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# Terrestrial and Freshwater Algae of Aldabra

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# Terrestrial and freshwater algae of Aldabra

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[Plate 18]

Contents



A preliminary account is presented of the terrestrial and freshwater algae found during the wet season 1968/69. Blue-green algae were by far the most abundant group, often conspicuous to the naked eye. Colonization of bare rock is almost entirely by heterocystous blue-green algae, with other algae, lichens and bryophytes playing a negligible rôle. On champignon and the drier parts of platin Scytonemataceae predominated. On parts of platin subjected to a frequent cycle of wetting and drying, there were large masses of colonies of *Nostoc commune*. Thin soils over platin with only a sparse angiosperm cover were often dominated by a *Nostoc–Riccia* community. However, in some areas of South Island sheets of various Oscillatoriaceae covered a similar substratum. It is suggested that this difference may be due to the activity of the tortoises. In the deeper waters covering the platin of South Island forms of *Wollea* were the predominant alga.

Chlorophyta were represented by a range of species, but these seldom formed a major part of the algal biomass. The rarity of diatoms and the absence of Chrysophyta were noteworthy.

Using the assumption that the heterocyst is an indicator of nitrogen-fixing ability, the evidence suggests that deficiency of combined nitrogen is a major factor during early successional stages on bare coral, but not one by the stage that an angiosperm cover has developed. Direct observation suggests that decay of blue-green algae is an important contributor to the formation of humus over bare rock, but gives little clue to the quantitative importance of these organisms as an agent of erosion.

## 1. Introduction

The geography and ecology of Aldabra atoll have been introduced by Stoddart & Wright (1967). The following account of the terrestrial and freshwater algae of this island is based on observations made during the wet season 1968/9. It can be considered only a very preliminary account due to the short period covered (December to early February), and the fact that many organisms will require culture studies before adequate naming. However, the scarcity of descriptions of terrestrial algae on coral atolls combined with their obvious importance on Aldabra suggests that such an account may be of at least temporary use. Generalizations presented do not refer to coastal or brackish habitats, unless this is specifically stated.

## 2. Results

### (a) *Relative importance of major taxa and life-forms*

In almost every site inspected the great majority of forms were blue-green algae. Sampling to obtain absolute values will have to wait until there is a detailed vegetation map to use as a basis, but it seems safe to state that over 99 % of all free-living algal material is blue-green algal. A summary (table 1) of the total species represented in various taxa also indicates that blue-green algae are in the majority, although the contrast is not so dramatic as when comparing biomasses. (The species lists used in making this comparison are based on card-index records of what were considered definable species when on Aldabra. In many cases they have not yet been given a binomial.) Even among the blue-green algae the great bulk of material is made up of only a few species.

Table 1. Species of terrestrial and freshwater algae distributed according to major taxa

| | | | |
|---|---|---|---|
| Myxophyta | 90 | Charophyta | 1 |
| Chlorophyta | 37 | Euglenophyta | 5 |
| Volvocales, 5 | | Cryptophyta | 1 |
| Chlorococcales, 14 | | Xanthophyta | 1 |
| Conjugales, 9 | | Bacillariophyta | 14 |
| others, 9 | | total | 149 |

Chlorophyta were widely distributed in temporary pools. Most species occurred in low numbers, but a few occasionally became abundant. As discussed below, the plankton vegetation of the pool by Takamaka Grove was unique in consisting almost entirely of Chlorophyta. The single charophyte was locally abundant in the Bassin Flamin region. The general absence of diatoms was striking. No instance was found of a microhabitat where diatoms were common, and the only place where they were found regularly was in the mucilage of certain submerged Nostocaceae. Many samples of *Cladophora* sp. were inspected from small pools, and not a single diatom epiphyte was found, in marked contrast to most regions where *Cladophora* is found. Euglenophyta were represented by occasional cells in small pools, and on South Island rarely as the dominant growth in tiny depressions in the platin. Xanthophyta were represented by a single species in two pools at Takamaka, while Cryptophyta were found only in a (brackish) pool south of Takamaka. No examples of freshwater Rhodophyta, Pyrrophyta or Chrysophyta were found.

