THE ALGAE OF THE MALHAM TARN DISTRICT

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MALHAM TARN (Yorkshire, O.S. one-inch sheet 90) lies in one of the best regions in Britain for investigations on freshwater algae. There is a rich and varied flora within a short distance of the good facilities available at the Field Centre. Further, if the advice of specialists is needed, the Windermere laboratory of the Freshwater Biological Association is not more than two hours away by road. Some problems can only be solved by intensive research but there are many others about which valuable information can be obtained by careful observation in the field and under the microscope. The references cited will assist those who are interested to obtain more information than can be given in this article. The floras of most general use for the beginner or non-specialist are Fritsch and West (1927), Smith (1933, 1950), Prescott (1951), Tiffany and Britton (1952) and Edmondson (1959). Here references are given to the relevant pages of Fritsch and West (1927) and Smith (1950) for descriptions and figures of most of the genera and species mentioned. These works are cited hereafter as F. and S. respectively with the page numbers given immediately after so that, for example, S.40 is p. 40 of Smith (1950). Where necessary references are also given to original papers. A word of advice is necessary to those who are not familiar with algae. Most of them are cosmopolitan and a few thousand are British. There is little doubt that over a thousand could be found in this area. Some of the genera are very large; for example, there are about 550 species of *Chlamydomonas* Ehr. and it is unlikely that the same species will be found in any two samples, even when they are collected from nearby places. Some genera are even larger; the diatom *Navicula* Bory has over a thousand species and the specific and infra-specific taxa of the desmid *Staurastrum* Meyen are about as numerous. Therefore it is a sound plan to begin by learning to recognize the genera, more than 450 of which are recorded in Britain. It is also true to say that relatively few freshwater algae are described satisfactorily, so that careful observations on selected species are of great value. There is no modern list of algae from this area but that given in West and West (1900-01) will be of help. The general classification of the algae used here is that of Fott (1959) whose book can be recommended also for the clear, simple German and many good figures.

THE TERRESTRIAL AND SEMI-TERRESTRIAL FLORAS

As most of the soils are calcareous, Blue-green Algae (Cyanophyta) and Diatoms (Bacillariophyceae) are well represented. On the Tarn Moss there is little bare peat for soil algae to grow on. However, the characteristic dusky purplish discoloration produced by *Zygogonium ericetorum* Kütz. (F.247; S.298) can be found on small patches, usually around the margins of temporary pools. There are larger, typical patches in the Fountains Fell area. Although often studied because of its remarkable appearance and resistance to drought, much remains to be discovered about this alga. For example, West's (1904) belief, which has often been quoted, that the success of small flowering plants such as Sundews (*Drosera* spp) and Sedges (*Carex* spp) on bare peat may depend to a great extent on the presence of this alga, could be tested experimentally in the field. Species of *Chlamydomonas* Ehr. (F.70; S.75) and *Coccomyxa* Schmidle (F.89; S.132) are common on the peat. These and other Green-algae (Chlorophyta) produce greenish slimes on the bases of old shoots of *Calluna vulgaris* (L) Hull and in the crowns of eroding tussocks of *Eriophorum vaginatum* L. The algae concerned are often said to be species of *Gloeocystis* Naeg. (F.90; S.116), a genus of uncertain circumscription. Careful descriptions of such algae based on examination of given populations at different times of year are needed. *Coccomyxa subellipsoidea* Acton (Jaeg, 1933) is the algal component of the enigmatic "primitive" lichen *Botrydina vulgaris* Bréb. (Acton, 1909; Jaag, 1933; Geitler, 1956) which is very common on the Tarn Moss. A very characteristic alga of acidic soils which flourishes on peat is *Euglena mutabilis* Schmitz (Lund, 1938). It is one of the few algae able to grow on natural substrata at pH 2 or less (Lackey, 1938; Prát, 1955; Fott, 1956).

The soil contains a flora of its own, though many of the algae are close relatives of aquatic forms and some also flourish on mud or in temporary puddles (see Petersen, 1935; John, 1942; Fritsch and John, 1942; Lund, 1945, 1947 and in the press, a). The seasonal periodicity of this community has rarely been followed even qualitatively, and then usually in agricultural and garden soils. In the wood flanking the back of Malham Tarn House there are very suitable areas for such observations on natural soils. It may be expected that, like vernal herbs, the algae will grow rapidly before the tree canopy develops. They are certainly abundant at this time but considerable numbers can still be found in summer under the carpet of *Mercurialis perennis* L. where moisture conditions are usually good. However, wherever dead leaves accumulate and do not decompose quickly, the exclusion of light causes a marked decrease in their numbers. Similarly the coniferous areas are poor in algae. Some workers believe that this is more from the inhibiting effects of the substances produced in conifer litter than from the prolonged covering of the soil surface.

The effect of even limited cultivation can be seen in the small flower beds near the house. These often bear macroscopic growths of Green-algae; *Vaucheria* DC (F.293; S.402), an alga long believed to belong to the Chlorophyta but now placed in the Xanthophyceae (Yellow-green algae), and *Cylindrospermum* (Cyanophyta, F.480; S.586) which forms small, shining dark blue or black slimes. The effect of disturbance can be followed easily, for areas recently dug and raked are much poorer in algae than the others. When inorganic fertilizers of the "compound" (NPK) type are sprinkled on the surface, the soil soon turns bright green from the vast multiplication of coccoid algae together with *Hormidium* Kütz. (F.154; S.146) and *Stichococcus* Naeg. (F.158; S.145). This effect can often be seen on the surface of the pots in which the Chrysanthemums are grown. On grassy, well trodden field paths the small dark greenish or blackish, more or less wrinkled, masses of jelly produced by *Nostoc commune* Vauch. (F.477) sometimes appear. This alga is known to the French as Crachats de Lune.

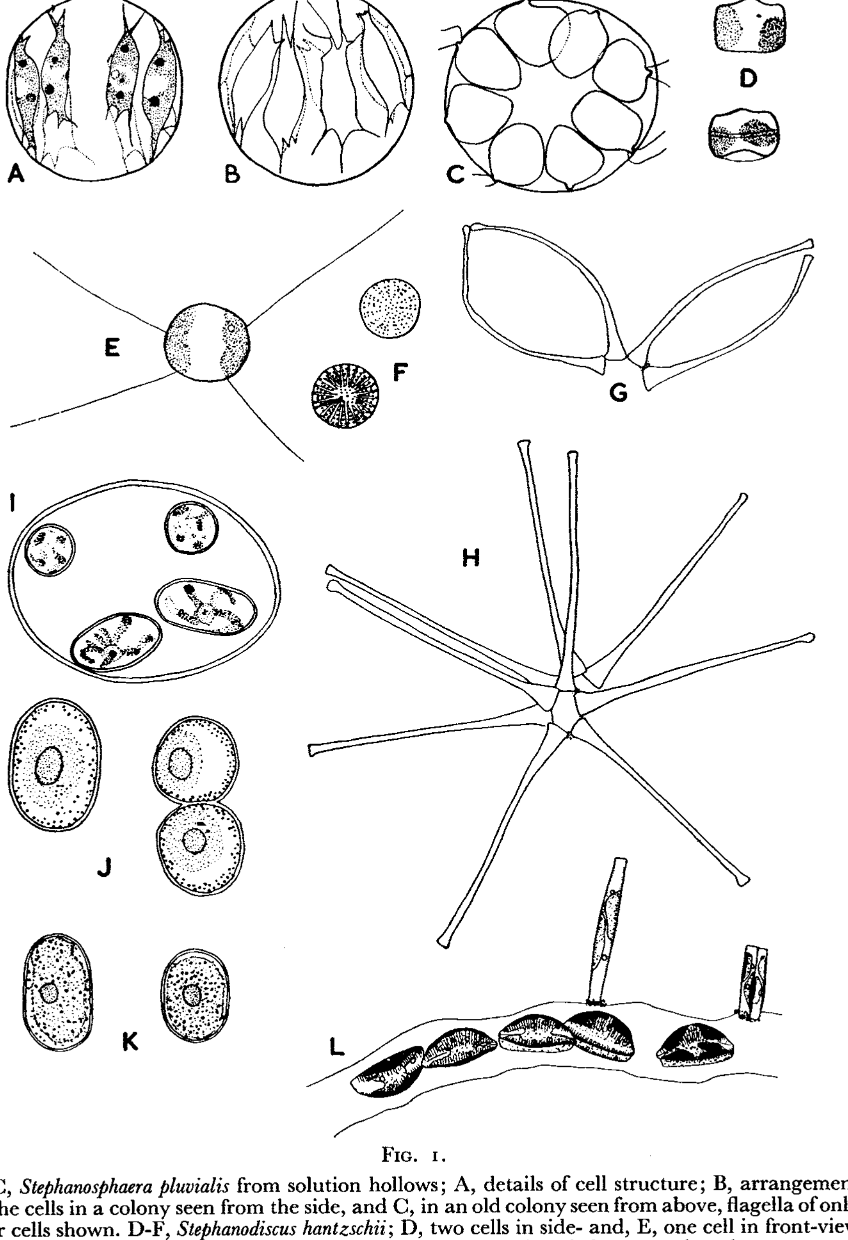


FIG. 1.

A-C, *Stephanosphaera pluvialis* from solution hollows; A, details of cell structure; B, arrangement of the cells in a colony seen from the side, and C, in an old colony seen from above, flagella of only four cells shown. D-F, *Stephanodiscus hantzschii*; D, two cells in side- and, E, one cell in front-view showing four of the spines; F, two cells, cleaned, mounted and drawn under phase contrast. G, *Asterionella formosa* var. *acaroides* and H, *A. formosa* var. *formosa*, both from a sample taken on 22 July 1959; only cell outlines shown. I, *Glaucocystis nostochinearum*, from a weed bed, a form with narrow elongate "endophytes". J, K, two *Mesotaenium* spp from jelly on mosses; the clear space between the marginal granules and chromatophore in J is occupied by purple sap. L, *Cymbella prostrata*, part of a colony, attached to the mucilage tube are two *Synedra* spp.

A-C, L × 500; D-F × 1,250; I, K × 640; J × 750; D, E, I-L alive, A-C killed in osmic acid and G, H in formalin.

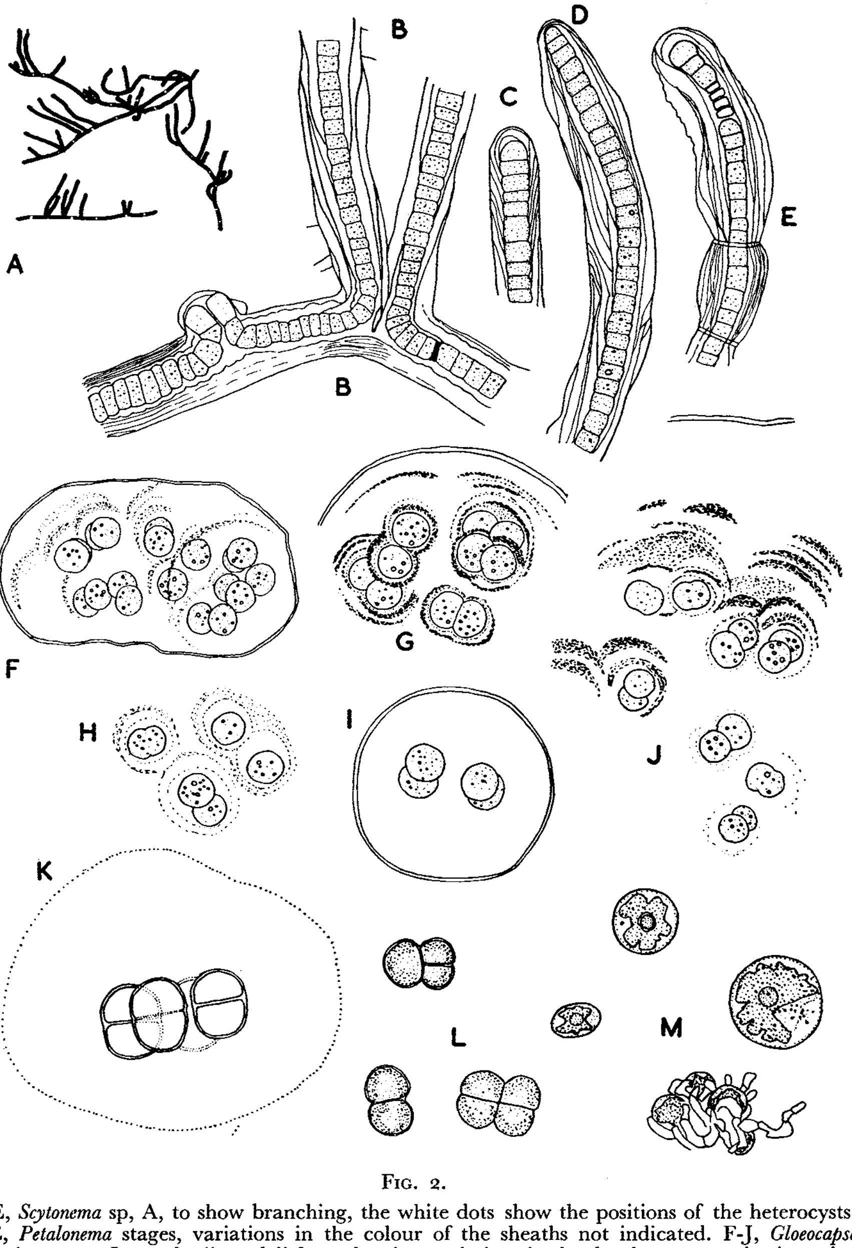


FIG. 2.

