P. CARVALHO

MICROCLIMATE AND DIVERSITY OF CRYPTOGRAMIC EPIPHYTES
IN A KARST DOLINE (TRIESTE, NE ITALY)

VARIAZIONI DELLA DIVERSITÀ FLORISTICA DELLE CRITTOGAME PRESENTI
IN UNA DOLINA CARSCICA E SUA DIPENDENZA DA FATTORI MICROCLIMATICI

Abstract - 212 relevés of epiphytic cryptogamic vegetation (lichens, mosses and liverworts) were carried out along eight transects in a typical Karst Doline near Trieste (NE Italy) in order to study the compositional variation in relation to the pronounced microclimatic patterns which are characteristic of Karst dolines. The epiphytic cryptogamic flora consists of 48 lichens, 13 mosses and 8 liverworts. The matrix of species and relevés was submitted to multivariate analysis (classification and ordination) to detect groups of relevés with similar floristic composition, groups of species with similar ecology, and compositional gradients characterized by indicator species. The distribution of indicator species within the doline was mapped by programs of automatic mapping. Different groups of indicator species revealed different distributional patterns inside the doline. Ecological indicator values were used for an ecological interpretation of the compositional gradient revealed by the ordinations. The main factors affecting the variation of epiphytic cryptogamic vegetation are the pH of the bark, air humidity, light and temperature. Dolines are characterized by a high diversity and a high richness of ecological niches, chiefly depending on the pronounced microclimatic variations; they host several aerohygrophytic species and some montane species which are otherwise absent from the Karst. Cryptogams have been used as indicators to draw an air humidity map of the doline, which essentially agrees with microclimatic measurements from other, similar biotopes.

Key words: Biodiversity, Bioindicators, Bryophytes, Cryptogams, Karst, Lichens, Microclimate, Vegetation.

Riassunto breve - 212 rilievi di vegetazione crittogamica epifita (licheni, muschi, epatiche) sono stati effettuati lungo 8 transecti nella dolina di Borgo Grotta Gigante presso Trieste. Lo scopo del lavoro è quello di studiare la variazione della composizione floristica in dipendenza della variazione dei parametri microclimatici tipica delle doline carsiche. Sono state ritrovate 48 specie di licheni, 13 di muschi ed 8 di epatiche. La matrice delle specie e dei rilievi è stata sottoposta ad analisi multivariata (classificazione ed ordinamento) al fine di individuare gruppi di rilievi con simile compostazione floristica, gruppi di specie con ecologia simile, e possibili gradienti ecologici. La distribuzione delle principali specie indicatrici nell’ambito della dolina è stata mappata utilizzando programmi di cartografia automatica. Diversi gruppi di specie presentano diversi modelli di distribuzione nell’ambito della dolina. Indici ecologici associati alle specie sono stati utilizzati per interpretare ecologicamente i gradienti di composizione floristica rivelati dagli ordinamenti. I principali fattori che influenzano la variazione floristica della vegetazione crittogamica epifita sono il pH del substrato, l’umidità atmosferica, la luce e la temperatura. Le doline si caratterizzano per la presenza di molte specie aeroigrofitiche e di alcune specie tipiche della fascia montana, altrimenti assenti sull’altipiano carsico presso Trieste. Esse presentano un’alta biodiversità.
ed una ricchezza di nicchie ecologiche che dipendono essenzialmente dalle pronunciate variazioni microclimatiche. Le criptogame sono state utilizzate come indicatori per redare una carta dell'umidità atmosferica della dolina, che concorda con i dati microclimatici pubblicati nella letteratura.

Parole chiave: Biodiversità, Bioindicatori, Bryofite, Carso, Criptogame, Licheni, Microclima, Vegetazione.

Introduction

Cryptogams, and especially lichens and bryophytes, were often used as phytoclimatic indicators. Important studies trying to correlate cryptogamic vegetation with bioclimatic differences between different geographic areas are those of Winiowski (1930) for Poland, Barkman (1958) for Holland, Pirio (1982) for Scandinavia, Palmer (1986) for the United States, and Sergio et al. (1989) for Portugal. Lichens and bryophytes are often more sensitive than higher plants to the variation of climatic parameters such as air humidity and the amount of rainfall, and, for this reason, they can be utilized as indicators even at a small scale, e.g. they can reveal microclimatic differences within relatively small biotopes (Nimis & Losi, 1983). The importance of lichens and bryophytes as phytoclimatic indicators is enhanced in climatically transitional areas, where even small changes in the relief are translated into wide microclimatic differences.

The Trieste Karst, in NE Italy, is one of such transitional areas: the climate of Trieste is intermediate between two major climate-types: the Mediterranean and the Central European climates. For this reason, small microclimatic changes determine impressive variations of the flora and vegetation. One of the most interesting Karst biotopes for studying the effects of microclimatic variations on the flora and vegetation are the dolines. These are more or less circular depressions, with depth varying from a few meters to about 40 m and diameter ranging from a few meters to about 1 km or more. They are one of the most typical features of the Karst landscape, and originated as a consequence of the action of rainwater on the underlying calcareous rocks. The vegetation of the dolines is quite different from that of the surrounding Karst Plateau (Poldini, 1972; 1980), and the main differences are related to the important microclimatic variations within the doline biotope (Poli, 1961).

The aim of this study is to carry out a detailed analysis of the spatial distribution of cryptogamic epiphytic vegetation in a typical Karst doline, and to try an interpretation of these variations in terms of microclimatic changes. Furthermore, considering that air humidity data are generally less available than rainfall and temperature data, an attempt was made to map air humidity patterns using cryptogams as bioindicators.

Survey area

The survey area, the Doline of Borgo Grotta Gigante, is located in the Trieste Karst, Region Friuli-Venezia Giulia, Province of Trieste. The margins are at an elevation of 250 m (fig. 1), whereas the bottom is at 212.2 m, with a depth of ca. 40 m. The largest diameter ranges from 275 m (NE-SW) to 270 m (NW-SE), the smallest from 235 m (N-S) to 220 m (W-E).