The rarity of flagellates seems a distinctive feature of the flora, as compared with the floras of temporary pools from some other regions. Only one flagellate was at all common, the calcified loricate *Phacotus lenticularis* Ehr. One particular comparison will be made. The author studied habitats in Sierra Leone in 1967 which had much the same physical characters and at much the same climatic season, the beginning of the rains. However the Sierra Leone pools were developed over a series of laterite pans, and thus differed markedly in their chemistry. In the Sierra Leone pans blue-green algae were again widespread and abundant, but small flagellates were also often abundant in temporary pools. Chrysophyta, unrepresented in the Aldabra samples, were especially common.

The generalizations about the relative preponderance of blue-green algae over green algae apply only to the free-living forms. The situation with lichens is the reverse. Most lichens contained green algae, and forms with blue-green algae were uncommon.

### (*b*) *Types of algal habitat*

There seems no simple way of classifying those habitats showing obvious algal growths. However, comparison of sites according to the following five factors gives some understanding of the range of such habitats.

FIGURE 1. *Stachytarpheta jamaicensis* growing among colonies of *Nostoc commune* on West Island.

(Facing p. 251)


PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

(1) *Relation to water-level.* A series of habitats may be traced ranging from those never holding water through those undergoing frequent cycles of wetting and drying during the wet season to ones submerged for long periods. As discussed in more detail below, the algal flora showed a change from dominance by Scytonemataceae to one by Nostocaceae through this series.

(2) *Depth of soil overlying rock.* In general a series of habitats with obvious algal growths from ones with no soil cover to ones with such cover shows a correlation with the previous series related to water-levels. However, there are some sites with a continuous layer of soil but seldom inundated. The relative freedom of such sites from angiosperm cover was in many cases obviously due to the activities of man or of tortoises.

(3) *Size of habitat, especially pools.* In the Cinq Cases region the flora of small pools in the platin. was often very different from that of the large areas of water covering several acres. A variety of causes probably influenced such differences; one obvious one is the effect even one tortoise turd can have on an isolated pool. The few cases mentioned earlier where Euglenophyta were dominant in tiny depressions in the platin were all ones where the algal layer had developed over rotting turds. Some algae were recorded only from the larger areas of water, e.g. *Spirogyra* spp., *Chara zeylanica* Kl. ex Willd.

(4) *Effect of surrounding vegetation.* The flora of small pools in the *Casuarina* grove behind the settlement on West Island showed obvious differences from that of small pools on the platin As an algal habitat the pools in the *Casuarina* grove differed from those outside in at least three obvious ways: lower light intensity; smaller temperature range (maximum recorded temperature of 37 °C against 41.5 °C outside); deep brown colour of water associated with *Casuarina* 'needles'.

(5) *Effect of tortoises.* One local effect of tortoises was mentioned in (3) above, and others are dealt with later.

### (*c*) *Distribution of algae in various habitats*

Champignon with only sparse angiosperm cover generally had a scattered thin cover of blue-green algae. On convex surfaces the rock might be almost free of any algae, while in small concavities the algae developed a dark blue-green turf. These algal growths almost all belonged to the Scytonemataceae, with a few epiphytic cells and colonies of Chroococcales where the growth was more luxuriant. Boulders with a shaded undersurface near the ground often had this covered with a thin blue-grey powdery film where Chroococcales predominated. Growths of lichens and bryophytes were almost absent on rocks, except occasionally where there was a humus layer developing. Lichens were almost entirely confined to being epiphytic on trees and shrubs.

Bare platin surfaces generally above the water-level resembled the surfaces of champignon in that they often developed a thin layer of Scytonemataceae. Small depressions, however, were frequently filled with masses of irregular colonies of *Nostoc commune* Vaucher. These colonies imbibe water very rapidly after a storm. Various such masses on West Island were followed during the survey, and were found to be remoistened and dried out many times during the period. Depressions which were deep enough to have a permanent covering of water during the wet period had a much more varied flora, described later.

