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Some aspects of the ecology of limestone solution - hollows at gait barrows, north Lancashire

Lowe, Christopher J.

SOME ASPECTS OF THE ECOLOGY OF

LIMESTONE SOLUTION — HOLLOWS

AT GAIT BARROWS, NORTH LANCASHIRE

by

Christopher J. Lowe, B. A.

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Departments of Botany and Zoology,
University of Durham.

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* This print is not available in every copy of
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ACKNOWLEDGEMENTS

INTRODUCTION

In August 1978, I was shown several limestone areas near Carnforth, North Lancashire. Of these, Gait Barrows, a newly-created Nature Reserve, was especially impressive, for both its massive pavements and varied flora. Many water-filled or well-vegetated solution-hollows occupied the former, and amongst the latter were some heathery patches of scrub, which seemed anomalous in such a base-rich setting.

Notes and memories of that visit prompted these studies. The original aim was to relate the apparently acidophilous scrub to the solution-hollows, but early in the research it became clear that the two habitats were not causally linked, as was first thought. The study thereafter evolved into a concerted investigation of the solution-hollows. The five Chapters of Part I embrace their physical and chemical qualities, and the phyto-sociological analysis of the inhabiting plants. Part II incorporates a discussion of the geological processes responsible for the precise character of the Gait Barrows pavement, and a consideration of some postulated patterns of botanical development.

PART I

CHAPTER   1

THE   SETTING   FOR   THIS   STUDY

1 : 1   Geographical   Position

Gait Barrows, a 'grade one' site of 70 hectares' extent in North Lancashire, was acquired by the Nature Conservancy Council in 1977 and designated as its 'Silver Jubilee' National Nature Reserve. (Photograph 1). It lies in the centre of a broadly triangular region of distinctive topography, which Oldfield (1960) has christened "Lowland Lonsdale". This area projects bluntly into the North-Eastern part of Morecambe Bay, and is bordered to the North-West by the Kent Estuary. Its Eastern, and longest, edge corresponds to a wide, glaciated trough presently occupied by the section of the M6 motorway immediately North of Carnforth.

The precise location of Gait Barrows (National Grid Reference — SD 4777 - 4877) in relation to these environs is depicted on the accompanying MAP 1. Arnside, a small coastal resort, is about three kilometres distant; Silverdale is the nearest substantial settlement; and the County boundary with Cumbria (formerly Westmorland) passes less than one kilometre to the North of the Reserve.

Commemorative   Plaque

Excavated   Zone
(roadway   for   quarry - traffic)

3&4

Runnels   on   Southern   Pavement

Undissected Limestone of Study - Area
(with mineral-vein in foreground)

5&6
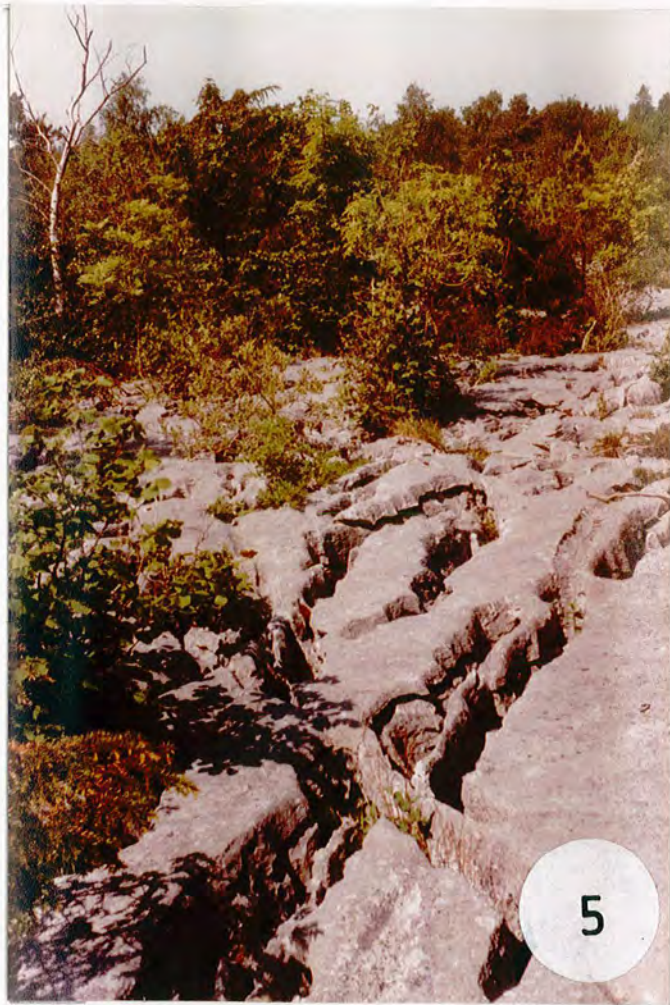
Dissected   Margin   of   Pavement
(and   increasing   woodland)

Main   Gryke - System
(looking   North-West)

Pot - hole

'Tadpole' - type Hollow

code '20'

Solution - Hollows (mainly 'Aquatic')

Solution - Hollows (mainly 'Terrestrial')

A Well – Vegetated Site
('7H')

Large, Open Hollow
(Site 'J',
nearly two square metres in extent.)

Site '32' — Floral Diversity

Site 'G' with Sedum acre

Polygonatum odoratum

Site 'X' with Juncus tufts
(also renowned for high pH-values)

Site 'U', with dry, friable substrate

Patch of Scrub, with Calluna vulgaris

MAP 1

1 'LOWLAND LONSDALE'

RIVER
KENT

15m

N

ARNSIDE

Arnside
Knott

61m

GB

SILVERDALE

LM

61m

15m

Warton
Crag

MORECAMBE
BAY

15m

M6
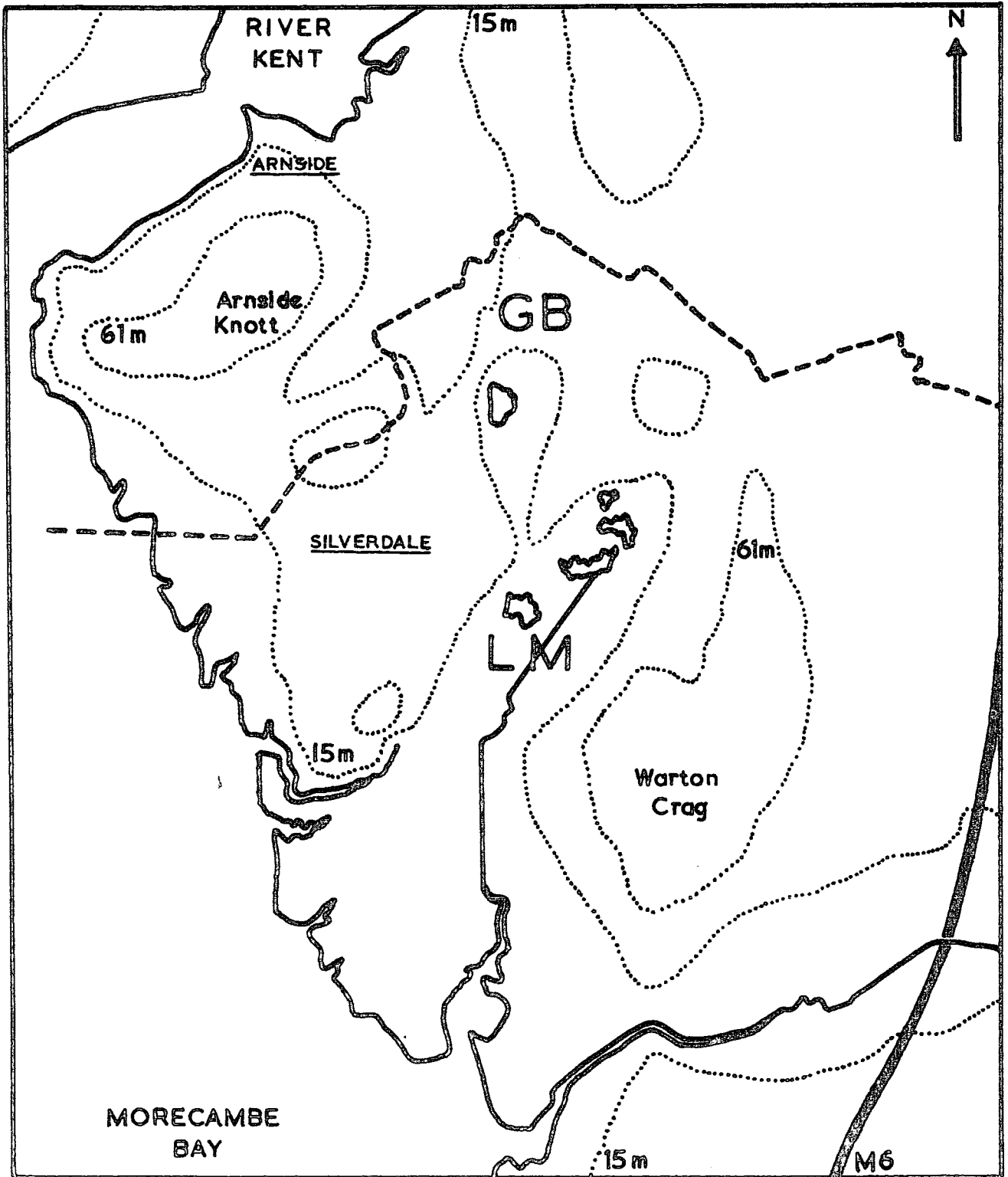
⬚ — generalised contours

--- — County Boundary

GB — GAIT BARROWS

LM — LEIGHTON MOSS

1 : 2   Site Description

1 : 2 : 1   Lowland Lonsdale: Topography

Lowland Lonsdale consists of a geological fretwork
which is closely reflected in its contrasting and broken
relief.   Upstanding Carboniferous Limestone ridges, which
reach 160 metres (525') above sea-level at Arnside Knott and
Warton Crag (see MAP 1), alternate with fault-governed and
glacially-excavated valleys.   Much of these drift-filled
and low-lying tracts is ill-drained, and dominated by open
meres, reedswamp, or similar aquatic vegetation, as at the
Leighton Moss R.S.P.B. Reserve.   Whereas the limestone
exposures are frequently well-wooded, the lower slopes
and reclaimed valley-floors are mainly devoted to pastoral
farming.

1 : 2 : 2 Gait Barrows Reserve: General Description

Gait Barrows National Nature Reserve, as MAP 2 shows,
also has a similar, but smaller-scale, variety of environments.
Its Southern part is occupied by the open water — fen — alder
carr sequence of Little Hawes Water, plus the base-rich grass-
land of neighbouring meadows.   The Northern half, as Ordnance
Survey Sheet 97 suggests, is predominantly wooded (see Section
1 : 3 : 3 below).   However, this portion of the Reserve also
includes relatively bare limestone, in the form of massive
pavement (see Section 1 : 3 : 4 below), which, despite its
limited extent (12 ha), constitutes "the most important
feature" (Ratcliffe, 1977) of Gait Barrows.   The same

MAP 2
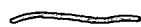
⌒	Boundary of Gait Barrows Reserve.
⌒··⌒··	Main internal paths.
⸛·········	Outlines of three chief areas of surviving, undamaged pavements; the square inset indicates the part drawn on MAP 3.
⊙	Memorial cairn (see Photograph 1).
W	Woodland
X	Excavated zone
══	Lane past Reserve.
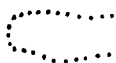
2 GAIT BARROWS HABITATS

N

W W W W W W W W

W X X X X X W

W X X X W

X X X W

X X X W

W W X W

W W X W

W W X X W

W W X X W

Little Hawes
Water

HAWES WATER

100 m

Silverdale

account of the Reserve defines the pavement as "probably the finest example in Britain of this extremely local habitat". (Ratcliffe, 1977, op. cit.)

1 : 2 : 3 Gait Barrows Reserve: Conservation Value

The Gait Barrows limestone pavement is not well known, partly because it was until 1977 in private owner-ship, and partly because the surrounding woodland almost completely screens the interior of the Reserve. Precise references to the area, in both geological and botanical literature, are few. Ward & Evans (1976) visited Gait Barrows during a concensus of all Carboniferous Limestone regions of Britain. They applied a floristic index to pavements, whereby their conservation value was assessed in respect of species-richness in general and occurrence (ranked on a scale of abundance) of plants of sparse dis-tribution in particular. Of 537 individual pavements examined, Gait Barrows gained by Ward & Evans' reckoning a total score of 475, well above the second-placed site, Hutton Roof Crags, a complex of 13 pavements situated in Cumbria, just to the East of Lowland Lonsdale. Moreover, five out of six species in Ward & Evans' 'Group A' plant-list, which they regard as "most dependent on the pavement habitat for the maintenance of important populations", are found at Gait Barrows.

Thus this Reserve is of outstanding interest, as well as of the highest-priority conservation value. Just-ification for intensive research there requires no further

elaboration.   Indeed, it is salutory to note that Ward &
Evans based their floristic index on the gryke-inhabitants
only (S. D. Ward, pers. comm.).   A substantially greater
diversity accrues if the vegetation of solution-hollows,
disturbed areas, and woodland (see Section 1 : 3 : 3) is
also taken into consideration.

1 : 3   The Physical Nature of Gait Barrows Pavements

1 : 3 : 1 Altitude

One of the distinctions of Gait Barrows is its "unusually
low elevation" (Ratcliffe, 1977) of between 25 and 40 metres
(about 80' to 130') above sea-level.   In this, it differs con-
spicuously from not only almost all of Lowland Lonsdale's other
Carboniferous Limestone outcrops, (see Section 1 : 2 : 1), but
also the more extensive and better-known pavements of Craven
and Ingleborough in Yorkshire, which are at heights above 335
metres (1 100').   Ward & Evans (1976) stress the importance of
low altitude, and vegetation components associated with this,
in contributing to Gait Barrows' premier position as a site
for conservation.

1 : 3 : 2 The Limestone

The limestone rock comprising the Gait Barrows pave-
ment is of Lower Carboniferous age.   No exact horizon can be
attributed to these strata, however, as geological documentation
of the site is minimal.   In appearance, the rock is compact and

resistant; seemingly without macro-fossils; of a generally
pale coloration and homogeneous texture; and massively and
more-or-less horizontally bedded. Further details of the
Gait Barrows geology are given in Chapter 6.

1 : 3 : 3   Habitat-divisions   of   the   Limestone   Areas

Locally-based commercial enterprise has removed con-
siderable quantities of limestone peripheral to the now-sur-
viving pavements. Such limestone was more accessible, and
also presumably more picturesquely sculptured by weathering,
than the rock comprising the more central areas of the site,
and was marketed as 'water-worn' rockery-material. Similar
exploitation has occurred elsewhere, for example at Farleton
Knott, Cumbria (Ratcliffe, 1977) and Ingleborough, Yorkshire
(Goldie, 1973). Excavation is done by machinery which takes
off the top, and botanically vital, limestone bed. Lateral
damage to pavement-surfaces is thus rapid and irrevocable.
Depredation of this sort led to strong concern for the future
of the pavement, and the eventual purchase of the Gait Barrows
National Nature Reserve.

The resultant stripped portions of the pavement are
still very obvious as broken, rubbly areas — a form of horiz-
ontal scree — generally lightly vegetated and noticeably one
'step' below the relict pavement in its reduced extent. (See
Diagram 1 below). Several broad roadways created by and for
the now-defunct quarrying operations (Photograph 2) divide the
remnants of the Gait Barrows pavements into three discrete parts,
of which the central one is the study-area investigated in this
project.

<u>Diagram 1</u>

<u>GENERALISED CROSS-SECTION</u>

<u>OF EXCAVATED AREAS</u>

rubbly & scrub-covered surface.

surface (smooth) of
relict pavement.

thickness of
one bed of limestone.

quarried blocks
not collected

←————— <u>excavated area</u> —————→
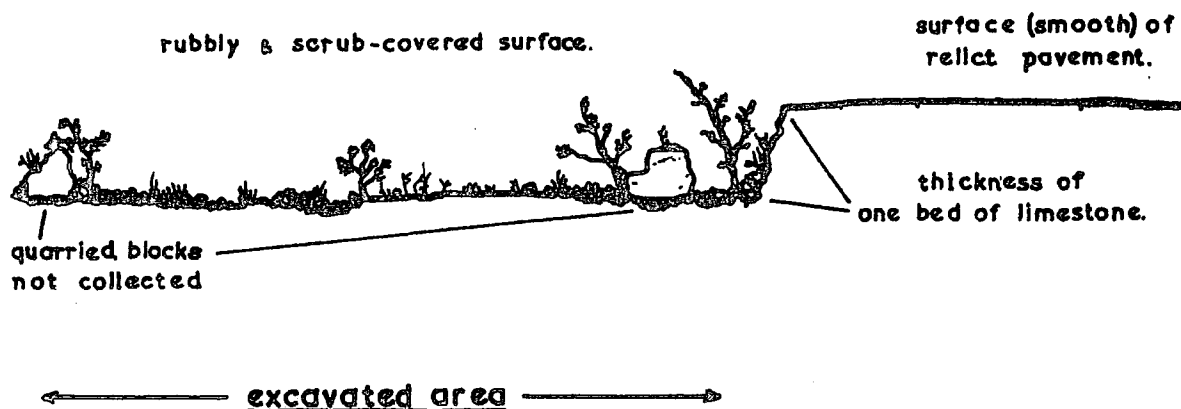
Parts of the Reserve from which limestone has been
extracted merge into a second type of habitat, where fairly
well-grown mixed woodland has developed. With increasing
distance from the main pavements, the limestone supporting
this vegetation becomes progressively fragmented and buried
under leaf-litter and drift-derived soils. These three
habitats — 'classic' pavement; lower-level, man-made
surfaces of shattered rock; and dense woodland — form a
quasi-concentric pattern, as suggested by MAP 2, although,
of course, detailed examination of the Reserve reveals many
discrepancies in this morphological and vegetational zoning.

In the following Section, only the study-area of the
central pavement is described.   Its features are plotted
on MAP 3.

1 : 3 : 4   The Morphology of the Central Pavement

The Northern part of the central section of pavement is flat or at most very gently undulating.   South of the line A ———— B on MAP 3, this horizontality is marred by a slight flexure in the bedding of the rocks which tilts the pavements perceptibly towards the Little Hawes Water embayment (MAP 2).   Much of the Southern area — though more noticeably so on the Eastern pavement — has a different morphology characterised by runnels (Photograph 3) rather than solution-hollows, a change which is in response to the increased slope.

Much of the actual bedrock-surface is exceedingly smooth;   many hours of kneeling on the limestone in relative comfort testifies to this!   The only common disfiguration is provided by frequent and intersecting mineral-veins of secondary in-filling material, whose chemistry, though dominantly calcitic [1], permits a greater resistance to weathering than does the host-rock.   Such veins therefore protrude above the general pavement-level by a few millimetres.   Diagram 2, below, and Photographs 4 (foreground), 8, 9 and 10 show this feature.   The main mineral-vein attains 10 centimetres in thickness, but most examples are minor features.   Their relationship to solution-hollows is discussed in Section 6 : 2.

A further distinction of the central areas of the Gait Barrows pavement is the noticeable paucity of longitudinal fissures known as 'grykes'.   In marked contrast to many better-known and more typical pavements, such as those above Malham Cove, Yorkshire, it is possible at Gait

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1   See Appendix A .

Barrows to take several positive strides across uninterrupted
limestone, and the customary rectilinear pattern of dissection
is largely absent.   (Photograph 4).   Such a condition of the
surface of the pavement is termed 'massive'.   Towards the
woodland edges surrounding the pavements, this quality de-
generates as gryke-frequency increases, as described earlier
in Section 1 : 3 : 3. (See also Photograph 5).

The few existing grykes are characteristically deeply
etched into the bedrock, with vertical sides, modest width,
and in some cases irregular 'beaded-edged' outline.[2]   They
are concentrated into two or three chief systems, (Photograph
6), the major one cutting diagonally across the Northern part
of the pavement at a bearing of 340°.   This is marked on MAP
3.   Towards such fissures the pavement-level becomes slightly
bowed, as Diagram 2 shows.   Some of the grykes, especially at
the rare intersections of more pronounced forms, have devel-
oped into genuine pot-holes.   (Photograph 7).

Whereas grykes and pot-holes are endowed with vertical
outlets for drainage and fine in-washed material (cf. Ivimey-
Cooke, 1965), runnels and solution-hollows are more truly
superficial features of the limestone-surface, penetrating
less than the depth of one bedding-plane, and being invar-
iably floored with solid rock.   Runnels are long, trough-
like depressions, often aligned down-slope, which sooner or
later transmit lateral drainage to some vertical exit such as
a gryke.   Solution-hollows are usually perfectly enclosed,
a character which is demonstrated on many of the photographs,
though a number of the Gait Barrows forms are projected into

2 Appendix B lists dimensions of grykes.

MAP 3

The line A ——— B divides the horizontal from slightly
tilted strata (see text).

This map shows the study-area (central pavement — C),
flanked by similar massive pavements to East E and West W.