The microclimate of the dolines was thoroughly studied by Poli (1961); according to this author, it differs from the prevailing climate on the Karst Plateau having higher relative air humidity, weaker wind action, and a pronounced thermic inversion. An elevation drop of 30 m in a doline climatically corresponds to an elevation increase of 360 m (in January of 660 m). Although no specific climatic study was ever carried out on the Doline of Borgo Grotta Gigante, its microclimatic features should correspond to those sketched by Poli (1961) for large dolines. The bottom of the doline is colder than the margins, as a consequence of the progressive decrease in temperatures from the upper to the lower parts of the doline, and the S-side (N-exposed) is also colder than the N-side (S-exposed). These microclimatic features are reflected in the floristic and vegetational characters of the doline, particularly on its south side (north-exposed), which is occupied by the Asaro-Carpinetum betuli (Lauti, 1964). This is an extrazonal association (Poldini, 1985) characterised by the presence of many species of Fagetalia, although Fagus is missing. According to Lauti (1964), this is a consequence of the strong continental character of the doline. Later, Poldini (1980) demonstrated that the dolines also have a function as refuge areas for montane species, as a consequence of thermic inversion, and considered them as oases of a more continental climate immersed in a Submediterranean climatic region.

Only a few studies deal with the cryptogamic flora and vegetation of these peculiar biotopes (Gerdol, 1982; Nimis & Losi, 1984; Nimis, 1983; Nimis & Losi, 1983). According to

![Fig. 1 - Map of the survey area with location of the 53 trees in which the relevés were carried out. The trees are numbered as in tab. 1.](image-url)

- L'area studiata con la posizione dei 53 alberi sui quali sono stati effettuati i rilevamenti. La numerazione è quella di tab. 1.
NIMIS & LÖS (1983) the lichen flora of the dolines hosts several species with a more or less suboceanic distribution in Europe. This is mainly due to the higher air humidity prevailing in the doline biotope, so that dolines have a continental character for temperatures, but a suboceanic character as far as air humidity is concerned.

Data and methods

The data for the present study consist of 212 relevés of epiphytic vegetation (lichens and bryophytes), carried out according to the method presented by HÖRZIG et al. (1987) and LIEGENDOERFER et al. (1988) for monitoring air pollution. A fixed size (30 x 50 cm) sampling grid subdivided in ten rectangles was used to compute the frequency of each species (i.e. the number of grids units in which it occurs). In tab. I, frequencies 9 and 10 were subsumed under frequency 9 for reasons of space.

Relevés were disposed along eight main transects, oriented in different directions (N-S, O-E, NW-SE, NE-SW) from the center of the doline, between 9 and 30 m from the lowest point (see fig. 1). They were mainly taken on Quercus petraea, the most common tree species, and also on Quercus cerris, Carpinus betulus and Ostrya carpinifolia. For each tree, four relevés were carried out:
- 2 relevés at an height of 30 cm, at the north and south sides of the trunk;
- 2 relevés at an height of 1.3 m, at the north and south sides of the trunk.

A further data source utilised for the ecological and phytogeographic interpretation, are the indicator values and the phytogeographic diagnoses given by WARRI (1980) for lichens and by DÜLL (1984,1985 and 1991) for bryophytes. These are as follows:

Ecological indicator values of lichens by Wirth:

pH classes (pH):
1 - Extremely acidophytic, pH < 3.3
2 - Strongly acidophytic, 3.4 < pH < 4
3 - Very acidophytic, 4.1 < pH < 4.8
4 - Moderately acidophytic, 4.9 < pH < 5.6
5 - Subneutrophitic, 5.7 < pH < 7.0
6 - Neutrophitic, 7.0
7 - Moderately basiphitic, 7.1 < pH < 8.5
8 - Basiphitic, pH > 8.5

Moisture classes (H):
1 - Extremely hygrophytic
2 - Strongly hygrophytic
3 - Very hygrophytic
4 - Mesophytic
5 - Very xerophytic
6 - Strongly xerophytic

Light intensity classes (L):
1 - Strongly skiyophytic
2 - Very skiyophytic
3 - Moderately photophytic
4 - Very photophytic
5 - Strongly photophytic

Ecological indicator values of mosses and liverworts by DÜLL:

pH classes (pH):
1 - Extremely acidophytic, pH < 3.0
2 - Between 1 and 3, mainly on very acid substrate
3 - Acidophytic, 3.0 < pH < 5
4 - Between 3 and 5
5 - Moderately acidophytic, 5 < pH < 6
6 - Between 5 and 6
7 - Subneutrophitic, 6 < pH < 6.9
8 - Between 7 and 9
9 - Basiphitic, pH > 7.0

Moisture classes (H):
1 - Strongly xerophytic
2 - Between 1 and 3, i.e. mainly on dry sites
3 - Very xerophytic
4 - Between 3 and 5, places moderately fresh to becoming dry for longer periods
5 - Mesophytic
6 - Between 5 and 7, colonising moderately but permanently moist places
7 - Rather hygrophytic
8 - Between 7 and 9
9 - Strongly hygrophytic

Light intensity classes (L):
1 - Strongly skiyophytic
2 - Between 1 and 3, i.e. only on shady sites
3 - Skiyophytic
4 - Between 3 and 5
5 - Moderately photophytic
6 - Between 5 and 7
7 - Photophytic
8 - Between 7 and 9
9 - Strongly photophytic

The ecological indicator values are given, for each species, in the floristic list. However, for a small number of species, ecological values are not available. It is important to stress that these ecological indices permit only a first qualitative evaluation of ecological requirements.

Data analysis proceeded in the following steps:
1) Numerical classification, based on Minimum Variance Clustering and Euclidean Distance, of relevés and of species, in order to obtain floristically similar groups of relevés and ecologically similar groups of species;
2) Reciprocal ordering of relevés and species, in order to reveal possible ecological gradients, and to extract a reduced number of indicator species;
3) Concentration Analysis (AOC) of the matrix of relevé and species groups, to analyse the correlation among them;
4) Principal Component Analysis (PCA) of the matrix of ecological data and relevé groups, in order to analyse the correlation between compositional variation in the data set and the variation of some main ecological factors;
5) Principal Component Analysis (PCA) of the matrix of phytogeographic data and relevé groups, to analyse the correlation between compositional/ecological variation in the data set, and the variation of phytogeographic affinities of the relevé groups;
6) Plotting the distribution of the indicator species of each species group within the doline. These maps are based on the average frequencies of each species within each station (tree), which includes four relevés;
7) Plotting the distribution of air humidity within the doline; the basic data are weighted averages of the humidity index calculated for each tree;
8) Estimate of the substratum acidity of each relevé, based on weighted averages of the acidophytism index, for each relevé.