The masses of *Nostoc commune* colonies usually overlay a thin layer of humus, and it seems reasonable to surmise that the alga itself gives rise to this humus. At least on West Island, a few angiosperms germinate and grow rapidly directly in the *Nostoc commune* mounds (figure 1, plate 18). Strangely, the two species most frequently found in this habitat, *Portulaca oleracea* and *Stachytarpheta jamaicensis*, are both probably recent introductions. However, it appears that in most cases angiosperms do not develop on the flat surfaces of platin until there is a development of a humus-containing layer covered only thinly by *Nostoc* colonies. It is tempting to consider this situation as the next stage in a succession, though in many cases it is now probably a relatively stable micro-community influenced, as mentioned earlier, by activities of man or tortoises. On West Island thin layers of soil overlying relatively flat rock developed a covering of *Riccia* sp. during the period December to February. Mingled with this were many small colonies of *Nostoc* and other blue-green algae. This community occurred on man-made tracks, as a zone between bare rock and forest, and as patches in an otherwise relatively well developed covering of herbs. All transitions could be found from a blue-green alga plus *Riccia* covering to a herb community with only minor growths of alga and liverwort. Angiosperms particularly associated with communities transitional between the two types were: *Tephrosia pumila* var. *aldabrensis*, *Phyllanthus maderaspatensis*, *Portulaca quadrifida*, *Sida parvifolia*, *Bulbostylis* sp., *Dactyloctenium pilosum*. All except the first are annuals. In parts of South Island a different type of community was often found overlying a thin layer of soil. This was dominated by sheets of various species of Oscillatoriaceae. Such a community was found near the camps at Cinq Cases, Takamaka and Dune Jean-Louis.

The bodies of water standing for at least much of the wet season included the bulk of the algal species. They will be described briefly under three headings.

(i) *Small pools, mostly less than* 2 *to* 3 m$^2$ *in area.* The flora of these was rather variable. Sometimes it consisted almost entirely of a single planktonic species, usually either a *Chlorella* sp. or an *Ankistrodesmus* sp. Much more frequently there was a mixed flora with blue-green and green algae, the former predominating. In the deeper pools containing a humus layer, there was usually a crust of blue-green algae or Chaetophorales on the sides of the pool, sometimes partly endolithic. Floating masses of blue-green algae were common, either Nostocaceae or Oscillatoriaceae. In some pools planktonic blue-greens were also abundant, including several gas-vacuolate forms. In other pools filamentous greens were conspicuous. Floating masses of *Oedogonium* sp. were not uncommon in all regions of Aldabra, though most common on West Island. They were often obvious by their white or yellowish coloration as seen from the surface. *Cladophora* sp. was found in a number of pools on West Island, mostly ones in the *Casuarina* grove. It was not found elsewhere. Possibly this is a regional difference within Aldabra, but it might also be due to the fact that the main *Cladophora* season lasted only a couple of weeks and so could be missed easily. Where it occurred it appeared to grow very rapidly, but also to be grazed heavily.

(ii) *Large areas of platin submerged on South Island.* It appears that exceptionally large areas of the region round Cinq Cases were submerged during the 1968/9 wet season. Here various colonial forms of Nostocaceae were common in the water. These were mainly attached rather than planktonic forms or floating on the surface. Colonies of *Wollea* sp. were particularly common; the typical form of this organism was not found on West Island. The other genera important in the sheets of water around Cinq Cases were *Aphanocapsa* and similar Chroococcales, *Spirulina*, *Oscillatoria*, *Lyngbya*, *Nostoc*, *Spirogyra* and *Oedogonium*. *Spirogyra* spp. were apparently confined to the larger areas of water, but the other genera were also well represented in small pools. *Chara zeylanica* was locally abundant at the edge of Bassin Flamin, together with the angiosperm, *Naias* sp. The *Naias*, however, was also found at many other sites in the region. The only other angiosperm which approached being a true submerged aquatic was a

*Bulbostylis* sp., which apparently germinated and grew well under water, although it was also common in other areas only occasionally submerged.

(iii) *Takamaka pools*. There are three medium-sized pools near the trail running past the Takamaka Grove. One of these is brackish, but is included here for comparison. The floras of these three pools were all markedly different, and would repay a detailed investigation. They are referred to here as Takamaka pool I (the most northerly), Takamaka pool II (next to the actual grove of takamaka trees, *Calophyllum inophyllum*), Takamaka pool III (about 200 m south of pool II). Pool III is the brackish one. Pools I and III apparently dry out after the wet season, whereas pool II is possibly permanent. Algal samples were collected from these pools on 18 January 1969 and 2 February 1969.