3 CENTRAL PAVEMENT

N

W

E

C

A ————————————————————————————— B

25 M
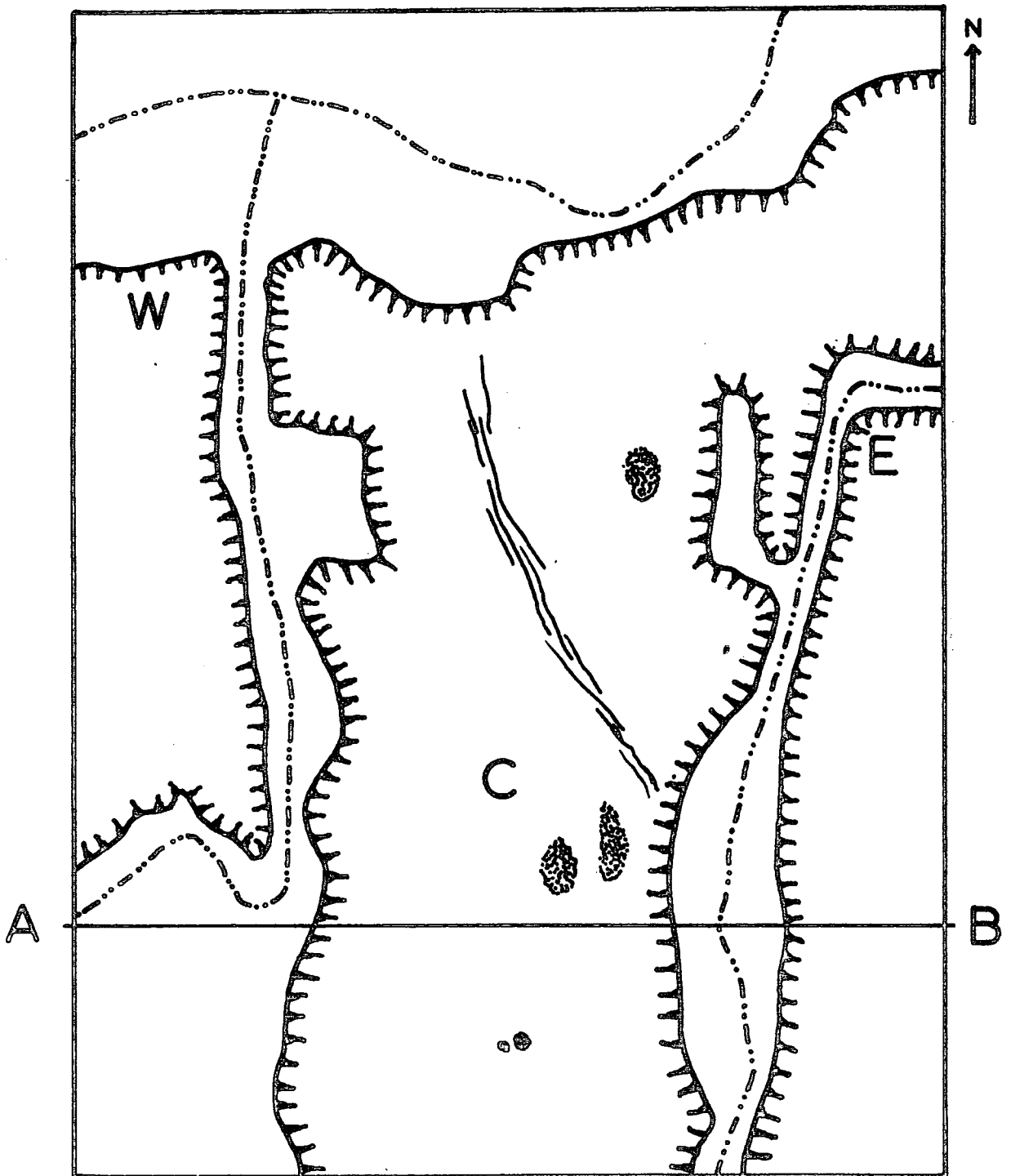
```
...─..─..    paths

         perimeter of massive pavement

  ⊕,      standing stones

          main gryke-system

          patches of scrub
```

runnels such that the dual-feature resembles a tadpole in
overall shape. Hollow '20', on Photograph 8, is an example.
The relationship between runnels and solution-hollows, there-
fore, is closer than that between these features and either
grykes or pot-holes. Both runnels and solution-hollows
customarily contain some form of accumulated substrate and/
or standing water, with associated organic material.

The principal subject of this investigation is the
vegetation of the solution-hollows of the central pavement
at Gait Barrows, and their physical parameters and the main
phytosociological data are dealt with in Chapters 3 and 4
respectively. The possible origin and evolution of these
features, in both geological and botanical terms, is examined
in Part II.

Diagram 2   PAVEMENT MORPHOLOGY

mineral-vein
protruding.

cross-section
of runnel
or hollow.

bowed effect.

bedrock

bedding-plane.

major but infrequent
gryke.
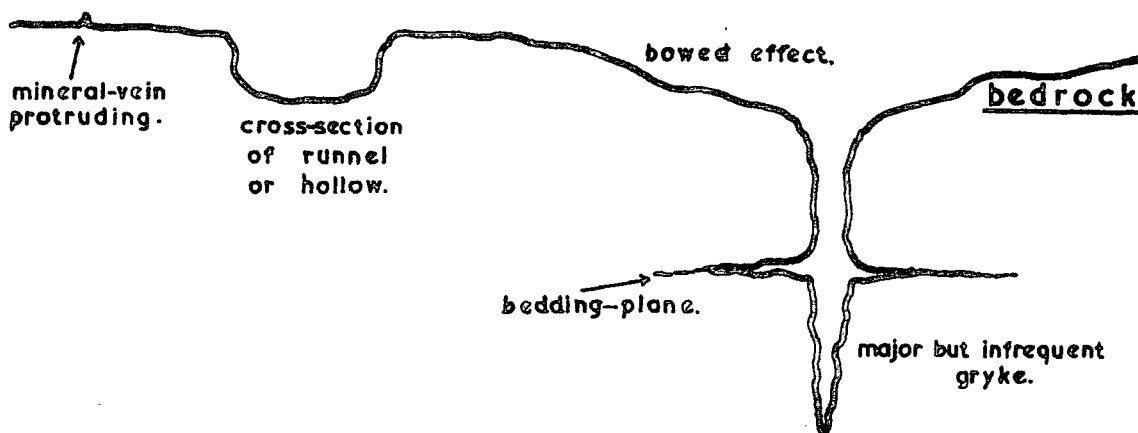
SUMMARY of SECTION 1 : 3

The Northern part of Gait Barrows consists of
exposed Carboniferous Limestone. Much, how-
ever, is heavily dissected and densely wooded.
Peripheral parts of the bare and open pavement
have been destroyed by quarrying for water-worn
limestone. The remaining pavement is divided
into three sections, of which the central one,
displaying an unusually coherent surface of
hard, smooth, massive and generally flat-bedded
lithology, is the study-area for this project.
The pavement-morphology comprises infrequent
but well developed grykes; occasional pot-
holes; runnels, more commonly found on the
more inclined strata; and solution-hollows.
These last-named feature are the main subject
of the investigations described in subsequent
Chapters.

CHAPTER 2

FIELD - WORK METHODS

(N.B. The statistical- and computer-techniques are described in the appropriate places in ensuing Chapters.)

2 : 1 Dates of Visits

A reconnaissance visit to Gait Barrows was made between May 2nd and May 6th. The main field-work was done from May 15th to June 2nd, followed by a third stay (June 18th — 22nd) when most of the final results were obtained. Some observations were added on July 5th and 6th, a brief overnight stop at the site. In Tables, dates are converted to the numerical form, i.e. '6/7/81'.

2 : 2 The Sample of 100 Sites

2 : 2 : 1 Choice of Sites

Field-work began with the designation of 100 solution-hollows comprising the sample studied. These are hereafter referred to as 'sites' or simply 'hollows'. Selection was random in that no preference was exercised except to fulfil the following criteria:

(a) hollows were taken from as comprehensive an area of the central pavement as possible, including surfaces East and West of the main gryke-system and North (61 sites) and South (39 sites) of the flexure (line A - B on MAP 3) separating the horizontal and tilted beds;

(b)   an equal number of water-filled, i.e. 'pools-in-
      hollows', and silt-containing, well-vegetated,
      sites was chosen.   These will subsequently be
      referred to as 'aquatic' and 'terrestrial' sites
      respectively, and contrasting examples of these
      two types occur on Photographs 9 and 10.

The hollows which do not form part of the sample of
100 were missed purely by accident, are relatively few, and
generally representative of the whole population, so that
their exclusion has not materially affected results. Sites
outside the sample proper are occasionally mentioned in the
text, for comparative purposes.

Many of the sample were later tested by auguring or
probing, to ensure that they were truly solution-hollows and
not choked pot-holes.   One site was rejected and a near-by
hollow substituted.   However, without inflicting unwarranted
disturbance on well-vegetated sites, it is impossible to check
that all of them are genuinely limestone-based.   A similar
ambiguity concerns long, narrow, open-ended hollows, which
are, at least, transitional between true hollows and runnels.

2 : 2 : 2   Marking   of   Sites

Sites were firstly marked with chalk numbers.   These
survived long enough for the selected sample to be finalised,
and were then reiterated by discreet symbols about three centi-
metres in size, printed on the limestone with black 'felt-tip'
pen;   such a marking is visible on Photograph 8.   Vegetated
sites were numbered from '1' to '50', whilst water-filled

hollows were accorded letters from both UPPER- and lower-
case alphabets. Eight sites shared both characteristics,
and were therefore designated by both a number and a letter,
for instance '7H' and '19e'. This necessitated the use of
additional symbols, such as '&'. In the following accounts,
site-codes are always put in single inverted commas, as in
the foregoing examples. For lists of sites, inverted commas
are placed only before the first- and after the last-named
code.

In case the printed symbols were somehow obscured or
erased, a detailed dossier of the locations of all the 100
hollows was compiled. From this it may be feasible to re-
construct the sample with total accuracy for further study.

2 : 3   The Physical Dimensions of Sites

2 : 3 : 1 Length and Width Measurements

The length and width of each site was assessed with
a metal tape-measure. As often and as nearly as possible,
the two axes intersected at 90° and approximately over the
centre of the hollow, but some sites such as '18d', shown
in the foreground of Photograph 10, were too asymmetrical
to permit this. Runnels extending from the hollows were
not included in these measurements.

2 : 3 : 2 Depth Measurements

'Depths-to-bedrock' were measured by means of a thin,
cylindrical, metal probe, calibrated in centimetres, placed
vertically in the depression and read off against a stiff,

wooden bar which rested on the limestone 'plateau' each side of the hollow.   Diagram 3, below, demonstrates the method.
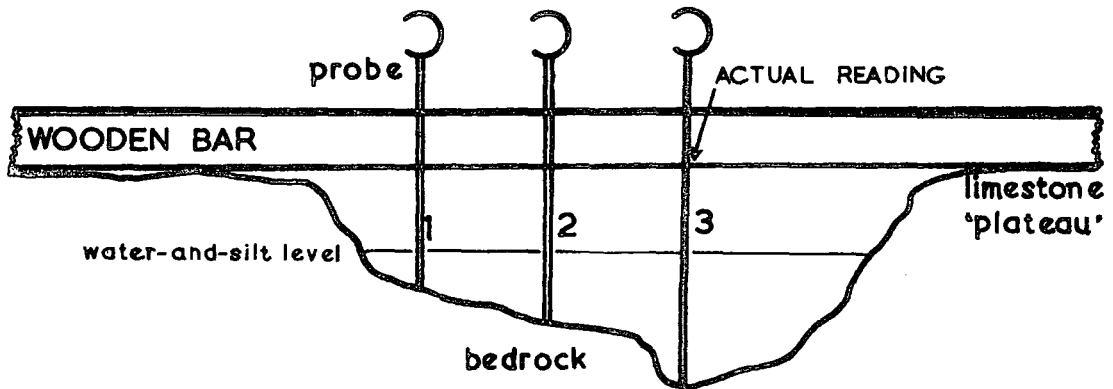
Diagram 3   DEPTH-SOUNDING

Levels of silt and water were taken by the same procedure.   Depth-of-water is a very variable phenomenon, subject to recent weather conditions inter alia, and in a quantified sense has been largely discounted in these studies.   The importance of water-levels in general is discussed elsewhere, in Sections 4 : 3 and 5 : 4, for example.

In theory, depth-measurements obtained by this method are maxima for each site, ascertained after thorough testing to locate deepest points.   Diagram 3 (above) shows the trial-probes (1 and 2) before the actual reading is accepted at the third attempt.   With vegetated sites, and even many pools-in-hollows, however, such determinations cannot be standardized entirely, as the base is partially concealed.   Some hollows have abruptly deeper, but very narrow, areas, not easily detected.   Several alleged maxima were therefore probably under-

recorded. On the other hand, existence of these miniature chasms confers an exaggerated impression to overall depths. Clearly, discrepancies in the initial estimate of depth-to-bedrock are reflected in the other depth-statistics. Since the depth of the site may be very influential in botanical terms, this unreliability is a pity. Further measurements to improve accuracy were ruled out by lack of time, though four sites were subjected to a fuller survey whereby a more detailed profile of the base of those hollows could be drawn. (See Section 3 : 3 : 3).

2 : 4   Chemical Assessments

2 : 4 : 1   pH - Measurements

A portable 'PYE UNICAM 293' meter with detachable electrode was used to take pH-measurements of the water in the solution-hollows. Table I summarises this field-work. Drying-out later in the season curtailed sampling, and inserting the electrode, especially uncapped, into inadequate depths of water, or into sludgy conditions, often elicited artificially-reduced pH-readings. Growing familiarity with the meter allowed false or doubtful determinations to be recognized, and the sites involved were re-tested. Some water-samples were checked independently by Mr. Leslie Rose. Thus, particularly for the two main sets of data (numbers 3 and 4 in the Table below), reasonable confidence obtains as to their accuracy. Readings are distinguished to two decimal places, i.e. to 0·05 of a pH-unit.

TABLE I   pH-testing

No.	Date	Time of day	Total Sites Tested*	Total no. of rdgs.	Comment
1	4/5/81	12·00-13·30	17	17	Equipment-trial
2	15/5/81	11·30-15·40	30	42	High values recorded
3	30/5/81	10·30-15·30	45	100	Major tests)
4	18/6/81	09·00-11·30	26	63	of all sites) available)
5	21/6/81	07·00-09·00	16	33	Early morning sampling

* out of 55 hollows which were at one time wet
enough to be considered 'aquatic' in nature.

The procedure outlined below for pH-testing evolved
during the early sampling-occasions, and was specifically ad-
hered to during the main sessions.

(a) Preparation   (actually on the limestone pavement)

     i/ test water-temperature of pools with ordinary therm-
        ometer;

    ii/ adjust 'Unicam' meter accordingly;

   iii/ test 'Unicam' battery;

    iv/ switch to 'stand-by' for recommended warming-up period;

     v/ couple electrode to meter;

    vi/ draw appropriate columns in field-work notebook, ready
        for entries of time-of-day, temperature, pH-value.

(b) Testing pH-meter

     The meter was buffered at each set of tests, using 7·0
     and 9·2 solutions prepared in the laboratory beforehand.

(c) Sampling   (for any given site)

   i/ place thermometer in water;

  ii/ insert electrode so that bulb immersed, and apparatus balanced and steady;

 iii/ switch 'Unicam' meter from 'stand-by' to 'recording pH', and activate stop-watch;

  iv/ record temperature (and remove thermometer to next site);

   v/ check duration of 30 seconds from stop-watch, read off pH-value from now-stabilized indicator-needle;

  vi/ record pH in notebook, and switch back to 'stand-by';

 vii/ rinse electrode thoroughly with distilled water;   and

viii/ transfer meter and accessories to next solution-hollow.

2 : 4 : 2   Soil - samples

Using an improvised sampler — a 15-mm diameter cork-borer with a rod-and-plunger adaptation to eject the soil — two soil-cores were collected from the hollows for laboratory analysis.   The small size and fragility of the sites precluded more intensive soil-sampling.

2 : 5   Phytosociological   Methods

Sites were treated as units irrespective of size. The dichotomy of 'aquatic' and 'terrestrial' sites (Section 2 : 2 : 1) was accepted as a subjective but obvious and valid categorization, and both groups of hollows were given identical phytosociological treatment.

For inclusion in the phytosociological data, terrestrial plants had to be rooted in the soil trapped on the base of the hollow.   Plants growing from rocky crevices on the sides were discounted, because this rupestral environment mimics that of

the grykes rather than being a true component of the solution-
hollows habitat. Thus eliminated were a very small number of
species and occurrences, such as scattered ferns (for example
<u>Asplenium ruta-muraria</u>) and patches of liverwort.

Lichens have not been considered at all in this study,
except incidentally in the discussion concerning the formation
of solution-hollows and early colonization, in Chapters 6 and
7. Mosses, however, are included (cf. Zotov, 1941; Ivimey-
Cooke, 1965). Scientific names are according to Watson (1968).
Mr. M. J. Wigginton kindly confirmed the identifications.

Algae tenanting aquatic sites were classified as
either <u>Nostoc sp</u>. or 'filamentous green algae', which was
represented in both suspended and settled-out material. As
different genera could not be defined in the field (see full
details in Appendix C), the composite term 'filamentous
green algae', abbreviated to 'fga', is used throughout, and
is regarded for phytosociological purposes as a single species.
Section 5 : 1, below, deals further with algae.

Nomenclature and taxonomic order for vascular plants
follow Clapham, Tutin & Warburg (1981), whose 'Excursion Flora'
was used as the definitive text for identification; sources
such as McLintock & Fitter (1965) were also referred to. Of
the higher plants, most were already known, and less familiar,
or later-emerging, species were checked as vegetation devel-
oped, the chief objective being to have all plants named, and
comprehensive lists made, before the actual phytosociological
analysis was done. Local botanists provided assistance with

some difficult plant-groups. By this method, the eventual
phytosociological values were assessed efficiently, without
delays posed by problems of identification. Conventionally,
some plants were reserved to generic status only, since they
were difficult to ascribe to species-level, or were possible
hybrids. These include <u>Salix sp.</u> and <u>Hieracium sp.</u> All
scientific names are underlined, as in the foregoing examples.

The 'Domin' scale of cover-abundance, (see, e.g.
Kershaw, 1973; Chapman, 1976), was used for phytosociological
values. Sites were assessed in late May, and again on June
19th and 20th, this second analysis providing the more comp-
rehensive and standardized results. The symbol 'χ' denotes
one or two plants only; the other extreme, i.e. cover-value
10, was represented by a few instances of 'fga'. A very small
number of impersistent species, such as <u>Erophila verna</u>, which
disappeared from hollows before June 19th but had previously
been listed, were accorded a nominal cover-value of 1. Sapling
trees (such as <u>Fraxinus excelsior</u> or <u>Pinus sylvestris</u>) were
also given a nominal value, of 2, unless their foliage was
deemed sufficiently spreading and thick to influence a greater
proportion of the site.

2 : 6   Documentation

Information gained in the field was written in a note-
book on site, and later transcribed to one or (usually) both
of two sets of documents:

   (a) file-index cards, each side of which — representing
       a single solution-hollow — was divided into compart-
       ments according to a master-plan, so that all data

relevant to that site were located in a brief space;

(b) charts of systematic facts, such as pH-measurements or phytosociological cover-values, so that a ready comparison of phenomena could be made, either from site to site, or over a period of time, if successive sampling was carried out.

During fine, calm weather, cards and charts were sometimes directly amended and added to in the field.

CHAPTER 3

THE PHYSICAL AND BOTANICAL CHARACTERISTICS

OF THE GAIT BARROWS SOLUTION-HOLLOWS

3 : 1   Physical Characteristics

3 : 1 : 1 General Morphology of the Hollows

Detailed morphological studies of the solution-hollows of a limestone pavement have not been found in the literature. The most thorough qualitative description is by Sweeting (1973), with which the more summary accounts of other authors (such as Zotov, 1941, and Ivimey-Cooke, 1965) broadly agree as to the hollows' physical attributes, including contained water and/ or accumulated sediments. (See Appendix D for definitions quoted from other sources).

As the photographs of Gait Barrows indicate, a wide range of forms may occur on the same pavement. A catalogue of various types is given in Section 3 : 3 : 2, Table VII. Some hollows, such as 'U' and '25', exceed the largest dia- meter (60 centimetres) mentioned by Sweeting in her earlier work (in Dury, 1966), and approach the maximum dimensions given in Sweeting (1973).

The distribution of hollows over the pavement-surface is also a variable phenomenon. At Gait Barrows, there is in many cases ample feature-less limestone between neighbouring

sites — some data concerning proximity are given in Appendix
'E(iv)' — whereas at Sulber, North Yorkshire (Ward & Evans,
unpublished material, 1975) and in New Zealand (Zotov, 1941),
hollows are closely packed together, with only narrow, arete-
like partitions of fretted rock separating adjacent pits.