For data analysis, we used the package of programs by Wilki & Orloci (1980) and Andaar (1991).

All maps were obtained by computerised automatic mapping, with the program package SURFER (Golden Inc., Colorado, U.S.A.), in order to avoid subjectivity in the cartographic expression of the results. The program used is based on a grid, whose mesh size depends on the minimum and maximum values of the input data. The interpolation method utilised to create a regular grid starting from points (trees) irregularly distributed on the study area, is based on the values of the 10 stations nearest to a given point. The influence of a given point on the others is inversely proportional to their distance.


Results

A total of 69 cryptogams (48 lichens, 8 hepatics and 13 mosses) was recorded in the 212 relevés. The matrix of relevés and species (tab. 1) was submitted to classification, and the results are summarised in fig. 2. Eight main groups of relevés and six groups of species were formed.

The reciprocal ordination, carried out on the same data, is shown in fig. 3a (relevés) and 3b (species). The relevés are arranged along a typical horse-shoe (fig. 3a), with the exception of relevé groups 3 and 6, whose centroids are positioned near the origin of the axes. The centroids of the remaining relevé groups are arranged in the following sequence, from left to right: 1, 2, 4, 5, 8, 7, 9, and 3. In fig. 3b the species with high scores on the first two Principal Components are those which are more related with the compositional gradient revealed by the ordination (indicator species).

The relationships between groups of relevés and of species were studied by AOC, and the results are shown in fig. 4. The relevé groups are disposed along a curved line, in a sequence similar to that already discussed for fig. 3a: 1, 2, 4, 5, 6, 7, and 8. This suggests that such a sequence reflects an ecological gradient. Relevé group 3 has low scores on both Canonical Variates, which means that it is not significantly correlated with the gradient, as in the ordination of fig. 3a. Tab. 1 reports all relevés, with the relevé groups disposed in the sequence suggested in fig. 4.

Before attempting an ecological interpretation of the ordinations each group of species and of relevés will be briefly commented on, based on the results showed in fig. 3 and 4.

Species group 1 (50 species) - Indicator species are: Anomodon viticulosus, Cladonia coniocrea, Chrysothrix candelaris, Hyperphysicia adgulutinata, Parmelia glabrata, Pertusaria flavida and Graphis scripta. This is by far the largest species group, although many of the species are quite rare within the doline. In the ordination, most of the other species of this group have point projections near the origin of the axes (within dashed line in fig. 3b), due to their low frequency. Most species are rather acidophytic, fairly hygrophytic and heterogeneous for light requirements. The indicator species of this group have higher frequency at the E-NE sides of the doline, between 11 and 20 m from its bottom (fig. 5).

Species group 2 (3 species) - This group includes only Candelariella reflexa, Lepraria sp. and Normandina pulchella, which are most frequent at the SE-W sides of the doline, between 20 and 30 m from its bottom (fig. 6). These species are widely different as far as the ecological requirements are concerned.

Species group 3 (5 species) - This species group consists of Frullania dilatata, Hypnum cupressiforme, Parmelia caperata, Parmelia perlata and Phyllycis argenta. They are associated with relevé groups 8 and 7 (fig. 4), and can be considered as rather acidophytic, rather hygro- and photophytic. Their intermediate ecological requirement agrees well with their highest frequency above 20 m from the bottom, at the SW side of the doline (fig. 7).

Species group 4 (2 species) - This group includes only two species: Metzgeria furcata and Rudula complanata. Their occupancies have a maximum in relevé group 6 (fig. 2), although they occur in all relevé groups (tab.1). They are most frequent above 20 m at the SE side of the doline, and below 20 m at the SW side (fig. 8). Ecologically, they are subnephtophytic, meso- and rather photophytic.

Species group 5 (3 species) - The most frequent species is Neckera complanata; two
Tab. 1 - Table of the species and of the 212 relevés. The relevés are numbered as in fig. 1, with the following additional specifications: P = Quercus petraea, Q = Quercus cerris, O = Ostrya carpinifolia, C = Carpinus betulus, M = on the bole, B = at the base of the trunk, S = south-facing, N = north-facing. Numbers associated to the species refer to species group numbers (see fig. 2).
further bryophytes are included: *Anomodon attenuatus* and *Porella platyphylla*. They are associated with relevé group 1 (fig. 4), and can be considered, in general, as subneutrophic, mesophytic, and rather skiphytic. This group is more or less restricted to the bottom of the doline (fig. 9).

**Species group 6** (6 species) - This group includes: *Acrochaete gemmata*, *Bacidia rubella*, *Himalayabrya nivea*, *Leucodon sciuroides*, *Phaeophyscia chlorantha* and *Orthotrichum sp.* It is related with relevé groups 2 and 3 (fig. 4). The species of this group could be considered as subneutrophic, mesophytic and heterogeneous for light requirements. They are most frequent on the N side of the doline from 9 to 22 m from the bottom (fig. 10).

The eight relevé groups will be also commented on, based on the results shown in fig. 3a, b and fig. 4.

**Relevé group 1** - Number of relevés: 33. Average number of species per relevé: 6. Lichen species: 13%. In the ordination (fig. 3a) this group is located at the extreme left of the horse-shoe (with negative scores on the first Principal Component). It is associated with species groups 4 and 5 (fig. 4). The main phorophytes are *Quercus petraea* and *Ostrya carpinifolia*.

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Fig. 2 - Classification of relevés and species into groups, based on minimum variance clustering, and on the data in tab. 1. The contingency table gives the occupancy counts in the blocks of the structured table species/relevé groups (binary data).

**Classificazione di rilievi e specie in gruppi**, basata sulla minima varianza e sui dati di tab. 1. La tabella di contingenza fornisce le frequenze nei blocchi dei gruppi specie/rilievi della tabella strutturata (dati binari).

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Fig. 3a - Arrangement of relevé points in the reciprocal ordering of relevés and species, based on the data in tab. 1. Symbols refer to relevé group numbers, as in the dendrogram of fig. 2. Circled numbers give the position of the relevé group centroids.

**Disposizione dei punti dei rilievi nell’ordinamento reciproco di rilievi e specie**, sulla base dei dati di tab. 1. I simboli si riferiscono ai numeri dei gruppi, come nel dendrogramma di fig. 2. I numeri cerchiatì forniscono la posizione dei centroidi dei gruppi.

Fig. 3b - Arrangement of species points in the reciprocal ordering of relevés and species, based on the data in tab. 1. Only those species are named, that have high scores on the first two Canonical Variates.

**Disposizione dei punti delle specie nell’ordinamento reciproco di rilievi e specie**, sulla base dei dati di tab. 1. Vengono nominate solo le specie che hanno alte coordinate sulle prime due Variabili Canoniche.

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Fig. 4 - Canonical Analysis (AOC) of species and relevé groups based on the data of fig. 2. Symbols refer to relevé groups, as in the legend, numbers to species groups, as in fig. 2.

**Analisi Canonica (AOC) dei gruppi di specie e rilievi sulla base dei dati di fig. 2. I simboli si riferiscono ai gruppi di rilievi come in legenda, i numeri ai gruppi di specie, come in fig. 2.**
the former more frequently than the latter (tab. II). The highest frequency is on the N-side of the trunk, and below 20 m from the bottom of the doline (tab. III).

**Relevé group 2** - Number of relevés: 33. Average number of species per relevé: 11. Lichen species: 41%. Most relevés are from the south-exposed side of the trunk. The most frequent phorophyte is *Quercus petraea*, followed by *Quercus cerris*; the relevés are more frequent above 20 m from the bottom (tab. II and III). This group is associated with species group 6 (fig. 4).

**Relevé group 3** - Number of relevés: 28. Average number of species per relevé: 7. Lichen species: 56%. Most relevés were on *Quercus petraea*, on the S-exposed side of the trunk, and mainly located on the N side of the doline, below 20 m from the bottom (tab. III). This group is also associated with species group 6, but less strongly than relevé group 2 (see occupancy counts in fig. 2). This group it is not very significant in the ordination, its centroid being located near the origin of the axes (fig. 3a).

**Relevé group 4** - Number of relevés: 14. Average number of species per relevé: 14. Lichen species: 55%. All relevés included in this group were on *Quercus petraea*, mostly on the S-exposed side of the trunk. The frequency distribution in the doline is highest on the SE side above 20 m from the bottom (tab. III). This group is associated with species group 2 (fig. 4), and is located in the central part of the horse-shoe (fig. 3b).

**Relevé group 5** - Number of relevés: 58. Average number of species per relevé: 10. Lichen species: 65%. The main phorophytes are, in decreasing order of frequency: *Quercus petraea*, *Quercus cerris* and *Ostrya carpinifolia*, mostly on the SE and SW sides of the doline, above 20 m from the bottom. This relevé group has the highest incidence of relevés from the N-exposed side of the trunks (tab. III), and is also associated with species group 2 (fig. 4).

**Relevé group 6** - Number of relevés: 11. Average number of species per relevé: 9. Lichen species: 50%. The relevés of this group occur preferentially on the S-side of the trunk of *Quercus petraea* and *Carpinus betulus* (tab. III). The distribution on the doline is rather heterogeneous: the relevés have high frequency below 10 m and above 20 m, mainly at the SE and S sides of the doline, but also at the NW side. It is associated with species group 4 (fig. 4). In the ordination, this relevé group, as relevé group 2, has the centroid with the point projection near the origin of the axes (fig. 3a).

**Relevé group 7** - Number of relevés: 8. Average number of species per relevé: 6. Lichen species: 73%. These relevés were taken on *Carpinus betulus*, without preferential exposure on the trunk. This small group is restricted to the bottom of the doline (up to 10 m) at the NE and S sides (tab. III). It is associated with species groups 1 and 3 (fig. 4) and in the ordination is located at the positive extreme of the horse-shoe (fig. 3a).

**Relevé group 8** - Number of relevés: 33. Average number of species per relevé: 7. Lichen species: 79%. The most frequent phorophyte is *Quercus cerris* followed by *Quercus petraea*, mainly below 20 m from the bottom, at the NE and S sides of the doline, like the previous group. The frequency of relevés exposed on the N-side of the doline is rather high, mostly on the S-exposed side of the trunks (tab. III). This group is associated with species groups 1 and 3 (fig. 4).

Information about ecological factors which might be responsible for the floristic-vegetational variation found within the doline, was obtained from ecological indices, both for lichens and bryophytes; they are reported in tab. IV and V. These data were submitted to PCA,
and the results are shown in fig. 11. The sequence of relevé groups in the ordination based on ecological data (fig. 11) is well-related to that based on floristic data (fig. 3a). The first Principal Component explains 50.5% of the total variance, the second 18.2%. The first Component reflects a trend in increasing acidophytism, separating subneutrophic (1, 2 and 3) from more acidophilic stands (4, 5, 6, 7 and 8). This trend is more evident in fig. 12, where the relevé groups are arranged according to their angular seriation in fig. 3a. Relevé groups 3 and 6 are excluded, due to their point projections near the origin of the axes, which is indicative of a scarce correlation with the overall compositional gradient. A gradient of increasing acidophytism is evident in fig. 12, both for lichens and bryophytes. Furthermore, acidity and bryophyte number per relevé, are inversely correlated (fig. 13).

The second Principal Component separates skio- and hygrophytic stands (relevé groups 1, 7 and 8) from photo- and mesophytic stands (relevé groups 2, 3, 4, 5 and 6). These results indicate that the cryptogamic flora reacts to differences in air humidity and light intensity within the doline; near the bottom of the doline (relevé groups 1 and 7), air humidity is higher...
than at the top (relevé groups 4 and 5), and light intensity has an opposite behaviour. The ecological differences between relevé group 8 and relevé groups 2, 3 and 6 could be explained by the highest percentage of relevés on the N-side of the trunk in this group (tab. III).

The phytogeographic data reported in tab. VI were also submitted to PCA in order to analyse the phytogeographic affinities of the relevé groups; the results are shown in fig. 14. If the figure is interpreted on the basis of the previous ecological characterisation of relevé groups, a correlation is evident between ecological requirements of species and their distributional patterns. Relevé groups 1, 7 and 8, taken in shaded sites, have the highest frequency of northern species, whereas relevé groups 2, 3, 4 and 5 taken in more illuminated sites, have the highest incidence of southern species. Thus, temperature seems to play an important role on the floristic-vegetational variation within the doline, as the species which extend their distribution ranges more widely towards the north are most frequent near the bottom of the doline, which, because of thermic inversion, is also its coldest part.

Finally, an attempt was made to map the distribution of air humidity in the doline, by using the indicator index for xerophytophytic conditions. The map (fig. 15) shows a trend in increasing air humidity from the top to the bottom of the doline, the area with lowest xerophytophytic values being that near the bottom (up to 10 m of elevation). The ecological differences along the sides of the doline could be explained by different topography. The high values of air humidity obtained on the E and NE sides (i.e. those facing W and SW), are due to the very high inclination slope, producing deep shade conditions, and hence low evapotranspiration rates. According to field observations, the E portion of the bottom also has a very reduced light intensity and lower temperatures. The low value of air humidity, above 20 m from the bottom, on the NW side (-facing SE) is due to the low inclination slope, to the other open canopy of the woodland, and to the effect of the dry Bora-wind blowing during autumn-winter.

Summarising, the main factors responsible for the floristic-phytogeographic variation of epiphytic cryptogamic vegetation in the doline are: acidity of the bark (depending on the phorophyte), temperature (depending on exposure and on thermic inversion), light (depending on canopy closure and topography), and air humidity (mainly depending on exposure and topography).

**Phytosociological interpretation**

The eight relevé groups obtained by numerical classification cannot be considered as associations in the phytosociological sense, as not all of them have a set of species occurring with high frequency within one relevé group only. They can be treated as nodes arranged along the compositional gradient. For this reason, the basic units for a phytosociological interpretation of the data are clusters formed at lower fusion levels in the dendrogram of fig. 2. They are:

- Cluster A: includes relevé group 1;
- Cluster B: includes relevé group 2;
- Cluster C: includes relevé groups 4 and 5;
- Cluster D: includes relevé group 8;
- Cluster E: includes relevé group 7.

Relevé groups 3 and 6 were not taken into consideration, as they do not have any differential species.

**Cluster A:** this group corresponds well to the union Neckeria-Anomodon viticulosus (Gams, 1927) Szafirn, 1955 (tab. I). Of the characteristic species, the following are present in our data set: Neckeria complanata, Anomodon attenuatus, Anomodon viticulosus and Porella platyphylla. This union is considered as a subneutrophytic and fairly hygrophytic synusia occurring on trees with a nutrient-rich bark (Barkman, 1958).

According to Gerold (1982) in the Karst area it occurs only at the base of large trees with rough bark, inside deep dolines; this is confirmed by our study, this union having been

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<tr>
<th>Relevé groups</th>
<th>Lichens</th>
<th>Bryophytes</th>
<th>Phorophytes</th>
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<td>Ostrya carpinifolia</td>
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Tab. II - Percentages of cryptogams and main phorophytes for each relevé group.

- Percentuali di crittogami e principali forofiti per ogni gruppo di rilevii.

<table>
<thead>
<tr>
<th>Relevé groups</th>
<th>Transects in the doline</th>
<th>Elevation range (m)</th>
<th>Exposure on the tree</th>
<th>Height on the tree (m)</th>
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Tab. III - Percent distribution of different parameters in the relevé groups.

- Distribuzione percentuale dei diversi parametri nei grappi di rilevii.
found on Q. petraea, mostly on the N-exposed side of the trunk, at the bottom of the doline.

Cluster B: this group corresponds to the union Leucodontetum sciuroides Störmer, 1938 (tab. I). This, according to Gerdoü (1982), is characterised by the constant presence of species of the Anemondontion europaei such as Leucodon sciuroides (the characteristic species of the union), Hamalothecium sericeum and Porella platyphylla and by the high frequency of Tortulina laevipilae species. In our relevés these species are also associated with Orthotrichium sp., Acrocorynium gemmata, Bacidad rubella and Phaeophyscia chloaetha. This synusia is subneutrophitic, photophytic and less hygrophytic than the Neckero-Anemondontetum viticulosi. In our doline this union has been found mainly at the base of Q. petraea, and also on Q. cerris, mainly on the S-exposed side of the trees, and is more frequent above 20 m from the bottom. Differences of exposure may explain the different ecological requirements between this and the former union.

Cluster C: this cluster corresponds to the union Parmelietum caperatae-perlatae (Barkm.) Delzenne & Gehu (tab. I). The characteristic species is Parmotrema chinense. Other high-frequency species present in our relevés are: Normandina pachella, Phlyctis argena, Cladonia coniocrana and Parmelia caperata. In the study area the synusia is mainly found between 20
and 30 m from the bottom, chiefly on Quercus petraea. These data are in agreement with the ecological requirements reported for this union by Nijs (1982), which are: acid pH (from 5.0 to 6.2), high air humidity and diffuse light.

**Cluster D:** This cluster, which cannot be assigned to any described union for lack of characteristic species, represents fragments of Calicion vegetation (tab. I). The only characteristic species present is Chrysothrix candelaris, with Parmelia glabrata, Parmelia sulcata and Pertusaria flavida as companion species. These relevés were mainly taken Quercus cerris from the bottom of the doline to ca. 20 m, and the ecological requirements cited in the literature for Calicion-synusiae are the following: very acid pH (from 3.8 to 4.9), high air humidity and abundant diffuse light (Barkman, 1958; Nijs, 1982).

**Cluster E:** These few relevés are very poor in species (6 as average per relevé), and represent only fragments of the alliance Graphidion scriptae Oxner, 1928 emend. Barkm., 1958 (tab. I). The characteristic species is Graphis scripta, associated with Parmelia sulcata. According to Barkman (1958) this alliance has a distinct preference for smooth-barked trees. Most associations are acidophytic (pH from 5 to 6), moderately to strongly hygrophytic and moderately photophytic. The relevés were taken on the bark of Carpinus betulus near the bottom of the doline.

**Discussion and conclusion**

In the biotope analysed in this study, the most important factors influencing the variation of epiphytic cryptogamic vegetation seem to be: pH, light intensity, air humidity and temperature. The pH clearly separates bryophytes and lichen communities; the former are mainly located at the base of the trunk, which are more exposed than tree trunks to dust deposits coming from the surrounding calcareous environments. However, the bases of the trunks, especially in the humid environment of the doline, are also more humid than the boles. Thus, it is probable that pH has only a secondary role in separating communities dominated by bryophytes from those dominated by lichens, the main factor being instead water availability.
Air humidity and light are inversely correlated, and seem to have an influence on the diversity of epiphytic vegetation. The average number of species per relevé tends to be higher near the upper margin than near the bottom of the doline, where air humidity is higher and light intensity is lower. Near the bottom of the doline the species tend to be more hygro- and skiohyphic than near the margin. In my opinion, in this habitat the light factor seems to be more relevant than the water factor. Although air humidity is generally higher near the bottom of the doline, its values are relatively high throughout this biotope than in the surrounding Karst Plateau, so that the importance of air humidity as a limiting factor is probably reduced. On the contrary, light intensity is clearly much higher near the margins than near the bottom of the doline. Temperature also plays an important role on the distribution of the epiphytic flora, as demonstrated by the fact that the species which extend more widely towards the north are more frequent near the bottom of the doline.

In conclusion, this study has shown that also for epiphytic cryptogams, as for higher plants, dolines represent a complex environment, with several different ecological niches, mainly dependent on microclimatic patterns within the biotope. This determines the presence of complex compositional gradients, and higher biodiversity values than those typical of the surrounding Karst Plateau. This fact should be taken into consideration for the management of Karst ecosystems and for the preservation of local biodiversity, especially considering that there are projects for transforming parts of the Trieste Karst into a large conservation area. Furthermore, cryptogams have confirmed their sensibility to microclimatic variations, and can be profitably used to obtain information on microclimatic patterns at a small scale.

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Tab VI - Occupancy of the relevé groups in different phytogeographical subdivisions of Europe, calculated as percentages of the total occupancies for each relevé group.

- Tasso di occupanza dei gruppi rilevati nelle diverse suddivisioni fitogeografiche europee, calcolati come percentuale dell’occupanza totale per ogni gruppo rilevato.

**Floristic List**

**Lichens**

*Acrocoma gemmata* (Ach.) Massal. - A species with a distribution ranging from the South-Boreal to the Mediterranean zones, with subatlantic affinities. It grows on rough, nutrient-rich bark of mature trees, mostly in woodlands or open situations. In the Trieste Karst it is generally confined to deep dolines. pH: 5; H: 3; L: 2 - 3.

*Agonoma albojuncta* (Stenb.) P. James - This species is known from many European countries, but this is the first record for Italy. In the doline of Borgo Grutta Gigante A. albojuncta was found on *Quercus petraea* in a sheltered and rather humid situation, and associated with the following lichens: *Acrocoma gemmata*, *Candelariella reflexa*, *Normandinia polchelli*, *Phaeopychia chlorantha* and *Philytis argenta*. *Bacidia circumspecta* (Norrlin & Nyl.) Malme - An ephiphytic species, occurring principally on eutrophic bark. It is widespread, but rare, being known from western and central Europe. In Italy it was only reported from Toscana (Nen, 1993), and is now also known from the Friuli-Venezia Giulia region, where it was collected on *Quercus petraea*. pH: 4; H: 3; L: 2 - 3.

*Bacidia rubella* (Hoffm.) Massal. - A widespread species ranging from central Europe to the Mediterranean mountains. It occurs on isolated broad-leaved trees with rough and nutrient-rich bark, mainly on *Quercus*. Sensitive to air pollution, and generally not common in the Trieste Karst. pH: 5; H: 3 - 4; L: 3 - 4.

*Caloplaca holocarpa* (Hoffm.) Wade - This is, as presently understood, a variable and common species ranging from the Arctic to the Mediterranean zone. *C. holocarpa* is a nitrophyte species, found on eutrophic and nutrient-rich substrata, both on bark and on rocks. The identity of ephithic and epyphytic populations is not certain. pH: 5 - 7; H: 5; L: 3 - 4.

*Candelariella reflexa* (Nyl.) Lettau - This species is widespread in Submediterranean parts of Europe. It is found in nutrient-enriched habitats, and is moderately tolerant to air pollution. It is very common in NE Italy. pH: 3 - 4; H: 3; L: 3 - 4.

*Cetraria olivetorum* (Nyl.) Cult. et Cult. - This lichen is found on acid bark, mostly in humid situations. *Cetraria olivetorum* has a subatlantic distribution in Europe. In the Friuli-Venezia Giulia Region it is generally confined to humid beech-forests of the montane vegetation belt. This is the record at the lowest altitude for that area. pH: 3 - 4; H: 2 - 3; L: 3 - 4.

*Chaeothea ferruginea* (Sm.) Migula - A widespread species in the Northern Hemisphere, ranging from the Boreal zone to central Europe. It occurs on bark, principally in fair well-lit and humid situations. It is tolerant to SOX air pollution. In the Trieste Karst it is rare, and restricted to *Quercus cerasi*. pH: 2 - 3; H: 2 - 4; L: 2.

*Chrysothrix candelaris* (L.) Laundon - This species occurs on dry, shaded sides of rough-barked trees; rarely on rocks and walls. It is a subcosmopolitan lichen, known from the Boreal to the Submediterranean zones, absent from Arctic-Alpine and desert areas. In the Trieste Karst it is usually found on old specimens of *Quercus cerasi* inside the dolines. pH: 2 - 4; H: 3; L: 2 - 4.

*Cladonia coniocraea auct. - A widespread and common species, ranging from the Arctic to the Mediterranean zones. Chiefly on acid bark of living or recently dead trees and wood, less often on soil. pH: 3 - 4; H: 3 - 4; L: 3 - 4.

*Collema flavicolum* (Ach.) Ach. - This species has a wide distribution from the Arctic to the Temperate zones. It is found on a wide variety of substrata, including bark, siliceous rocks and often among mosses, in rather shaded and humid situations. pH: 5; H: 3 - 3; L: 2 - 4.

*Collema subflaccidum* Degel. - A subcospean species, with a wide distribution in both Hemispheres. It occurs on bark, in relatively moist and shaded situations, being less frequent on rocks.

*Dimerella pinetis* (Ach.) Veza - This species is found on shaded, more or less acid bark, at tree bases or in deep crevices, occasionally on wood, mosses and rocks. A common lichen, often overlooked, with a wide distribution from the Boreal to the Mediterranean zones. pH: 2 - 4; H: 2 - 3; L: 2 - 3.
Graphis scripta (L.) Ach. - A widespread species ranging from the south of the Boreal to the Mediterranean zones. It is preferentially found on smooth-barked trees such as Fagus, Carpinus and Corylus, in humid situations. In the Trieste Karst it is restricted to dolines. pH: 3 - 5; H: 2 - 3; L: 2 - 3.

Glycera truncigena (Ach.) Hepp - This is a widespread, but rather rare species, with a distribution ranging from central Europe to the Mediterranean and temperate regions. It grows on the roots of trees such as Acer, Ulmus, Prunus and Quercus. pH: 4 - 5; H: 2 - 3; L: 2 - 3.

Hypermecina adstringenata (Fröls) H. Mayrb. et Poelt - On the nutrient-rich bark of tree trunks, rarely on shaded, vertical surfaces of calcareous or siliceous and nutrient-enriched rocks and walls. It has a subatlantic range in Europe. pH: 3 - 5; H: 3 - 3; L: 3 - 4.

Lecanora argyrella (Ach.) Malme - A widespread species with a holartic distribution, frequently confused with other related species. It grows on smooth bark, in rather nutrient-poor situations.

Lecanora chiaanera Nyol. - This lichen has a holartic distribution, and occurs also in the Southern Hemisphere. It is found on bark and wood, mainly of deciduous trees and also worked timber, with a very wide ecological amplitude. Common in the Trieste Karst. pH: 4 - 5; H: 3 - 5; L: 2 - 5.

Lecanora intumesens (Rebent.) Rabenh. - This epiphytic species is widespread throughout Europe. In Italy it is most frequent in beech forests of the montane belt, and this is the record at the lowest elevation in NE Italy (see Núes, 1993). pH: 4; H: 3; L: 2 - 3.

Lecanora palisida (Schreber) Rabenh. - This lichen has a wide distribution from the south of the Boreal zone to the Mediterranean montains. It occurs in shaded and rather humid situations, on rather acid bark, mostly of deciduous trees. In the Trieste Karst it is generally confined to the dolines. pH: 4; H: 2 - 3; L: 2 - 3.

Lecidella glaucophracta (Ach.) Has. s.lat. - This species occurs on bark and has a very wide ecological amplitude. It is found from the Arctic to the Mediterranean zones. It is moderately tolerant to SO2 air pollution. pH: 3 - 5; H: 2 - 5; L: 4 - 5.

Lepraria sp. - The genus Lepraria comprises several species, which, after the monograph of Laurenz (1992) can be identified at species level only after a chemical analysis. Most of the species, according to Laurenz (1992), occur on rocks, bark and rock, less frequently on soil.

Normandinia pulchella (Borr.) Nyol. - N. pulchella is a cosmopolitan species, with a subatlantic distribution in Europe, extending east to the Carpathian Range (Tretjak & Núes, 1989). It mostly grows on heaptics and on other lichens, and is fairly common in NE Italy. pH: 4 - 5; H: 2 - 3; L: 4.

Opegrapha fuscens (Pers. - This lichen is found on the smooth, nutrient-rich bark of broad-leaved trees, mostly in humid and shaded situations. O. fuscens is a Northern Temperate species, ranging from central Scandinavia to the Northern Mediterranean mountains. pH: 4 - 5; H: 2 - 3; L: 2 - 3.

Parmelia caperata (L.) Ach. - A widespread temperate species, with a subatlantic range from the southern part of the Boreal zone to the Mediterranean region; on more or less acid-barked and broad-leaved trees. One of the most common and abundant species of the Trieste Karst, often covering the entire trunks. pH: 3 - 4; H: 4; L: 4.

Parmelia glabrata (Lamy) Nyol. - This species has a very wide distribution in Europe, from the Boreal to the Mediterranean zones. It is found on more or less smooth bark or wood, occasionally on rocks. pH: 4; H: 2; L: 3.

Parmelia subaurita (L.) Nyol. - This species is widely distributed in the Northern Hemisphere, from the Boreal to the Mediterranean zones. It occurs on bark, especially on neutral- to acid-barked trees, less frequently on trunks and rare on rocks. It is moderately tolerant to air pollution. pH: 2 - 3; H: 3 - 5; L: 3 - 4.

Parmelia sulcata Taylor - P. sulcata is a very common species, occurring on trees, rocks and occasionally on soil, mostly on acid substrata and in rather humid situations. It is distributed from the Arctic to the Mediterranean zones. pH: 4 - 5; H: 3 - 5; L: 4.

Parmotrema chinesia (Osbeck) Hale et Ahti - A species with a very wide distribution, reported from all Continents. In Europe it has a rather subatlantic range, and is also frequent in the Mediterranean mountains. It grows on well-fit, broad-leaved trees, and also on siliceous rocks and walls. In the Trieste Karst
a wide distribution in Europe, occurring on a wide variety of substrata and in diverse habitats. It is generally rare, and not well-developed in the Trieste Karst. pH: 3 - 5; H: 2 - 3; L: 2 - 3.

Scoliciosporum umbrianum (Ach.) Arnold - This species grows on a wide variety of substrata, including calcareous rocks, walls, wood, bark, and man-made substrata. It appears to be tolerant to air pollution. It is an inconspicuous, but widespread lichen, ranging from the Boreal to the Temperate zones. pH: 5; H: 2 - 5; L: 2 - 5.

Strigula mediterranea Etayo - Salazar - This species was described from the Crimea Peninsula as Porina schizospora Vainio, and later transferred to Strigula by Etayo in 1993. It occurs on smooth bark, amongst mosses on sheltered trunks of old trees, mostly Quercus, Ulmus and Fraxinus. It is known from the Crimea Peninsula, Italy and Spain. For Italy it was reported from Tuscany and Calabria and is known, after this work, also from the region Friuli-Venezia Giulia.

Theleopsis rufella Nyl. - This lichen is found on mature, broad-leaved trees in humid, but not too shaded situations. It is known from Temperate Europe, where it has a wide distribution and is only locally common, and was also reported from Macaronesia and North America. It is generally very rare throughout Italy. pH: 2 - 3; H: 2; L: 3.

Bryophytes

Anomodon attenuatus (Hedw.) Hue. - A subcontinental species ranging from the Arctic zone to central Europe. It grows on damp shaded logs and rocks. pH: 7; H: 5; L: 5.

Anomodon viticulosus (Hedw.) Hooker & Taylor - A temperate, almost cosmopolitan plant, common and sometimes locally abundant on basic substrata at low altitudes; rare elsewhere. It grows on rocks, walls and trees. pH: 8; H: 4; L: 4.

Brachythecium velutinum (Hedw.) B. S. G. - A variable species forming green or yellowish-green patches on shaded tree boles, rocks and walls. It ranges from the sub-Boreal to the Mediterranean zones. pH: 5; H: 4; L: 5.

Cololejeunea calcarea (Libert.) Schiffn. in Engler & Prantl - A very minute liverwort, scattered or in small thin patches. It grows on other bryophytes, on rocks, particularly limestone, and very rarely on bark. It is a widespread temperate species. pH: 9; H: 7; L: 4.

Furullania dilatata (L.) Dum. - A widespread temperate species, from the sub-Boreal to the Submediterranean zones. It grows on trees and rocks. pH: 5; H: 4; L: 5.

Furullania tamarisci (L.) Dum. - This is a southern temperate species, occurring from central Europe to the lower mountains of the Mediterranean zones. It grows on rocks and bark in sheltered or open habitats, forming glossy, reddish-brown patches. pH: 5; H: 4; L: 7.

Homalia trichomanoides (Hedw.) B. S. G. - A temperate species, found on damp, shaded rocks, walls, soil banks and tree trunks. H. trichomanoides has a gametophyte resembling that of Neckera, but the stems never have paraphyllia or flagelliform branches. pH: 7; H: 6; L: 4.

Hypnum cerenumm (Hedw.) B. S. G. - This moss grows on dry, exposed walls, on hard-packed soil, tree trunks and sand-dunes; common especially on basic substrata. It is distributed from the sub-Boreal to the Mediterranean zones. pH: 6; H: 2; L: 8.

Hyphnum caprifolii Hedw. - A species with a very wide distribution, from the South-Boreal to the Submediterranean zones. It forms green or pale green patches on a variety of substrata, in sheltered or exposed habitats, especially of acidic type. Very common. pH: 3 - 4; H: 4; L: 5.

Lejeunea cavifolia (Ehrh.) Lindb. - A small plant, forming thin patches. It is found on damp shaded rocks, on bark and also on other bryophytes. It is a suboceanic-montane species with a wide distribution, from the Boreal to the Mediterranean zones (including Macaronesia). pH: 6; H: 6; L: 5.

Leptodon smithii (Hedw.) Web. & Mohr - This species has subatlantic distribution in Europe. It occurs on bark, mostly on basic substrata, occasionally on basic walls or rocks, forming dark green patches. pH: 6; H: 4; L: 8.

Leucodon sciuroides (Hedw.) Schwaegr. - This is a temperate species with a wide distribution, mostly found in open habitats, forming yellow-green patches on rocks, walls and tree trunks. pH: 6; H: 4; L: 8.

Metzgeria forata (L.) Dum. - A widespread and common species, from the sub-Boreal to the Submediterranean zones. It forms dense mats or scattered thalli growing through other bryophytes. It is found on the bark of various trees and shrubs in both sheltered and exposed situations, and also on dry shaded rocks. pH: 6; H: 4; L: 5.

Neckera complanata (Hedw.) Hue. - A species with strongly complanate, not undulate leaves, forming yellowish-green patches on usually shaded rocks, walls and tree trunks. A common moss with a very wide distribution. pH: 7; H: 4; L: 4.

Neckera crispa (Hedw.) - A species with strongly complanate and transversely undulate leaves, forming yellowish-green to golden, lax patches. It is found on basic rocks, on damp, calcareous soil and rarely on trees. It is known from Europe and Macaronesia. pH: 6; H: 4; L: 4.

Orothricium sp. (Hedw.) - A large, world-wide genus of about 250 saxicolous and corticolous species, some of which show considerable morphological variations. The specimens collected were growing in small tufts and were always sterile, so that their identification was not possible.

Plagiomnium affine (Funk) Kop. - This is a temperate species with a wide distribution, ranging from the sub-Boreal to the Submediterranean zones. It forms spreading green patches or scattered shoots on damp soil in woods, being very rare on bark. pH: 5; H: 5; L: 5.

Porella platyphylla (L.) Pfeiff. - A species with a very wide distribution, from the sub-Boreal to the Mediterranean zones. It occurs on a wide variety of substrata including sheltered tree boles, walls, rocks and soil. pH: 6; H: 4; L: 5.

Porella platyphyllaidea (Schwein.) Evans - This is an orphletic species, known from central Europe and North America. It grows on bark and rocks, mostly in humid situations. The species is poorly understood, and requires a detailed taxonomic revision. pH: 7; H: 2; L: 7.

Radula complanata (L.) Dum. - A very common species, ranging from the sub-Boreal to the Submediterranean zones. It occurs in habitats with high air humidity on deciduous trees, less commonly on rocks. pH: 7; H: 5; L: 7.

Ulotrichopsis cristata (Hedw.) Brid. - A common species with a distribution ranging from the Boreal to the Submediterranean zones. It grows on branches of trees and shrubs, mostly on Corylus, Fraxinus, Salix and Sambucus in yellowish-green turfs. pH: 3; H: 6; L: 4.


Acknowledgements

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References