A-E, *Scytonema* sp, A, to show branching, the white dots show the positions of the heterocysts; B-E, *Petalonema* stages, variations in the colour of the sheaths not indicated. F-J, *Gloeocapsa sanguinea* sensu Jaag; the "purple" form showing variations in the development and orientation of the sheaths or their absence (I). K, *Chroococcus limneticus* Lemm., from the tarn plankton. L, *Pleurococcus* sensu lato. M, *Trebouxia* sp. showing variation in the size and shape of the cells and, bottom right, partially lichenized cells.

A × 20; B-E × 400; F-J × 750; K × 640; L, M × 700, except bottom right, × 400. All alive.

The most widespread alga in Great Britain is the so-called *Pleurococcus naegelii* Chod. (Fig. 2, L) or *Protococcus viridis* Ag. (F.209; S.166), which forms a bright but pale green powdery coating on trees, posts, stonework, rocks, etc. However, in fact, there are several algae involved, all of which may look very alike under natural conditions (e.g. Vischer, 1960) and practically nothing is known about their separate distributions in Britain. Until proper studies have been made, the discussion of their ecology will continue to be bedevilled by arguments as to which alga was being observed (e.g. Edlich (1936) re Fritsch (1922) and Fritsch and Haines (1923)).

This group of algae is well developed at Malham both on trees and on the limestone. A characteristic feature of the flat, loose limestone flakes common in and around areas of pavement is that this community is either on the outer parts of the undersides of the surface stones or on the upper surface of the stones beneath them. Such positions afford the "*Pleurococcus*" community the conditions it favours, namely, moderate illumination at all times of day or during a considerable part of it, freedom from direct precipitation, and relatively high humidity. In this group are the few British algae able to obtain their water from vapour. Similar growths are found in the entrances to cracks and holes in limestone cliffs.

The ill-effect of being wetted by water is the reason for the absence of these pleurococcoid algae in the larger rain tracks on the branches and boles of the trees in the Tarn House wood. Just to one side of such tracks they may flourish, probably because here the humidity of the microclimate is high and perhaps also because nutrients carried down in these tracks diffuse outwards, particularly in a dry period after rain when there will be a lateral gradient of moisture. In addition this may be a good area for collecting the separate species and genera because Edlich (1936) says that they occupy different positions in relation to dampness. Thus outside the rain-track areas, his *Apatococcus* extends higher up the bole than his *Pleurococcus*.

These algae and the associated lichen, *Lecanora conizaeoides* Cromb., whose algal partner (gonidium) is a species of *Trebouxia* Puymaly (F.106; S.224), and with which they may at first be confused, are eaten by Psocids whose ecology was first studied in detail at Malham (Broadhead and Thornton, 1955).

Near the bases of trees some intermixture with the soil flora is likely. *Hormidium* and the *Hormidium*-stage of *Prasiola* Menegh. (F.164; S.195) may extend a little way up the bole, while *Stichococcus* is often present near or in the base of the pleurococcoid community.

Trebouxia (Fig. 2, M) may be found almost anywhere in these powdery coatings but is almost always more or less completely immersed in fungal hyphae, so that there are all stages between fully developed lichens and lichenized algae. Several of the genera mentioned in this section, especially *Coccomyxa*, include species or infra-specific taxa which are the algal components of lichens. In some books on lichens *Protococcus* Ag. is the commonest Green-alga mentioned as a gonidium. This name has been applied to such a variety of algae that it is best deleted, like *Conferva* L. Even if it is the *Protococcus* of old authors or the *Pleurococcus* of modern ones, it is still far less common as a gonidium than was originally believed. The number of lichens which have been investigated properly is still not very large and nearly all our knowledge of the algae of

British lichens is based on the assumption that they are the same as in the populations existing elsewhere. There is, then, scope for much careful observation on natural and cultivated gonidia.

The algal flora of Moss tussocks and liverworts has received little attention in Britain. Round (1957) described the diatom flora of Bryophtya over which water seeped intermittently. At Malham, algae, including diatoms, can be found in moss tussocks which are only wetted by direct precipitation (the xerophytic community of Beger, 1927), while in areas rich in Bryophytes every gradation from terrestrial to aquatic conditions can be found. Diatoms offer certain technical advantages as organisms to study, and the ecology of those in mosses offers fascinating opportunities for research on their relation to light, temperature, moisture and nutrient conditions at various levels within the tussock or stratum. An extraordinary unexplained feature of the diatom assemblages at Malham and elsewhere (e.g. Round, 1957) is that certain species, such as two of *Melosira* Ag. (F.354; S.462), are often common in mosses and yet absent in the soils except for empty frustules, though even these are rare. Many mosses, particularly in wet summers, have greenish or almost blackish slimes on them produced by *Coccomyxa* and a desmid *Mesotaenium* Naeg. (Fig. 1, J, K; F.229; S.305). Under and at the margins of these slimes the moss is dead or unhealthy. My own casual observations suggest that the algal growths cause the death of the moss leaves, not that they colonize already damaged areas, but no detailed study of the interrelationships of these plants has been made.

On walls, including those of Malham Tarn House, can be found orange, brick-red, yellow or yellow-green powdery to fluffy growths of *Trentepohlia* Martius (F.200; S.179), all the British species of which are exclusively terrestrial. In general the more exposed the plants, the brighter they are coloured. In view of the frequent difficulty of identifying the species there is still need for detailed descriptions of natural communities of these supposedly well-known algae.

An inside wall of one of the outhouses is the only known British habitat of the monotypic *Prasiococcus calcarius* (Boye Pet.) Vischer (1953). This is restricted to highly calcareous substrata in nature and was originally discovered in a grotto in similar abundance and with similar intense coloration to that of the Malham community (Petersen, 1915, sub *Pleurococcus calcarius* sp. nov.).

The flora of the surfaces of permanently or intermittently wetted rocks and cliffs is especially interesting. The idea that the distinction between *Scytonema* and *Petalonema* "appears to be convenient" (Desikachary, 1959, p. 450) can scarcely be held if the blackish, almost mossy tussocks of *Scytonema* Ag. (F.482; S.588) are examined. The Scytonema-stage is best developed in the drier situations and the Petalonema one in wetter places (for illustrations and discussion, see Jaag, 1945). Apart from cliffs, this alga is common on low banks of tufaceous soil and slate close to Mastiles Bridge (Gordale Beck), where the percolating water ensures wet enough conditions for the production of the massive, beautifully lamellate sheaths of the *Petalonema* stage (Fig. 2, A-E).

Two other blue-green algae whose taxonomy has been confused because of a failure to distinguish between phenotypic and genotypic features, are the coccoid *Gloeocapsa sanguinea* (Ag.) Kütz. (Fig. 2, F-I) and *G. alpina* Naeg. emend Brand (see Jaag, 1945). These algae, together with certain lichens, cause much of the bluish-black discoloration of the limestone in the Malham area, although sometimes it is of inorganic origin; possibly soot. Jaag (1945) and Gemsch (1943) have shown that these and similar brownish or rust coloured algal discolorations on acidic rocks, which can also be seen not far from Malham, are produced by the same species. This was previously called *G. sanguinea* when the sheaths around the colony were brownish or reddish and *G. alpina* when they were bluish-black. The pigment changes colour according to the pH of the substratum, being bluish on alkaline and reddish on acidic material, hence the colour of the coatings of the predominantly limestone rocks round Malham. In the drier and more exposed situations the algae form a very thin layer over the rock which when wet is slippery to the touch and can only be removed by scraping. The sheaths are highly stratified and coloured. Under wetter conditions, more obviously mucilaginous layers are formed, and when these are also in more shady positions they can often be rubbed off with a finger quite easily. Then the sheaths are usually paler and less stratified. Sometimes careful investigation of a rich growth will show that the outer colonies are more stratified and highly coloured than the inner which are protected from the higher illumination and more violent fluctuations in moisture. These growth forms have also been given separate names (see Jaag, 1945).

In the Alps the blackish or reddish discolourations produced on rock faces by *Gloeocapsa* often form prominent features well known to climbers because of their dangerously slippery surface when wet. These Tintenstriche (for a fine picture see Jaag, 1945, Tafel, 9, b) are also striking features of the more spectacular Norwegian fiords. The most prominent streaks in the Malham area are on the vertical cliff of Malham Cove.

On wet enough rocks many diatoms may be found and reddish, papery or almost leathery sheets of *Phormidium purpurascens* (Kütz.) Gom. together with small bluish blobs of jelly produced by *Nostoc* spp. The determinations of the last are difficult because the most valuable taxonomic character, the spore, is so rarely produced, and a careful study of them would be valuable.

Strata of *Phormidium* (F.471; S.576) are not always reddish but may be various shades of bluish-green to almost black. This is a common soil alga but usually exists there as separate threads. However, if soil samples are kept in the manner suggested in Appendix I, the typical strata will probably appear after some weeks. In all these habitats *Chroococcus* may also be found. In addition the only British planktonic species is common in the tarn (Fig. 2, K).

A rich and varied flora may be found in the fissures of the flat areas of limestone so common in the district. These grikes (see Proctor, 1960, Fig. 3) contain a variety of micro-habitats. Here may be found bare rock with the *Gloeocapsa* community, Bryophyte communities of diverse type, each with its algal flora, and at the bottom richly calcareous soil. All these communities are undescribed.

Aquatic habitats

(1) *Temporary pools or puddles*

(i) *On Rock*

There are numerous small, shallow solution hollows on the limestone pavement, and scattered ones elsewhere. The bottom and sides of these are often reddish or brick coloured, especially when dry. If this reddish material is scraped off it will be seen to consist of vast numbers of round cells. These are the cysts of *Haematococcus pluvialis* Flotow (*Sphaerella lacustris* (Girod) Wittr., F.79, *Haematococcus lacustris* (Girod) Rostaf., S.110), an alga common in bird-baths. If they have been dry for some time and are placed in a dilute nutrient solution (see Appendix I), they will probably germinate and a population of green, or more or less reddish, free-swimming cells will arise. As the numbers increase the cells will become more and more reddish and finally encyst once more (concerning this alga see Droop, 1953, 1954, 1955, 1956). If they are sub-cultured before this stage, or while they are still green, they can be maintained in the motile stage continuously. *Stephanosphaera pluvialis* Cohn (F.80; S.111) is another common green-alga in solution hollows (Fig. 1, A-C). This beautiful colonial organism provides a good example of an alga which was thought to be very rare because the wrong places were examined. It is widespread and often abundant on limestone in England (Lund, 1950a), Ireland and parts of Spain (Margalef, 1949) but in the rest of Europe and America it is characteristic of non-calcareous rock (e.g. Pascher, 1927; Droop, 1952; Skuja, 1956; Smith, 1950). In England and Ireland I have been unable to find it on acidic rock. A special search was made in the English Lake District because *Stephanosphaera* is so common on the surrounding limestone. In Finland (1952, 1953) Droop found it on granite but not on nearby marble. He believes that the absence of vegetation round the solution hollow is one of the main factors determining its distribution. This seems to be true of the English Pennines, Irish Burren and the Baltic Skerries, and probably of Sweden too because Skuja (1956) says it is widespread on naked rock. It is not clear why this should be so, for it grows much better in an inorganic culture solution if soil extract (see Appendix I) is added, yet Droop found in Finland that even if a pool had pale yellowish water the alga was absent. A similar situation exists at Malham where an abundance of bryophytes on the rock around the pool seems to produce sufficient humic material to be deleterious. Margalef (1949) says that the sources of nutrients in the hollows he studied were vegetable detritus, pollen and sheep dung, and that the typical fauna was chironomid larvae; while Almsted (1933) records it as abundant in a pool rich in humus. At first sight these accounts seem to differ from those of Droop and myself. However, from the Swedish text, it is clear that what Almsted means by humus is bird dung, while Margalef's vegetable detritus may well be wind-borne dust. Swirenko (1926) alone records it from an apparently quite different habitat, namely, the plankton and weed beds of a lake near the Dnestr in Southern Ukraine. He suggests it may have come from the Carpathian Mountains.

A feature which the calcareous solution hollows of the English Pennines and of the Irish Burren, and the ice eroded, acidic pools of the Finnish Skerries have in common is the large number of pools in a given area, whereas in the English Lake District, for example, solution hollows are rare. Considerable amounts of soot may fall in the Malham area depending largely, no doubt, on the wind direction as in the English Lake District (Gorham, 1955, 1958; Proctor, 1960). There was, therefore, the possibility that these pools are at times as acid as those in Finland, notably shortly after re-filling. To test this, dust from a hollow on the carboniferous limestone near Orton, Westmorland, was placed in rainwater containing sulphuric and other acids resulting from industrial pollution, the sample being kindly supplied by Dr. E. Gorham. These hollows are of exactly the same type as those at Malham and each had been found to contain *Stephanosphaera* when wet. The acidity of the rain was neutralized almost at once. After 18 hours there were 18 mg of calcium per litre, so that it is clear that such solution hollows will always be calcareous.