Pool I had a flora dominated by two *Nostoc* spp. and *Naias* sp. *Phacotus lenticularis* was very common in the plankton. Many other small unicellular and colonial Chlorophyta were also present, though at low densities: *Chlorella* sp., *Ankistrodesmus* sp., *Tetraedron* spp., *Scenedesmus quadricauda* (Turp.) de Bréb., *Scenedesmus bijuga* (Turp.) Lagerheim var. *alternans* (Reinsch) Hansgirg, *Coelastrum microporum* Näg., species of *Closterium*, *Cosmarium* and *Staurastrum*. A few diatom species were also present, and the Xanthophyta, *Goniochloris* sp. Several species from this pool have now been obtained in axenic culture.

Pool II was brown in colour, with a bottom of deep silt, which was easily disturbed. Apart from a slight algal growth on the sides near the surface, the flora consisted entirely of minute non-flagellated cells, mostly Chlorophyta about 2 to 4 μm diameter. In contrast to any other pool on Aldabra with a mixed flora, blue-green algae were of negligible importance.

Pool III had conspicuous blue-green algal growths round the edges, and to a lesser extent floating on the surface. In contrast to pool I these were largely of Oscillatoriaceae, and Nostocaceae were absent. Pinkish growths of purple sulphur bacteria were also conspicuous on the mud and underneath the blue-green algal crust, as they were in many other brackish habitats on the island.

Besides the habitats discussed above, algae were occasionally conspicuous in other situations. Free-living forms were sometimes abundant on old tree trunks, but much more rarely than lichens. Growths of *Nostoc commune* Vaucher var. *flagelliforme* (Berk et Curtis) Born. et Flah. were often common among grass under coconut groves, e.g. to the north of the settlement on West Island, Ile Michel.

## 3. Discussion

There are apparently no detailed accounts in the literature concerning the distribution of terrestrial and freshwater algae on other coral atolls. However, what floristic accounts there are available do indicate that blue-green algae are important elsewhere (see, for example, Taylor 1950).

The micro-algae seem unlikely to provide much evidence on problems of speciation and endemism on Aldabra. But they do provide important circumstantial evidence on the mineral budget of the island. The main point concerns the availability of combined nitrogen, and rests on the assumption that nitrogen-fixation by blue-green algae is correlated with the presence of heterocysts. As heterocysts are now thought probably to be the actual site of nitrogen-fixation (Fay, Stewart, Walsby & Fogg 1968), this assumption seems justified here. Further, the presence of a source of combined nitrogen reduces or inhibits the production of heterocysts. It therefore seems reasonable to infer further that habitats consisting entirely or largely of heterocystous blue-green algae are ones where other organisms can not compete due to lack of combined nitrogen. Conversely, a conspicuous growth of non-heterocystous blue-green algae or of other algal phyla entirely devoid of intermingled heterocystous forms suggests a habitat with at least a moderate level of available combined nitrogen. Of the main terrestrial and freshwater blue-green algae the Nostocaceae and Scytonemataceae are heterocystous forms, and the species studied usually had frequent heterocysts present. The Oscillatoriaceae are not nitrogen fixers. Blue-green algal growths on bare rock were almost entirely of Nostocaceae and Scytonemataceae on Aldabra. It may thus be inferred that all the primary colonizers are nitrogen-fixing forms. In the later stages of (a theoretical) succession, blue-green algal growths sometimes consisted almost entirely of nitrogen-fixing forms, as in the turfs co-dominated by *Riccia* sp., Takamaka pool I and many of the sheets of water around Cinq Cases. On the other hand, as mentioned earlier, sheets of Oscillatoriaceae predominated on soil with a thin angiosperm cover in region of South Island, and nitrogen-fixing blue-green algae are absent from pools II and III. It is therefore reasonable to assume that these regions are locally less deficient in combined nitrogen. Various explanations can be put forward for these areas where nitrogen-fixers are absent. It is attractive to suggest that an increased rate of circulation of mineral nutrients through the ecosystem by tortoises may be one factor favouring a higher level of combined nitrogen. The relative success of non-nitrogen-fixing algae versus angiosperms, both presumably with rather similar mineral requirements, suggests that the mechanical action of tortoise grazing may itself favour the success of the algae.