3 : 1 : 2   Surface   Dimensions

Solution-hollows on Gait Barrows vary from almost
perfectly circular shapes (e.g. 'F' = 35 x 34 cms;   '17' =
63 x 61 cms) to narrow, more-or-less rectangular trenches
(e.g. 'j' = 160 x 22 cms;   '15' = 160 x 17 cms).   The mean
length of all sites is 85·14 cms, with a standard deviation
of 41·36;   the mean width of all sites is 44·10 cms, with a
standard deviation of 21·88.   Further statistics are given
in Appendix E .

Surface-areas of the sampled sites were calculated
by the formula $\pi r_1 r_2$, where:

r_1 =   half the length (long axis),   and

r_2 =   half the width (short axis).

(See Section 2 : 3 : 1).

Such a measurement presumes a perfect ellipse, which is often
an over-simplification.   Sites of a far-from-oval shape, such
as '18d' (Photograph 10) were assessed individually to avoid
serious discrepancies.   Minor irregularities of outline prob-
ably constitute compensating errors.   Hollow 'J' (shown on
Photograph 12) is the most extensive, approaching two square
metres in area.   Four other sites exceed one square metre.

At the other extreme, only seven hollows are smaller than 1 000 square centimetres.

This generally large size, compared, for example, to Sweeting's figures (1966), probably reflects the open and uninterrupted quality of the Gait Barrows limestone pavement. Ivimey-Cooke's study (1965) also embraced a wide variety of forms, including "variously-shaped con- cavities several square metres in extent", from which it may be inferred that the Burren solution-hollows possibly share similar morphological characteristics with those of Gait Barrows.

Surface-dimensions for aquatic and terrestrial sites were averaged separately, to see whether the data for these two main categories of hollow differed significantly. The measurements of length and width were adopted in this compar- ison, as they are more accurate than computations of area. Sites which have both aquatic and terrestrial characteristics were incorporated into both groups. For this reason, the samples are more than 50, and the means are greater than the overall mean quoted earlier in this Section.

TABLE II   Means and Standard Deviations (SD) of Surface Dimensions

		Aquatic	Terrestrial
length	mean	88·85	88·79
	SD	46·82	38·25
	variance of mean *	39·86	23·23
width	mean	45·37	44·06
	SD	17·87	20·52
	variance of mean *	5·91	8·09

* formula from Bailey (1979).

Such similar mean values, attended by large standard
deviations (see Table II), suggest no significance between
the differences of the two sets of data. From the sums of
the 'variances of means' for length (63·09) and width (14·00)
the standard deviations were worked out:

for length, 7·94;   for width, 3·74;

following which, values for 'd' are 0·241 and 0·351 respectively.
Both are far from significant. As expected, there is no real
difference in surface-dimensions between aquatic and terrestrial
parts of the sample.

3 : 1 : 3 Depths of Hollows

Depth-to-bedrock data, especially for vegetated sites,
were difficult to obtain accurately. (See Section 2 : 3 : 2).
Under-estimation is likely in some cases; in others, chance
sampling of deep-weathered cracks exaggerates the general base-
level of the hollows. Consequently, depth-measurements have
been grouped into 5-centimetre interval classes, and are plotted
on Graph 1 in the two main categories, aquatic and terrestrial.
'Dual-sites', such as '7H' and '19e', were allocated according
to the precise position of the maximum depth-probe. More often
than not, this occurred under vegetation rather than in standing
water.

The aquatic sites show a more concise and symmetrical
distribution, with over half of them (51%) having depths in a
modal class 10 - 15 centimetres. Shallower hollows imply
lesser depths of water, and sites in the first two classes,
i.e. forming the left-hand side of the graph, such as 'U' or
'b', were noticeably liable to dry out quickly. In contrast,

GRAPH 1

% FREQUENCY of SITES

—————— aquatic sites

— — — — terrestrial sites

DEPTHS-to-BEDROCK by 5cm-Interval classes

31
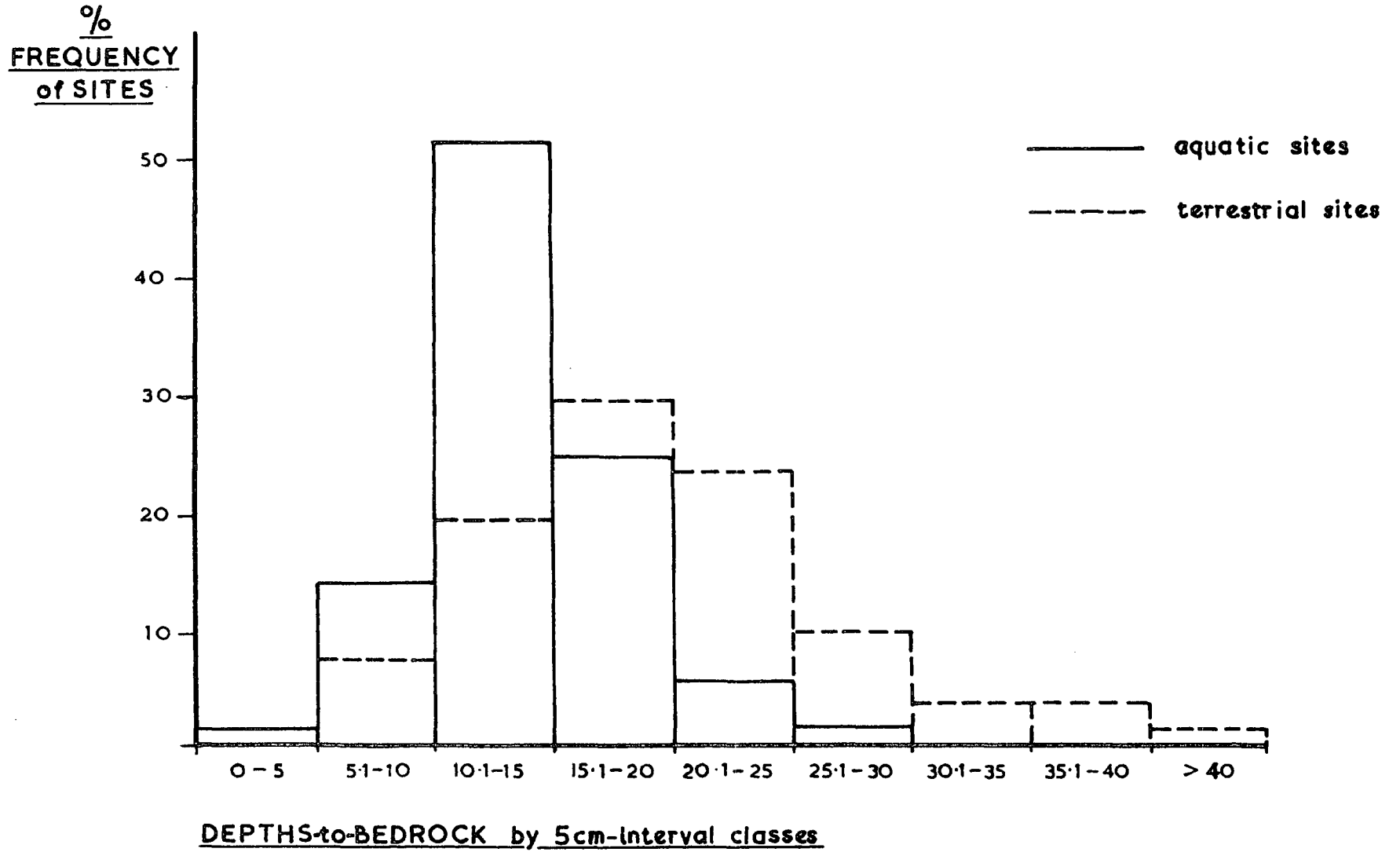
relatively deep areas, exemplified by 'X' and 'c_a', were characteristically full of water.

The terrestrial histogram on Graph 1 is displaced further to the right, favouring in particular the two classes comprising depths 15 - 25 centimetres (53% of individual sites), but with ten hollows even deeper than this. Site '31' registered a depth-to-bedrock of 50 cms!

These figures (actual, not percentages) were submitted to χ^2 -testing thus:

TABLE   III   <u>Depth of Hollows by Classes</u>

	Classes of depth-to-bedrock, 5-cm intervals						
	0 - 5	5·1 - 10	10·1 - 15	15·1 - 20	20·1 - 25	25·1 - 30	above 30 · 1
Aquatic	1	7	25	12	3	1	—
Terrestrial	—	4	10	15	12	5	5
Totals	1 *	11	35	27	15	6	5
Expected Occurrence		5·5	17·5	13·5	7·5	3	2·5

(N.B.   The last three classes have been combined to give a
        large enough sample, and the first class, 0 - 5 cms,
        asterisked above, is ignored because of its single
        entry.)

From the figures listed in Table III, the calculated value of χ^2, for five degrees of freedom, is 10·320. This is approaching 95% significance. The χ^2-value thus strongly suggests that the observed differences in the distributions

of depths-to-bedrock between aquatic and terrestrial hollows is significant rather than a matter of chance.

The biological significance of this is hard to fathom, partly because one cannot tell whether extra depth in terrestrial hollows precedes, or is consequent upon, the processes of terrestrialization. It is probable that already deep pits collect and retain solid particles more effectively, leading to an accumulation which is itself deep and stable enough for higher plants. This argument is expounded further in Chapter 7. However, such a hollow will still be water-logged as well. It may support emergent aquatic vegetation, but not be a truly terrestrial site. The counter-argument is that the addition of organic acids from soil and plant-life accelerates solution at the base of the hollow, in which case increased depth can be interpreted as more of a result than a cause of such developments.

3 : 2   Botanical Characteristics

3 : 2 : 1 General Facts

The number of plant-species recorded from the sampled solution-hollows is 83. This total is made up of a variety of growth-forms and taxonomic groups, as shown in Table IV. 'Woody species', it should be noted, are seldom well-developed, and Salix saplings in particular are usually less than 20 centimetres in height and still pliant.

TABLE IV   Groups of Plants

Name	No of spp.	% of total
woody species	8	9·6
ferns	1	1·2
forbs	47	56·6
grasses, sedges and rushes	16	19·3
mosses	9	10·8
algae	2	2·4
Totals	83	99·9

The dicotyledonous forbs (43; 51·8%) are themselves very varied, 18 families being represented, and no genus having more than three species. A full species-list for the solution-hollows is given in Appendix F .

Five descriptive terms, used principally in the next two Sections, and in Chapter 4, are defined below:

(1)   frequency: number of occurrences.

(2)   dominance: preponderance of given species within
                    a site, or group of sites, compared to
                    other species; this implies a relatively
                    (or very) high value on the Domin scale.
                    The term 'dominance' is not applied in
                    its functional sense of a species having
                    major influence within its community.

(3)   constancy: degree of presence of a species within
                    all sites of a stipulated group, recorded
                    as a percentage measurement, i.e. frequency
                    of species/total number of sites in group.

(4)   fidelity: measure of exclusiveness of a species to
                    a particular species-assemblage.

(5)   species-
       richness: simply the number of species within any
                    site, as a measure of diversity irres-
                    pective of scale (cf Krebs, 1978).

3 : 2 : 2 Botanical Contrasts

The solution-hollows differ botanically from other
(sub-)habitats of the limestone pavement. These distinc-
tions have not been systematically or quantitatively meas-
ured, but the following Table indicates some of the more
obvious contrasts of abundance and absence. The eight
species listed are frequent in and/or characteristic of
the various environments of the limestone complex, namely:

grykes and pot-holes (G);

rough, stony surfaces (see Section 1 : 3 : 3),
produced by excavation (X);

and   three patches of scrub, mentioned in the Intro-
       duction and marked on MAP 3 (S).

The more densely-wooded parts of the Reserve, rather distant
from the central pavement and correspondingly further removed
in floral composition (see Section 1 : 3 : 3), are excluded
from this consideration。 The last (right-hand) column in
Table V gives a qualitative statement of the species' status
in their respective habitats。

TABLE V   Species of Other Habitats

Name	Habitat	Status
Helianthemum nummularium	X	large patches
Hypericum androsaemum	G	very typical of deep grykes
Hypericum montanum	X	scattered but common
Saxifraga tridactylites	X	widespread and quite common
Thymus praecox	X	frequent over bare scree, and in grassy areas
Calluna vulgaris	S	notable quantities within limited area of this habitat
Eupatorium cannabium	G	quite numerous
Epipactis atrorubens	G,X	sporadic but characteristic。

None of these eight species occurs anywhere in the 100
sampled hollows. Several Pteridophyta, for example Phyllitis
scolopendrium and Polystichum aculeatum, could equally validly
have been selected as gryke-loving, hollow-avoiding species。
A number of plants do transcend the habitat-divisions。 For
instance, Teucrium scorodonia and Geranium robertianum occur
in 10 and 20 hollows respectively, and are plentiful elsewhere
at Gait Barrows； Hypericum montanum occupies six of the sampled
sites, and has also invaded large tracts of the rubbly, quarried
limestone； in similar places, Sedum acre, a frequent constituent
of the solution-hollows, seems equally well-adapted； and, lastly,

Potentilla erecta, though found in four of the more richly-
vegetated sites, is a rather more constant member of grassy
patches and scrub-communities peripheral to the pavement.

Nonetheless, the exclusivity of certain species to
certain parts of the limestone is a valid concept, and could
be supported by a second list of species characteristic of
the hollows but scarce or absent elsewhere. In this cate-
gory most of the aquatic plants would be placed, since only
the solution-hollows provide standing water, or at least pre-
vailingly moist conditions. Thus the flora of this habitat
is complementary to, rather than merely a microcosmic image
of, the pavement vegetation as a whole, and contributes an
extra botanical dimension to the wealth of Gait Barrows as
a Reserve.

3 : 2 : 3 Inter-site Variation

Floristic appearance varies considerably from site
to site. At one extreme there are water-filled hollows
with no emergent vegetation, exemplified by the large pool
'J' on Photograph 12. The other extreme is represented by
hollows packed with sediments and sustaining a variety of
herbaceous plants (Photograph 13), in the form of low-growing
mats, or taller mounds of grasses and sedges. Such a complex
gradation of assemblages requires the simplification afforded
by multi-variate data-analysis, and so the phytosociological
details were fed into the computer-program TWINSPAN (Hill,
1979), whose results are discussed in Chapter 4. As ensuing

comments in this Chapter frequently refer to 'aquatic' versus 'terrestrial' sites, suffice to say here that TWINSPAN ratified this major division of habitats, though agreement with the original allocations of individual sites was not perfect. Table VI shows the precise categories, and anticipates the detailed treatment in Chapter 4.

TABLE   VI   Summary of TWINSPAN Categories

	species	sites
aquatic	8 *	37
terrestrial	75	62
Totals	83	99

+ one site ignored.

(* In fact TWINSPAN separates only four species as truly aquatic. For practical convenience, another four species, related ecologically or taxonomically, are included here; and a fifth addition, Salix sp., could also be made.)

Graph 2 shows the frequency with which each of the 83 species occurs. The conventional 'reversed J-shaped curve' (Raunkiaer, 1928) is crudely apparent, with 29% of the species being recorded only once, and a long 'tail' of plants which are found in over 15 sites. Six out of the nine (including Salix sp.) aquatic types are members of this tail, and four of them are the most frequent of all species. These are: the two algae; the moss Fissidens sp.; and Juncus articulatus, the overall 'winner', occupying 56% of all hollows.

GRAPH 2

No. of Species

24

22

20

18

16

14

12

10

8

6

4

2

0

— terrestrial species
[74]

— aquatic species
[9]

1 2 3 4 5 6 7 8 9 10   14 15   19 20 21 22   24 25   27   32   38   45 47

No. of Sites

39
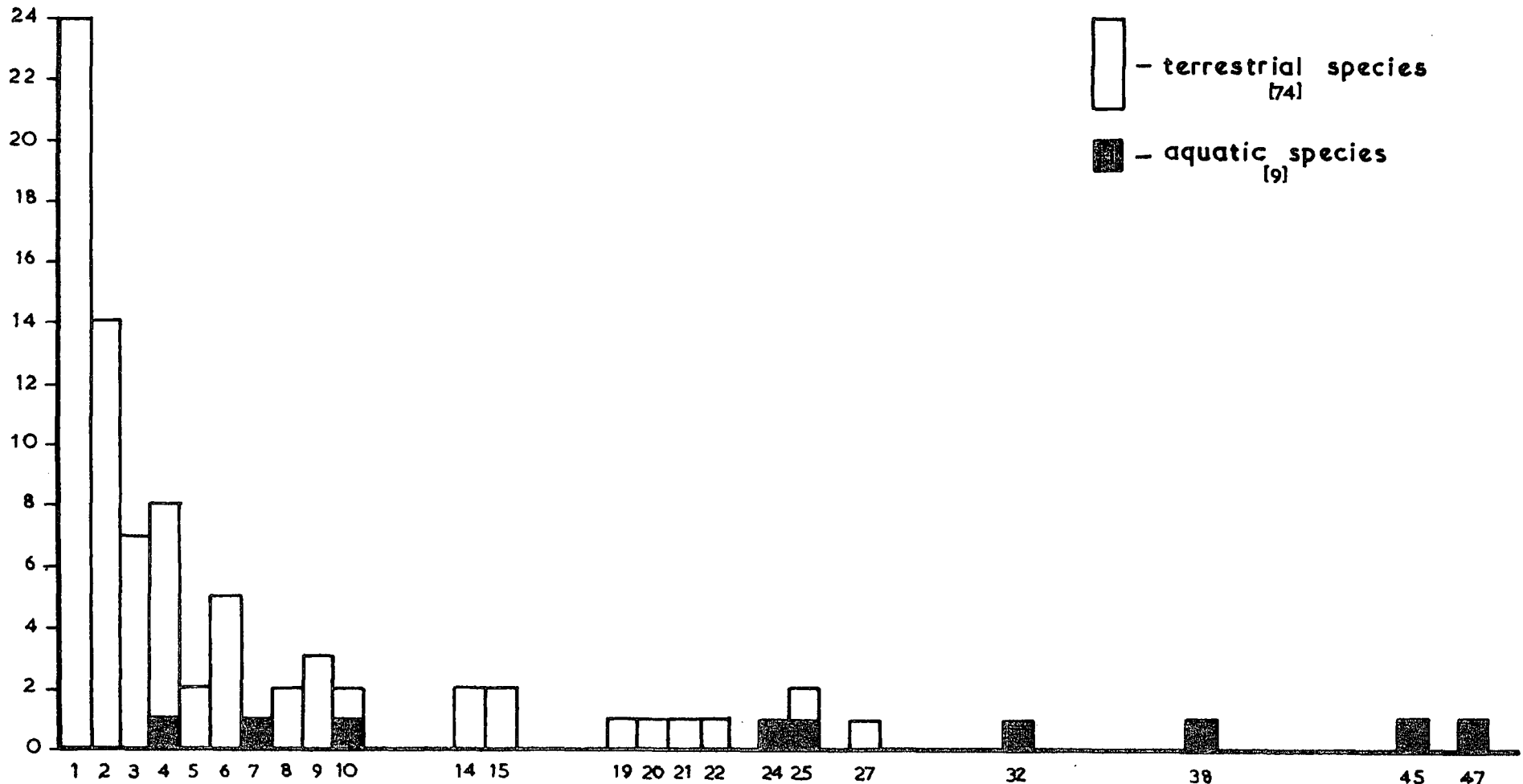
This reflects not so much a preponderance of aquatic sites as a relative paucity of aquatic species. If a new hollow were artificially created in the limestone-surface, and kept full of water, it would be comparatively easy to predict what its ultimate plant-life would be. A new site equipped with soil and left to develop terrestrial vegetation would draw its eventual tenants from a much wider range of species, and forecasting the outcome would be consequently much more speculative.

Graph 3 is a histogram of species-richness per site plotted against frequency of occurrence. Thus one may read, for example, that a single hollow, (actually 'b'), has no inhabitants, whereas the maximum vegetational diversity of 18 species occurs twice; these richly-endowed sites are '7H' and '32'.

The aquatic sites are clearly less diversely vegetated. 35 out of 37 such hollows (94·5%) contain only four, or fewer, plant-species. (The remaining two aquatic sites are 'E', five spp., and 'P', with seven spp.) Moreover, only nine (out of 62; 14·5%) terrestrial hollows share this low-order diversity. The contrast is evident, considerable, and complementary to the relative differences in numbers of aquatic and terrestrial species.

Three separate peaks of frequency are defined on Graph 3; in other respects, patterns are amorphous. The

GRAPH 3

No. of Sites for each 'score' (y-axis)

Total No. of Species per Site (x-axis)

SITES:

---- terrestrial (62)

········ aquatic (37)

according to TWINSPAN

first peak, at class (species-richness) 2, emphatically
represents the aquatic type of vegetation. Indeed, four
of the five apparently mis-placed terrestrial sites are
so designated only because TWINSPAN puts them in the
'terrestrial' category. Their original allocation was
within the aquatic half of the sample, as their codes,
'C, F, G, and Y' indicate.