The phenology of *Stephanosphaera* also needs more study. In May, 1948, May, 1951, July, 1957, and August, 1960, it was frequent in the Malham area, but in July, 1956, I could not find a single colony although the very same pools were full of water. I have had similar experiences on the Westmorland limestone. Unlike *Haematococcus*, the resting stage in *Stephanosphaera* is the zygote and it may be that once these are formed a period of rest must be undergone or that they must be dried out before germination is possible.

This alga has been discussed at some length in order to include observations made since the accounts of Lund (1950a) and Droop (1952, 1953) and to emphasize that here is an alga which, in its abundance near the Field Centre, ease of cultivation and largely unexplained ecology, offers excellent opportunities for research. Moreover, these solution hollows contain many other interesting algae which are either alleged to be very rare or are as yet unrecorded for Britain. Various types of pool can be found, though sharp distinctions between them are impossible. Where a considerable amount of black deposit is present, part of which is soot, sulphur bacteria may abound together with the large unicellular Blue-green alga *Synechococcus* Naeg. (F.458; S.557). This alga is remarkable in being one of the few coccoid Cyanophyta which can move, albeit slowly (Lund, 1950a). The means by which even filamentous Blue-green algae move is still not clear (see Fritsch, 1945) but the large cells of this alga make it a useful test organism. In some pools *Nostoc* is found in great abundance. In those rich in plant debris, because they are surrounded by a considerable growth of bryophytes or angiosperms, the flora is more like that in temporary pools on soil. If the whole bottom is covered with humic matter the effect of the calcareous substratum is largely lost and species of *Mesotaenium*, *Coccomyxa*, *Hormidium* and *Microspora* Thuret (F.162; S.148) appear. Birds probably play a large part in enriching the pools with organic matter and distributing the alga.

Among rarities in solution hollows are several flagellates, such as species of *Monomastix* Scherffel, *Pedinomonas* Korshikov (see Belcher and Swale, in the press), *Ochromonas* Klebs (F. Fig. 1, D; S.420) and *Chlamydomonas*, *C. gordalensis* Lund (1954) being only known from near Malham (this alga is placed in *Chlorogonium* Ehr. (F.79; S.81) by Ettl, 1958).

(ii) *On Soil*

Considerable numbers of cattle graze in the area and, in wet and boggy regions, make temporary puddles by trampling. They also influence the chemical nature, and so the algal content, of the water in these and other pools. Innumerable algae may be found in such pools and two of the best areas for them are the Ha Mire and Great Close Mire. In those dunged by cattle *Euglenineae* (e.g. *Euglena*, Ehr., *Phacus* Duj., *Lepocinclis* Perty and *Trachelomonas*

Ehr; F.407 *et seq.*; S.p.352 *et seq.*) and Volvocales (e.g. *Chlamydomonas*, *Chlorogonium*, *Carteria* Deesing, *Gonium* Müller and *Pandorina* Bory; F.59 *et seq.*, S.64 *et seq.*) often predominate. Among supposedly rare British flagellates found here are *Hymenomonas* Stein (S.419), possibly *H. roseola* Stein, species of *Pyrobotrys* Arnoldi (*Chlamydobotrys* Korsh., see Lund, 1942; Belcher and Swale, in the press) *Heteromastix angulata* Korsh. (Skuja, 1956), *Mesostigma viride* Laut. (Lund, 1937), *Lobomonas rostrata* Hazen, *Spermatozopsis exsultans* Korsh., *Chlorobrachis gracillima* Korsh. and *Myochloris* Belcher and Swale (in the press), the last a new genus discovered during a course held at the Field Centre in 1960. *Chlorobrachis gracillima* Korsh. is of uncertain status, some saying it is the zygote of *Pyrobotrys gracilis* (Korsh.) Korsh.,with which it was found at Malham, others that it is a separate organism (e.g. Korshikov, 1938; Hansen and Gerloff, 1952), so that here is yet another problem which might well be solved at the Field Centre.

The less polluted pools contain more Chrysophyceae (F.314 *et seq.*; S.405 *et seq.*), brownish coloured algae often given less attention in botany courses than their evolutionary, ecological and biochemical importance warrant. *Synura* Ehr. (F.325; S.417) and *Mallomonas* Perty (F.323; S.413) are common flagellates whose cells are covered by overlapping siliceous scales which may be spinous. Though the gross structure of these diagnostically important scales can be seen with a light microscope by the techniques used for diatoms (see Appendix II), their full beauty is only revealed in electron micrographs (e.g. Harris and Bradley, 1956, 1957, 1960; Manton, 1955). Chrysophyceae produce very characteristic resting spores which are also silicified. These are very common in post-glacial deposits in peat and underwater muds. There can be no doubt that the peat in the Tarn Moss, which has already been examined for its pollen remains (Pigott and Pigott, 1959), will contain such fossils. Unfortunately too little is yet known about them to be able to refer these fossils to given species. It may be that this will never be wholly possible because many look so alike, but more, careful, descriptions of living material are needed.

Many other kinds of algae occur in these pools, notably diatoms (F.334 *et seq.*; S.440 *et seq.*) and filamentous Green-algae such as *Microspora*, *Spirogyra* Link (F.245; S.299), *Mougeotia* Ag. (F.249; S.292) and *Zygnema* Ag. (F.243; S.296). *Spirogyra* is an algal "type" so generally used in botany courses that it might be thought to be too well known to be of interest. However, few of the approximately 300 named species are satisfactorily described and much remains to be learnt concerning their ecology and cytology.

It is clear, then, that the algae of any such puddle offer scope for intensive study but it should be pointed out that there are considerable difficulties in understanding their ecology. The physical and chemical conditions may fluctuate rapidly and the biochemistry of many of the species is complex and little understood (e.g. Provasoli, 1958). Many of the flagellates may be termed interface organisms in that they flourish when conditions are anaerobic in and near the mud surface and aerobic above. *Trachelomonas* is an example; the euglenoid cells live in cases impregnated with manganese and iron oxides. The cases may be so dark brown that the cells within are invisible. The manganese and iron are obtained in the form of ferrous and manganous salts or as complexes (chelates) with organic compounds. If a pool contains excrement there may be as good a supply of these substances in the water as a whole as at the mud surface but, in general, it is a good plan to collect a mixture of surface mud and the water overlying it. More than 250 species of *Trachelomonas* have been described, nearly all on the basis of the ornamentation of the envelopes. However, this feature is so variable that there can be no doubt that too much taxonomic importance has been given to it (Pringsheim, 1953). What are now needed are careful descriptions of cells as well as their envelopes, and the Malham area would provide a variety of "species" which could be examined and cultivated.

The Tarn Moss contains few such pools and these may be so transient that the flora is similar to that described for peaty soil. Desmids (F.253 *et seq.*; S.310 *et seq.*), which abound in less degraded bogs, are particularly disappointing in number and variety.

(2) *Permanent pools*

In permanent pools quite the reverse may be the case. Thus, in and around the fen area at the head of the tarn opposite the Moss and along the inflow are pools in which may be found many beautiful desmids. The word permanent is used to include pools which do occasionally dry up in periods of drought. Other places where such pools may be found are near Spiggott Hill and in Great Close Mire. The former pools are of interest because they contain drainage from the calcareous hillock and so show transitions between acidic and alkaline conditions. Proctor (1960) records calcium contents in this area ranging from 2·6 to 26 mg/l.

As in the temporary pools and puddles, a great variety of algae may be found but, as yet, so little is known about them that no notable ecological facts can be mentioned.

In many places there are calcareous springs with areas of more or less permanent water around them. These show transitions to the conditions in running water or on land and could, therefore, provide useful information on the effects of variations in flow and moisture on algae. They are usually rich in diatoms, concerning which information can be found in Round (1960a). Diatoms can be used as indicators of salinity and acidity. While many of them will grow over a considerable range of pH and of dissolved calcium, some are very sensitive to these factors and the general picture provided by an analysis of the whole population is usually clear. A good idea of the calcareous and non-calcareous assemblages can be obtained by comparing populations from boggy places round these springs and those in the Fountains Fell area.

(3) *Rivulets and streams*

The majority of the algal investigations in Britain are concerned with lakes, tarns, mires and ponds so that streams are relatively neglected. The Malham area offers good opportunities for rectifying this state of affairs, while the calcareous nature of most of them ensures a rich, varied and interesting flora. Moreover, in the Fountains Fell and Mastiles areas less calcareous or even strongly acidic streams can be studied, and the transition from one state to the other followed in a single stream.

In Gordale Beck live two of the rarest British algae, *Oocardium stratum* Naeg. (F.283; S.325), recorded by the Wests (1900-01) and rediscovered recently by Mr. C. A. Sinker, and *Chrysonebula holmesii* Lund (1953) which has not yet been found anywhere else in the world except here and in a branch of Cowside Beck (coll. C. A. Sinker). *Chrysonebula*, unlike *Oocardium*, is easy to find for, in spring, it covers large areas and can be seen from some yards away, appearing as almost white, jelly-like masses on top of the stones in the areas of rapid flow. It is remarkable that so abundant an alga should have been overlooked for so long.

Oocardium is one of the few desmids growing only in highly calcareous waters; the vast majority of the thousands of species and varieties of these algae cannot grow in such waters. The presence of a rich and varied desmid flora is a sure indication that the water is soft. The cells of *Oocardium* secrete tubes of mucilage around which lime is precipitated. In parts of Europe such as Bavaria and Yugoslavia (e.g. Wallner, 1933, 1934-35; Golubić, 1957) *Oocardium* is very abundant and an important element in the building of tufa. It often forms small nodules on the leaves of mosses. At present it is apparently very rare in the Malham area but careful examination of mosses and stones may reveal new localities.

Some good examples of tufa are to be found in Gordale and in a tributary of Cowside beck, as well as smaller ones elsewhere. There is no evidence that *Oocardium* has played any significant part in their formation but remains of blue-green algae can usually be detected. The species concerned have not been determined but it is probable that one of them is *Phormidium incrustatum* (Naeg.) Gom. which has been studied in the Cambridge area (Fritsch, 1949, 1950; Fritsch and Pantin, 1946). This alga or a nearly related form can be found in the upper parts of Gordale Beck. It forms a striking cover to the stones, being an unpleasant rusty-orange with greyish streaks. There has been much argument about the formation of tufa but there can be little doubt that one of the causes is the extraction of carbon dioxide from the water by photosynthesizing bryophytes and algae, with the consequent deposition of calcium carbonate, normally in the form of calcite.

Another blue-green alga depositing calcite is *Rivularia* Roth (F.488; S.600) which forms small hemispherical cushions or buttons on stones and rocks. When such cushions are bisected, the exposed section shows several layers of material, one on top of the other. These arise from the formation of successive layers of algal filaments with intervening bands rich in calcite, but it is not known whether they represent "annual rings" or not. *Rivularia* is, in many ways, a very convenient alga to study and it is to be hoped that those visiting Malham will pay more attention to it. It is easy to see and unlikely to be mistaken for any other organism. A plant can be marked since it is attached to stone. Apart from finding out how fast it grows and the nature of the "rings", it would be valuable to have information about grazing by animals and the effect of flow. The exact determination of all the species concerned awaits further study, as is the case with so many of the stream algae in the area. The diatoms alone (Round, 1960b) have been investigated, mainly those in the Malham Tarn Beck. Round compares the Malham communities with those from other British streams and rivers.

A curious but common plant in Gordale Beck and elsewhere is what appears, at first sight, to be an encrusting Green-alga. The more or less flat or raised bright green patches are a few millimetres across and, in general appearance, resemble those formed by a branched Green-alga, *Gongrosira* Kütz. (F.197; S.178), whose lime-encrusted thalli are common in calcareous waters. The Malham plant, however, appears to be lichen.

(4) *The Tarn*

This is a small lake (62 hectares) much of it 3 m or less in depth (maximum, 4·4 m) and 380 m above sea-level. There is one main inflow (Tarn Beck) and a few very minor ones. There is no large reed bed but extensive submerged vegetation. The drainage area is open, calcareous, grazed grassland with few trees. Strong winds are frequent and as the rainfall averages about 1,500 mm per year, there is often considerable flow down the Tarn Beck.

The margins of the tarn are very rich in algae, notably filamentous Cyanophyta, diatoms and Chlorophyceae such as *Oedogonium* Link (F.220; S.207), *Spirogyra*, *Cladophora glomerata* (L.) Kütz. (F.168; S.213), *Ulothrix zonata* (Web. et Mohr.) Kütz. (F.152; S.142) which is most common in spring, and *Chaetophora incrassata* (Huds.) Hazen (F.187; S.155). The last grows both on stones and on peat below the eroded face of the moss. One of the most striking features of the shores is the immense growth of epilithic diatoms in spring. The white of the limestone is masked by the rich brown produced by the myriads of these plants. A prominent species usually is *Cymbella prostrata* (Berk.) Cl. (Fig. 1, L) whose cells live within tubes of mucilage. The zig-zag colonies of *Diatoma elongatum* Ag. are also present but the greatest abundance of this diatom usually is in and around the mouth of the Malham Tarn Beck. Here, it and other diatoms may abstract so much silica in forming their elaborately sculptured walls that the concentration in the water is notably decreased. The competition of these diatoms and the planktonic forms for silica and other essential nutrients is discussed later.

Rivularia is also present here and small green blobs of *Coleochaete pulvinata* A.Br. are often common, especially in summer. *Coleochaete* Bréb. (F.202; S.168) shows an advanced form of sexual reproduction and this is one of the best species for following the process. Normally the plants are annuals, disintegrating in winter, but in Malham some, at least, can be biennials. In the second spring or early summer new threads can be seen radiating out from the dead ones with their empty female sexual organs. This unusual feature may be related to the incrustation of the jelly with lime, so that the death of the vegetative cells in winter does not lead to the break-up of the plant as a whole.

Large blobs of pale green jelly are often found in the detritus thrown up on the margins of the tarn. Similar blobs may be found attached to the stones and to other objects elsewhere. This apparent alga is a colonial ciliate *Ophrydium versatile* O.F.M. Such large numbers of *Chlorella* Beij (F.118; S.251) cells live symbiotically within the ciliates that the animal is sometimes mistaken for a palmelloid Green form such as *Tetraspora* Link (F.93; S.122). Similar algae may be found in other ciliates and are the cause of the brilliant colour of the Green Sponge and "Hydra", two organisms not recorded for Malham but common elsewhere. Unlike the *Chlorellae* living freely in soil, etc., the culture of these symbiotic forms has generally been found to be difficult and they are often placed in a separate genus, *Zoochlorella*.

Other organisms which harbour symbiotic algae of a bright blue-green colour can be found in the tarn, especially on the mud or among weeds. The rhizopod *Paulinella chromatophora* Laut. (Fig. in Geitler, 1959) contains two curved, band-shaped "chromatophores" which seem to be undoubted Blue-green algae. When the amoeboid cell within divides, one of the symbionts passes through the opening of the case into the new daughter individual. In *Glaucocystis* Itzigs. (F.493; S.564) the nature of these bodies is less clear. Here the cells, which are oval to ellipsoid, contain starch and form autospores like the Green-algae belonging to the Chlorococcales, and also contain radiating blue-green bands or short rods. The common view that this is a symbiosis between a colourless Green- and a pigmented Blue-green alga has become doubtful since Skuja (1953, 1956) discovered zoospores in a similar genus, *Gloeochaete* Lag. (F.494; S.565) and erected a separate division, Glaucophyta, for these organisms. Careful observations on these algae are still needed. *Glaucocystis nostochinearum* Itzigs. (Fig. 1, I) can often be found quite easily by collecting mud and plants from the beds of stoneworts (*Chara* spp). The development of the blue-green bodies in the cells is so varied that it is probable that this is either an aggregate species or contains several infra-specific taxa. *Gloeochaete wittrockiana* Lag. is much less common.

Chara Valliant (S.346) is one of the commonest genera of Stoneworts (Allen, 1950; Sledge, 1936). It and allied calcified forms have a long fossil history. These organisms have been considered as part of the Chlorophyta (Charophyceae), as a separate algal group, or even one not belonging to the algae, in the last two cases under the name Charophyta. In soft, peaty waters its place is taken by the uncalcified *Nitella* Ag. (S.345). Near the Tarn Moss there are extensive underwater deposits of eroded peat, but the effect of the overlaying hard water is such that here too *Chara* may be found, though not so luxuriantly as elsewhere. The ecology of the three Malham species needs much more study. For example, do growth and photosynthesis continue throughout the year? When is the main period of growth and how fast do the plants increase?

There are at least four different kinds of sediment in the tarn, two of which have been studied by Round (1953). His work is concerned with the smaller algae, particularly those able to swim over or creep on the substratum. Their distribution is affected in a considerable degree by the presence or absence of peat.

In the peaty area can be found one of the most remarkable algae, *Cladophora sauteri* (Nees) Kütz., which is sometimes placed in a separate genus, *Aegagropila* Kütz. (F.170; S.215). This alga forms what appear to be spherical or oval balls of moss, the origin and nature of which have often been discussed. Larch needles may become entangled in them and the whole mass reach the size of a grapefruit. In rough weather these "Cladophora-balls" are rolled about and are thrown up on the shores or accumulate in quiet areas such as the boat-houses. Species forming balls are usually found in lakes rich in lime, and Malham Tarn is the only lake in Britain, outside Ireland, which has a number of calcareous lakes, in which it can easily be obtained in quantity. The records for the English Lake District need confirmation.

Most species of *Cladophora* are marine and Selivanov (1939) found that the halogen content of Russian specimens of *C. sauteri* was exceptionally high (Br 0·3-0·8 mg/g and Cl 12 mg/g dry weight) for a freshwater organism. Moreover, the ratio of bromine to chlorine was low. He suggested that this might be a relict form, retaining the high content of bromine it had before leaving the sea. The Malham plants show the same feature (Br 1 mg/g; Cl 11 mg/g). Unfortunately for this attractive hypothesis other unpublished analyses of freshwater algae by Mr. F. J. H. Mackereth show that the halogen content of freshwater forms varies widely without any relation to possible migration from the sea. Thus *Spirogyra britannica* Godward contained 32 mg/g of halogens. (Br 0·5 mg/g; Cl 31 mg/g), nearly all as chlorine, while *Batrachospermum* sp. contained 1 mg/g of bromine and 0·5 mg/g of chlorine, that is about twice as much bromine as chlorine. Both these are genera of freshwaters, *Spirogyra* comprising some 300 species, none of which is truly marine and only about two of which extend into brackish water. Lastly *Cladophora glomerata* may contain about one-fifth the amount of bromine as *C. sauteri* and three times more chlorine than bromine (Br 0·2 mg/g; Cl 3 mg/g).

So little is known about the life-history and biology of these balls that they deserve attention. Equally, collection of large numbers, merely because they look so curious, would be regrettable since this rare organism might then become extinct in the tarn.

The plankton of the tarn is qualitatively that of a somewhat eutrophic body of water but quantitatively it is usually rather sparse, though considerable crops arise occasionally. The term eutrophic is applied rather loosely to bodies of water rich in dissolved salts essential to plant life, such as those of nitrogen, phosphorus and potassium. Consequently the plant production is high and, if the water is deep enough to permit prolonged thermal stratification in summer (which is not the case here), the lower layers become de-oxygenated. The opposite of this is an oligotrophic water body, with small amounts of essential elements, low production and no de-oxygenation of the lower layers of the water. In addition, a third type of lake, called dystrophic, is characterized by water which is brown in colour from the large amount of suspended and

Table 1. *Concentration of the major dissolved ions in the waters of the main inflow, the tarn and Windermere, English Lake District, all expressed as millequivalents per litre. Apart from* NO_3N, *and, in Malham Tarn*, $CaHCO_3$, *there is little change in these ions over the year or from year to year.*

	Tarn Beck	Malham Tarn	Windermere, North Basin
Date	19.6.58	18.6.58	25.4.56
Ca^{++}	4·000	2·365	0·300
Mg^{++}	0·247	0·197	0·055
Na^{+}	0·161	0·148	0·157
K^{+}	0·018	0·015	0·013
HCO_3^{-}	3·880	2·340	0·156
Cl^{-}	0·140	0·115	0·206
SO_4^{--}	0·381	0·294	0·155
NO_3N	0·019	0·001	0·019

colloidal peaty matter present. If there were a tarn in the Tarn Moss this would be dystrophic. Good examples of eutrophic waters are the meres of East Anglia, Shropshire and Cheshire, and of oligotrophic ones nearly all those on non-calcareous rock in the north-west of England and in Scotland. Dystrophic waters may be found not far from Malham in the more peaty areas of the Pennines.

Despite the vast difference in the total of the dissolved ions (Table 1), the plankton of Malham contains few species not seen in the oligotrophic north basin of Windermere. This is because most planktonic algae are able to tolerate wide variations in the amount of calcium bicarbonate and carbonate present. The reason why most highly productive bodies of water are rich in nutrients is that soils rich in lime are usually also relatively rich in essential elements, such as nitrogen and phosphorus, a feature generally strengthened by the fertilization due to relatively intensive farming and human sewage.

The spring crop of diatoms in Malham only once (1952) exceeded 1,000 cells/ml though another larger crop arose in the summer of 1950 (Figs. 3, 4; Table 2). In Windermere the diatom crop each spring is about 5,000-12,000 and sometimes even up to 30,000 cells/l (concerning *Asterionella*, see below). Green-algae in Malham rarely exceed 100 cells/ml; in Windermere they almost invariably do so, even reaching 1,000 cells/ml or more and including some relatively large species. The larger Chrysophyceae (*Dinobryon* and *Mallomonas*) are about as common as in Windermere. The Blue-green algae are about as numerous as those in the north basin of Windermere but less numerous than in the south basin of this lake.

Table 2. *Greatest number of cells per ml (filaments in the case of Anabaena) of the commoner plankton algae of Malham Tarn in the years* 1949-53 *respectively.* The figures for *Anabaena flos-aquae* include some threads of *A. circinalis* Rab., and those of *Rhodomonas* some cells of *Cryptomonas*. For descriptions of the *Rhodomonas* and *Gemellicystis* see Skuja (1948) and Lund (1956).

	1949	1950	1951	1952	1953
Anabaena flos aquae (Lyngb.) Rab.	6	7,100	34	508	36
Asterionella formosa Hass.	96	2,563	504	71	322
Dinobryon divergens (Imhof) Duj.	5	4,004	3,506	260	426
Gemellicystis neglecta Teil.	< 1	164	40	88	42
Mallomonas spp.	< 1	720	< 1	< 1	< 1
Rhodomonas minuta var. *nannoplanctonica* Skuja	146	2,356	1,300	586	472
Sphaerocystis schroeteri agg.	50	8	131	192	592
Stephanodiscus hantzschii Grun.	< 1	54	74	2,845	450
Uroglena americana Calkins	< 1	< 1	3,100	479	8,000

The cause of the relatively small amount of plankton in Malham Tarn is basically one of morphometry. Because the lake is so shallow macrophytes (*Chara*, *Potamogeton* L., *Myriophyllum* L.), attached algae and those living freely on the deposits are able to flourish. Light of sufficient intensity to permit photosynthesis at all depths is present over part of almost every day. These plants are, therefore, competing with the phytoplankton for nutrients. It would be of interest to have some comparative quantitative data on the fixation of carbon by these communities. For a number of reasons the plankton community has received more ecological attention than the benthic one, but it is almost certainly true to say that in the majority of British waters the latter community is the more important in relation to primary production.

Sledge (1936) points out that the Wests' (West and West, 1909) account of the plankton of the tarn gives the impression that desmids are numerous, a feature hardly to be expected in so calcareous a body of water and not found by him and Professor W. H. Pearsall. My observations support this view but, in fairness to the Wests, it should be mentioned that none of the algae they say were common are desmids and at least half the desmids they record are not planktonic. In a lake as shallow and wind-swept as this, material from the margins and bottom deposits is often found in suspension.

No detailed study of the plankton has been made but, thanks to the assistance of Mr. P. F. Holmes and his staff, it has been possible to make the observations recorded in Figures 3-6 and Table 2.

The periodicity of the diatom *Asterionella formosa* Hass. (Fig. 1, G) is shown for this tarn and the south basin of Windermere (Figs. 3-6). In the latter its cycle is regular and is determined mainly by the light and temperature conditions and the presence or absence of sufficient silica. Parasitism by fungi and floods (Lund, 1950b; Canter and Lund, 1948) also play a part, and this may also be true of the concentration of phosphate phosphorus. The cycle in Malham Tarn shows certain instructive similarities and dissimilarities. Severe parasitism is very rare. An epidemic, produced by the Phycomycete (Chytrid), *Zygorhizidium planktonicum* Canter (Canter and Lund, 1953), occurred in October 1951 (Fig. 4, P).

The relationship between the development of crops of *Asterionella* and the concentration of dissolved silica shows agreement with that in Windermere in two respects. First, no appreciable increase takes place when the concentration is below 0·4-0·5 mg/l. Second, when a large crop does develop the concentration of silica falls. On the other hand, the crop exceeded 1,000 cells/ml only once, while in Windermere 5,000-10,000 cells/ml are regularly produced in spring (Figs. 3-6; Lund, 1950, and other unpublished data). The detailed reasons for this difference are unknown but there can be little doubt that the main one is the competition for nutrients. In spring the chief competitors are likely to be the immense growths of diatoms on the stones and bottom deposits. The decrease in the concentration of silica is clear evidence for this. The vernal crop of *Asterionella* is about 100-500 cells/ml and, with the exception of the *Stephanodiscus* blooms in 1952 and 1953 (see later), is the main plankton diatom. The data in Lund (1950b) show that this is equivalent to the utilization of about 14-70 μg SiO_2 per litre of water but the actual decrease in SiO_2 in solution in the water during this period is about 1,000-2,000 μg (i.e. 1-2 mg) per litre (Figs. 3-5). The plankton, therefore, is of little importance in terms of primary production. Some reserve is necessary in making such comparisons. Thus the crop of *Asterionella* observed, the so-called standing crop, does not equal the production. It represents the difference between gain by growth and loss from all causes. In Malham, cells will be lost by parasitism, animal grazing, sedimentation to the bottom, by outflow and death from unknown causes. While an accurate computation of the amounts so lost is impossible, some general facts are known. The effects of parasitism are negligible here; no

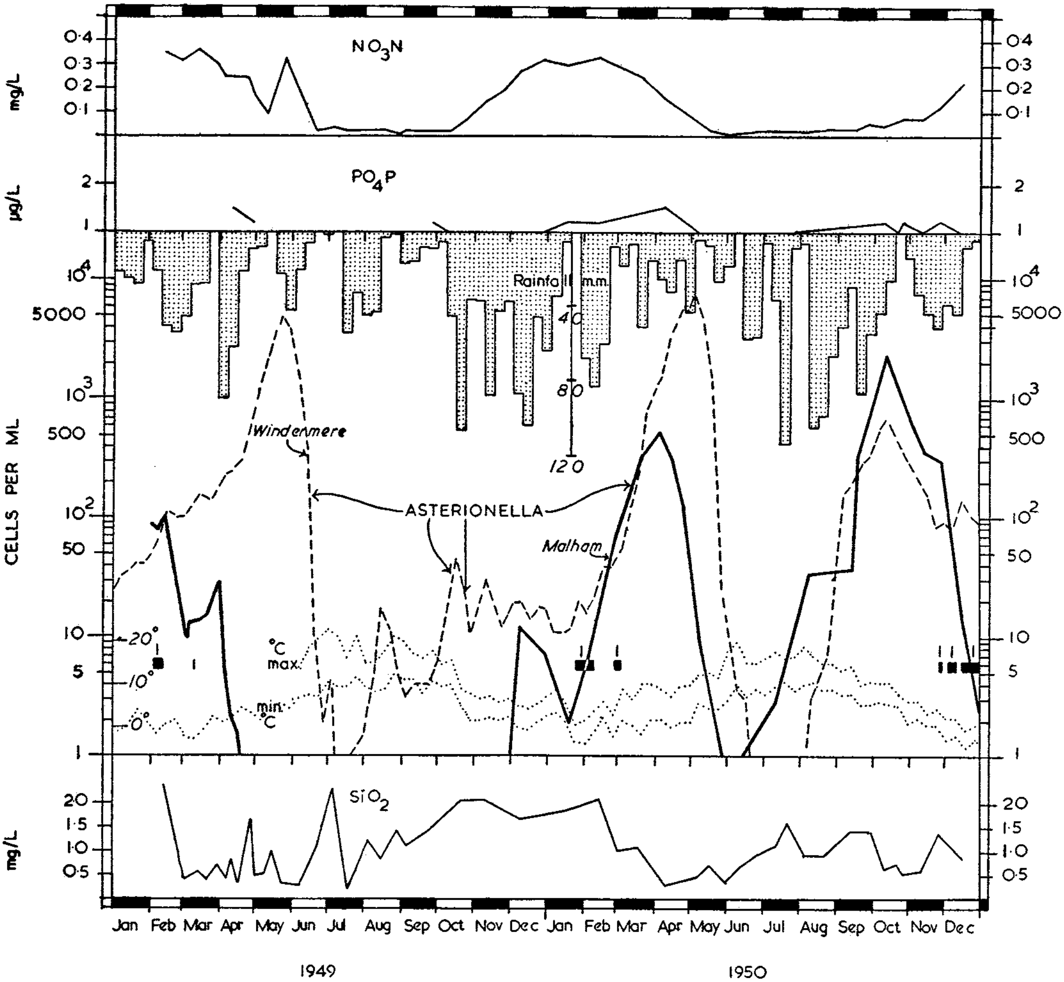
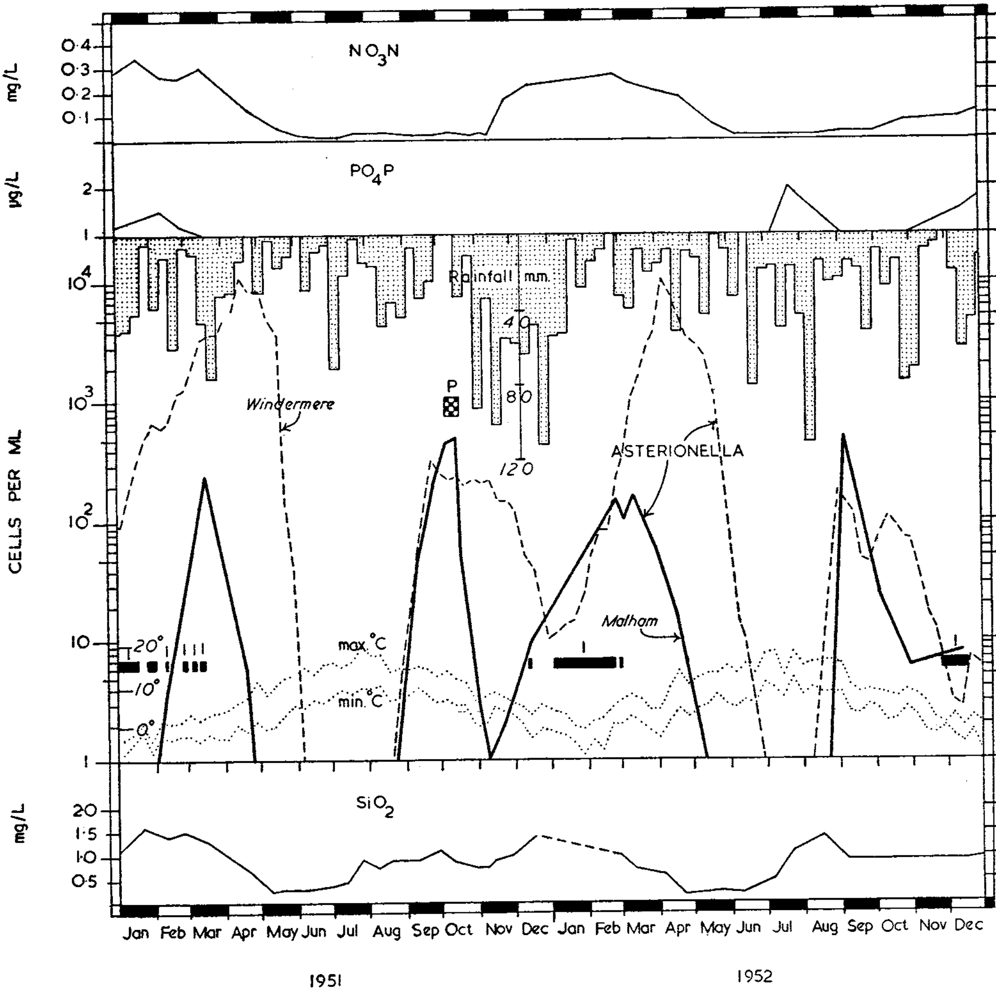


Fig. 3

Figs. 3-6.

The seasonal cycle of *Asterionella formosa* Hass. in the plankton of Malham Tarn and Windermere, south basin between 1949-53 and 1958-60 respectively, in relation to the concentrations of certain dissolved substances, air and water temperatures, rainfall and parasitism. Fig. 6, top, right-hand corner, the alkalinity of the tarn and the Tarn Beck between 1949-53 and 1951-53 respectively. I, above black rectangles, periods of ice-cover; P, period of severe parasitism. For other explanations see lettering on the figures.



NO3N
PO4P
mg/L
µg/L
CELLS PER ML
Rainfall mm.
40
80
120
P
Windermere
ASTERIONELLA
Malham
max. °C
min. °C
20°
10°
0°
SiO2
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
1951
1952

FIG. 4

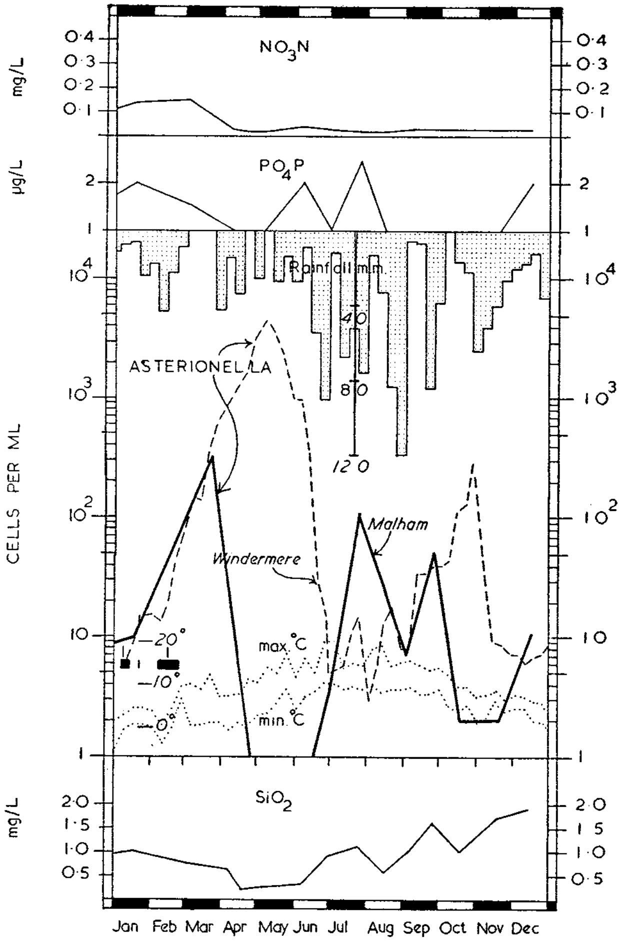

NO3N
mg/L
0·4
0·3
0·2
0·1
PO4P
µg/L
2
1
Rainfall mm
40
80
120
CELLS PER ML
10^4
10^3
10^2
10
1
ASTERIONELLA
Malham
Windermere
20°
10°
0°
max. °C
min. °C
SiO2
mg/L
2·0
1·5
1·0
0·5
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
1953

FIG. 5

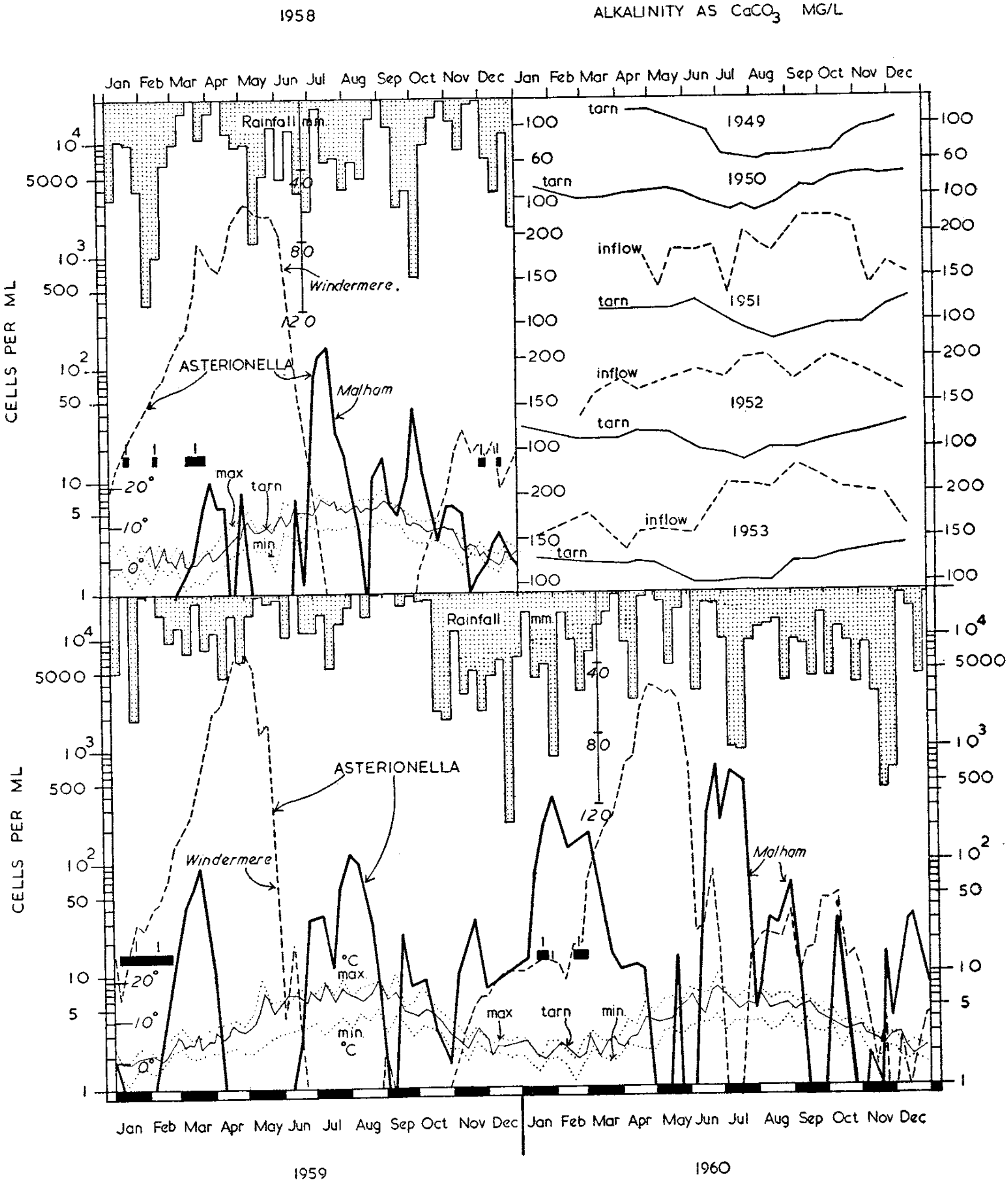

1958
ALKALINITY AS $CaCO_3$ MG/L
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Rainfall mm.
Windermere.
ASTERIONELLA
Malham
max
tarn
min
tarn
1949
1950
inflow
1951
1952
1953
CELLS PER ML
Rainfall mm.
ASTERIONELLA
Windermere
Malham
°C max.
min. °C
max tarn min.
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
1959
1960

FIG. 6

animals are known which graze extensively on *Asterionella*; in so shallow and stormy a lake much of the material falling to the bottom has a good chance of being resuspended; the volume of the lake and amount of rainfall in spring are such that the water in the tarn is unlikely to be replaced more than once, and, lastly, the frequency of dead cells in the colonies of *Asterionella* gives an indication of the deaths from unknown causes. Not even the most generous estimates of total loss can cover more than a fraction of the difference between the silica contained in the standing crop at its maximum and the total amount abstracted from the water; the differences between these two amounts in the years concerned being from about 14 to 140 times that incorporated into this crop.

Another difference from Windermere is that the crop in spring and at other times may start to decrease before the concentration of silica in the water reaches 0·4-0·5 mg/l. Clear examples can be seen in March 1951 and September 1952 (Fig. 4). It has been shown (Lund, 1950b) for Windermere that at this concentration *Asterionella* is unable to obtain enough silica in unit time to continue to multiply effectively. It has also been suggested (Lund, 1950b) that, if there is sufficient light for growth, the cells of *Asterionella* attempt to continue to do so. The result of this is that abstraction of silica from the water continues but fewer and fewer of the cells obtain enough to divide before death supervenes. Consequently there arises the catastrophic decline in numbers by the death of the cells observed during this final phase of utilization of silica. Observations on the rate of photosynthesis of *Asterionella* in this period (Talling, 1957) support this theory. The fact that similar catastrophic declines in the size of the population of *Asterionella* occur in Malham at levels of silica concentration above, or even far above, those limiting its growth in Windermere and elsewhere (see Lund, 1950b) suggests that the same effect is caused by insufficient amounts of another essential nutrient or, maybe, more than one such nutrient. The substances concerned are unknown but data are available for nitrogen ($N.NO_3$) and phosphate phosphorus ($P.PO_4$), (Figs. 3-6).

In spring the concentration of nitrate is often at or near its maximum. This is because much of the decomposable nitrogeneous organic matter arising in autumn and winter from the death of plants, or parts thereof, and of animals has been mineralized through the action of bacteria and fungi. In addition, the demand for nitrogen by the plants in the drainage area is only just beginning in spring as they restart growth. Consequently much of the nitrate in the soil can enter the tarn in the rain which has passed over or percolated through the soil before joining the inflowing streams. Nitrate nitrogen may then exceed 0·3 mg and is invariably more than 0·1 mg/l. Observations on other lakes and unpublished experiments show that *Asterionella* can grow at concentrations below 0·1 mg/l $N.NO_3$, while the vast crops in Windermere arise at levels below 0·3 mg/l $N.NO_3$. We can conclude, therefore, that the size of the spring crop of *Asterionella* in Malham Tarn is not limited by the amount of nitrogen available.

The position with regard to phosphorus is very different, though allowance must be made for the facts that *Asterionella* can abstract it from the water at very low concentrations, that the cells can store amounts in excess of those immediately necessary and then utilize this reserve for growth in the absence of further supplies, and that the minimal amount that a cell needs in order to divide is extremely small (Lund, 1950b; Mackereth, 1953). Nevertheless the concentration of phosphate phosphorus in the water of Malham Tarn is almost always extremely low. Indeed we do not know how low it falls for the method used is inaccurate at levels below about 1·5 μg/l PO_4P (i.e. 0·0015 mg/l), a level which is approximately the maximum concentration observed in the tarn. It is, therefore, not improbable that phosphorus is the element which limits the production of this and other algae in the tarn. In this connection it is of interest to realize that in recent years the amount of phosphorus entering the tarn each year will have increased. This is from the increased use at the Field Centre of synthetic detergents which contain much more phosphorus than does soap.

In summer the amount of phosphorus is lower than can be estimated and the concentration of nitrate nitrogen is also very low (Figs. 3-6). The latter falls to lower levels than in Windermere (Lund, 1950b), a feature which is, incidentally, characteristic of eutrophic lakes. Now, the main source of replenishment of plant nutrients is the inflow in all lakes in which replacement of the water takes place in a period of months rather than years. If, then, nutrients such as phosphorus and nitrogen and, at times, also silica are at such low levels in the tarn in summer as to limit production, a clear relationship might be expected between the development of *Asterionella* and the amount of rainfall. Figs. 3-6 show that this is not the case. *Asterionella* does not always increase after periods of considerable rainfall. This, however, is not unexpected because there are always about twenty species present in significant number in the plankton in summer. Which of these will predominate depends on a variety of circumstances which will vary on each occasion. Moreover, these include Green-Algae, Blue-green Algae and diverse flagellates as well as diatoms. It is reasonable to expect that in dry summers the crops will be smaller than usual because the opportunities for *Asterionella*, as well as its competitors, to increase markedly will be less than in wet years. This can be seen to be so in 1949 (Fig. 3) and 1959 (Fig. 6). The reverse should be true also, namely, that the chances of relatively large crops arising will be greatest in the wettest years. It is, therefore, noteworthy that the largest crop seen in the tarn arose in the very wet summer of 1950 (Fig. 3). Relationships of this kind involve the laws of chance. It is a case of a given trend being more probable under one set of environmental circumstances than another. Consequently, observations covering one or two seasons are unlikely to disclose such weighted chances. This is one of the reasons why long series of observations on the rise and fall of populations are so valuable. Observations carried on for eight years are more than twice as valuable as those covering four years, and those for four much more valuable than those for two. One of the advantages, then, of having permanent field stations of the types maintained by the Field Studies Council is that such observations can be made. In the present case, in addition to the eight years' records for *Asterionella*, there are also those for certain physical and chemical variables. The latter and rainfall have received some consideration but the temperature data are also instructive.

It is often said that diatoms are cold water stenotherms, that is they only flourish over a fairly narrow range of low or very low temperatures. The characteristic outburst of growth in early spring, seen so strikingly on the stony margins of Malham Tarn, supports this view. There are, however, other possible explanations of this correlation with low temperatures which cannot be discussed here. Where *Asterionella* is concerned this view can be seen to be incorrect. For most of the eight years only air temperatures were recorded, but from those of the water taken during the last two years (Fig. 6) it is possible to infer a reasonably close relationship between the maximum air temperature, particularly in summer, and that of the water. Nearly all the marked increases in the numbers of *Asterionella* in summer, including the greatest, that between June and October 1950, cover periods when the water temperature for all or part of the period, was, or almost certainly was, between 16°-20° C. The vernal increases on the other hand began at temperatures around 4° C. or even during or after ice-cover (Figs. 5, 6, 1953; 1960). Therefore this diatom is not a cold stenotherm. This supports the work of Talling (1957) and Lund (1949, Fig. 7; 1959, Fig. 6) which show that it should be able to increase, albeit slowly, even in winter and that, other conditions being favourable, the greatest rate of increase will be at the time when the water temperature is at or near the maximum for Britain. The reason why, in fact, the population is commonly at a minimum (Lund, 1950b) during this physically favourable period is one which has already been considered, namely, a shortage of essential nutrients.

In July 1959 there appeared, with startling suddenness, a crop of *Asterionella* consisting largely of curved or deformed cells, agreeing with the var. *acaroides* Lemm. (Fig. 1, G). The only other British records of this diatom are from Irish lakes (Round and Brook, 1959). Some believe that it is a separate taxon and others that it is an abnormal stage of *Asterionella formosa* Hass. The continuous records available for Malham Tarn enabled me to consider these two viewpoints. The details are given elsewhere (Lund, in the press, b) but the conclusion reached was that var. *acaroides* is simply a stage or phase in the growth of *Asterionella formosa.* The nature of this form and the factors governing its appearance remain unknown. Therefore, a careful study of it is still needed and Malham Tarn Field Centre could be the place where this will be done.

The alkalinity of the tarn varies considerably during the year but is never as high as in the Tarn Beck (Fig. 6, top right). In the tarn, the alkalinity is lowest in summer and highest in winter; in the inflow, the reverse prevails. The detailed causes of these cyclic changes are unknown, despite the vast number of estimations of alkalinity made all over the world. An explanation is suggested in Appendix IV. It seems unlikely that the algae, *Chara* excluded, play a large part in the precipitation of calcium carbonate in the tarn, prominent though their incrustations may be.

Some points concerning the size of the crops of plankton algae were discussed earlier but two of them deserve special consideration. *Stephanodiscus hantzschii* Grun. (Fig. 1, D-F) first appeared in some quantity in 1950 and has not been seen since the end of 1953. In small numbers it could be overlooked because of its small size. It is characteristic of eutrophic waters, notably slow flowing rivers and canals. It can withstand considerable pollution and relatively high concentrations of salts. Hustedt (in Huber-Pestalozzi, 1942) finds that, in Europe, it may also be abundant in oligotrophic mountain lakes, but then only for a short period after the break-up of the winter cover of ice. This was exactly the situation in Malham Tarn in the years 1950-53. In 1952 a large crop developed. The reason for this curious distribution in time and space is unknown.

The vast numbers of *Anabaena* in August 1950 (Table 2) gives a false impression of the abundance of these algae. The sample was taken just below the surface of the water. The cells have vacuoles containing gas and consequently rise to the surface in quiet weather. Bluish-green discolorations are often visible along the margin of the tarn or in the boathouses in summer from becalmed or cast-up surface scums of these algae. The cells may die under such conditions, liberating the pigments and so turning the water a milky blue-green. Such algae often form vast sheets under these conditions in eutrophic lakes and references to them are found in folklore. Throughout the world they are known as water-blooms or water-flowers. In England the history of the breaking of the meres, that is the sudden appearance of these superficial blooms, has been described by Griffiths (1939).

In any account of the algae of the Malham area mention must be made of its famous species, *Ochromonas malhamensis* Pringsheim (1952). Among the many fascinating features of this alga is the fact that we know nothing about its occurrence or ecology in nature, except that it appeared in a culture from a red film scraped off a stone somewhere in the tarn or on its margins. Similar organisms have arisen in cultures of algal material elsewhere but it is not yet certain that the Malham organism itself occurs anywhere else. This flagellate shows an extraordinary nutritional diversity. It can photosynthesize, take up organic particles and digest them internally (phagotrophy), or hydrolyse them outside its body, utilize a wide range of organic substances in solution and, in suitable media, grow in the light or dark. Yet it cannot grow either by photosynthetic or phagotrophic means alone. The existence of such an alga in pure culture presented physiologists and biochemists with an experimental organism of great potential value. Sub-cultures from that originally obtained at Cambridge have been sent to many laboratories and the results of numerous investigations on it have been published.

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I. Collection and maintenance

If the few, simple pieces of advice given here are followed much disappointment will be avoided.

Do not collect large numbers of samples except for some definite, limited purpose. From some habitats even one sample may contain far more algae than can be examined in the time available. The larger the mass of algae collected, the sooner they are likely to die. This is particularly so with aquatic species. Plankton samples should not be so thick that it is impossible to see through the bottle when it is held up to the light. This does not apply to translucent plastic bottles which have the advantages of being lighter than glass and being virtually unbreakable. Nevertheless a glass bottle is a useful addition because the sample can be seen within and an examination in the field with a $\times 15$ or $\times 20$ hand lens is often very helpful. All collecting bottles should be well washed and rinsed, particularly if they are cleaned with sulphuric-bichromate cleaning mixture. Chromium is very poisonous and for most purposes cleaning with a saturated solution of commercial calcium triphosphate is satisfactory and harmless.

Place reed stems, parts of underwater weeds, soil, bark or stones in polythene bags, boxes, cartons or tins. Even paper may suffice. Reed stems, etc., if put in bottles, should be out of water. Put just enough water in the bottle to maintain a saturated atmosphere when it is closed.

On return put the samples in a cool place. Bottles should be opened so that air, but not dust, can get in. If the bottle is full of water, remove at least half. Examine the samples as soon as possible, especially water samples. Rocks, soil and bark can be left till last.

Plankton can be collected with the special nets of bolting silk made for the purpose or by pouring water through a strong, relatively coarse filter paper. Whatmans No. 541 is suitable. Large filter papers are best and the filter funnel should preferably be a plastic one. Minute forms can be concentrated by centrifuging gently; a hand centrifuge is sufficient.

Many algae can be kept alive for days or weeks if they are placed in a moderately illuminated place. If it is cool, so much the better, but, in general, more algae are killed by neglect and exposure to too intense illumination than by normal room temperatures. But beware of central heating; the room may be too hot. Reasonable illumination is supplied by an unshaded north window. If this is not available, the bottles must be protected from direct sunlight. A shady corner in a back yard is excellent, except in very frosty weather. In summer, if in a north-facing room, the samples should be about 30 cm from the window, in winter they will need to be close to it and in towns this may always be necessary.

If algae are to be kept alive, they must not be crowded. A plankton sample collected with a net is unlikely to last long, so it is good practice to collect some water at the same time. This itself may contain enough plankton but, if it does not, add a few drops from the netted sample. Algae should not be placed indiscrimately in any kind of water, especially tap water which may contain poisonous amounts of chlorine, zinc or copper.

Algae collected from cold, fast flowing streams may die quickly no matter what precautions are taken. A good plan is to reduce the level of the water they are in until they are partially or wholly exposed. Provided the vessel is loosely covered or closed the atmosphere above will remain both saturated with moisture and well oxygenated. These algae should be kept cool or cold. Algae on bark will not keep well by this method or in any atmosphere permanently saturated with water vapour because fungi will rapidly cover the surface. Keep them moist for a day or two and then let them dry slowly for a similar period before replacing them in a moist atmosphere. Soil should be kept moist but not soggy.

Algae usually keep well in polythene bags and so can be sent through the post. For those which must be sent in water the precautions already given apply.

Many algae can be maintained for long periods and will multiply if the following further simple procedure is adopted. In following this and the other suggestions it should be remembered that, as in gardening, advice is helpful but experience is the best guide.

Soil algae are difficult to separate from the particles around them. Therefore, having collected as much of the surface of the soil as possible, place it in a dish, smooth it and pat it flat but not too tight. Now add enough water to saturate it and put cover glasses on the top. Leave the dish open until any excess standing water has evaporated and then cover it. Many of the algae are motile and will creep up on to the undersides of the coverglasses in a day or two. There they will multiply. Others will, in time, grow on to the coverglasses. Such samples can be kept for months provided the algae are not crowded out by bryophytes and other plants. The coverglasses can be taken off from time to time, mounted on a drop of water, examined and replaced on the soil. The same procedure with mud will yield a fascinating array of species. The mud must be saturated with water. The adherence of sand or silt to the coverglasses will not interfere with the use of immersion lenses because only the thickness of the coverglass is between them and the algae. The best dishes are plastic "disposable" petri dishes. Despite the word disposable they can be used over and over again. Small amounts of culture solution (see below) can be added to ensure rapid growth or a pinch of any commercial fertilizer sprinkled over the surface. By using different kinds of fertilizer variations in the flora may be produced.

Look for motile aquatic species on the illuminated side of the vessel of water, either at the top or bottom. In addition some algae flourish on the surface film, the so-called neuston community. If coverglasses are placed on the surface of water over filamentous algae, spores may settle on them, as well as other algae.

A great variety of algae will grow if the original sample is slightly enriched. If more water is wanted, add that from the habitat concerned or distilled water or rainwater. Alternatively the culture solution can be made up in such water after it has been sterilized by heating to about 80° C or by boiling. The bacteria will not all be killed but other algae will. To some fertile garden soil add an approximately equal volume of pure or natural water. Boil the mixture for a few minutes, leave to settle and decant off the supernatant liquid, filtering it if necessary. This soil extract is added at a strength of about 10% to a second solution containing sufficient $Ca(NO_3)_2$ and KH_2PO_4 to give concentrations of approximately 1 mg/l NO_3N and 0·1 mg/l PO_4P. The complete solution is sterilized by boiling for a minute or so. Variations in the type of soil used may be beneficial for some algae, for example, algae from acid bogs will flourish better with peat extract.

Another simple method of maintaining algae, particularly some flagellates, is to place a little of the mud, etc., from the habitat concerned in the bottom of a flask or tube and then to add culture fluid or enriched water to this so as to form, as it were, "a pond in a bottle". In this case the type of deposit will have a considerable effect on the flora. Peat, mud and clay are useful variants to try. If it is wished to enrich the water organically a small piece of meat, cheese, bean, pea, etc., can be inserted beneath the surface of the deposit.

II. Examination and preservation

Always examine algae alive first even if, as is generally the case with diatoms, the species can only be recognized by the use of methods which kill them. Observe them under low powers of magnification first; here a stereoscopic binocular microscope may be helpful. If all manner of algae are to be studied, a microscope with a 2 mm immersion lens is essential and for identifying species of diatoms this must be of the best quality. A water immersion lens magnifying about 50 times is very useful. It combines good resolution with a relatively long working distance. The latter is needed when algae are kept in "live" chambers. There are few better ways of learning about algae than by drawing them, and to do this accurately to scale a camera lucida or drawing prism is needed. Phase contrast is very helpful, especially for examining mucilage, flagellates and mounted diatoms.

Algae vary greatly in the length of time they will remain alive under a coverglass. If they are to be examined with lenses of short working distance the coverglass cannot be raised far off the slide. Hence it may have to be ringed directly using, for example, polystyrene (distrene), liquid paraffin or Noyer's cement. The algae will live longer if some kind of live chamber can be used. For example, the coverglass can be raised slightly by a complete strip of lens paper placed under its margins. As this is very absorbent the whole preparation can be kept wet easily. The simple chamber described in Lund (1959a) for another purpose also makes a good live chamber and it is easy to make several of different depths so that observations can be made under low power water or oil immersion lenses.

Permanent mounts of algae can be made but only by tedious processes and, in many cases, with difficulty. For temporary observations the best fixative is osmic acid, although cells full of fat will rapidly turn black, but such cells are, in any case, unsuitable for discerning the nature of the internal structures. Osmic acid (Os_2O_4) is expensive and slowly decomposes in solution but a few precautions will conserve the supply. Use a 1% or 2% solution made up in clean, dust-free distilled or deionized water. Buy it in the ampoules which contain about 250 mg. Keep it in a well stoppered, narrow mouthed, black bottle and remember it is highly irritant to eyes and nose. It will then last for more than six months. Fix the algae either by placing a drop of water containing them in the centre of a coverglass and inverting this over the top of the bottle, or by adding a drop of the acid of equal volume to a similar drop on a slide. Only trial will determine which method is best but, if both are equally good, fixation by the vapour conserves the supply. Osmic acid fixes the cells and their contents in a remarkably life-like condition. Some features become clearer because it begins to decompose at once in the light and so lightly blackens them. The drawback is, of course, that after a few hours everything is so black that observation is difficult.

Formalin (about 4% in water) is the best general preservative, except for delicate forms, but trying to identify algae in formalin can be a thankless task. If the material is to be kept permanently, add a little glycerol to the stock formalin solution and then it will not dry up. In any case seal the tube with wax or polystyrene solution.

A few algae, notably Cyanophyta such as *Scytonema*, *Phormidium* and *Oscillatoria*, can be preserved dry. They will swell up again on rewetting but the cell content may be much altered.

Iodine has several uses. Make up a concentrated stock solution. Add iodine crystals to a saturated aqueous solution of KI until this is itself saturated with iodine. If some of this is now diluted about 100 times and, on standing, iodine crystals appear, add more of the saturated solution of KI to this stock until this trouble is cured. Algae may be fixed and preserved by using this solution at about 1-2%. This will kill delicate flagellates without destroying them, but it will discharge the gas vacuoles of Cyanophyta. Preservation is possible if, afterwards, the sample is topped up with the formalin-glycerol mixture. For testing for starch use the solution diluted to a pale straw colour; for cellulose use it at full strength, then remove as much as possible before adding strong H_2SO_4 (2 vols. glycerol in 1 of water added carefully to 3 vols. conc. H_2SO_4). A blue or blue-violet colour should appear. For staining flagella use it at about half strength. Decolorization to any desired degree can be obtained by adding dilute sodium thiosulphate. The best method of using iodine in the field is to have a suitable amount of the stock solution already in a bottle and then to add the sample until it is diluted to approximately 1% or 2%. Iodine penetrates polythene, so bottles once so used will have to be kept for this purpose. It attacks cork.

Innumerable stains are recommended. For most purposes 1% aqueous solutions of methylene blue, gentian violet and acid fuchsin will suffice. For fat, Sudan IV is satisfactory. Chlor-zinc-iodide will stain cellulose and starch. It should be remembered that the word cellulose is used here in a general sense because ordinary cellulose and mercerized cellulose differ in their staining reactions. An expensive but, for some purposes, excellent stain is ruthenium red. Buy an ampoule and, to conserve it, do not make up a solution but add it as the solid. Dip the end of a mounted needle into the stain and then into the water.

Algae and their contents vary in their avidity for stains and the following procedure will ensure that allowance is made for this. Add a small drop of the stain to the edge of the coverglass on one side. Then the algae near this side will be heavily stained and those near the other unstained. It necessary it can be made to flow under the coverglass by removing water from the other side with a piece of absorbent paper, then a spectrum of staining is obtained. Some algal mucilages will not stain, or if they do, they contract strongly in the process. If some Indian ink is added to the mount the mucilage will stand out against the black background. This should be standard procedure with plankton algae. Do not use the ink directly but dilute it first by about 50%.

The identification of diatoms involves special procedures in order to bring out the detailed ornamentation of their siliceous walls. Some genera can be recognized quite easily alive but this is rarely the case with species. First, it is necessary to remove all the organic matter in the cell and, of the many methods proposed, the following will suffice for all the kinds of material likely to be encountered.

If only a small amount of material is present and is not very heavily contaminated with other organic matter, or if the diatoms are especially delicate, incineration is best with or without treatment with hydrogen peroxide. This is usually the best method for small samples of plankton. It also keeps the natural arrangement of those cells which are in colonies or filaments while the other treatments break them up. In addition corrosive acid fumes are not produced. The diatoms (not too many) in a few drops of water are placed on a No. 1 or 0 coverglass which is itself placed face upwards on a metal plate above a bunsen burner. A No. 2 coverglass is unsuitable because it is too thick. The sample is dried with gentle heat. During this process 100 volume H_2O_2 is added drop by drop, taking care that the reaction is not so violent that the water runs over the edge of the coverglass. Finally, heat strongly but not so powerfully that the glass buckles or melts. When cool the coverglass is mounted face downwards on the slide (see later).

When there is plenty of material or a large amount of organic matter, lime, silt, etc., a more drastic procedure should be adopted. First let the sample stand until the particles have sedimented, apart from any fine clay or colloidal matter. Decant or siphon off the supernatant liquid. If heavy particles, such as large sand grains, are present, these can be removed by a second sedimentation. In this case the sample is well shaken and left for a minute in which time these particles will fall to the bottom. The supernatant matter is decanted off and the sandy deposit thrown away. Acid treatment follows. If there is much calcium carbonate or ferrugineous matter this can be dissolved in HCl, heating if necessary. Again leave to settle, and to cool, and pour off the acid. Repeat once or twice, after first refilling with water so that most of the HCl is removed. If such substances are absent or present in insignificant amounts this preliminary treatment is unnecessary. Now add an equal or slightly larger volume of concentrated H_2SO_4 and about one quarter the volume of HNO_3. The mixture is boiled in a fume cupboard until either the liquid becomes colourless or white fumes of boiling H_2SO_4 are evolved. In the latter case crystals of $NaNO_3$ or KNO_3 are added carefully to the boiling mixture until the liquor is colourless or nearly so. Leave to cool and add water carefully until the volume of the liquid is at least twice as big. The liquor will become hot again when this is done. Leave to cool and then run on to an acid hardened filter paper such as Whatman's No. 541. Wash with diatom-free water until it is free of acid or nearly so. Use BDH Universal Indicator as a guide, when it no longer turns pink on addition washing is complete. The material can also be washed by repeated centrifuging. Finally pipette some of the mixture on to coverglasses, leave to dry and mount.

If no fume cupboard is available an alternative procedure described by Priimachenko (1960) can be used, though this is not so drastic or satisfactory. It has, however, the great advantages that no heating is necessary and no irritating corrosive fumes are produced. It is, however, a good plan to cover the vessel containing the material between operations. It is satisfactory for plankton but only partially so for mud, etc. In the latter case, however, some of the diatoms will be cleaned sufficiently, especially if only small amounts are treated at a time. Sediment, decant and remove unwanted matter as in the previously described acid treatment. Add to the diatomaceous material an equal or greater volume of conc. H_2SO_4. Leave for 5 minutes; then add a saturated aqueous solution of $KMnO_4$, approximately 3-4 drops per 5 ml of liquor in the flask. After 2-3 minutes add 3-4 drops of a saturated aqueous solution of oxalic acid which should decolorize the liquor more or less completely. Thereafter the procedure is the same as in the preceding method. If this method does not work well, increasing the amount of the H_2SO_4 added at the beginning or of oxalic acid at the end may help.

In order to see the finer markings on the walls of diatoms they must be mounted in a material of high refractive index. Several such mountants are on the market. They are usually dissolved in benzene and it is a good plan to wet the coverglass, on to which the diatoms have dried, with benzene before adding the mountant in order to drive out the air in the cells. If a phase contrast outfit is available this will increase the ease of resolution. Commercial mountants may not be of high enough refractive index to resolve the marking of some diatoms (e.g. small *Nitschia* spp). If this difficulty arises a specialist should be consulted. On the other hand some diatoms have such thick walls that certain diagnostically important features may be difficult to see in standard mountants. It is, then, a good plan to make one mount in such a medium and another in a medium of lower refractive index, such as polystyrene. A suitable polystyrene mountant can be made by adding 15 gm of polystyrene to 30 ml of xylene containing 5 ml of dibutylphthalate as a plasticiser. All these mountants dry very slowly in air and if an oven is available the slides should be heated in it at about 80° C until the solvents are driven off.

The siliceous scales on *Synura*, *Mallomonas* and certain other Chrysophyceae should be mounted in the same manner. Cleaning should be carried out on a coverglass by the first method described. The fine spines of *Stephanodiscus* are mostly easily seen by examining a dried unmounted sample.

III. List of Genera

The algae collected from a given place at one time may be very different from those in another season or year. This, combined with the lack of full records of the hundreds of species in the district and the difficulties beginners will have in making correct identifications, would make species lists of limited value. Therefore, instead, the places where the genera concerned are most likely to be found are indicated by letters as follows:

A. Soil other than peat. Especially near Malham Tarn House.
B. Peat, bases of old *Calluna* stems, eroding tussocks of *Eriophorum*, etc., on the Tarn Moss.
C. The three largest pools on the Moss and the flushed zone between Spiggot Hill and the Moss.
D. Bark of trees, palings, bryophytes, and rock over which water either does not trickle or does so only occasionally.
E. Rock with water trickling over it frequently; bryophytes present or absent.
F. Solution hollows on limestone pavement.
G. Temporary puddles; especially in Ha Mire and Great Close Mire.
H. Permanent or semi-permanent pools in mires, fens and carr.
I. Streams, rivulets, outflow of springs.
J. Among macrophytes or on mud of Malham Tarn.
K. On stones, macrophytes and other algae, or peat in the Tarn.
L. Plankton.

If a description of the genus cannot be found either in Fritsch and West (1927) or Smith (1950) and there is no reference to it in the present paper, a suitable original paper is cited. The divisions and classes are those of Fott (1959). For lists of species West and West (1900-01) and Round (1953, 1960a, b) can be consulted.

CHLOROPHYTA

1. CHLOROPHYCEAE

(a) *Free-swimming*

Carteria	GH	Heteromastix	GJ	Pyramimonas	G
Chlamydomonas	ABCGH	Lobomonas	G	Pyrobotrys	G
Chlorobrachis	G	Mesostigma	GJ	Spermatozopsis	G
Diplostauron	H	Monomastix	F	Stephanosphaera	F
Eudorina	L	Pandorina	GHL	Volvox	L
Gonium	GHL	Pedinomonas	G		
Haematococcus	F	Phacotus	JL		

(b) *Non-motile, not clearly filamentous*

Ankistrodesmus	CGHJL	Elakatothrix	L	Pleurococcus	D
Asterococcus	CL	Eremosphaera	C	Quadrigula	L
Botryococcus	HL	Gemellicystis (Lund, 1956)	L	Scenedesmus	GHJL
Characium	CHIK			Schizochlamys	C
Chlorella	AD	Glaucocystis	JL	Sphaerocystis	L
Chlorococcum	AD	Gloeochaete	J	Stichococcus	AD
Coelastrum	HJL	Kirchneriella	L	Tetraspora	GH
Coccomyxa	BD	Oocystis	L	Tetraedron	HL
Crucigenia	HJL	Palmodictyon	H	Trebouxia	D
Dactylococcus	A	Paulschulzia	HL	Trohiscia	AD
Dicranochaete	HK	Pediastrum	HJL		
Dictyosphaerium	L	Planktosphaeria	L		

(c) *Filamentous*

Aphanochaete	K	Microspora	CH (if very wet B)	Ulothrix	IK
Binuclearia	C			Uronema	K
Bulbochaete	K	Microthamnion	CH		
Chaetophora	IK	Oedogonium	IJ		
Cladophora	IK	Prasiola (Hormidium-stage)	D		
Draparnaldia	HIK				
Hormidium (correct name is Chlorohormidium Fott)	ABD	Stichococcus	ABD		
		Stigeoclonium	IK		
		Trentepohlia	D		

2. Conjugatophyceae

(a) *Not filamentous*

Actinotaenium (Teiling, 1954)	CH	Euastrum	CH	Spirotaenia	H
Arthrodesmus	CHJL	Gonatozygon	H	Staurastrum	CHJL
Closterium	CGHJ	Mesotaenium	ABD	Staurodesmus (Teiling, 1948)	HL
Cosmarium	CHJL	Micrasterias	H	Tetmemorus	C
Cylindrocystis	ABC	Netrium	CH	Xanthidium	CH
Docidium	H	Penium	CH		
		Pleurotaenium	H		

(b) *Filamentous*

Desmidium	CH	Mougeotia	CGHJ	Zygnema	CGH
Gymnozyga (Bambusina)	CH	Sphaerozosma	H	Zygogonium	B
Hyalotheca	CH	Spirogyra	CGHJK		
		Spondylosium	H		

CYANOPHYTA

(a) *Not filamentous*

Achromatium	HJ	Chroococcus	CEL	Holopedium	J
Aphanocapsa	E	Coelosphaerium	J	Merismopedia	CHJ
Aphanothece	EJ	Eucapsis	J	Microcystis	L
Chamaesiphon	I	Gloeocapsa	DE	Synechococcus	CF
Clastidium	I	Gloeothece	DE	Synechocystis	CF

(b) *Filamentous*

Anabaena	L	Lyngbya	IK	Rivularia	IK
Arthrospira (incl. Spirulina)	HJ	Microcoleus	A	Schizothrix	EI
Beggiatoa	HJ	Nostoc	AEF	Scytonema (incl. Petalonema)	E
Calothrix	EIK	Oscillatoria	GHJ	Stigonema	DE
Cylindrospermum	A	Phormidium	AIK	Tolypothrix	CH
Dicothrix	EIK	Plectonema	I		
		Pseudanabaena	J		

CHRYSOPHYTA

1. Chrysophyceae

(a) *Free-swimming*

Chromulina	CGH	Hyalobryon	H	Ochromonas	CGH
Chrysococcus	CGH	Hymenomonas	G	Synura	CGHJ
Dinobryon	HL	Mallomonas	CGHJL	Uroglena	L

(b) *Non-motile, not filamentous*

Chrysonebula	I	Chrysopyxis	C	Lagynion	HK

(c) *Filamentous*

Phaeothamnion	H

2. Xanthophyceae

(a) *Not filamentous*

Botrydiopsis	A	Characiopsis	CHJ	Ophiocytium	CH
Centritractus	HL	Chlorobotrys	C		

(b) *Filamentous*

Bumilleria	A	Heterothrix	A	Tribonema	CH
Heterococcus (Monocilia)	A				

3. BACILLARIOPHYCEAE (for full lists see Round (1953, 1960a, b))

Achnanthes	EHIK	Denticula	EI	Navicula	ACEGHIJK
Amphipleura	IH	Diatoma	EIK	Neidium	HJ
Amphora	HJK	Diploneis	J	Nitzschia	ACGHJK
Asterionella	L	Epithemia	LK	Pinnularia	CH
Caloneis	HJ	Eunotia	CH	Rhopalodia	EIJK
Campylodiscus	J	Fragilaria	EHIKL	Stauroneis	AGHJ
(springs)	I	Frustulia	CHK	Stephanodiscus	L
Ceratoneis	EI	Gomphonema	EHIK	Surirella	HJ
Cocconeis	HIK	Gyrosigma	J	Synedra	HIK
Cyclotella	L	Hantzschia	A	Tabellaria	CH
Cymatopleura	J	Melosira	EI	Tetracyclus	E
Cymbella	EHIK	Meridion	EI		

RHODOPHYTA

Asterocytis	IK	Lemanea	I	Rhodochorton (Chantransia)	I
Batrachospermum	I				

EUGLENOPHYTA

Astasia	GHJ	Distigma	GJ	Peranema	GHJ
Colacium (on Crustacea and Rotifers)	HL	Euglena	ABGHJ	Phacus	GHJ
		Lepocinclis	GHJ	Trachelomonas	GHJ
		Menoidium	GHJ		

PYRROPHYTA

1. DINOPHYCEAE

Amphidinium	GH	Gymnodinium	GH	Massartia	GH
Ceratium	L	Hemidinium	CBH	Peridinium	HL
Glenodinium	GH				

2. CRYPTOPHYCEAE

Chilomonas	G	Cryptomonas	CGHJL	Rhodomonas	JL
Chroomonas	GHJ				

IV. The alkalinity of Malham Tarn and Tarn Beck

The changes in the alkalinity are caused by factors which must also be involved in the formation of tufa. It is important to discover to what extent they are biologically controlled.

The alkalinity is usually given, for convenience, in terms of $CaCO_3$ but could equally well be expressed in other ways (e.g. as ions, Table 1). The processes governing the deposition of lime depend on the fluctuations of a complex equilibrium, the overall effect of which may, however, be expressed simply as follows: $CaCO_3$ (solid) $\rightleftharpoons$ $CaCO_3$ (dissolved) $+H_2O+CO_2 \rightleftharpoons Ca(HCO_3)_2$. Therefore the abstraction of carbon dioxide from the water, for example in photosynthesis, can lead to the precipitation of lime or chalk. The addition of CO_2, for example in respiration or microbial decomposition, will lead to the solution of $CaCO_3$, part of the carbonate already in solution being transformed into bicarbonate. The result will be the same whether the CO_2 acts directly on a piece of wet marl or tufa, or indirectly through its action on carbonate ions in solution. In soft waters $Ca(HCO_3)_2$, which is about thirty times as soluble as $CaCO_3$, accounts for virtually all the calcium in solution and there is no precipitation of lime.

The marked fall in the alkalinity of the Tarn begins between late May and the end of June, and is followed by an increase between September and October (Fig. 6, top right). The alkalinity rarely falls below 100 mg/l $CaCO_3$ but in 1949 fell to 60 mg/l and was very low between August and October. Two inferences may be made from these facts. First, that the great algal growth visible in the Tarn from February until April or May does not lead to any large deposition of $CaCO_3$. It must lead to some deposition and this appears to be detectable, for there is a gentle fall in alkalinity between February and April (e.g. 1950, 1952, 1953). The slight rise which follows, from April to May, could be a reflection of the end of the algal peak.

Second, if the great vernal outburst has so little effect, it seems unlikely that the summer crops will have more. Indeed, the date when the sharp fall in alkalinity occurs is not correlated with any observed mass increase of algae. This is, however, the period when the Higher Plants are growing, while *Chara* may well be active too. The former reach the surface about the end of June or early July when the alkalinity drops sharply. They die down in the autumn when the alkalinity rises. The exceptionally fine summer of 1949 will have been very favourable for the growth of macrophytes, while the inflow was greatly reduced. This is the period of lowest recorded alkalinity.

There are, however, certain features which do not support the view that the precipitation of lime is predominantly caused by the photosynthesis in the great weed beds. If it were, the tarn might be expected to have almost the same alkalinity as the inflow in the latter part of the winter at least. As this is not so there appear to be some other factors leading to a decrease in the alkalinity of the water after it has entered the tarn. It is also curious that the alkalinity is highest in the inflow, which also contains macrophytes and algae, at the time when it is lowest in the tarn.

Temperature changes can scarcely be the sole explanation of these inconsistencies, though they must play some part in the changes observed. The summer decrease in the tarn could be related to temperature. The higher this is, the less CO_2 can be held in solution and hence the greater the precipitation of lime. The absence of such a fall in alkalinity in the beck might seem to be explicable on the grounds that the water is colder in summer than it is in the tarn and hence more CO_2 can be dissolved in it. However, this is not the case in winter. Indeed the water may be warmer for the tarn is often frozen.

The cycle in the inflow, then, seems difficult to explain on the grounds of photosynthesis and seasonal changes in temperature. It is, however, explicable on biological and physical grounds. In winter the amount of run-off water arriving from the drainage area will be relatively high compared with the seepage, that is the water which has percolated through the soil. The former will abstract CO_2 from the atmosphere at or near ground level; the latter will be enriched in addition, on its way through the soil, by the CO_2 evolved directly or indirectly by the organisms in the soil, that is by soil respiration. If the water sinks deeper, as it often does in limestone, it will also be enriched by CO_2 under pressure, as is well seen at mouths of springs. In summer, seepage and spring water will become more important, because rainfall is usually less than in winter and evaporation is always greater. The finer the summer the more marked this change will be (cf. 1949). Therefore, the higher levels of alkalinity in the beck in summer arise because the water is more heavily charged with CO_2.

Taking these viewpoints as correct, a hypothesis can be erected to explain the changes in alkalinity observed in the tarn and the beck. In summer the beck water is relatively cool and supersaturated with the carbon dioxide it has gained by its passage through soil and rock. As it passes into the tarn it is losing gas to the atmosphere. However, the stream is short and the water enters the tarn before equilibrium is reached. In the tarn there is time for the remaining excess CO_2 to be lost. Hence the alkalinity of the tarn is always lower than that of the inflow. Further, in summer, the temperature of the tarn is higher than that of the beck so that less CO_2 can be contained in solution. Lastly, after the end of May, photosynthesis by the macrophytes will be considerable. These factors explain the diametrically opposite courses of the alkalinity curves in the tarn and beck.

The relative importance of the various factors is unknown. Since the estimation of alkalinity is simple, some of the assumptions made here could be tested directly. So far as the macrophytes are concerned, estimations are needed of the rate, and so amount, of their photosynthesis and of the size of the crops produced before an approximate figure for the amount of CO_2 they abstract from the water can be given.