the cave entrance due to temperature and humidity change, this lack of moisture places a stress on many hygrophilous bryophytes which would only find sufficient moisture on or near the cave floor where moisture can be gained through capillarity. The occurrence of large limestone blocks prevents this near the entrance and largely explains the variation in species-richness. Water relations and substratum type are therefore important factors for distribution and biodiversity.

Acknowledgements

We express our thanks to Dr. A.J.E. Smith, M. 0. Hill, A. Harrington and L. Ellis for checking critical bryophyte material. We are also grateflil to a BP Amoco Royal Society Research Fellowship awarded to the junior author during the period of investigation and to the warden and staff at Malham Tarn Field Centre for their generous assistance and logistic support.

References

BLOCKEEL, T. L. & LONG, D. G. 1998. A check list and catalogue of British and Irish bryophytes. (Cardiff: British Bryological Society).

CARTER, J. 1971, Diatoms from the Devil's Hole Cave, Fife: Scotland. Nova Hedwigia, 21: 657-681.

CHAPMAN, P.1993. Caves and Cave Life. London : Harper Collins.

CLAUS, G. 1962. Data on the ecology of the algae of Peace Cave in Hungary. Nova Hedwigia, 4: 55-79.

CLAUS, G. 1967. Bioluminescence in *Melosira varians*. Int. J. Speleol., 2 : 407-408.

COX, G., BENSON, D. & DWARTE, D. M. 1981. Ultrastructure of a cave-wall cyanophyte, *Gloeocapsa* NS 4. Arch. Microbiol. 130:165-174.

CUBBON, B. D. 1970. Flora records of the Cave Research Group of Great Britain from 1939 to June 1969. Trans. Cave Res. Gp. Great Britain) 12: 57-74.

CUBBON, B. D. 1976. Cave Flora. in : FORD, T. D. & CULLINGFORD, C. H. D. (Eds.) : 423-452. The Science of Speleology. London : Academic Press.

DALBY, D. H. 1966. The growth of *Eucladium verticillatum* in a poorly illuminated cave. Rev. Bryol. Lichenol, 34: 288-301.

DOBAT, K. 1966. Die Kryptogamenvegetation der Höhlen und Halbhöhlen im Bereich der Schwabischen Alb. *Abhandlung zur Karst- und Hohlenkunde*, E3: 1-153.

DOBAT, K. 1970. Considerations sur la vegetation cryptogamique des grottes du Jura Souabe. Ann. Speleol., *25* ; 871-907.

DOBAT, K. 1 998a. Flore (Lichens, Bryophytes, Pteridophytes, Spermatophytes). In: JUBERTHIE, C. & DECU, V. (Eds.): I310-1324. Encyclopaedia Biospeologica, Vol.2. Bucharest:Societé de Biospeleologie, Academie Roumaine.

DOBAT, K. 1 998b. Flore de la lumiere artificielle (Lampenflora - Maladie Verte). In: JUBERTHIE, C. & DECU, V. (Eds.): 1325-1335. Bncyclopaedia Biospeologica. Vol.2. Bucharest:Societé de Biospeleologie, Academie Roumaine).

HILL, M. 0., PRESTON, C. D. and SMITH, A. J. E. 1994. Atlas of the bryophytes of Britain and Ireland. England: Harley.

JAROS, W. 1964. The influence of the cavernous microclimate on the variability of the lichen *Lepraria crassisima*. Acta Biologica Cracowviensia Ser. *B*. 7 : 89-105.

LAMMERMAYER, L. 1916. Die grdne Pflanzenwelt der Höhlen. I. Teil. Denk. Akad. Wiss., 92:107-148.

MAHEU, J. 1906. Contribution a l'étude de la flore souterraine de France. Ann. Sci. Nat. 3:1-189.

MASON-WILLIAMS, A. 1962. Supplementary report on cave flora. In: CULLINGFORD, C.H.D. (Ed.). 389-391. British Caving 2nd edn. London.

MASON-WILLIAMS, A. 1966. Further investigations into bacterial and algal populations of caves in South Wales. Int. J. Speleol. 2: 389-395.

MASON-WILLIAMS, A. & BENSON-EVANS, K. 1958. A preliminary investigation into the bacterial and botanical flora of caves in South Wales. Cave Res. Group of Gt. Brit.

Publication 8. 70 pp.

MASON - WILLIAMS, A. and BENSON-EVANS, K. 1967. Summary of results obtained during a preliminary investigation into the bacterial and botanical flora of caves in South Wales. Int. J. Speleol., 2 : 397-402.

PURVIS, 0. W., COPPINS, B. J., HAWKSWORTH, D. L., JAMES, P. W. & MOORE, D. M. 1992. The Lichen Flora of Great Britain and Ireland. London : Natural History Museum.

STACE, C. 1991. New Flora of the British Isles. Cambridge : Cambridge University Press.

WIGLEY, T. M. L. & BROWN, M. C. 1976. The physics of caves. In: FORD, T. D. and CULLINGFORD, C. H. D. (Eds.) : 329-358. The Science of Speleology. London: Academic Press.

ZHANG, Z. & PENTECOST A. 1999. Bryophyte communities associated with travertine formation at Yorkshire National Park, U.K. Carsalogica Sinica 18 : 366-374.