It was expected that a single peak further along
the graph would similarly express the modal frequency of
species-richness for the genuinely terrestrial hollows of
individually higher indices of diversity. In fact, twin
maxima appear, at classes 9 and 13. The adjacent and inter-
vening frequencies are sufficiently low to draw attention to
the preferred values, and to suggest that they are real and
not merely accidental. A proposed explanation is deferred
until the following Chapter, where a far more detailed anal-
ysis of the plants constituting these sites is possible using
the TWINSPAN results.

3 : 3   Relationships between Physical and Botanical
Characteristics

3 : 3 : 1 Surface-area v. Species-richness

Surface-areas (see Section 3 : 1 : 2) of all sites
were plotted against their species-richness scores.   Graph
4 is a scatter-gram of these values.   No relationship at all
(correlation co-efficient = — 0·058) exists between these two
factors in the aquatic half of the sample, where the species-
diversity is normally low and quite independent of the size
of the hollow.   The correlation co-efficient is negative on
account of the extra-large sites with negligible variety of
plants; some of these hollows, such as 'J' and 'U', are so
extensive that the scale of the graph cannot accommodate them
in their proper positions.

For terrestrial sites, however, the correlation co-
efficient is 0·437, and with the large sample (51), this is
highly significant.   Smaller sites, therefore, are unlikely
to support as great a variety of terrestrial plant-species as
are the more extensive hollows, and the highest scores of 18,
18 and 17 species (for sites '7H, 32 and 31' respectively)
are in surface-areas of more than 5 000 square centimetres,
amongst the top 15% of the sample as measured by this para-
meter.   Intuitively, however, it is felt that other physical
factors besides surface-area influence the botanical charac-
teristics of a site, so that the conclusion derived from this
statistically significant correlation must be restrained.
Surface-area is by no means an entire or deterministic
explanation of variable species-richness.

No. of SPP./Site

SURFACE-AREA related to SPECIES-RICHNESS

GRAPH 4

44

3 extra-large sites

SURFACE AREA in 1000's square centimetres

x = terrestrial   ● = aquatic
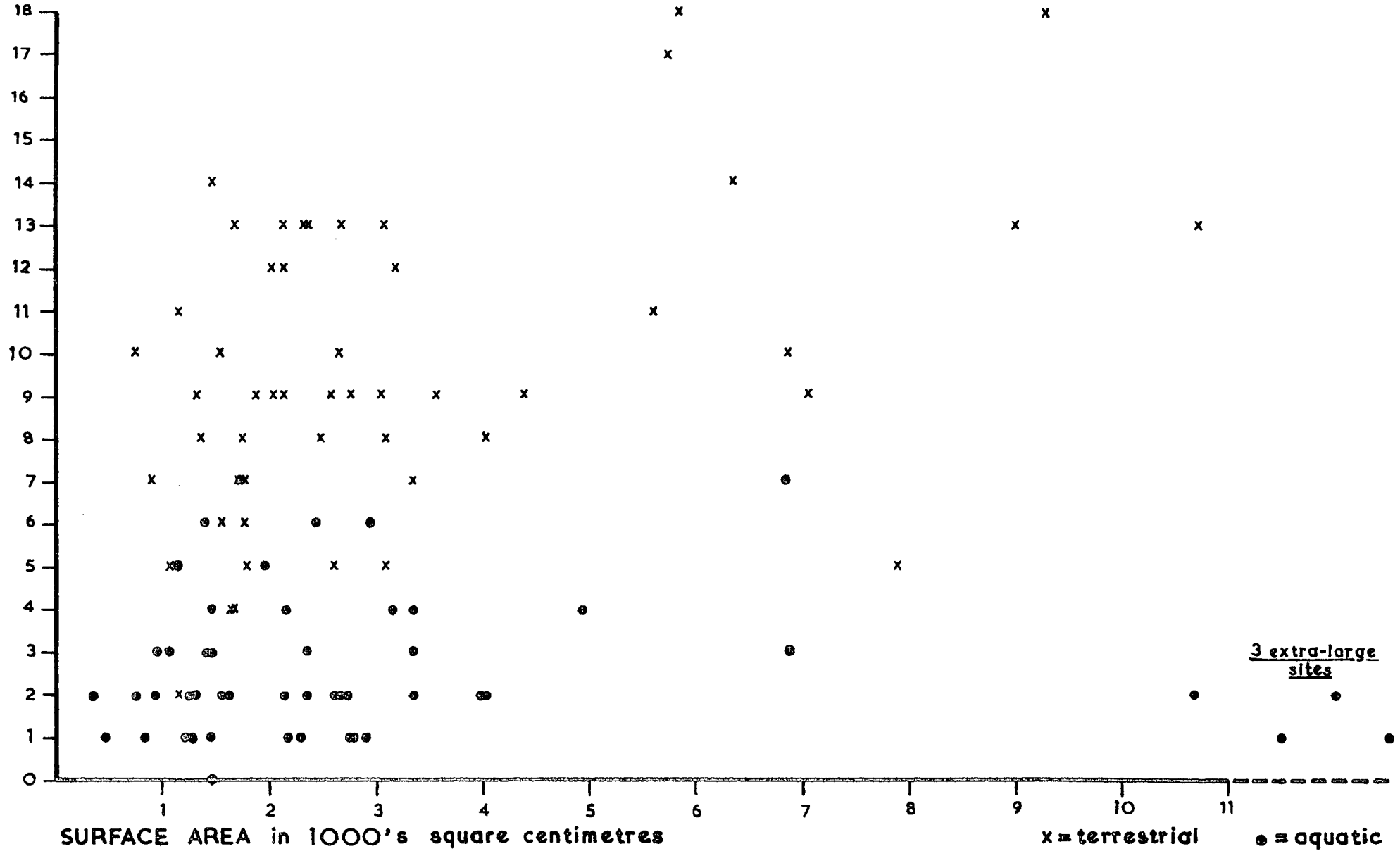
3 : 3 : 2 Special Morphology v. Botanical Characteristics

Amongst the diversity of forms exhibited by the Gait
Barrows solution-hollows are several genera of sites which
are distinctive in outline and depth. Whilst it is unreal-
istic to equate absolutely botanical characteristics and
morphology, some of these genera are consistently assoc-
iated with certain types of vegetation. Table VII is a
summary of these relationships.

The sites described in Table VII constitute a minority
only of the total sample studied, so the correlations are of
limited applicability. The remainder of the hollows, mostly
more conventional in shape and size but by no means uniform
in appearance, express the full range of hydrological and
floristic options, from pools with only algal contents to
dry areas of varied vegetation. Chapter 4 examines the
detailed patterns revealed by the TWINSPAN results.

3 : 3 : 3 'Double - basin' Hollows

Particularly as water-levels diminished, it became
evident that the limestone base of some sites consisted of
a concentric 'hollow-within-a-hollow' form. An un-named
depression near 'G' shows this modified profile, and can
be seen in Photograph 14. The vestiges of moisture necess-
arily collect in the lower, usually central, areas of such
'double-basins', which were also observed to be the foci of
sediments and vegetation. Silts accumulating here are more
sheltered, and remain damp for longer periods. Thus, for

TABLE VII

Genera of Distinctive Sites

Aquatic or Terrestrial	Type Description	Examples	Associated Vegetation	Photographs
A	large, flat, shallow; oval but irregular outline; rather fretted, undercut edges; water always present, but not deep; 'swimming-pool' type.	J S	Nostoc dominant, in spheroidal aggregations.	12
A	neat, oval shape; amongst smallest sites; relatively deep (i.e. depth approaching width in dimension).	I, O, g, u.	'fga'-rich; little else, but Juncus articulatus or similar emergent plants may be there.	
A/T	regularly oval shape; smooth and sheer sides; water generally deep but well below rim of hollow; 'bath-like'.	P 19e 31 46r	mixed aquatic species + some terrestrial development, in form, often, of mound with coarse vegetation; total appearance resembles garden-pond.	10
A/T	runnel-type, i.e. long, narrow, moderately deep, with exit; but usually half-choked with sediment.	t 41 44	some aquatics + mosses downstream of terrestrial mound of tufted species such as grasses, especially Festuca rubra.	

TABLE VII (continued)

Aquatic or Terrestrial	Type	Description	Examples	Associated Vegetation	Photographs
T		underneath dimensions problematical, as sites totally filled with soil; no room for standing water; size average; outline variable, from round to irregular.	12 13 14 36 50	all terrestrial plants, generally weedy, + mosses, forming slightly domed mat, spreading to surrounding limestone; rich in species.	
T		round; very open and exposed, and dry out rapidly.	G U	only Sedum acre on shallow, infirm sediments.	14 17

47

two reasons, they create a more permanent and stable substrate, whereas dry, exposed material readily crumbles to fragments capable of being removed by wind. Even where soils are plastered over the whole floor of the hollow, the 'double-basin' sites are likely to have at least some area with a greater depth of sediment, and are therefore preferentially endowed to receive and sustain colonizing plants.

Very many of the aquatic hollows have some emergent vegetation, frequently tufts of _Juncus articulatus_, but sometimes mounds of species such as _Carex lepidocarpa_, as in '48w'. (Photographs 9 and 10 portray examples of such sites.) This vegetation normally occupies not the shallower margins of the pool but the deeper middle, and is often entirely surrounded by a moat of clear water. The details of the base-sections of the hollows remain obscured, however, in these circumstances. A sufficient number of the 'double-basin' type of profile was recorded from the more visible sites (15 out of 54; 27·8%) to suggest that this shape is a fairly common feature. Several hollows outside the sampled 100 also demonstrate this profile. Recurrence of this pattern of centrally-positioned plant-life and encircling water implies that 'double-basins' confer an advantage in terms of the establishment of higher plant-species.

On June 21st, four hollows, 'C, F, O and o' were selected for detailed depth-measurements. (See Section 2 : 3 : 2). The profiles obtained from the two first-named sites are reproduced on Graphs 5a and 5b. The 'double-basin'

form is clearly shown, as is the close correspondence of trapped organic matter ('F') and plant-life (<u>Fissidens</u>, in 'C') to the deeper, inner parts of the base-section.

GRAPH 5a

DEPTH of SITE 'C'

showing 'DOUBLE-BASIN' PROFILE

rim

damp conditions and erect, rooted FISSIDENS

depth-to-bedrock
in cms

inner, deeper basin

horizontal scale 4 cms
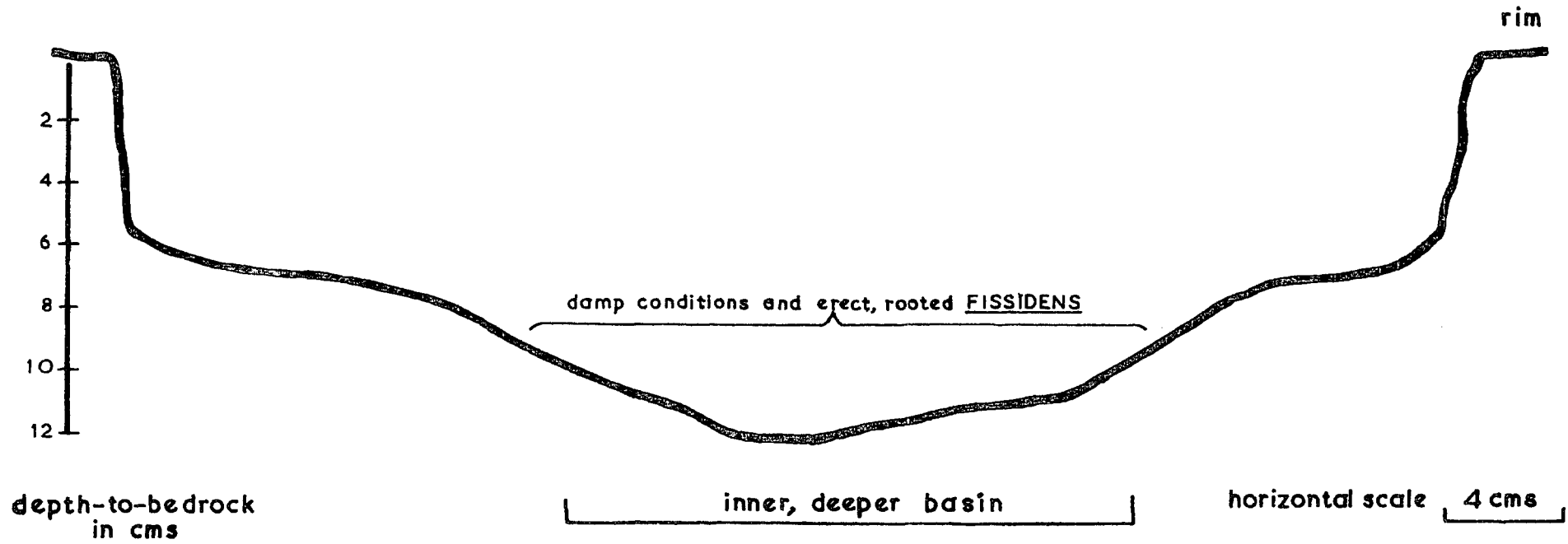
GRAPH 5b   DEPTH of SITE 'F'

showing 'DOUBLE-BASIN' PROFILE

depth-to-bedrock in cms

water-level + leaves, Nostoc, etc.

inner, deeper basin

rim

4 cms horizontal scale
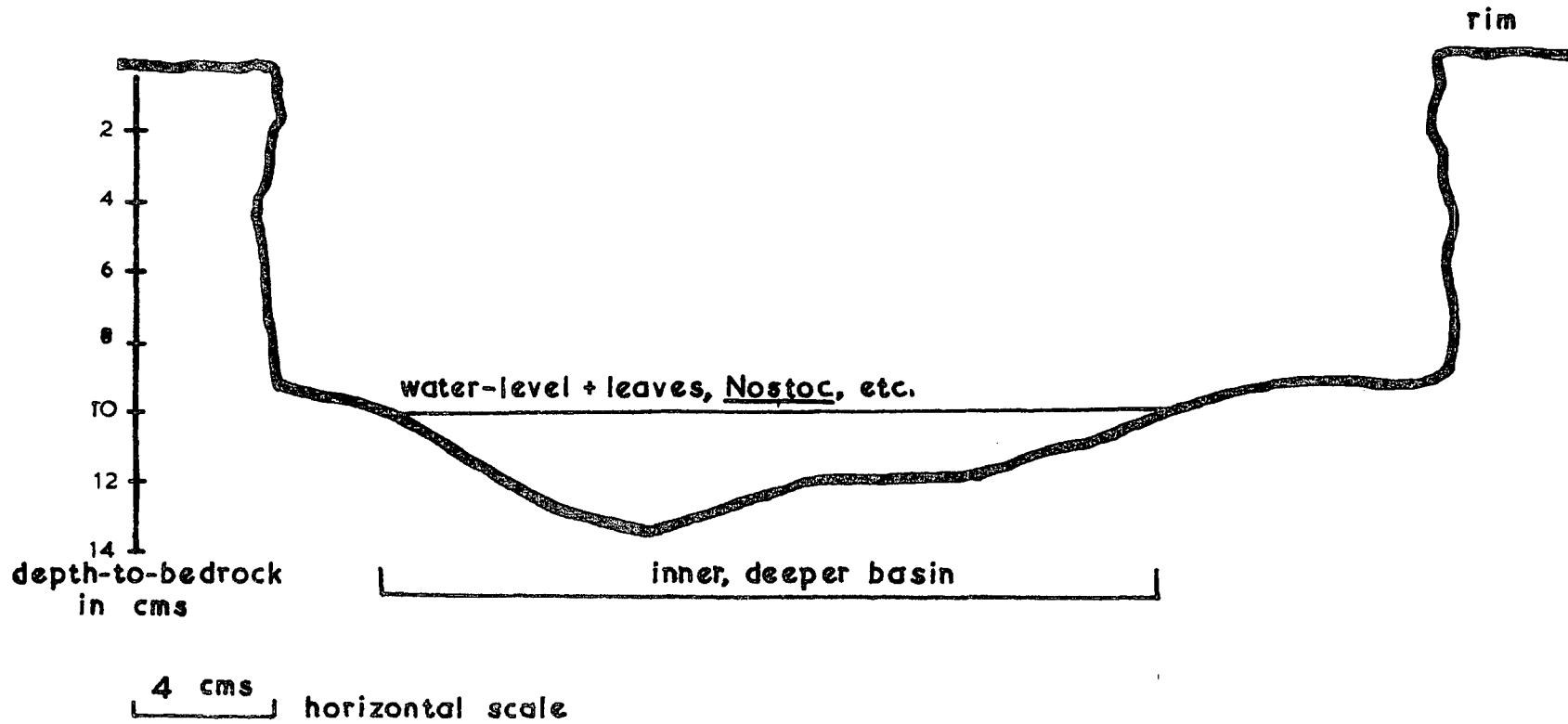
CHAPTER   4

PHYTOSOCIOLOGICAL   ANALYSIS

4 : 1   The TWINSPAN Program

The main body of phytosociological data collected on
the Gait Barrows pavement (see Section 2 : 5) was transferred
to computer data-sheets and thence to punched cards, and pro-
cessed by the TWINSPAN * program (Hill, 1979). This is a
FORTRAN program primarily designed for detailed phytosocio-
logical descriptions where populations of species are related
to a number of sampled sites. The classification of the 100
solution-hollows making up the sample in this case is done
first, and the arrangement of species is based on the result-
ant order of sites, so that ecological relationships are emph-
asised. For these reasons, TWINSPAN is a very relevant pro-
gram to the research undertaken at Gait Barrows.

(* TWINSPAN = Two-way Indicator Species Analysis)

4 : 2   The Primary Division of Samples

The primary division, or "crude dichotomy" (Hill, 1979),
effected by TWINSPAN creates two unequal groups of sites, those
occupying the left-hand area of the Table[1], comprising 62 hollows;
and those to the right, which contains 37 hollows. These two
groups are dealt with below, in Sections 4 : 4 and 4 : 3 res-
pectively. One site ('b') had no species in it at all, and

1 A copy of this table of results is attached to this thesis.

has been ignored by the TWINSPAN algorithm. For complete-
ness' sake, it should perhaps be placed at the extreme right-
hand end of the table.

4 : 3   The Aquatic Sites

The 37 sites constituting the right-hand part of the
table of samples are clearly those characterised by 'aquatic'
species of plants almost exclusively, with algal represent-
atives often dominant.   Only three of these sites have Domin-
scale cover-values of less than 5 for filamentous green algae
('fga') and/or Nostoc sp. (See Section 2 : 5).   Juncus
articulatus occurs in almost half of these sites (17 out of
37; 45.9%), often abundantly.   However, these three species
('fga', Nostoc and Juncus articulatus) also occur fairly widely
in sites on the left-hand side of the TWINSPAN table, and of at
least equal importance, therefore, in distinguishing the two
parts of the basic dichotomy is the almost complete absence,
in the 'aquatic' sites, of genuinely terrestrial plant-species.
The only records are for Sedum acre in two hollows ('h' and 'i'),
and Poa annua and Cratoneuron filicinum, once each, at minimal
cover-abundance.   In fact the relatively small total of twelve
species embraces the entire flora of these aquatic hollows.

The right-hand side of the table can thus be summarised
as: generally wet hollows, such that the flora is nearly
completely aquatic in preference; species-poor, the mean of
38 sites being 2.26, and the maximum diversity (in 'P') being
only seven species; and with a corresponding tendency towards

obvious dominance, especially by algae. All these sites
have 'letter' codes, thus reinforcing the prima facie div-
ision of the sample established at the outset of the study.
(See Sections 2 : 2 : 1 and 2 : 5). Several aquatic sites
are shown in the photographs and both 'fga' (hollow 'm') and
tufts of Juncus articulatus (hollow 'n') can be seen on print
number 9.

The main sub-division of the aquatic sites clearly
adopts an algal criterion. Group 'a$_1$' comprises 11 sites,
the home of Nostoc, which is present in all these hollows,
and achieves high cover-values in eight of them (72·7%).
Other species — Juncus articulatus, for instance — are
few in number, subordinate in cover-value terms, and incor-
porate no truly terrestrial types apart from one occurrence
of Sedum acre (site 'i', cover-value 5). Sites 'J, N and s'
contain much 'fga' as well as Nostoc, and are thus separately
categorized as 'a$_1$ left', a trio of mixed algal components
and even fewer contributions from additional species than in
the principle 'a$_1$ right' samples.

Category 'b$_1$' comprises the remaining 26 aquatic
hollows, with characteristically low species-diversity, the
mean being 2·35 species, and the total number of species
represented being 12. This category is dominated by 'fga'.
Only two sites, 'M' and 'y', have a Domin-value of less than
5. Relatively little Nostoc exists here, (8 sites; 30·8%),
and those pools with high cover-values for Nostoc are placed
in a third sub-category, 'b$_1$ left', in which Juncus articulatus

is 100% constant, and often co-dominant with 'fga'.

In fact the splitting produced by TWINSPAN at levels 2 and 3 for sites already accepted as definitely aquatic is governed simply by the permutations of presence — usually, as it happens, this means abundance — of the three chief aquatic plants, namely 'fga', Nostoc, and Juncus articulatus. Table VIII summarises the combinations. None of the 37 pools has sufficient quantities of other species to allow groupings based on wider criteria. Further comment on the precise distribution of, say, Fissidens or Tortella tortuosa, which are scattered throughout the aquatic categories, is deemed unprofitable.

TABLE VIII   Summary of TWINSPAN Division
                     of Aquatic Sample

		fga	Nostoc	Juncus
(8)	'a₁ right'		✓	+
(3)	'a₁ left'	✓	✓	
(15)	'b₁ right'	✓	+	+
(11)	'b₁ left'	✓	+	✓
(37)				

The figures in brackets, at the left of the Table, are the number of sites in each sub-division. A tick ('✓') means 100% constancy of that species within that grouping, whereas ' + ' indicates scattered presence only.

Group 'b₁ left' includes several sites with marginally greater diversity of vegetation than in other aquatic hollows,

and the highest-scoring ('P', with seven species) member is
actually placed immediately next to the crucial boundary with
the terrestrial part of the sample, as if TWINSPAN were sym-
pathetic to 'P's attempt to graduate to the terrestrial side
by virtue of its accumulated solid material and relatively
varied floristics!

It must be stressed that this analysis of the aquatic
sample, as described above, is an artefact of seasonality, for
algae, especially 'fga', are prone to short-term fluctuations
which would affect the precise allocation of aquatic sites to
the available sub-categories. The terrestrial sites, in more
ways than one, offer more solid substance for discussion, and
the details are set out in the following Section.

4 : 4   The Terrestrial Sites

The left-hand part of the TWINSPAN table comprises
the terrestrial sites. The first sub-division splits off
only two hollows, numbers '1' and '49', from the other 60
sites. Hollows '1' and '49', are both dominated by __Sesleria
albicans__, and only one other species and three other species
respectively occur in these two sites, all at very low levels
of abundance. In some ways these hollows are pocket lime-
stone grasslands, or at least representative of that fragment
of calcareous meadow occupied by __Sesleria__ tufts. The very
low (for terrestrial sites) species-richness scores are in
part a result of this __Sesleria__ dominance, and also attrib-
utable to the relatively small surface-area of '1' and '49'
(see Section 3 : 3 : 1). __Sesleria albicans__ is found in a
few other sites (code-numbers '2, 6_2, 21 and 32'), but less

overwhelmingly and as a fellow-member with at least five and as many as 17 other plant-species; thus these sites are manifestly more varied, and aptly segregated from '1' and '49'. Only one other site, coded '10', among the genuinely terrestrial group is as species-poor as these two 'grasslands'.

The remaining 60 terrestrial samples are sub-divided at level 3 roughly equally into the following two categories:

'a', with 26 sites (43·3% of terrestrial group);

'b', with 34 sites (56·7% of terrestrial group).[1]

The characteristics of group 'a' are:

i/ species-rich hollows, the mean being 8·89 species, and the maximum score 18 (in '7H'); sites 'G' and 'U' are exceptions to this generalization (see Section 3 : 3 : 2, and Table VII).

ii/ containing a large proportion of the total terrestrial flora (43 out of 75; 57·3%), including.....

iii/ an abundance of relatively low-growing, 'common', 'weedy' or even man-influenced types, such as Cardamine hirsuta, Veronica spp., Plantago major and Poa annua, which, if occurring together, create a 'farm-yard' effect.

iv/ recurrent Sedum acre, (20 out of 26; 76·9%), though usually at moderate cover-value only, and Geranium robertianum (16 out of 26 sites; 61·5%).

v/ strong representation of the mosses Bryum pseudotriquetrum and Cratoneuron filicinum, with combined occurrence in 22 out of the 26 hollows (84·6%).

vi/ only a scattering of properly aquatic species; for example, algae are restricted to three sites only (codes '7H, G and z'), and then only at low levels

---

1 These divisions, remember, are at level 3; the 'a1' and 'b1' aquatic groupings (Section 4 : 3) are defined at level 2.

of abundance; other 'semi'-aquatics (see Section
(4 : 5) occur more commonly and occasionally with
high cover-values, but in association with several,
more terrestrial, species, and thus never truly
dominantly.

vii/ the inclusion within these 26 sites of all those
defined in Table VII, Section 3 : 3 : 2 as physio-
gnomically 'flatter', where accumulated silt and
decaying mossy material has filled the hollows to
the level of the surrounding pavement. This def-
icient relief is emphasised by the low-growing
habit of the plants concerned, often members of
the group described under point iii/ above.
Such sites look less exciting, which is perhaps
why none of them is featured in the photographic
record, fully representative though this was meant
to be.

Category 'b' of the terrestrial sample is charac-
terised by a number of features as set out below, some of
which are in marked contrast to the definitive elements of
category 'a' sites:

i/ high species-richness, again, the mean for these
34 sites being 8·65 species, the maximum again
18 species (in hollow '32'), and the proportion
of the total terrestrial flora being even greater
than for 'a', viz. 60 out of 75 (80·0%).

ii/ four exceptions to this generally varied vegetation
are sites 'C, D, F and Y', which have achieved men-
tion already in Section 3 : 2 : 3. (See also the
Graph 2). TWINSPAN evidently regards them as
terrestrial because algae are virtually absent.
It is also true that three of these hollows had
only transient pools, (see Section 5 : 3). If,
therefore, these entries are removed from the
TWINSPAN ordination, this part of the table of

results becomes more coherent, and the mean species-richness improves to 9·47.

iii/ low-growing forbs are relatively poorly represented. Only <u>Prunella vulgaris</u> occurs more frequently in category 'b' than in category 'a', and <u>Poa annua</u>, for example, is reduced to two occurrences only, at cover-values 6 in site '17' and X in site '18'.

iv/ <u>Sedum acre</u> and <u>Geranium robertianum</u>, both characteristic species of group 'a' sites, are limited here to a minimal presence in only three and four hollows respectively, always at low cover-values.

v/ aquatic and semi-aquatic species are, however, well represented; in contrast to category 'a' sites, either 'fga' or <u>Nostoc</u> contributes to the flora of 14 out of 34 hollows (41·2%) and <u>Juncus articulatus</u> occurs, usually at moderate cover-values, in 24 out of 34 hollows (70·6%). The moss <u>Fissidens sp.</u> is even more characteristic of 'b' sites, being found in 28 (82·4%).

vi/ more importantly, category 'b' sites are endowed with a much greater proportion of taller, leafier plants, such as <u>Ranunculus spp.</u>, <u>Filipendula vulgaris</u>, <u>Succisa pratensis</u>, sedges (e.g. <u>Carex flacca</u>), and grasses (<u>Gramineae</u>). Though several species of this growth-habit, like <u>Typha latifolia</u> and <u>Polygonatum odoratum</u>, occur in only a single site, the overall impression is of more profuse, robust and erect vegetation, and, by implication, the exclusion of lower-growing herbs. In particular of the grasses, <u>Festuca rubra</u> is almost confined to 'b' hollows, and <u>Molinia caerulea</u> is even more partial. Table IX summarises these occurrences:

TABLE IX	'a' sites		'b' sites	
	occur-rences	cover-values	occur-rences	cover-values
F. rubra	4	medium	11	high
M. caerulea	nil	-	6	mostly high

vii / the physiognomic cross=section of a typical class
'b' hollow is shown in Diagram 4, below. These
sites are generally deeper and moister than the
category 'a' sites. (See the equivalent point
vii/ above).

Diagram 4   CROSS-SECTION of
'b' HOLLOW

bedrock base hidden
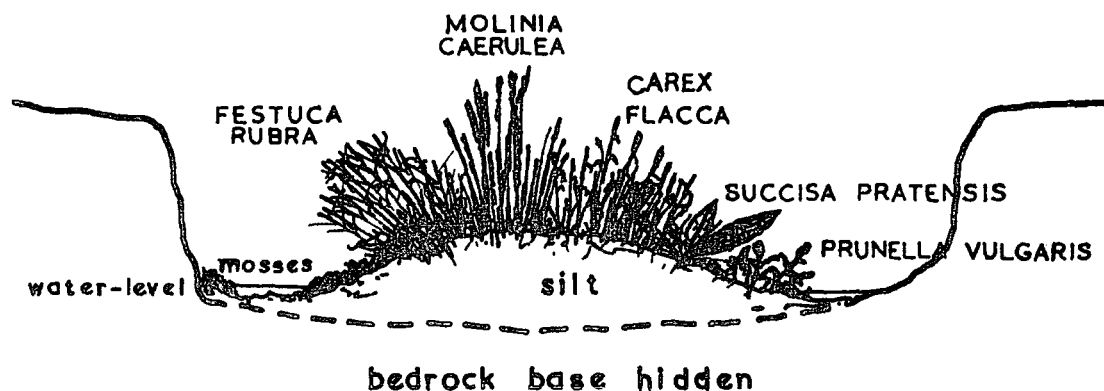
viii/ trees which contribute to the hollows' flora are
generally computer=placed in this second category
('b'). The chief exception is Salix sp., which,
like other semi=aquatics, is represented in both
'a' and 'b' sites.

Table X summarises the TWINSPAN divisions of terres-
trial sites. Overlap inevitably arises to thwart the perfec-
tion of these distinctions. The mosses Bryum pseudotriquetrum
and Cratoneuron filicinum are probably the two most catholic
species, acting seemingly as either early colonists or gap-
fillers, and in whichever role being less selective as to
their fellow=inhabitants.

The generalisations which make up Table X, below, are
further elaborated in the final summary, Table XIV.

TABLE X   Summary of Terrestrial Sites

Category 'a'		Category 'b'	
2 sites species-poor, Sesleria-dominated grassland	26 sites species-rich, flat, dry, weedy areas	30 sites species-rich, damper sites, leafier, tufted growth	4 sites aberrant sites (Fissidens — Juncus) i.e. 'C,D,F,Y'

4 : 5   Analysis of Species

The TWINSPAN operation orders species on the basis
of the arrangement of sample-sites already produced.   In
this investigation, the chief plant-division is created to-
wards the end of the species-list, such that four species
are separated from the remaining 79.   Of these four, three
— 'fga', Nostoc, and Juncus articulatus — have already
gained prominence in the foregoing description. (Section
4 : 3 in particular deals with this group.) They are the
truly aquatic members of the truly aquatic sites, and their
precise distribution is adopted by TWINSPAN as its criterion
for detailed classification of these water-filled hollows.
(See Table VIII). They clearly form a recurrent (but not
obligate — only nine sites throughout the whole sample have
all three species) association, though all readily occur
elsewhere, particularly in the terrestrial 'b' group; and
Juncus articulatus especially contributes to the vegetation
of non-aquatic hollows, albeit at lesser abundances. Juncus
articulatus is in fact the single most frequently-occurring
plant-species, being found in 47% of the total sample.

The fourth species of this primary division is

Epilobium parviflorum, of sparse occurrence (7% of sites)

at low cover-values (often single specimens only) scattered

across the TWINSPAN table.

A secondary demarcation is shown in the same general

area of the species-list, and suggests affinities between a

further set of four species, viz:

Danthonia decumbens,

Fissidens sp.,[2]

Tortella tortuosa,

and   Pseudoscleropodium purum.

These species can be regarded as semi-aquatic in preference.

For example, Danthonia decumbens, a nationally widespread

grass, is described (Hubbard, 1976) as growing "usually in

somewhat moist or wet places". As mentioned earlier (see

Section 3 : 2 : 3), a ninth plant, Salix sp., which is next

on the TWINSPAN list, could be added to these semi-aquatics.

The remaining 74 species are thus designated as

terrestrial. Two categories, divided at level 3, separate,

broadly speaking, the relatively low-growing, mat-forming

weeds (36 species, top part of TWINSPAN table), from the

more erect, leafier, and often tufted forbs. The dicho-

tomy is not strict, for Dactylorhiza fuchsii and Inula conyza,

for example, are placed anomalously in the upper part of the

table, whereas Cerastium fontanum occurs below the dividing-

line. However, in all such cases of apparent mis-placing,

cover-values of plants involved are usually minimal; occur-

rences are few; and the list-position is usually very near

2 Fissidens adianthoides was the only member of this genus
   to be identified, and possibly the only one present.

the crucial boundary anyway. As for the analysis of the samples described earlier (Section 4 : 4), the overall impression holds true, emphasised and confirmed by the allocation of all the tree-species (except <u>Pinus sylvestris</u>) to the lower list, whilst the three common terrestrial mosses, (<u>Bryum pseudotriquetrum</u>, <u>Mnium undulatum</u> and <u>Cratoneuron filicinum</u>) contribute to the category of low-growing forms.

Plant-species in the second half of the TWINSPAN list are almost entirely confined to, and characteristic of, terrestrial sites category 'b', until, of course, one reaches the minority of semi-aquatic and aquatic species at the very bottom of the table. The occurrences of plants from this second half of the terrestrial species-list in the sites of terrestrial group 'a' are relatively few, and are catalogued below, in Table XI.

TABLE XI   <u>Occurrences of Lower-list Species</u>
<u>in Group 'a' Sites.</u>

Species	Occurrence	Sites	Cover-value
Hypericum montanum	3	'50' '14' '22'	X X X
Cerastium fontanum	1	'37'	1
Lotus corniculatus	1	'22'	1
Galium sterneri	1	'42'	2
Centaurea nigra	1	'7H'	2
Festuca rubra	4	' 3' '20' '42' '50'	2 5 5 4

<u>Festuca rubra</u>'s apparent infidelity, however, is

substantially offset by its 33% constancy, and high level of dominance, in terrestrial category 'b', where it frequently associates with two other tall species, as Table XII shows.

TABLE XII   Recurrent Association of Species

Species	Site - numbers											
	41	44	27	16	39	t	32	21	6_1	6_2	2	43
Festuca rubra	8	8	9	-	4	8	7	8	8	6	9	4
Carex flacca	8	5	-	7	5	-	2	4	-	-	-	-
Succisa pratensis	7	3	6	6	4	6	2	X	2	-	-	1
	The entries in the columns above are Domin-scale cover-values for each species per site. The figures below are the species-richness scores for each of the sites.											
Total number of species	5	9	7	5	8	13	18	11	13	14	13	13

The independent occurrences of the three species on the Gait Barrows pavement were:

Festuca rubra   —   four other sites (see Table XI),
Carex flacca   —   two other sites,
Succisa pratensis   —   eight other sites.

In other words, they are not merely excessively common plants which are bound to coincide, but form a true association. Moreover, the arrangement of samples on Table XII suggests that the Festuca — Carex flacca — Succisa partnership may inhibit species-richness, which declines in the hollows concerned as the Festuca-dominated association strengthens.

A second interesting association, involving far too

few sites to be considered significant, concerns the two
species whose occurrences, with cover-values, are plotted
on Table XIII.

TABLE XIII   Another Association of Species

Species	Site - numbers i) association			ii) independent occurrence			
	'2'	'21'	'6₂'	'1'	'49'	'32'	'19e'
Sesleria albicans	4	4	4	9	9	1	-
Fraxinus excelsior (saplings)	2	2	2	-	-	-	1

It is tempting to see here a microcosm of the transition between
calcareous grassland and ash-rich limestone woodland!

TABLE   XIV   Summary of TWINSPAN Results

This Table shows the proportions of various groups of plants,
expressed as percentages, occurring in various categories of sites.

	terrestrial			aquatic			
	'grass-land'	a	b	b₁ left	b₁ right	a₁ left	a₁ right
terrestrial							
low-growing, weedy annuals	o	●	◉	o	o		o
taller forbs, grasses, etc.	o	o	◉				o
aquatic							
'semi'-aquatic plant-species.		◍	◍	◉	◉	◉	◉
true aquatics.		◉	◍	●	◍	◍	●

(Format based on Huntley & Birks, 1979).

symbol		value
o	–	≤ 2%
◉	–	2·1 – 10%
●	–	10·1 – 25%
◍	–	25·1 – 50%
● (large)	–	>50%

The left-hand column briefly defines groups of species. The different-sized circles denote the occurrence of species within these groups, expressed as a percentage of the total possible occurrences within each category of sites.

CHAPTER 5

ALGAL CONTENTS and pH - VALUES

of POOLS - in - HOLLOWS

This Chapter, as the title suggests, deals only with aquatic
sites.

5 : 1   The Algal Presence

55% of the sampled solution-hollows on the Gait Barrows
pavement support algal life.   This figure includes all the so-
called 'aquatic sites', and where water-levels are maintained
persistently, algal quantities are normally high;   of 37 such
hollows, all but three (8·1%) have Domin-scale cover-values of
8 or above.

Visually, the algal material occurs in four different
expressions:

   i/ dense, free-floating strands ('algal scum');
   ii/ similarly bright, pale green furry growths, presumably
       attached, clothing sediments on the base of the hollow;
   iii/ dark olive-green, globular masses;
   iv/ thick, rubbery, leaf-like forms of a similar colour to
       those described in iii/ above.

The latter two categories are both ascribed to the genus Nos-
toc, which forms "large, macroscopic, mucilaginous colonies"
(Bold & Wynne, 1978).   The spheroidal aggregations, iii/,
are heterocysts, and very typical constituents of many Gait
Barrows pools such as those occupying sites 'J' (Photograph 12)
and 'S'.   The other two categories, i/ and ii/, despite their

different appearance, were found under microscopic analysis
to consist of the same genera, mainly _Spirogyra_ and _Zygnema_,
and are therefore both included under the heading 'filamentous
green algae' ('fga'). (See Section 2 : 5). A list of algal
components of 'fga' is given in Appendix C.

5 : 2   Observed High pH - Values

Many pools-in-hollows, as well as containing abundant
algae, provided unexpectedly high pH-values. During trials
with the pH-meter at the beginning of May, site 'P' produced
a reading of 9·35, and site 'S' registered 9·50. The 'official'
pH-sampling on May 15th gave maxima of 10·25 and 10·35 for the
water in hollow 'X' (Photograph 16), tested respectively at
about mid-day and in late afternoon. Initial scepticism as
to the veracity of these results was dispelled by immediately
checking the meter against the 9·2 buffer-solution, with satis-
factory correspondence; and later by having water from 'X' in-
dependently tested. (See Section 2 : 4 : 1).

Such high pH-values are unusual in nature, but not
without precedent. Williams (1966) reported a mean pH-value
(118 samples) for pools on limestone pavements of 7·8, but
some of his individual readings exceeded pH 10. Indeed,
slightly lower but comparable pH-values, shown in Appendix
G, were registered with the same apparatus to that used at
Gait Barrows in meres and drainage-ditches — respectively
much larger, and flowing, bodies of water — on Leighton
Moss Reserve (see MAP 1), about 2 kilometres from Gait

Barrows. This wetland receives base-enriched drainage from surrounding Carboniferous Limestone. Apparently reservoirs attain values as high as 9·8 after treatment with sodium bi-carbonate $(Na(HCO_3))$. (Water Board employee, pers. comm.) Thomas (1930) reported maxima of pH 12 in the admittedly exceptional conditions of pools containing rain-washed lime-waste.

Observations at Gait Barrows suggested a possible correlation between algal abundance and high pH-values. This hypothesis is supported by the comment (Ratcliffe, 1977) that on Cousa Downs Reserve in Cornwall, pH-assays reached 10 in "shallow pools when the aquatics are photosynthesising". 'Juncus Pool 1', mentioned in Appendix G, also had a notice-able algal scum.

5 : 3   The Relationship between Algae and pH.

To test this presumed relationship, Kendall's Rank Correlation was applied, scoring ranked pH-values of 32 sites determined on May 30th — if several readings were taken at one pool, a mean-value was calculated — against Domin-scale rankings for 'fga' (not Nostoc) assessed on May 24th for the same sites. Since many 'fga' rankings were equal, as a result of general prolificity and therefore repeated cover-abundance figures of 8, 9 and even 10, a modified formula recommended by Siegel (1956) was used. The computed value for T_B (correlation co-efficient) is:

·246 ;

and for t :   1·962 , which, for infinite
degrees of freedom, is significant to 95% level.   The
probability of chance accounting for the alleged corr-
elation would be even less if the fourth-ranked site in
terms of high pH-value ('p' , mean pH = 9·575) had been
accorded, as well, a high value for algal presence.   In
fact, 'fga' were not recorded here.   This is almost cer-
tainly an error.

     The conclusion is, therefore, that a strong positive
correlation exists between abnormally high pH-values and
algal abundance in the Gait Barrows solution-hollows.
Algae are known to tolerate extreme environments in general
(see, for instance, Alexopoulos & Bold, 1967) and high pH's
specifically (Trainor, 1978).   Conversely, there is also
evidence that algae actively modify the chemistry of their
surroundings.   Hutchens (1948) noted that in laboratory
cultures of <u>Chilomonas</u> of initial pH 6·0, increases had
taken place thus:

                    after 48 hours, pH = 7·5;
                    after 72 hours, pH = 8·3.

The main agency by which alkalinity increases is "preferential
absorbtion of particular constituents" (Fogg, 1972) of the
culture-medium during photosynthesis by the algae present.
Possibly the Gait Barrows pools undergo a similar process.
Since they are generally small, relatively undisturbed, and
isolated from other biochemical effects, the comparison to
laboratory conditions is perhaps not far-fetched.

The mechanism of pH-change as described in the literature is accentuated when CO_2 is in short supply. Under these circumstances, "the utilization of bicarbonate in photosynthesis may result in the pH of media rising as high as 11 or more". (Fogg, 1972, op. cit.) In alkaline waters (such as those of Gait Barrows pools) "little if any free carbon dioxide exists" (Trainor, 1978), and bicarbonate is plentiful. Conditions in the hollows thus seem correct for the following postulated series of events:

(1) algal development and photosynthesis;

(2) depletion of already deficient CO_2;

(3) dependence thenceforth on calcium bicarbonate in pool-water;

with(4) consequent raising of pH, to the high values recorded at Gait Barrows;

and (5) precipitation of carbonates.

A soft, greyish, mealy deposit irregularly covering the limestone walls of some hollows testifies to phase (5). A further stage — of drastically diminished algal presence — was noted on July 5th, (see Section 5 : 4 : 1), and may be analogous to Hutchens' (1948) discovery that above certain pH-levels, algae died. Whether the effect at Gait Barrows was an algal response to intolerably high alkalinity or merely a seasonal phenomenon irrespective of water-chemistry, is not known. Unfortunately, it was not possible to take pH-readings on this last occasion to see if pH-values had dropped in accordance with declining algae, and so the argument that pH-values vary directly with fluctuations in

algal activity could not be further substantiated.

These conclusions remain somewhat tentative; two months' observations are scarcely sufficient to secure an absolute conviction that algae are responsible for high pH-values. Nonetheless, the main observations at Gait Barrows fit the pattern outlined above, and supporting evidence is also offered by the relationship of pH-values to times-of-day. Many of the higher measurements were made during the hotter parts of fine days, such as May 30th, when algal photosynthesis is encouraged by warm, sunny conditions. Early morning pH-readings (June 21st) were rather lower than corresponding values at the same sites but taken at a later hour (on June 18th), a change which perhaps reflects algal inactivity overnight. More systematic experiments, however, are needed to elucidate and confirm the hypotheses described in ths Section, incorporating a set of control-data to counter the effect of falling water-levels. These not only debilitate algal life, but make accurate pH-testing much more difficult.

The association between algae and pH established in this Section applies, strictly speaking, to one point only in time, namely late May. The next Section examines trends shown by the two phenomena during the study-period, and also refers to a potentially influential third condition, the drying-out of pools.

5 : 4   Temporal Variations

5 : 4 : 1 Algal Performance

As part of the main phytosociological programme, algal cover-values were recorded on two dates, May 24th and June 20th. These dates are hereafter abbreviated to '1' and '2'.

The trends affecting aquatic sites, 35 of which can be directly compared from '1' to '2', are graphed below. Actual numbers of sites are given in the relevant columns. These categories of change are largely independent of whether Nostoc or 'fga' comprised the algae. Some sites of 'unchanged status' had, in fact, small increases of either Nostoc or 'fga'

GRAPH 6   ALGAL PERFORMANCE

Frequency of sites (%)
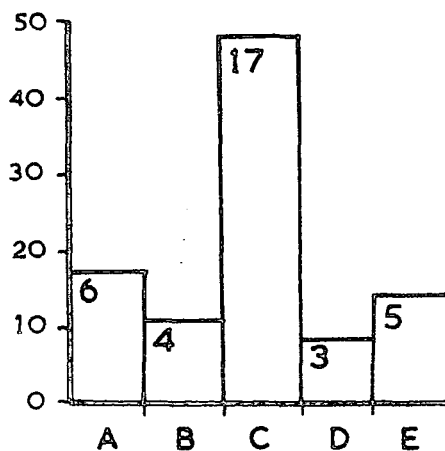
(numbers = sites)

Algal trends

A = considerable increase;
B = slight increase;
C = unchanged;
D slight decrease;
E = considerable decrease.

balanced by an equivalent decline in the other, and sampling-error possibly accounts for much of the apparent fluctuations involving a small plus or minus in cover-values between '1' and '2'.

The truly aquatic sites are divided by TWINSPAN partly on the basis of their algal components (see Section 4 : 3). Sub-group 'a$_1$ right', comprising 8 hollows, has <u>Nostoc</u>, usually attaining cover-values of 7 or more, but no 'fga'. Most of these sites ceased to be pools by date '2', and it may be that the occurrence of <u>Nostoc</u> is associated with this phenomenon. 18 'terrestrial' sites (according to TWINSPAN — they may in the first place have been designated as aquatic) also had some algal constituents, almost always at low cover-values. <u>Nostoc</u> was more characteristic of these sites than was 'fga', (13 out of 18 (72·2%) compared to 8 out of 18 (44·4%)), customarily occupying marginal pools surrounding other vegetation, or the runnel-type exits of some hollows (see Section 1 : 3 : 4), where drainage dampened the bedrock. This prevalence of <u>Nostoc</u> probably reflects the greater propensity of 'terrestrial' sites to dry out, and the 11 hollows which demonstrated <u>un</u>changed algal-values in the sampling-period were either abnormally deep and consequently retentive of water, such as '46r', or inhabited by <u>Nostoc</u> only, which remained even after serious desiccation, as in site '&$_B$'. Of the two sites which showed a marked decline, i.e. 'C' and 'D', both suffered nearly complete loss of water. The other five terrestrial sites registered slight alterations of algal abundance. Minor increases in three sites (16·7%) were in each case from nil to very little,

and are probably not so much real developments as the result
of more careful examination of the pools.

Between the two dates in question, major changes in
algal-frequencies are relatively few, and the only discern-
ible pattern is that Nostoc spp. are more typical than 'fga'
of areas prone to desiccation.   Under the duress of this
condition, (and/or low CO_2 (see Section 5 : 3) and high pH-
values), relative survival capacities of different algae may
become important in the maintenance of algal populations.
For example, blue-greens such as Nostoc thrive in low-CO_2
environments (Trainor, 1978), and some species of Zygnema
endure drying-out and respond quickly to subsequent wetting
(Bold & Wynne, 1978).

A brief return to Gait Barrows on July 5th showed
that the 'fga' quantities had much reduced during the inter-
vening fortnight beween visits.   Some pools seemed to have
been entirely swept clear of suspended material.   Graph 7
below summarises a rapid survey of 'fga' cover-values done
early the following morning (July 6th) for 25 aquatic sites.
Field-notes of that occasion refer to "dead, sludgy material"
inhabiting the pools, presumably the remnants of algae.
Necessarily, few terrestrial sites ever had 'fga'-levels
conducive to vast decreases, but hollows '18d, t and z'
subscribed to the general trend in falling from Domin-scale
values of 4 or 5 to nil or χ .

As Graph 7 shows, some aquatic sites more efficiently
retained their 'fga', and this is difficult to explain.   Many

GRAPH 7   LATER ALGAL PERFORMANCE

Frequency of sites

(%)

```
50 ┤
      ┌──────────┐                          ┌──────────┐
40 ┤  │          │                          │ 12 Sites │
      │          │                          │          │
30 ┤  │ 8 Sites  │                          │          │
      │          │                          │          │
20 ┤  │          │   ┌──────────────────────┤          │
      │          │   │     5 Sites          │          │
10 ┤  │          │   │                      │          │
      │          │   │                      │          │
 0 ┼──┴──────────┴───┴──────────────────────┴──────────┴──
         I              II              III
```
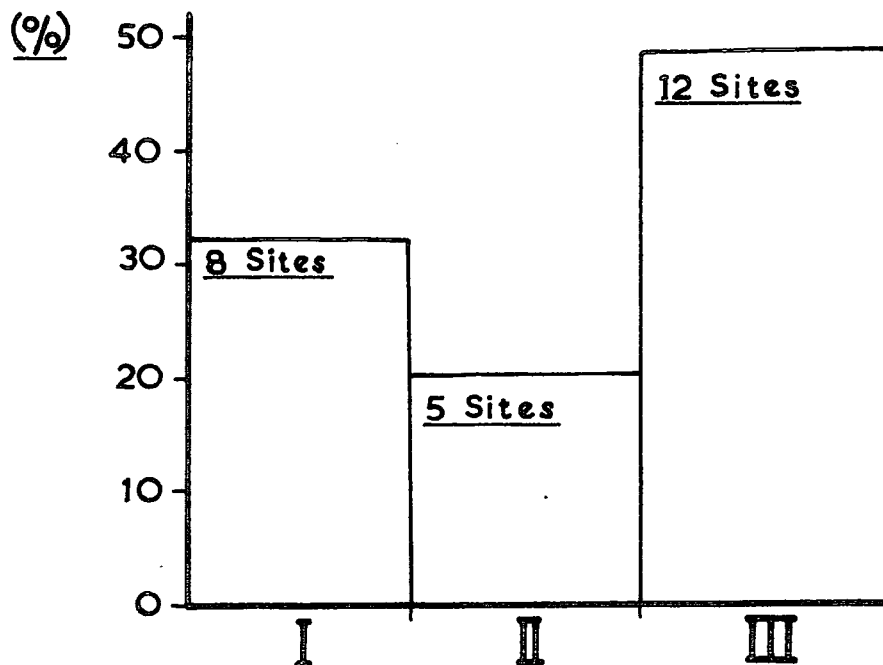
I   'fga'-levels maintained;

II   considerable decline, but 'fga' still present;

III   decline to nil from previous 'fga' abundance.

of these hollows belong to TWINSPAN category 'b₁ right', but this is only to be expected, because this sub-division was (initially) characterised by dominant 'fga', and, in any case, other members of the same group, such as 'T' and 'c$_b$', suffered sharp declines in their algal content.

Desiccation during the interval between June 20th and July 6th cannot be discounted. Weather-conditions in North Lancashire are not known for this period; severe evaporation is considered unlikely, but drying-out of some sites may have occurred. Water-levels prevalent in early July were, however, totally changed by a heavy and prolonged downpour on July 5th,

just before the pools were examined in what was obviously a freshly replenished state, with the remaining floating algae visibly diluted and most hollows newly full of clear water.

A more tenable explanation of the declining algal presence is simply that the algal scums are a seasonal phen- omenon in the Gait Barrows solution-hollows, and that the July 6th observations coincided with the main dying-back. Some sites had progressed further in this event than others. Moreover, it may be that the high pH-values, recorded up to June 18th, are inimical to 'fga', and contributed to their decline. (See Section 5 : 3). <u>Nostoc</u> aggregations, how- ever, are much more permanent, surviving desiccation and being conspicuous in some pools even in early February, during the preliminary visit to the Gait Barrows pavement.

<u>5 : 4 : 2   pH - values</u>

The five sessions of pH-testing, from May 4th to June 21st, afford comparisons of values at different times during the field-work season.   No equivalent phytosociological data exist for the earliest dates, and it is therefore not possible to say whether algae proliferated during the fortnight when pH-values reached their zenith.   Table XV shows the trends in pH between the main sampling-dates:

May 15th,   i.e.   '2',

May 30th,   i.e.   '3',

June 18th,   i.e.   '4'.

(These numbers correspond to those listed in Table I, Section
2 : 4 : 1).

TABLE XV   pH - trends

	increasing pH-value		decreasing pH-value		static	
	(i)	(ii)	(i)	(ii)	(i)	(ii)
from '2' to '3'.	21/28	75%	5/28	18%	2/28	7%
from '3' to '4'.	6/27	22%	19/27	70%	2/27	7%

Column (i) in each category of pH-behaviour shows the actual number of sites out of those available for comparison, and (ii) shows the percentage of sites in each category.

Thus, most sites (75%) reached their maximum pH by the end of May (date '3'); in so doing, five pools (out of 21; 24%) increased by more than one full pH-unit. Of the five (18%) whose values decreased during the same period, two exhibited only very marginal declines ($\geq$ 0·05 pH-units).

Contrastingly, a very similar proportion of pH-values (70%) dropped between the next two sessions ('3' and '4'), and of the six sites where against-the-trend increases were noted, two were again only marginal ($\geq$ 0·10 pH-units).

It has already been postulated, but by no means fully tested, that algae may be responsible for pH-variations. Another possible cause, which also varies temporally, is loss of water from the pools, a condition which becomes more pre-valent as spring- and early summer-temperatures produce evap-oration. Drought ultimately renders pH-testing impossible. Even in the so-called aquatic sites, the number sampled fell

from 43 on May 30th to 25 on June 18th. It is therefore difficult to establish a correlation between approaching aridity and progressively reduced pH-values, but some evidence for such a relationship can be derived.

Six sites — 'C, F, G, Q, Z_B, and 18d' — gave pH-values on May 30th, but dried out thereafter. The mean of the measurements from these six sites is a markedly low 7·85. Pools-in-hollows 'x, V, y, and R' had pH-values respectively of 7·55, 8·10, 8·40, and 8·90 (mean = 8·24) on May 15th, when appended comments in field-notes were, for example, "depth barely sufficient", and "electrode hardly immersed". The two mean values stated above should be viewed in the light of the overall mean pH-value for aquatic sites, which is 8·62, from 97 measurements taken throughout the study-period.

In contrast, hollows with persistent water-levels — not necessarily of great depth, but tending not to dry out — maintain relatively high pH-values. A selection of such pools is listed in Table XVI, below, with mean pH-measurements taken, unless otherwise stated, during the last chief sampling-session, June 18th (date '4'), when the effects of desiccation were noted in other sites, despite recent fairly wet weather (76·4 mm of rain in the preceding fortnight).[1]

There is, therefore, a suggested correlation between relatively low water-levels, due to evaporation and/or drainage, and pH-values lower than the mean; and stable water-levels and pH's higher than the norm. TWINSPAN allocates

1 Rainfall figures for Leighton Moss nearby, courtesy of
  Mr. John Wilson.

TABLE XVI   High pH-values
                            in persistent pools

code	pH	code	pH
I	9·35	a	9·55
J	9·73*	c_a	8·75
M	8·80	c_b	9·60
O	9·05	g	9·625
P	9·56	u	9·175
S	9·75		
X	9·85		

*   reading taken on May 30th.

the six sites of low pH and early-season aridity to the
'terrestrial' groupings, and amongst the aquatic sites
some with fairly rapid desiccation properties are placed
together, such as 'j, i and o' in sub-group 'a_1 right', as
if to reinforce the argument that depth and duration of
water-levels play an important role in the life-history
of the hollows.   It is, however, difficult to 'prove',
or attach significance to, the proposed association. The
main handicap is the lack of quantified measurements of
persistence of water-levels.   As with some other parts
of the study described in this Chapter, progress towards
more conclusive information can be made only with a sys-
tematic programme of monitoring pH-values and related
phenomena, as a separate research-topic in its own right.

5 : 5   Site '46r'

Many visitors to Gait Barrows 'know' the hollow now designated as site '46r'. It is readily distinguished even at a distance by its tall and evidently flourishing specimens of Typha latifolia, an unusual plant for limestone pavement. Site '46r' is a large, deep hollow, but water is often restricted to the base of the vegetation. Consequently, pH-assays refer to the immediate environment of Typha's roots. These values are consistently the lowest of all pH-surveys done, as the following details show:

TABLE   XVII   pH-values in '46r'

date	pH-values
30/5/81	6.85
18/6/81	7.20
	7.35
21/6/81	6.60

Either the occurrence of Typha latifolia in this site is a response to abnormally low alkalinity (by Gait Barrows' standards), or else the plant itself is altering the chemistry of its own surroundings.

5 : 6   Soil - Chemistry

The method of soil-sampling is explained in Section
2 : 4 : 2.   In the event, only two soil-cores were obtained,
partly because of the risk of damaging sites, and it was hoped
that these would offer some hint of chemical conditions.   The
details, inadequate to provide a full section in this Chapter,
are given in Appendix H;   some implications of the data are
discussed in Section 7 : 5 of Part II.

SUMMARY of CHAPTER 5

A positive correlation exists between high
pH-values and algal abundance in the pools
occupying solution-hollows on the pavement
of Gait Barrows. Algal photosynthesis is
proposed as the modus operandi whereby the
relationship occurs, and the chemical pro-
cesses documented for laboratory conditions
may be enacted in the limestone pools. No
evidence, however, was found for fluctua-
tions in parallel of detailed pH-values
and algal abundances. The effect of vary-
ing water-levels is probably superimposed
on the pH-algal relationship. One site
shares the distinctions of relatively low
pH-values and an unusual plant-species,

Typha latifolia.

PART II

CHAPTER   6

GEOLOGICAL   CONSIDERATIONS

6 : 1   Limestone   Pavements

6 : 1 : 1 Introduction

Limestone 'pavements' consist of more-or-less
horizontal surfaces of bare rock in the form of 'clints',
which are analogous to paving-slabs, separated by 'grykes',
which are joints widened by solution.   Pavements are "of
almost infinite morphological variety" (Sweeting (in Dury),
1966), and have thus aroused considerable interest and con-
troversy.   It is particularly true of the Morecambe Bay
limestones that "no two outcrops of pavement are exactly
alike" (Sweeting, 1966, op. cit.), and therefore elucidation
of their precise origin is even more difficult, a problem
exacerbated by the sparsity of geological research on such
sites as Gait Barrows.

6 : 1 : 2 The Origin of Pavements

The present character and appearance of any limestone
pavement such as Gait Barrows is a function of two main sets
of events, viz:

i/ the original creation of a stripped limestone platform;
and ii/ the subsequent, and usually current, modifying processes
which act on such a surface.

Williams (1966) has very adequately summarised the arguments concerning the first stage. Moisley (1955) has stressed the importance of recurrent, impermeable shale-bands ("laminae"), each of which protects the directly under-lying limestone stratum, until glacial exhumation selectively exposes such strata in the form of wide plat-forms. This accounts for the 'step-and-stair relief' of many Karst areas, including those of North-West Yorkshire. The Morecambe Bay limestone topography is not so arranged, however, much of it being somewhat chaotic as a result of faulting (see, for example, Sweeting (in Herak & Stringfield) 1972, or Moseley, 1973). It is impossible to judge whether the Gait Barrows pavement specifically owes its origin to over-lying shales. The surroundings offer little geol-ogical evidence of the calibre of that easily deduced from the vertical exposures of much of the limestone further East, and the general geological relationships are rendered uncer-tain by the absence of Geological Survey maps of this part of the country.

Parry's (1960) explanation for the occurrence of pavements relied on late-Glacial snow-accumulation to in-itiate active solutional stripping in certain localities. His research, again, was done in the rather different ter-rain of North-West Yorkshire, and his main hypothesis has negligible relevance to Gait Barrows, where both low alti-tude and lack of containing relief preclude durable snow-cover.

Pigott (1962) recognized that 'pavementation' —
the term used by Parry — coincides with intensive glacial
erosion.   Pigott suggested that moving ice removed weath-
ered debris from the limestone surface, and produced a
freshly smoothed platform, often synonymous with a bedding-
plane.   Gait Barrows lies in an obviously glaciated region,
and it is logical to postulate that this particular pavement
was glacially scoured as the ice progressed Southwards and
seawards.   Erratics of Silurian grit from further North con-
firm this.   Perched limestone blocks (see MAP 3), which
Sweeting (1966) calls 'pseudo-erratics', also occur on the
Gait Barrows pavement.

Exactly how deeply glacial action penetrates is
largely speculative.   Really severe scouring might remove
so much rock that the new surface is totally free of evidence
of previous incision, and the pavement so caused would be
virtually without grykes, like that at Gait Barrows.   Such
intensive glacial modification may apply to low-lying sites
such as Gait Barrows, and may thus obviate arguments arising
from the structural nature of the limestone (see Section
6 : 1 : 4).

Once bare limestone surfaces have been produced,
several factors subsequently influence the detailed quality
of the pavements, and indeed continue to govern present pro-
cesses.

6 : 1 : 3 Lithology

Carboniferous Limestones are generally compact and resistant, and are much more conducive to the formation of Karst features than, say, the relatively light-weight and incompetent oolites and chalks. Within Carboniferous Limestone facies, however, lithological variations "are probably the most important cause of contrast between one pavement and another" (Sweeting (in Dury), 1966).

The Gait Barrows limestone is an extremely pure form. Spectrophotometric analysis of two specimens of rock submitted on July 5th determined 99% + calcite; no insoluble residue was detected. Gait Barrows limestone consists of comminuted fossiliferous material (a mixture of brachiopods, echinoids, lamellibranchs and others) identifiable only in thin-section (Mr. D. Schofield, pers comm.). Such a coarse-grained, highly-calcitic — by virtue both of organic content and cementing matrix — rock is designated as 'biosparite' (Dr. H. Goldie, pers. comm.), and is probably similar to the lithology of the Arnside Knott area (MAP 1) as described by Sweeting (in Herak & Stringfield, 1972).

These sparry limestones are "relatively impermeable and insoluble" (Sweeting & Sweeting, 1969), and also less affected by frost-action, which is probably minimal at Gait Barrows in any case, than other limestones. Grykes in such limestones are typically infrequent and usually narrow. For these reasons, massive, sparry limestone beds correspond to the "most extensive" (Parry, 1960) and "more conspicuous"

(Sweeting (in Waltham), 1974) developments of pavement. Moreover, because of their reluctance to weather, this type of limestone generates smooth surfaces, for which the Gait Barrows pavement is notable (see Section 1 : 3 : 4), especially in contrast to Hutton Roof, whose limestone is "pseudo-brecciated" (Sweeting (in Herak & Stringfield), 1972), and of a very rugged micro-topography.

In many of their characteristics, therefore, the Gait Barrows pavements are generically and morphologically similar to the better-known massive examples of the Burren, in Western Ireland, and Scar Close on Ingleborough, North Yorkshire, where "uninterrupted and unbroken clint-surfaces of over 200 square yards (170 square metres) occur" (Sweeting (in Dury), 1966).

Lithological character also has a specific effect on the aquatic properties of solution-hollows, for, according to Jennings (1971), "in thick beds lacking porosity, solution-hollows ...... can hold water until it is entirely lost by evaporation".

6 : 1 : 4   Structure

Structural weaknesses within the limestone permit entry by rain-water, and thus the onset of "enlargement of voids" (Jennings, 1971) and steadily increasing permeability which lead to classic Karst scenery and drainage. Of these structural weaknesses, joints "are the most important single factor" (Jennings, 1971), in that solution-widening of joints produces the pattern of grykes which typifies limestone pave-

ment. "The frequency and orientation of grykes is controlled by the jointing" (Jones, 1965). Joints are particularly important in massive-bedded facies, such as the Gait Barrows limestone, because bedding-planes in such conditions offer fewer opportunities for solution; and major joints, which penetrate several strata, are more crucial than minor joints whose depth terminates within a single bed of limestone.

Horizontality of limestone strata aids the formation of pavements, though this (Sweeting (in Waltham), 1974) is not essential. (Indeed, Parry (1960) uses the lack of absolute correlation between bedding-planes, i.e. structure, and landform to illustrate that erosional elements, too, are of some importance.) Gait Barrows, however, is an example of generally flat pavement, and it is probably significant that the more dissected areas of open limestone correspond to the slightly inclined beds of the Southern portion of the pavement (see Section 1 : 3 : 4; Photograph 3).

6 : 1 : 5   Drift - cover

Jones (1965) argued that superficial features of a limestone pavement are formed under a drift-cover. Although it is true that biological action from peat-derived waters accentuates solution, and that some pavements are emerging from areas of 'bygone drift', authorities such as Sweeting and Williams assert that sub-aerial chemical weathering has been sufficient, even in the post-Glacial era, to fashion the present appearance of pavements. The latter states (1966)

that rain-water is powerful enough "without the addition of soil-acids of biological origin". Certain (calcareous) drift may preserve rather than destroy pavements.

It would nonetheless be interesting to know the post-Glacial history of Gait Barrows, especially as the solution-hollows discussed next (Section 6 : 2) are either residual, if Jones' ideas (1965) are correct, or more recent and still undergoing formation, if one accepts the more generally-held beliefs. Solution under a drift-cover is said to be uniform rather than discriminately channelled, and features produced in this way are distinctively rounded instead of "fretted and rough" (Williams, 1966). Gait Barrows, in both these respects, offers circumstantial evidence of having been buried, for its pavement is extremely smooth, and edges to grykes and runnels are usually not sharp. (Small areas of jagged and pocked limestone in the solution-hollows are interpreted in Section 6 : 2 : 2.) Furthermore, some of the local woodland grows over drift, and neighbouring pastures show only sporadic limestone outcrops penetrating the drift-cover.

6 : 1 : 6 Stage

Geological features reflect the stage of development they have reached within a sequence or cycle of events, and limestone pavements are no exception to this general truth. Parry (1960) believes that most limestone surfaces were once more perfect, and are now subject to a "process of fairly rapid decay with the accumulation of debris on the surface, and the formation of shallow grykes" (Parry, 1960). Gait

Barrows displays neither of these developments, and looks
very fresh; in 'age' as well as appearance, therefore, it
may compare with Scar Close, in contrast to which Goldie
(1973) considers the much-dissected Malham pavements
"physiographically older". Encroaching vegetation
reduces the visible area of pavement, and this may be
happening at Gait Barrows as peripheral woodland spreads.

6 : 2   Solution - Hollows

6 : 2 : 1 Terminology

Solution-hollows are well distributed in areas of
Karst topography — they are, for example, "quite common in
Yorkshire" (Williams, 1966), and Zotov's (1941) study con-
cerned those of Mount Cass, New Zealand — but they are not
among the best-known of limestone features, and different
authors have adopted different names. The classic, Slav-
onic term is 'kamenitza', variously spelt; Williams (1966)
confirms that these are "roughly equivalent" to solution-
hollows; Sweeting (1966) uses the name 'clint-hollows';
Zotov (1941) referred to them as 'solution-cups'; and
Jennings (1971) applies the phrase "solution-pans, (Amer.
'tinajitas', etched pot-holes)".

Jennings (1971) classifies solution-hollows under the heading 'Minor Solution Forms ...... developed on partly-covered Karst', which is a valid description for the Gait Barrows examples in that despite their small scale they contribute importantly to the vegetation of an otherwise largely abiotic surface.[1] Jennings points out that such partial cover may represent an early stage of colonization or a relict condition after removal of a previous vegetation-cover. The status of the Gait Barrows solution-hollows in this respect is further discussed in Chapter 7.

However they are labelled, these hollows comprise a distinctive, though variable, genus of limestone feature, intermediate in scale between the tiny effects of rain-pitting, or solution by persistent but local dripping (for instance, from perched blocks (Jones, 1965) or by spray (Williams, 1966)), and the much larger swallow-hole or doline-type depressions, where advanced solution, sometimes aided by general collapse, creates a real 'land-form' of markedly greater extent.

6 : 2 : 2 The Origin and Development of Solution-Hollows

The occurrence (and precise distribution) of solution-hollows requires the massive and horizontal style of limestone pavement. Where the clint-surface is less intact, by virtue of excessive solution, hollows are few or absent. In part-icular, co-existence between hollows and grykes is ipso facto rare, since the more extensively that grykes are developed, the greater is the reduction of flat, bare limestone on which

1 Lichens are of course present on even the most open expanse of Gait Barrows pavement.

hollows are almost invariably sited. (cf. Williams, 1966:
"The density of runnels depends largely upon the frequency
of grykes ...... ").

Gait Barrows demonstrates this negative association.
Where, as near the woodland edge, the limestone is more gener-
ously dissected by grykes, hollows are relatively few, and of
those which are found in such situations, many, such as 'N',
or '40q', are long and narrow, occupying residual ledges be-
tween grykes. Thus, the availability of an appropriate
surface-area is an essential factor, and this itself depends
on the precise conditions of lithology, structure and process,
as discussed in Section 6 : 1.

The chief mechanism for hollow-formation is *in situ*
solution, as it is for almost all superficial limestone fea-
tures. Williams (1966) confirmed this by measuring $MgCO_3$ and
$CaCO_3$ parts-per-million in water from pools on the limestone
pavements of the Burren, Western Ireland. The vastly higher
values compared with those of rain-water "can only be accounted
for by corrosion of the limestone" (Williams, 1966). Sweeting
(in Dury, 1966) asserts that water dissolves $CaCO_3$ until "the
solution becomes saturated or even super-saturated", and that
the duration of the pool-in-hollow correlates with the amount
of $CaCO_3$ taken up. The fact that solution by rain-water is
sufficient to create hollows suggests that these features are
active rather than residual, and formed in open air rather than
under closed cover. This further implies that the Gait Barrows
pavement may still be evolving, and that the situation examined
in 1981 will not necessarily be identical in years to come.

Minute topographic variations on the pavement may be
expected to influence the precise distribution of superficial
features, but at Gait Barrows it is not possible to distin-
guish many embryonic hollows where rain-water accumulates.
Lithological irregularities, also, may enable differential
chemical weathering to take place, whereby solution-hollows
are created, although Ivimey-Cooke (1965) claims that "flaws
in the rock, such as isolated chert fragments, do not gener-
ally develop into solution-cups". Sweeting (in Dury, 1966)
suggests that hollows "are often aligned in series in the
directions of jointing", but at Gait Barrows the paucity of
visible structures within the limestone, at least as indicated
by opened grykes, renders this correlation tentative. None-
theless, the incidence of long axes of the solution-hollows
(approximately North-South) accords fairly well with one main
trend of major grykes (Parry, 1960); and some hollows, for
example 'I' and 'z', have revealed the existence of latent
joints [2], which also correspond to their long axes.

Networks of mineral-veins (see Section 1 : 3 : 4,
and the relevant photographs) traverse the limestone, and
over half the hollows examined (53%) are crossed by these.
The frequency of veins allied to the abundance and size of
solution-hollows makes this coincidence not remarkable.
Moreover, seldom do veins apparently dictate the major
axes of the hollows; occasionally they terminate the
excavated area as if inhibiting rather than encouraging
solution-processes; and some sites, such as 'D' and 'T',
are notably by-passed by conspicuous veins lying only a

2 latent joints = "thin and hair-like, only apparent when
the rock is broken up" (Jennings, 1971).

short distance away. The following Table, extracted from field-notes, shows the variable and inconsistent relationship between solution-hollows and mineral-veins.

TABLE XVIII Solution-hollows v. Mineral-veins   (selected entries)

Code	Comment	Interpretation
C	vein cuts across one edge	not significant
F	two veins but not axially placed	not significant
G	largish vein across middle	possible focus of solution
c_a	major vein truncates end of hollow	significant
18d	veins govern odd shape (Photograph 10)	significant
t	many veins dissect this runnel-type site	not significant
48w	vein goes through hollow, but at wrong angle	accidental
6_2	cluster or network of veins	not significant
24	several veins	very significant
32	veritable artery, 10 centimetres in thickness, crosses this hollow	significant

The interpretation 'significant', above, means that it seems probable that the existence of the vein had some effect on the origin or the morphology of the site involved.

Using physical parameters by themselves, it is difficult to arrive at a coherent explanation for solution-hollows' being etched into the limestone-surface at the precise spots where they occur. Considering the diversity of forms which Gait Barrows exhibits (see Chapter 3), perhaps a single, over-riding cause is not to be expected.

Authorities generally agree that biotic factors play
an important part in the development of solution-hollows.
Zotov (1941) believes that small-scale corrosion is initiated
under miniature mats of mosses, such as Tortella phaea, which
was found in almost all the solution-cups he studied.   Amongst
the mosses which occur in the Gait Barrows hollows are Tortella
tortuosa, related to Zotov's T. phaea, (in 25% of the sites),
and Fissidens sp.;   both of these are mentioned, as well, by
Ivimey-Cooke (1965), who considers them as important in the
'pioneer phase' of the development of solution-hollows in the
Burren and on Hutton Roof respectively.   Mats or mounds are
a conspicuous vegetational feature of the hollows at Gait
Barrows, and often, especially when Bryum pseudotriquetrum
(22% occurrence) is a component species, exhibit the storeyed
arrangement of:

> leafy shoots,
>
> decayed matter,
>
> rhizoids,

on the base of the site, which Zotov (1941) thought was instr-
umental in producing acidic drainage and peaty substrate, below
which solution of the limestone took place.   If such mats are
the initiators of the hollows, however, the earliest stages of
development should be apparent.   Accumulations of mosses on
the Gait Barrows pavement seem to be in already well-established
solution-hollows, and the mossy growths on the smooth, upper
pavement, i.e. directly on unaffected clint-surfaces, prove
to be unfixed and unstable.   For example, small patches of
Tortula ruralis and Bryum argenteum on the central pavement

had been moved, presumably by wind-action, so as to obscure the code-number '15' printed on the nearby limestone, and loose aggregates of moss are frequently blown into hollows. (Personal observations, May 24th).

It seems equally correct, therefore, to regard species of mosses as among the early colonists in a favourable habitat provided by other agencies. Once hollows exist, it is no doubt true that they act as "foci for the accumulation of lichens and moss-spores" (Sweeting, in Dury, 1966). She considers that such vegetation "tends to increase the CO_2-content of the water, and the hollow deepens". Jennings (1971) comments that not only are CO_2-values enhanced by the organic matter, but that the "fine clastics may seal off the flattest, lowest parts of the bottom" so that limestone-solution is concentrated "on the steep to over-hanging sides of the pan", i.e. where CO_2-renewal coincides with least protection of the rock. Such an interpretation accords with observations at Gait Barrows insofar as some precipitous edges of the hollows show an irregular, fretted appearance at the junction of rock and water. As water-levels drop, so a zone of pocked and friable limestone emerges, in some instances — site 'M' demonstrates this well — covered with a pinkish-grey scummy deposit of weathered $CaCO_3$ (see Section 5 : 3), indicating that chemical action has been both pronounced and recent.

Quite probably, the basal attack described by Sweeting (1966) and the "rock-air-water line" focus of Jennings (1971) are complementary, or at least alternative, processes, and not mutually incompatible.

Rates of solution of limestone are difficult to
determine, and local factors have considerable effect. Two
statements, however, may shed helpful light on the develop-
ment of Gait Barrows solution-hollows. Firstly, Zotov (1941)
believes that the 'solution-cups' he studied had formed since
the deforestation of the area, and therefore over a period of
a few hundred years. Such a rate of solution would destroy
the pavement in the geologically near-future. More rele-
vantly, Sweeting (in Waltham, 1974) describes a 20-year
vigilance over a defined portion of limestone pavement in
Yorkshire, where "small solution-hollows have developed
during the period of observation that did not exist at the
beginning of the experiment".

Not all geological processes are imperceptibly slow.
The writer has witnessed recognizable reduction of limestone
coastal features from marine erosion in as little a time as
five years. It will be interesting to see how long Gait
Barrows retains its present character of intact pavement.

SUMMARY of CHAPTER 6

The Gait Barrows pavement is a glacio-Karstic feature, i.e. its formation has been dependent on erosion by moving ice, followed by chemical weathering (solution) of the limestone surface, either sub-aerially or under a drift-cover. No sign of this is visible, but circumstantial evidence, and certain details of micro-morphology, imply that the pavements are in fact exhumed.

The high ratio of clints to grykes which characterises the Gait Barrows pavement is a function of several inter-related factors: the sparry nature of the rock; its horizontal bedding; and its relative freedom from major joints. Massive pavement of this type lends itself to the formation of solution-hollows which Gait Barrows has in some abundance, but the incipience of these minor solutional forms is hard to determine. Early in their history, they collect not only standing water but also sediments and plant-colonists such as lichens, mosses and algae; some authorities believe that this biotic material actively instigates the process of formation.

CHAPTER 7

PATTERNS OF BOTANICAL DEVELOPMENT

7 : 1 Introduction

The geological processes discussed in Chapter 6 produce a palimpsest on which post-Glacial events are successively inscribed. Subsequent developments at Gait Barrows have been the generation of a cover of natural vegetation, and also the imprint of man, including recent spoliation of the pavements, as recorded in Section 1 : 3 : 3.

7 : 2 The Early Vegetational History

The limestone tracts of Lowland Lonsdale have experienced a conventional floristic history (Oldfield, 1960). Pioneer plants included Juniperus and Betula; both are still present at Gait Barrows. Bare outcrops of limestone in Pollen Zone IV were colonized by Corylus, which grew in grykes. Ulmus glabra (probably subsp. montana) partially replaced this in Zone VI a, and was itself superseded by Pinus, which reached its maximum in Pollen Zone VI b, actually "growing on the solid limestone" North of Hawes Water (Oldfield, 1960, op. cit.), i.e. in the very near vicinity of Gait Barrows.

Incomplete though the evidence is bound to be, one may entertain visions of the pavements about 5 000 B.C. as being well-vegetated, and, moreover, regard present specimens

of _Juniperus_ and _Pinus_ as having a long and true pedigree
(Oldfield, 1965). Nowadays, the woodland parts of the Gait
Barrows Reserve, though of an obviously secondary nature,
contain representatives of other long-established species
which once contributed importantly to British forest-lineage,
such as hornbeam (_Carpinus betulus_) and small-leaved lime
(_Tilia cordata_). The latter species is usually a relict
of uncleared land (Pigott & Huntley, 1980). The central
pavement at Gait Barrows has about 20 species of woody plants,
most of which probably have their ancestral roots in history
as firmly as their physical roots are in limestone! The
total assemblage is suggestive of a lengthy and varied
tree-cover.

Vegetation change resulting from deforestation by
man, rather than solely for climatic reasons, is now a well-
explored argument (e.g. Iversen, 1956; Turner, 1962; Penn-
ington, 1974). Oldfield's (1963) conclusions for Lowland
Lonsdale are that a fluctuation of conditions took place,
dependent upon human incursions, for pastoral land-usage
and later 'Landnam' cultivation, and retreats. Oldfield
reconstructs a continuing alternation of woodland cover and
farmland reclamation through more recent, i.e. post-Roman,
times. Much of this history is related to ownership by the
influential Furness Abbey.

Details for Gait Barrows specifically are so far
lacking. Lousley (1950) commented that "the wooded pavements
of Middlebarrow, Gait Barrows, and Cringlebarrow have crowded,
well-grown trees, which form a continuous canopy". If this

is literally true, it may mean that the present open pavement
has been revealed in the last half-century. Observations by
Sweeting (in Waltham, 1974) that new solution-hollows appeared
during a 20-year study of Yorkshire limestone (see Section
6 : 2 : 2) also suggests that the vegetational development
of the Gait Barrows sites _may_ have taken place within living
memory. Further research on a local basis might elicit the
relevant facts.

7 : 3   The Origin of Plants

The 100 solution-hollows studied at Gait Barrows con-
tain a total of 83 vascular plant-species. Why such a large
variety? Calcicolous species in Britain much outnumber cal-
cifuges (Grime, 1979, _inter alia_). The Arnside district of
North Lancashire is botanically richer than any other 10-km.
square of its latitude (54° 10' North), and comparable to
famous areas in, for example, Kent (Information Board, at
Leighton Moss Reserve). Petty (1902) listed 400 species
for 'Silverdale' alone. Within the immediate vicinity of
the Gait Barrows pavements to-day is a wide variety of hab-
itats, both natural and man-made. Amongst these are the
wet-land environments of Leighton Moss (MAP 1) and Hawes
Water (MAP 2). It can readily be envisaged that the
anomalous _Typha latifolia_ plants in site '46r' originated
as either wind-borne or bird-carried pappus from one or
other of these localities. Wildfowl such as mallard
(_Anas platyrhynchos_) and shelduck (_Tadorna tadorna_), as
well as gulls (_Laridae_), flight over Gait Barrows daily.

The "reservoir of suitable species" (Grime, 1979) available to colonize new habitat is, therefore, large, and there is little problem in explaining the occurrence of any particular plant, calcicole, arable weed, or true aquatic, in the total list gathered from the Gait Barrows solution-hollows. Local availability, plus the dispersal powers of reproductive units, allows the sites' potential for varied flora to be realised. This potential is in part a function of the precise habitat-characteristics; that at least some of the hollows are wet for some of the time grants opportunity to a different range of plants for successful colonization. The moisture-bearing capacity is a fundamental reason for the solution-hollows' flora being not simply a mirror-image of the general vegetational composition of limestone pavement, as has been mentioned already in Section 3 : 2 : 2. The hollows are thus validly a member of the "clearly defined minor habitats" recognized by Ivimey-Cooke and Proctor (1966) in the "complex mosaic of fragmentary patches" constituting limestone pavement.

7 : 4   Aquatic v. Terrestrial

The distinction of aquatic and terrestrial sites is intrinsic to this study. TWINSPAN results broadly reiterate the prima facie division. Divergences between the original, subjective dichotomy and the TWINSPAN allocations are explicable in vegetational terms — TWINSPAN uses vegetational criteria, and thus moves sites such as 'C, Q, and Y' with no dominance of aquatic vegetation, algae in particular,

from aquatic to terrestrial categories, and treats sites of mixed character (for example, '7H, 19e, 46r and 48w') as terrestrial.

For the moment, let us consider 'aquatic' and 'terrestrial' as purely physical conditions irrespective of floristic composition. 'Aquatic-ness' is a temporary state; sooner or later (most) pools evaporate and hollows dry out. This may happen seasonally. The duration of the Gait Barrows investigation was inherently too brief for this to be fully witnessed. Thus, 'aquatic' is a valid concept within the limits of this study, but less so over the total life-history of any site. As if to confirm the transience of so-called aquatic sites, TWINSPAN sub-divides these on the very ephemeral criterion of algal abundance and distribution.

Another expression of their impermanence is that all hollows, including the now-terrestrial sites, begin in an essentially aquatic state. "Water collects in pools and basins, and as a result of solution by stagnant water such basins are enlarged" (Sweeting, 1973). The embryonic stages depend on weather-conditions; the persistence of standing water reflects the balance of rainfall and evaporation, creating a wet-dry-wet sequence. Eventually increased depth-to-bedrock permits increased permanence of water, particularly on limestone of weak porosity (Jennings, 1971), which is perhaps the case at Gait Barrows. It is probably at this stage that lateral extension and the production of sheer sides occurs.

Slightly worrying is the apparent lack of hollows at Gait Barrows in the earliest phase of formation. One would expect them to be manifest particularly after showers, when rain-water lodges briefly in miniature topographic depressions. Site 'b' is the nearest approximation amongst the sampled 100. It is shallow (4·4 cms. depth-to-bedrock), desiccates quickly, and, significantly, has no plant-species at all.

There is, though, absolutely no evidence that the terrestrial condition is anything other than secondary, i.e. that terrestrial developments require a relatively 'mature' environment in the form of an already well-excavated hollow. Thus, aquatic status is not temporary merely in the sense that the hollows may fairly easily dry out, but also in that many sites lose their original identity and become, ultimately, terrestrial. The direction of change is, however, one-way only, and it is hard to envisage advanced terrestrial sites returning along the path they have already travelled. Many Gait Barrows hollows, including those subjectively classified as owing an allegiance to both states, and others transferred by TWINSPAN from aquatic to terrestrial, suggest a position between the two extremes. The rate of transition, and whether it is enacted by continuous and gradual evolution, or by a more irregular development, is beyond the scope of this discussion.

The terrestrial condition, in purely physical terms, implies a solid substrate. Gait Barrows limestone is not as clean as it looks; a hand placed on dampened rock picks up copious quantities of black specks. This material is washed or blown into hollows, and accumulates there. Depressions

consisting of a 'double-basin' profile are especially
efficient at trapping such silt (see Section 3 : 3 : 3,
including Graphs 5 a and 5 b). Site 'b', mentioned ear-
lier, has as yet negligible silt-content.

A clear picture emerges, therefore, that the Gait
Barrows solution-hollows are susceptible to change, and not
simply static features of ever-lasting characteristics. It
may be repeated here that they are active rather than resid-
ual, a conclusion reached already (Section 6 : 2 : 2) on
geological grounds, and certainly not just the long-abiding
remnants of a former, more widespread, vegetation. The
modes of alteration in floristic terms are outlined in the
next Section.

7 : 5   Vegetational Developments

Previous writers (Ivimey-Cooke, 1965; Sweeting (in
Waltham), 1974) affirm the importance in both corrosion and
colonization processes of rock-hugging lichens, which minutely
fragment the limestone-surface and also provide an organic
veneer. Lichens encrust rock irrespective of topography,
however, and their presence in well-formed solution-hollows
has not been studied in this investigation. Probably they
are less important than algae and saxicolous mosses. Of the
former, Nostoc's ability to survive desiccation, its N-fixing
capacity, and relatively bulky biomass, are all valuable to
the early stages of terrestrialization. The role of mosses
has been stressed by Zotov (1941) and Sweeting (1966) in part-
icular. At Gait Barrows, several species are abundant, and

the part they play in the early processes is discussed in
Section 6 : 2 : 2.

In terms of succession, Fissidens seems especially
important. Not only does it occur in 45% of the sites,
but its dominance in otherwise poorly-vegetated hollows,
and persistence (usually in lesser quantities) where a
larger variety of plants has become established, suggests
that Fissidens is a bridge between primitively aquatic and
progressively terrestrial characteristics. Its leafy form,
when decayed, contributes to the developing depth of sub-
strate. Site 'C', shown on Graph 5a, (Section 3 : 3 : 3),
demonstrates the manner in which Fissidens growths direct
the terrestrialization process.

The autochthonous accretion of what is by now an
organic soil absolves the hollow from dependence on the
accidental arrival of wind-blown material. Milestone though
this may be in the physical development of the site, it does
not automatically confer terrestrial status in vegetational
terms. Hollows which are large enough, such as 'P' and 'X',
or simply very deep, like 'I', (see Section 3 : 3 : 2, Table
VII), retain their pools, and despite captured sediments and
home-produced humus, vegetation is still of an aquatic type.
Algae may well remain dominant. Of vascular species, Juncus
articulatus emerges very commonly from silt in water-filled
hollows. Its tufts often form single-species stands, and
create vegetational islands encircled by clear water (see
Section 3 : 3 : 3, and Photographs 9 and 10); often, this
is the limit of development in truly aquatic sites.

Elsewhere, _Juncus articulatus_ seems to have been the starting-point of more terrestrial growths, and hollows where this progress has taken place, perhaps by virtue of accelerated build-up of solid substrate, become — both visually and according to TWINSPAN — terrestrial. Usually these sites are allocated to TWINSPAN terrestrial category 'b'. Some low cover-values of _Juncus articulatus_, for example in '19e' and '23', might be interpreted as relict populations gradually being overwhelmed by species of drier habitats, such as _Festuca rubra_ and _Molinia caerulea_. Longer-term studies are needed to confirm this, but it may well be that one pathway from aquatic to terrestrial character, in vegetational terms, is by means of _Juncus articulatus_. If this is so, it is obviously more typical of deeper sites where retained moisture is prevalent, and a transition involving a vegetational factor is necessary.

In shallow sites, however, the main physical attribute of a terrestrial condition, namely soil, is reinforced at an earlier stage by drought or drainage, and allows a truly terrestrial flora to develop. At Gait Barrows, one plant more than any other species seems instrumental in effecting the beginnings of terrestrial succession in shallow sites. _Sedum acre_ is the most frequently-occurring dry-land species in the sampled sites (see Section 4 : 4). In some instances, e.g. site '24', it is very dominant; often it partners saxicolous mosses mentioned earlier; and in two depauperate hollows, 'G' and 'U' (see Section 3 : 3 : 2, Table VII; and Section 4 : 4), _Sedum acre_ is virtually the only inhabitant. Its ecological suitability as a primary colonist in such circumstances is

mainly tolerance of the drought typical of "shallow soils
...... developed particularly on basic or calcareous rocks"
(Harder et. al., 1967); resistance to rabbit-grazing (Tan-
sley, 1939) may also be a useful asset. Sedum acre prob-
ably helps to stabilize the substrate within the hollows,
although loose, wind-blown fragments of the plant are not
uncommon. It seems, too, to withstand at least temporary
saturation when its surroundings are flooded by rain, and
in fact Sedum acre occupies two sites which are classified
as aquatic (see Section 4 : 3). It is equally character-
istic of the newly-exposed, rubble-strewn limestone of the
quarried zone. A congener, Sedum telephium, is also pres-
ent in the Gait Barrows solution-hollows, (nine sites), but
is not regarded as exhibiting the same pioneering spirit.

Another stonecrop, Sedum album, is, however, a com-
parably early invader of open limestone in Gotland (Denmark)
(Gimingham et al., 1966). This species, like S. acre at
Gait Barrows, is associated with other primary colonizers,
especially Tortella tortuosa, and also with "an accompanying
accumulation of a skeletal soil". This lichens — mosses —
succulents pattern noted by Gimingham and his co-workers is
the first phase of a "dynamic sequence representing the early
stages in a colonization succession". The roles performed
by the two species of Sedum in their respective localities
are very similar, and each introduces a more complex, varied
vegetation which supersedes the Sedum-phase.

Following this, however, it is difficult to give a
synoptic account of vegetational development. Morphology

of the hollows, and even detailed topography of silt- and
humus-accumulations, influence vegetational change. Sites
with little relief, where sediments and/or vegetation mats
have choked the basin to pavement-level, drain spontaneously
outwards, aridity is even more prevalent, and plants are
more exposed. Under such circumstances, the inhabiting
flora tends to comprise lower-growing species whose life-
cycle is annual, and whose seed-production is relatively
rapid and early. Poa annua in several sites, for instance,
had died by July 5th. Such hollows are generally placed by
TWINSPAN in its terrestrial category 'a', and have been des-
cribed as 'physiognomically flatter' sites (see Sections
3 : 3 : 2 (including Table VII) and 4 : 4).

Deeper, more sheltered, partially water-filled sites
(terrestrial category 'b') give rise to a very contrasting
flora, dominated in general by a mound of taller and tufted
species, surrounded and in-filled by the relict moisture-
loving community, particularly mosses. This type is also
treated in Section 4 : 4, and Diagram 4 attempts to portray
such a hollow. The accumulation of sediments, and later,
and more importantly, decayed plant-material, may create a
pronounced feature whose topmost zone is quite possibly above
the normal levels of both standing water in the surrounding
hollow and saturated soil, so that leaching of minerals is
accentuated. The chemical analysis referred to in Appendix
H suggests downward removal of calcium (but not other bases), or
at least the failure of this element to penetrate upwards
by capillarity.

The phenomenon of increasing calcium with depth is especially marked in the soil-core extracted from site '19e', which is tenanted by a group of plants, _Molinia caerulea_, _Carex pulicaris_ and _Carex hostiana_, all at cover-values of 5 or more, characteristic of slightly drier and nearer-to-neutral conditions. One hollow does not, of course, make for a hypothesis, but as it happens two neighbouring sites, uncoded and outside the sampled 100, have precisely the same tussocky appearance and component species. Moreover, their exact disposition is very similar in all three vegetation mounds, with _Carex hostiana_ forming the outside of the assemblage, and _Molinia caerulea_ occupying the innermost, highest area. Possibly this arrangement reflects some detailed, intra-site conditions.

Species-richness is likely to be adversely affected by the development of mounds of coarse, tufted vegetation. This has already been demonstrated (Section 4 : 5) with respect to _Festuca_-dominated sites. Reduced diversity is seen as a physical response, because of the shading and competition at root-level exerted by grasses and some robust forbs, rather than a problem of soil-chemistry, for hollow '32', which also shows relative calcium-deficiency in the upper part of its soil (see Appendix H), nonetheless has a very high species-richness score. The tendency towards acidic conditions in '32', though it does not inhibit diversity of flora, may be responsible for the occurrence of one particular species, _Potentilla erecta_, which is associated more closely with acid-to-neutral chemistry of the substrate rather than a lime-rich environment.

Although acidification within the solution-hollows is a trend which merits at least brief consideration, the present evidence suggests that such effects are limited in importance. The statement made in the Introduction (p. ix) to this study, that there is no real link between the sites investigated and the patches of "apparently acidophilous scrub", remains valid.

One special pattern, recognized by TWINSPAN even though it applies to only two sites, is the establishment of Sesleria albicans in company with a dearth of other species (see Section 4 : 4). Reasons for the assumption of a dominant status by this particular grass have been put forward by Mrs. Jean Dixon (pers. comm.), who is currently studying Sesleria albicans at Bradford University. Early investment in root-development, rather than above-ground growth, enables Sesleria to survive drought at a stage when other plants might succumb. It is, however, tolerant of a moderate amount of temporary swamping, such as the Gait Barrows solution-hollows experience. Seeds, which are heavy, disperse only very locally; though a relatively small number is produced, germination has been found to reach 96%, and the result of these biological traits is the concentration of Sesleria-seedlings around the parent plant. Strong tillering and culm-production from established specimens will eventually over-shadow and crowd out potential competitors, and prevent new colonists. The chief disadvantage of Sesleria albicans is its rather slow start in above-ground development. Presumably this

is not a severe drawback in relatively shallow, open sites, where seasonal desiccation can be relied on to suppress the less deeply-rooted species while _Sesleria albicans_ gains a secure footing.

The foregoing paragraphs endeavour to explain some of the more obvious patterns of floristic development in the Gait Barrows solution-hollows. The precise composition of well-vegetated sites, however, is almost impossible to summarise or predict. The three richest hollows, '7H, 31 and 32', encompass _in toto_ 40 different plant-species. This is 48.2% of the available floral diversity. Only eleven of these species are shared between two of the sites, and no species occurs in all three sites. Though their starting-points may have been similar, and the initial routes by which their terrestrialization progressed also probably parallel, their destinations, so far as this study is concerned, have been remarkably different. It seems that once a substantial depth of substrate is available, without surfeit of moisture, the membership-subscription to join the terrestrial hollow dramatically drops, many more species can 'afford' to belong to the growing community, providing that they have the res-idence-qualification of calcicoly, and exactly which plants do turn up becomes more a matter of accident than design.

SUMMARY and CONCLUSIONS

The characteristics of this phytosociological study
of solution-hollows on the Gait Barrows limestone pavement
are that it is:

  i/ floristic, concerning plant-species composition,
  rather than functional;

  ii/ synecological, rather than autecological;

  iii/ non-destructive;

  iv/ intensive in scale, dealing with small, enclosed and
  more-or-less self-contained areas on a whole-site
  basis, i.e. not sampled by quadrats, transects, or
  other partial method;

and v/ subjected to multi-variate ordination of both samples
  and species by means of TWINSPAN computer-program.

The Gait Barrows solution-hollows are numerous, and
morphologically both well-developed and varied. Their occur-
rence is entirely consonant with the complex of lithological
and structural qualities of the Gait Barrows limestone, and
the massive style of pavement consequently engendered. The
exact initiation of solution-hollows, however, is difficult
to determine. Once instigated, though, processes of vertical
and lateral corrosion are responsible for their enlargement.
Perhaps the chief historical puzzle at Gait Barrows concerns
a putative drift-cover. Since this would have been an imp-
ortant link between geology, topography and the developing
vegetation, its absence from the present pavement constitutes
a 'missing link'.

The present plant-life of the solution-hollows is, however, not a relict of former more widespread vegetation; nor is it closely related to other extant floral communities in other limestone sub-habitats such as the grykes. The first stage — water-filled sites — entails temporarily dominant algae, with whose abundance unusually high pH-values are associated. A variety of events — accretion of sediments, especially in the lower part of a 'double-basin' profile; accumulation of both living and dead Nostoc and mosses, particularly Fissidens; growth of emergent veg-etation, notably Juncus articulatus; or drying out and sub-sequent colonization by Sedum acre — instigates the transition from the at least seasonally aquatic state to an at least part-ially terrestrial condition. This dimorphism is a fundamental property of the sites investigated at Gait Barrows, though some hollows probably retain their pools permanently, because they are unusually deep, and other sites merely destroy the pavement-surface without contributing a diverse flora.

Following the early stages of development, the sequence is less easy to define. Morphological characteristics affect the precise degree and expression of the process of terrestrial-ization, and the visual extremes are represented by tussocky, species-poor Sesleria- or Festuca-dominated mounds and much more varied, herbaceous sites. Species-availability is high, fidelity is minimal, pattern concerns physiognomy and growth-form rather than actual floristic composition, and prediction in terms of the occurrence of species is virtually impossible.

APPENDIX

APPENDIX A

Chemical Analysis of Vein-Material

The results set out below were obtained from photospectrometry of samples from the main vein at Gait Barrows:

(a)   c. 85% calcite   ($CaCO_3$);

(b)   5 — 7% dolomite ($CaCO_3$, $MgCO_3$);

(c)   4 — 5% quartz   (SiO_2);

(d)   3 — 4% magnesite ($MgCO_3$);

(e)   trace   rhodocrosite ($MnCO_3$).

_____

c. 100%

The analysis was kindly done by Mr. R. G. Hardy of the Department of Geology, Durham University.

These results correspond closely to those determined by Mr. Leslie Rose (pers. comm.), who treated vein-material to acid-digestion which left a residue of 4% sludge, presumably the equivalent of the quartz in the table above. This, with the dolomite which may contain minute quantities of iron, may be the ingredient allowing for greater resistance of the mineral-veins compared to the surrounding limestone.

APPENDIX   B

Dimensions of Grykes on Central Pavement

The measurements of gryke-width and gryke-depth, in centimetres, are recorded below.   They were taken from 40 localities, found at random in the relatively few genuine grykes of Gait Barrows' central pavement.

	width	depth
mean of 40 sites	21·425	106·15
maximum dimension located	less than 40	c.175·00

The equivalent mean values for grykes determined during morphometric studies of the Ingleborough (North Yorkshire) limestone (Goldie, 1973) are:

width   20·42   cms, with Standard Deviation of 10·08;

depth   107·00   cms, with Standard Deviation of 49·0.

This similarity of mean values is further evidence that the Gait Barrows pavements are morphologically of the same style as the better-known Yorkshire examples such as Scar Close (see Section 6 : 1 : 3).

APPENDIX   C

Identifications of Algae

Samples of pool-water from the Gait Barrows solution-hollows
were brought back for laboratory examination.   Mr. Graham
Patterson kindly undertook the microscopic identification
of genera of algae;   the table below describes the appear-
ance in the field and the genera represented in eight sites:

Code	Macro-characters	Genera represented
u	Nostoc weed + 'fga'	Nostoc sp.; Zygnema sp.
S	Nostoc spheroids	Nostoc sp.
X	'fga' of usual form	Spirogyra sp., 90%, + some Oedogonium sp.
m	rather paler, more net-like or web-like form	Zygnema sp., 80%, + Closterium sp., 10 % + Pediastrum sp., 10 %.
h	as for 'm', above	Oedogonium sp.
O	ditto	mainly Zygnema sp., with Cosmarium sp. and Oedogonium sp.
T, V	green sludge coating muddy substrate	Closterium sp., + Oedogonium sp.

The samples were collected on June 22nd and identified the
following day.

APPENDIX D

Definitions of 'Kamenitzas' (Solution-hollows)

Source	Quotation
Zotov, 1941	"undrained circular pits" ;
Sweeting, 1966	"shallow and pan-like, with steep rims and flat bases" ;
Williams, 1966	"small cup- or saucer-shaped depressions" ;
Jennings, 1971	"basin- or dish-shaped depressions" ;
Herak & Stringfield, 1972	"small, shallow dish-like depressions" .

Herak & Stringfield (1972) continue ...... "on consolidated calcareous blocks (solution-hollows) are a clear expression of marginal corrosion due to a lack of vertical joints which might enable the sinking of water, and thus corrosion in a vertical direction."

This seems an admirable summary of the situation which obtains at Gait Barrows.

APPENDIX   E

Physical Dimensions of Sites

E i/ Long axes

Greatest = site 'N' = 225 cms;

Smallest = site 'R' =   28 cms.

E ii/ Short axes

Widest   = site 'U' = 130 cms;

Narrowest = sites'O', = 16 cms.
                  'R'

Eiii/Distances between sites

Nearest neighbours = sites '45&$_A$' and '&$_B$'

$\qquad\qquad\qquad\qquad$ = 14 cms apart;

Furthest distant   = site 'O' in the central part of
$\qquad\qquad\qquad\qquad\qquad$ the pavement and several hollows
$\qquad\qquad\qquad\qquad\qquad$ at radius of approximately 7 metres.

E iv/ Surface - areas

Most extensive = site 'J' = almost two square metres,
$\qquad\qquad\qquad\qquad\qquad\quad$ = 19 637·5 sq. cms;

Least extensive = site 'R' =   351·9 sq. cms.

APPENDIX F

Full List of Plant Species

Asplenium trichomanes,
Pinus sylvestris,
Taxus baccata,
Ranunculus acris,
R. bulbosus,
Erophila verna,
Cardamine hirsuta,
Viola riviniana,
Hypericum montanum,
Cerastium fontanum,
Sagina procumbens,
Arenaria serpyllifolia,
Linum catharticum,
Geranium robertianum,
Trifolium repens,
Lotus corniculatus,
Filipendula vulgaris,
Rubus sp.,
Potentilla erecta,
Fragaria vesca,
Crataegus monogyna,
Sorbus aucuparia,
Sedum telephium,
S. acre,
Epilobium parviflorum,
E. montanum,
E. ciliatum,
Rumex sp.,
Betula pendula,
Corylus avellana,
Salix sp.,
Fraxinus excelsior,

Centaurium erythraea,
Veronica officinalis,
V. serpyllifolia,
V. arvensis,
Euphrasia officinalis,
Prunella vulgaris,
Teucrium scorodonia,
Plantago major,
Galium sterneri,
Succisa pratensis,
Senecio jacobaea,
Inula conyza,
Solidago virgaurea,
Cirsium vulgare,
Centaurea nigra,
Serratula tinctoria,
Leontodon autumnalis,
Mycelis muralis,
Hieracium sp.,
Taraxacum sp.,
Polygonatum odoratum,
Convallaria majalis,
Juncus articulatus,
J. subnodulosus,
Dactylorhiza fuchsii,
Typha latifolia,
Carex hostiana,
C. lepidocarpa,
C. flacca,
C. pulicaris,
Festuca rubra,
F. ovina,

APPENDIX F

Full List of Plant Species (continued)

Lolium perenne,   Polytrichum sp.,

Poa annua,   Fissidens sp.,

Briza media,   Tortula ruralis,

Sesleria albicans,   Tortella tortuosa,

Holcus lanatus,   Bryum pseudotriquetrum,

Agrostis stolonifera,   B. argenteum,

Danthonia decumbens,   Mnium undulatum,

Molinia caerulea,   Cratoneuron filicinum,

                               Pseudoscleropodium purum,

Nostoc sp.,

'filamentous green algae'.

APPENDIX G

pH - values at Leighton Moss

date	site 1 'Juncus Pool', one	site 2 'Juncus Pool', two	site 3 Causeway Dyke
22/5/81	8·95	9·60	
	9·05	9·80	
	9·55	9·80	
31/5/81			9·20

APPENDIX H

Soil - Chemistry

Sample	Ca	Mg	K	Na
'32' upper	344	6·4	13·8	2·1
'32' middle	325	7·2	12·7	2·5
'32' lower	349	4·6	8·9	2·3
'32' base	369	6·6	9·6	1·9
'19e' upper	264	9·8	6·5	8·7
'19e' middle	400	4·2	2·8	2·5
'19e' lower	520	3·4	2·8	2·3

All units are parts-per-million.

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