Two further clues to the nitrogen economy of the island can be obtained by considering the legumes and the lichens. Legumes form only about 4% of the total angiosperm flora, and probably less of the biomass. Eight specimens each of *Tephrosia pumila*, *Abrus precatorius*, *Cassia aldabrensis* and *Gagnebina commersonianus* from West Island were dug up (and replanted) and inspected for nodule formation. All four species showed presence of nodules, but in all cases only few, and many plants lacked them altogether. They were developed best on *Tephrosia pumila*, one of the species often associated with the nitrogen-fixing blue-green alga plus *Riccia* sp. community. The evidence thus suggests that nitrogen-fixation by legumes is of negligible quantitative importance on Aldabra. The evidence for lichens is similar; their algae are not nitrogen fixers.

The above circumstantial evidence all supports a hypothesis that lack of combined nitrogen is probably one of the main factors in the early stages limiting the rate of development of vegetation from bare rock, but is of much less importance by the time a soil is developed. However, it should be pointed out that other nitrogen-fixing organisms like soil bacteria might possibly play an important part in the overall nitrogen economy, and it is well known that nodules of *Casuarina* fix nitrogen (Stewart 1966).

The rarity of diatoms and the absence of Chrysophyta indicate the likelihood of the lack of available silicate for their growth, which is perhaps not surprising on a coral atoll. The presence of diatoms in blue-green algal mucilages is an anomaly that requires explanation. Possibly the mucilage permits the diatom to obtain silicate otherwise unavailable.

It seems worth stressing that the algal vegetation of Takamaka pool II was different from that of any other pools investigated, particularly in view of the fact that the adjacent forest is different in floristic composition from elsewhere in the island. The most likely explanation is that the total, or balance of, nutrients is markedly different in this pool from elsewhere. An important step in obtaining an explanation of this phenomenon would be to obtain a comparative mineral budget of the Takamaka region with that of another region of South Island.



PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The last topic that will be discussed briefly is whether the blue-green algae are important in formation of humus and in erosion of rock surfaces. A quantitative estimate of either process would not be easy, but superficial observations suggests the likelihood that they are important contributors to the development of humus. At the present time most angiosperms grow on rock which has developed at least a very small pocket of soil, and it would appear that these first small soil pockets are often formed by decaying blue-green algae. However, it is much harder to speculate about their possible roles in erosion, or in local deposition of calcium carbonate. Some algal processes will certainly favour the erosion of the coral surface, as release of extracellular materials with chelating properties (Fogg & Westlake 1955; Whitton 1965) and the mechanical and other effects of partly endolithic forms. However, superficial observations provided no convincing clues to the importance of these processes as compared with other erosional agents. It may be mentioned that conspicuous growths of lime-depositing blue-green algae were absent, but some filamentous green algae were often encrusted with calcareous particles.

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## References (Whitton)

Fay, P., Stewart, W. D. P., Walsby, A. E. & Fogg, G. E. 1968 Is the heterocyst the site of nitrogen fixation in blue-green algae? *Nature, Lond.* **220**, 810–812.
Fogg, G. E. & Westlake, D. F. 1955 The importance of extracellular products of algae in freshwater. *Verh. int. verein. theor. angewandte Limnol.* **12**, 219–232.
Stewart, W. D. P. 1966 *Nitrogen fixation in plants*. University of London: Athlone Press.
Stoddart, D. R. & Wright, C. A. 1967 Geography and ecology of Aldabra Atoll. *Atoll. Res. Bull.* **118**, 11–52.
Taylor, W. R. 1950 *Plants of Bikini and other northern Marshall Islands*. Ann Arbor, Michigan: University Press.
Whitton, B. A. 1965 Extracellular products of blue-green algae. *J. gen. Microbiol.* **40**, 1–11.

FIGURE 1. *Stachytarpheta jamaicensis* growing among colonies of *Nostoc commune* on West Island.



PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES