ECOLOGY OF TERRESTRIAL PLANTS IN THE ANTARCTIC WITH PARTICULAR REFERENCE TO BRYOPHYTES

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Abstract: Ecological and phytosociological studies of Antarctic terrestrial plants were reviewed with particular reference to bryophytes. The terrestrial vegetation of the maritime Antarctic consists of two tundra formations of non-vascular cryptogams and of herbs. A scheme of vegetation units (sub-formation, association, sociation) of these formations was established, and their ecological conditions and development have been studied in detail by many authors. The vegetation of the continental Antarctic, however, remains insufficiently studied. The continental vegetation is much more simple in both flora and physiognomy, but it provides several important subjects of ecological interest. Environmental factors related to the vegetational pattern include: water availability, temperature, stability and texture of substrata, chemical edaphic conditions, exposure to wind and sun, degree of snow accumulation, and biotic factors, on which many observations have been made with interesting results.

Autecological studies on Antarctic mosses, combining field observations with experiments under controlled conditions, have recently been expanded, which are concerned with growth, reproduction, productivity, nutrients, photosynthesis, and respiration. Some selected species of Antarctic mosses have been physiologically studied in comparison with temperate plants of the same species. These studies are effective in understanding relationships between the moss life and environment, especially the adaptation to Antarctic extreme conditions.

Last were proposed and discussed some problems for future studies, such as taxonomical problems to be revised, scheme of vegetation units covering the whole Antarctic, autecological studies on the world-wide basis, and the nature conservation.

1. Introduction

What was once known as "Terra australis incognita" is at present a more familiar area and its land and life have become one of the popular topics in several scientific fields. The terrestrial vegetation of the Antarctic, which consists of two flowering plants and cryptogams such as bryophytes, algae, fungi and lichens, was formerly recorded simply as tundra formation, but in the twenty years since the IGY (1957–58), there has been noticeable progress in its ecological and phytosociological studies, along with an increase of taxonomical information.

The purpose of the present paper is to review recent ecological and phytosociological studies of Antarctic terrestrial plants, with particular reference to bryophytes. The area concerned includes both maritime and continental Antarctic (HOLDGATE, 1964) of the Antarctic botanical zone delimited by SKOTTSBERG (1960), and in some cases, observational data from the Subantarctic islands, such as South Georgia, are presented.

The most extensive investigations have been made by the botanical staff of British Antarctic Survey, who established a scheme of vegetation units and tried a detailed analysis of the environmental conditions, principally on South Georgia and in the maritime Antarctic. Autecological studies on Antarctic plants, combining field observations with experiments under controlled conditions, have been performed also by the British staff and by the members and co-workers of the Institute of Polar Studies, Ohio State University, U.S.A. Ecological work by Japanese researchers carried out in the Ongul region of East Antarctica is further important because it deals with the vegetation of continental Antarctic. Beside these activities by systematized team-works, there are some scattered contributions from other countries.

2. Vegetation Units and Their Distribution

2.1. Maritime Antarctic

The first ecological study in the maritime Antarctic was carried out by HOLDGATE (1964) on Signy Island (60°43′S, 45°38′W; in South Orkney Islands) where a British permanent station has been established since 1947. He recognized three formations of cryptogamic plants which were developed in relation to habitat types: 1) *Andreaea—Usnea,* 2) *Polytrichum—Dicranum* (=*Chorisodontium*), and 3) *Drepanocladus—Brachythecium—Acrocladium* (=*Calliergon*) formations. A few years later, LONGTON (1967) surveyed the vegetation over a wider area extending from Candlemas Islands (57°05′S, 26°45′W; in South Sandwich Islands) to Neny Island (*ca.* 68°S, 66°W; in Marguerite Bay). His system of vegetation units consisted of two formations: A) Antarctic cryptogam and B) Antarctic phanerogam, the former formation had six sub-formations which were differentiated on the basis of physiognomic criteria.

Studies of the vegetation of Signy Island, which has very favorable sites for the development of plant communities, were further expanded by GIMINGHAM (1967), GIMINGHAM and SMITH (1970) and SMITH (1972). SMITH (1972) presented an extremely detailed account of the island's terrestrial vegetation based on an analysis of floristic and edaphic data, and the classification of communities given by him has now been accepted as the standard system of vegetation units in the maritime Antarctic. The two largest units to be recognized were categorized on the basis of life form and included A) Antarctic non-vascular cryptogam tundra formation and B) Antarctic herb tundra formation. Within the cryptogam formation, eight sub-formations were described on the basis of the growth form of the predominant species or genera, and comprized a total of 15 associations differentiated according to the degree of constancy of one or more species in physiognomically similar groups of communities. Each association was further subdivided into one to ten sociations determined by the dominancy of particular species.

The classification system proposed by SMITH (1972) is summarized as follows:

A. Antarctic non-vascular cryptogam tundra formation
  1. Fruticose lichen and moss cushion sub-formation
    a. *Andreaea—Usnea* association, incl. 10 sociations
    b. Bryophyte and lichen assemblages of rock micro-habitats
    c. *Tortula—Grimmia antarctici* association, incl. 4 sociations
    d. *Pottia austro-georgica* association, incl. 1 sociation
  2. Crustose lichen sub-formation
    a. *Caloplaca—Xanthoria* association, incl. 6 sociations
    b. *Buellia—Lecanora—Lecidea* association, incl. 1 sociation
    c. *Placopsis contortuplicata* association, incl. 1 sociation
  3. Moss turf sub-formation
    a. *Polytrichum alpestre—Chorisodontium aciphyllum* association, incl. 7 sociations
    b. *Polytrichum alpinum* association, incl. 2 sociations
  4. Moss carpet sub-formation
    a. *Brachythecium* cf. *antarcticum—Calliergon* cf. *sarmentosum—Drepanocladus uncinatus* association, incl. 6 sociations
  5. Moss hummock sub-formation
    a. *Bryum algens—Drepanocladus uncinatus* association, incl. 2 sociations
    b. *Brachythecium austro-salebrosum* association, incl. 1 sociation
  6. Encrusted moss sub-formation
    a. Lichen encrusted *Bryum—Ceratodon* cf. *grossiretis—Pohlia nutans* association, incl. 1 sociation
  7. Alga sub-formation
    a. *Prasiola crispa* association, incl. 1 sociation
    b. *Nostoc* association, incl. 1 sociation
  8. Snow alga sub-formation
    a. *Chlamydomonas nivalis—Raphidonema nivale—Ochromonas* association, incl. 1 sociation
  9. Miscellaneous cryptogam assemblages
B. Antarctic herb tundra formation
  1. Grass and cushion chamaephyte sub-formation
    a. *Deschampsia antarctica—Colobanthus quitensis* association, incl. 3 sociations

SMITH (1972) described and illustrated various examples of environmental patterns for the communities of the five most wide spread associations.

Recently SMITH and GIMINGHAM (1976) compared the above vegetation units (associations and sociations), recognized by field observations on Signy Island, with groupings derived from an objective approach using statistical procedures, and concluded that the results of the various analyses strongly supported the validity of the community grouping proposed in the subjective classification.

LINDSAY (1971) and ALLISON and SMITH (1973) investigated the vegetation of South Shetland Islands (61–63°S, 53–63°W) located southwest of the South Orkney Islands. They were able to classify the communities according to SMITH's (1972) system and were able to recognize an almost identical system of sub-formations and associations, in spite of the fact that in the South Shetland Islands the moss turf subformation is less conspicuous (LINDSAY, 1971) and calcicolous communities are reduced in occurrence (ALLISON and SMITH, 1973). It is noteworthy that LINDSAY (1971) made an attempt to correlate aspects of plant succession in the coastal areas with factors such as exposure, salt spray and nitrogen supply.

Another work by SMITH and CORNER (1973) deals with the more southern section of the maritime Antarctic, including Arthur Harbour (Anvers Island), Goudier Island (Wincke Islands), Argentine Islands, Darboux Island and Cape Pérez (64°46′–65°26′S). The flora of this region is scarcely different from that of the South Orkney and South Shetland Islands, but the vegetation becomes sparser, the communities being less complex as a result of a smaller diversity of habitats and a less frequent supply of available moisture. *Chorisodontium aciphyllum*, which is a major component of the moss turf subformation, is less frequent in the south because of the greater limitation of water availability and has its southernmost limit of distribution on the Argentine Islands. On the other hand, *Polytrichum alpestre*, which is more tolerant of dryness, increases a dominance in the moss turf sub-formation.

2.2. Continental Antarctic

2.2.1. Ongul Islands and vicinity

The plants of the Ongul Islands (69°S, 39°35′E), where Syowa Station of Japanese Antarctic Research Expedition has been established since 1957, and its vicinity have been surveyed in various ways by Japanese workers. The moss flora of this region was first dealt with by HORIKAWA and ANDO (1961, 1967), and later revised and supplemented by OCHI (1976) and NAKANISHI (1977).

MATSUDA (1963, 1968), from his observations on East Ongul Island, has found that moss communities consisting of *Ceratodon purpureus, Bryum argenteum* and *B. inconnexum*, are distributed chiefly on the west side of the island, where they develop on southwest-facing slopes. He concluded that such a pattern of community distribution is due to the better conditions of these slopes in the western part which are protected from the northeasterly prevailing wind and hence receive much heavier snowdrift which brings better water availability in summer. The westerly distribution of moss communities was also observed on West Ongul Island by FUKUSHIMA (1968), KOBAYASHI (1974) and by SHIMIZU (1977). KASHIWADANI (1971, 1973) gave a small account of the mosses in his treatment of lichen ecology.

KOBAYASHI (1974) outlined the aspect of the terrestrial vegetation of the Ongul Islands and Prince Olav Coast, roughly classifying the vegetation into the following communities: 1) Moss, 2) Moss-lichen, 3) Lichen, 4) Alga-lichen, and 5) Alga. More detailed systematic studies on both the moss and the lichen communities in the Ongul region were carried out by NAKANISHI (1977). He recognized for the moss communities six sociations differentiated by species composition: 1) *Ceratodon purpureus,* 2) *Bryum inconnexum*, 3) *Ceratodon purpureus—Bryum inconnexum,* 4) *Bryum argenteum—B. inconnexum*, 5) *Bryum antarcticum—B. inconnexum*, and 6) *Desmatodon* sp.—*Bryum inconnexum*, and he suggested that these sociations could be integrated into the *Bryum inconnexum* association, which is considered to be related to the lichen encrusted *Bryum* spp.—*Ceratodon* spp.—*Pohlia nutans* association of the maritime Antarctic established by GIMINGHAM and SMITH (1970). NAKANISHI further investigated the distribution of the moss communities in relation to water availability and the direction of the prevailing winds.

2.2.2. Other continental areas

RUDOLPH (1963) observed the vegetation in a plot, 400 by 93 feet, on Cape Hallett (72°18′S, 170°18′E), Victoria Land. His vegetation map included an alga community with green (principally *Prasiola crispa*) and blue-green algae, a moss community of *Bryum argenteum*, and a lichen community consisting of *Xanthoria, Parmelia, Caloplaca, Buellia*, etc., each being classified into three types: heavy, patchy, and scattered, on the basis of coverage. He stated that in summer availability of water and nitrogenous debris appeared to be the major factors influencing the distribution of the vegetation components.

A classification of terrestrial vegetation near McMurdo Sound (77–78°S, 164–166°40′E) made by LONGTON (1973a) is noteworthy because it is concerned with the vegetation of the southernmost area so far studied. He recognized the following hierarchical units of communities.

A. Antarctic non-vascular cryptogam tundra formation
  1. Fruticose and foliose lichen sub-formation
    a. *Usnea* association, incl. 2 sociations
  2. Crustaceous lichen sub-formation
    a. *Caloplaca—Xanthoria* association, incl. 2 sociations
  3. Short moss turf and cushion sub-formation (incl. encrusted moss sub-formation)
    a. *Bryum* association
      i. *B. argenteum* sociation

ii. *B. antarcticum* sociation
iii. *B. argenteum—B. antarcticum* sociation
iv. *Bryum* sp. sociation
b. *Sarconeurum* association
i. *Sarconeurum glaciale—Caloplaca darbishirei* sociation
4. Alga sub-formation
a. *Prasiola* association, incl. 1 sociation
b. *Nostoc* association, incl. 1 sociation

As sub-formation dominated by mosses, only one (new sub-formation) has been differentiated which consists of three species of *Bryum* and *Sarconeurum glaciale*. The *Sarconeurum* association appears to tolerate more arid conditions than the *Bryum* association.

Generally speaking, the moss vegetation of the continental Antarctic is simpler in both flora and physiognomy. Sub-formation of (tall) moss turf, moss carpet, and moss hummock, which are common in the maritime Antarctic, are not found in the continental area. It is of interest that *Bryum argenteum*, a well-known cosmopolitan moss, is common in the continental Antarctic, but in the maritime Antarctic it is less frequent (LONGTON and MACIVER, 1977).

3. Community Development and Environment

Every author who has studied the Antarctic terrestrial vegetation emphasizes that water availability in summer is the greatest single influence on the development of cryptogamic communities. Other environmental factors related to pattern within the vegetation include: stability and texture of substrata, chemical edaphic conditions (nitrogen, pH, etc.), exposure to wind and sun, degree of snow accumulation, and biotic factors. It must be borne in mind that the these factors are closely correlated with each other and inseparable in considering their influence to plants.

Low temperatures in the Antarctic have been considered by many to be one of the most critical factors which limit the growth of plants, but temperature seems related to plant life as a secondary factor through limiting water availability. Most of the Antarctic organisms are not psychrophiles, but rather are cold tolerant or cold adapted (RUDOLPH, 1971). It may be true that Antarctic mosses, which are seemingly tolerant of coldness, are actually tolerant of dryness. Examples of Antarctic mosses which are strongly tolerant of long coldness below 0°C and hence of dryness, were demonstrated by HORIKAWA and ANDO (1967), LONGTON and HOLDGATE (1967), and GREENE and LONGTON (1970).

3.1. Water

Water availability, which is, as already stated, the most important environmental factor related to the differentiation of community structure, affects the plants in combination with other factors such as exposure to wind, degrees of snow accumulation and temperature. The observations by MATSUDA (1963, 1968) and subsequent Japanese authors (KOBAYASHI, 1974; NAKANISHI, 1977; SHIMIZU, 1977; YAMANAKA and SATO, 1977) on the Ongul Islands and vicinity show that the distribution of moss communities is strongly correlated with water availability through the pattern of snowdrifts which are affected by the direction of the prevailing winds.

SHIMIZU (1977), from his study on West Ongul Island and Teöya, recognized four habitat types based on the availability of water from snowdrifts and he analyzed the development of several moss communities in relation to each habitat type.

NAKANISHI (1977), in the ice-free area of the Ongul region, investigated the frequency of occurrence of the six moss sociations that he recognized, in different habitat types classified by the pattern of ground water supply: 1) Small snowdrift type, 2) Medium snowdrift type, 3) Large snowdrift type, 4) Lake-shore type, 5) Seepage type, and 6) Stream type. The results showed that, for instance, the *Ceratodon purpureus* sociation was distributed more frequently in rather dry habitats of drift types, while the *Bryum argenteum—B. inconnexum* sociation was restricted to the habitat with a constant supply of water, such as the seepage and the stream type.

It is well-known that the growth form of mosses has a close connection with water availability, and the significance of this fact has been noted for Antarctic mosses by several authors (GIMINGHAM, 1967; LONGTON, 1967; GIMINGHAM and SMITH, 1971; LINDSAY, 1971; SMITH, 1972). The following examples are from the observations by SMITH (1972) on Signy Island: Short cushion mosses (*Andreaea, Grimmia*) are characteristic of the drier and more exposed habitats; tall turf mosses (*Polytrichum alpestre, Chorisodontium aciphyllum*) are usually restricted to well-drained slopes or gravelly porous ground; carpet mosses (*Brachythecium, Calliergon, Drepanocladus*) dominate in permanently moist or wet habitats on level or gently sloping ground. As regards the carpets composed of pleurocarpous moss species, SMITH (1972) stated that in wetter situations they may develop a turf-like growth form, whereas in drier habitats they form a thin mat of more or less procumbent shoots. It is noteworthy that SMITH (1972) described and mapped various examples of small-scale distribution of communities arranged as a response to environmental gradients. Many of the small-scale patterns are closely correlated with gradients of water availability, for example, a zonation along the margins of swampy areas.

LONGTON and HOLDGATE (1967) described the marked zonation of bryophyte communities around fumaroles on Candlemas Island, South Sandwich Islands, which was correlated with a combination of temperature and moisture gradients.

GIMINGHAM (1967) studied the rate of water loss and rehydration of certain mosses on Signy Island, and detected strong positive correlations between the water holding capacity of a species and the moisture level of its habitat. For example, species of *Acrocladium* and *Brachythecium* growing on wet ground hold most of their water externally and it is lost rapidly under conditions of high evaporation stress, but rehydration is also fast. On the other hand, in species of *Andreaea* which occur in drier conditions, far less water is held externally, and water loss is much slower than in the case of *Acrocladium* and *Brachythecium*. Rehydration was also fast but it involved the uptake of less water than in *Acrocladium*.

Studies on the same subject were later expanded by GIMINGHAM and SMITH (1971), who determined experimentally the effects of colony form (*i.e.*, packing and arrangement of shoots) on water loss and water uptake in desiccating atmospheres.

3.2. Chemical edaphic condition

As elsewhere, habitats of calcareous rocks and soils in the Antarctic support the growth of particular calcicole species. On Signy Island, SMITH (1972) observed that calcicolous moss communities developed on local outcrops and knolls of marble, were dominated by *Grimmia antarctici, Tortula fuscoviridis* and *T.* cf. *grossiretis* (*Tortula—Grimmia antarctici* association). *Marchantia berteroana*, the only hepatic of the Marchantiales found in the Antarctic, seems calcicolous and it sometimes occurs in association with the above species of mosses. A *Pottia austro-georgica* association, a *Bryum algens—Drepanocladus uncinatus* association and a *Brachythecium austro-salebrosum* association are also characteristic of base-rich substrata.

According to SMITH and CORNER (1973), in southern parts of the maritime Antarctic, such as the Argentine Islands and neighboring localities, calcifuge genera, *e.g.*, *Andreaea* and *Racomitrium*, are associated with species of *Bryum, Grimmia* and *Tortula* which on Signy Island tend to be typical calcicoles. The mosses seem to have, in these southern regions with harsher conditions, a wider tolerance for substrata with more varied chemical composition and their edaphic requirements become less specific.

Species also exist which prefer to grow in sites of high nitrogenous enrichment as near rookeries of sea birds, *e.g.*, *Prasiola crispa* (green alga), some blue-green algae and certain lichens such as species of *Xanthoria* and *Caloplaca*. Among the mosses, *Bryum argenteum* is a nitrophilous representative (RUDOLPH, 1963; HORIKAWA and ANDO, 1967). NAKANISHI (1977) noted that in the Ongul region, the most ornithocoprophilic community was the *Bryum argenteum—B. inconnexum* sociation, while the *Bryum inconnexum* sociation and the *Bryum antarcticum—B. inconnexum* sociation both seemed to have some relation to the excrements of birds. On the other hand, SCHOFIELD and AHMADJIAN (1972) stated that *Bryum argenteum* and *B. antarcticum* displayed no consistent preference for habitats rich in organic nitrogen so far as one can determine from field notes on herbarium specimens.

Many members of the family Funariaceae, in temperate regions, are known to be characteristic of substrata with a high pH and a high nutrient content. Thus it is of interest that COLLINS (1969) found a vigorous colony of a species of the Funariaceae, not previously known from within the Antarctic botanical zone, in a fumarolic area on new surfaces recently extruded on Deception Island.

3.3. Temperature

The temperature at plant level is often much higher than the value of air temperatures as given by standard meteorological observations and the environment at this level seems fully favorable for plant growth. Data of moss communities exemplifying this ecologically important fact have been presented by many authors (MATSUDA, 1964a, 1968; HOLDGATE, 1964; RUDOLPH, 1966a, b; LONGTON and GREENE, 1967; LONGTON and HOLDGATE, 1967; GREENE and LONGTON, 1970; LONGTON, 1970, 1972a, 1974a; ALLISON and SMITH, 1973; LONGTON and MACIVER, 1977; COLLINS, 1977).

The data provided by MATSUDA (1964a, 1968) from East Ongul Island showed that, in summer, the temperature in the moss communities (*Bryum argenteum, Ceratodon purpureus*) sometimes became over +16°C, rarely ascending as high as +19°C, while air temperature increased to only +3°C; in winter, the air temperature fell to −40°C, but the temperature of mosses under the snow was never below −20°C. Diurnal fluctuations of temperature in the moss community were not recognized during winter, but in summer they were considerable, namely, during the day the temperature exceeded +15°C but at night it decreased to −5° to −10°C.

In February on Galindez Island (*ca.* 64°S), LONGTON and HOLDGATE (1967) observed a temperature as high as +30°C in a *Drepanocladus uncinatus* community when the air temperature was +7.8°C. Another interesting report was made by LONGTON and HOLDGATE (1967) from cushions of a species of *Grimmia* on Deception Island, when the air temperature was +0.4°C on December 9. Under these conditions they found that the mean temperature in the moss cushions on north-facing sunny rocks was +11.2°C, while cushions on south-facing shady rocks gave a mean value of 0°C.

COLLINS (1977) reported that for about 80 percent of the summer the temperature of *Polytrichum alpestre* (at 5 mm below the surface of its colonies) on Signy Island ranged between −5° and +5°C and rarely ascended above +25°C, while the summer temperature of *Drepanocladus uncinatus* was slightly lower and never exceeded +25°C. Such a difference of the temperature was, he explained, due to the longer duration of snow cover and wetter condition in the habitat of *Drepanocladus uncinatus*.

3.4. Exposure to wind and sun

Strong wind, sometimes carrying sand and snow crystals, causes physical damage to Antarctic vegetation and also excessive evaporation from the substratum and the plants themselves. The exposed habitats are also unfavorable for plant growth because snow accumulation is limited there, thus giving rise to unsheltered conditions with low temperatures in winter and a paucity of water supply in summer. Observations by LONGTON (1967), LINDSAY (1971), SMITH (1972), ALLISON and SMITH

(1973) and others showed that the drier sites exposed to wind are occupied only by lichens and small cushion-forming mosses such as *Andreaea* spp. which are tolerant of desiccation. Conversely, mosses with a carpet or a large, loose cushion growth form, are characteristic of moist ground and are found in the more sheltered, wetter habitats.

As already stated, the moss communities on East and West Ongul Islands are mostly distributed in the western parts of the islands which are sheltered from the prevailing winds and better endowed with water availability due to a greater snow covering. Additional studies by NAKANISHI (1977) on other localities near Syowa Station also showed that most of the moss communities were developed on the leeward side of wind-barriers facing west-northwest to southwest.

SMITH (1972) reported examples of wind erosion, supported by the effects of melting snow and ice in spring, resulting in the destruction of large parts of peat banks of *Polytrichum alpestre* and *Chorisodontium aciphyllum*, on Signy and some other islands. Wind erosion on a smaller scale was seen on the ripple systems formed on the surfaces of *Chorisodontium aciphyllum* banks, in which the ridge crest and windward slope of moss waves were encrusted by lichens and blue-green algae (SMITH, 1972; COLLINS, 1976b).

North-facing slopes which receive more insolation and hence are warmer and supplied with much melting water, are more favorable for the growth of plants. SMITH (1972) mentioned that although vegetation was by no means restricted to habitats with northery aspect, certain communities including those formed by *Polytrichum alpestre* and *Chorisodontium aciphyllum*, many of the larger moss carpet stands and communities of the two phanerogams are generally found in such situations. LONGTON (1967) had earlier noted a similar distribution pattern.

3.5. Biotic factors

The influence of animals such as seals, penguins and other sea birds, are locally effective in restricting the development of vegetation. These animals destroy the vegetation by trampling and causing an accumulation of guano and other organic matters. Their excrement is an important source of nutrients for plant growth, but excessive salts in or near rookeries are toxic to most plants, except a few ornithocoprophilous lichens, remarkably nitrophylous green algae, such as *Prasiola crispa*, and some blue-green algae. Several examples of damage to moss vegetation by seals and birds on Signy Island were pointed out by SMITH (1972).

The biotic relationship between mosses and lichens or blue-green algae is one of the interesting problems in the Antarctic ecosystem, which, however, remains insufficiently studied. Invasion by lichens and blue-green algae onto drier parts of moss communities is common in the Antarctic, and various cases of it were observed on Signy Island by SMITH (1972) and COLLINS (1976b).

LONGTON (1973b) reported the occurrence of radial infection pattern induced by the development of fungal hyphae in colonies of *Drepanocladus uncinatus*.

MATSUDA (1964b, 1968) analyzed the developmental process of a combined cushion-like colony of *Ceratodon purpureus* and of *Bryum inconnexum* in relation to cyclic covering with blue-green algae. HORIKAWA and ANDO (1967) reported that blue-green algae disturb the growth of Antarctic mosses, inducing abnormal leaf forms, while SCHOFIELD and AHMADJIAN (1972) suggested a symbiotic relationship in which the alga (*Nostoc* sp.) may obtain the necessary moisture from mosses, and the mosses nitrogen.

3.6. Succession with a change of environmental conditions

Botanical evidences from moss succession which suggests a recent decrease in the cover of persistent ice and snow, were observed on Signy Island (SMITH, 1972; COLLINS, 1976b) and on Argentine Islands (CORNER and SMITH, 1973). According to the survey on Signy Island, older peat banks formed by turf-forming mosses (mostly *Chorisodontium aciphyllum*) have been re-exposed by recent ice and snow recession and subsequently re-colonized by the same moss. Formation of new banks of the *Chorisodontium* was also observed and they were developing at the expense of the moss carpet communities (*Calliergidium, Calliergon, Drepanocladus*), and of another new bank of *Polytrichum alpestre* which was invading the moss cushion communities (*Andreaea, Grimmia, Dicranoweisia*).

If the trend of decreasing persistent snow cover were to continue until its winter depth and duration is relatively short, erosion of the moss banks would commence, an example of which is exhibited by the deep isolated banks with eroded edges on the west coast of Signy Island which are considered to have formerly been larger in extent.

4. Autecology

4.1. Growth and reproduction

Antarctic mosses characteristically exhibit small rates of growth and little sexual reproduction. Their reduced fertility is due to: 1) Quantitative unbalance of male and female plants, with the absence, sometimes, of either sex, 2) Spatial separation of male and female plants, 3) Reduced chance of fertilization because of paucity of liquid water, 4) Abortion of gamentangia and sporophytes from low temperatures and too short a growing season (HORIKAWA and ANDO, 1967; LONGTON and GREENE, 1967; GREENE and LONGTON, 1970; RASTORFER, 1971; LONGTON, 1972a).

It seems that the fertility of mosses is reduced with increasing altitude and latitude, but SMITH and CORNER (1973) noted that in the Argentine Islands mosses produced sporophytes which had been seen only very rarely or not at all in the South Orkney Islands located in more northern latitudes, and that this was due to largely to the increased duration of sunshine.

Various modes of vegetative reproduction in Antarctic bryophytes have been mentioned by SAVICZ-LJUBITZKAJA and SMIRNOVA (1961, 1963, 1964, 1972), TAKAKI (1962), HORIKAWA and ANDO (1967), GIMINGHAM and SMITH (1970), GREENE and LONGTON (1970), SMITH (1972), and LONGTON and MACIVER (1977). They include reproduction by: 1) Fragments of shoots, 2) Separation of innovations or buds, 3) Fragile leaf apices, 4) Various kinds of bulbils or gemmae, 5) Secondary protonemata developed from stems, leaves or rhizoids.

Detailed systematic studies on growth and reproduction have been carried out by certain authors with the following species of mosses.

1. *Polytrichum alpestre*

A series of studies on *Polytrichum alpestre* by LONGTON and GREENE (1967), LONGTON (1970, 1972a, b, 1974c) and COLLINS (1976a, 1977) are noteworthy. Selected interesting facts which these studies revealed are:

a) The seasonal growth of shoots is innately marked by: 1) Some shoot apices which failed to survive the winter and died, and 2) A segmented appearance due to a variation in leaf size through the season. Therefore, the series of annual growth and production can be analyzed by tracing these features.

b) Field colonies of *P. alpestre* show clinal reduction in size with increasing latitude, *i.e.*, with increasing climatic severity the annual growth rate estimated by segment weight, segment length and number of leaves per segment decreases; for example, on the Falkland Islands (51°42′S) they are respectively 2.6 mg, 5.3 mm, 37 (overall means for all specimens scored); on South Georgia (54°17′S) 1.9 mg, 4.3 mm, 30; and on Signy Island (60°43′S) 0.7 mg, 3.5 mm, 18. Experimental studies indicate that these features are all subject to phenotypic plasticity, but also suggest the presence of pronounced inherent differences between colonies from different environments.

c) Antheridia begin to develop during the late summer (February–March), overwinter as juveniles, and mature in the next summer. Archegonia are usually initiated in late spring (October–November) and mature in summer, only rarely overwintering.

d) Sporophytes, developed after fertilization during summer, overwinter in the early calyptra in perichaetium stage, and mature with spore liberation in the next autumn (March–April), 15–17 months after fertilization.

COLLINS (1976a) has made a close analysis of growth and population dynamics of *P. alpestre* on Signy Island.

2. *Pohlia nutans* and *P. cruda*

CLARKE and GREENE (1970) investigated the reproductive phenology of these two species at three separated sites: Disko Island (Greenland), Great Britain and South Georgia, and found that in both species, the start of gametangial production is considerably later in the year at both polar sites, but once produced, the gametangia matures more quickly.

CLARKE and GREENE (1971) performed another study on the same species, in which moss samples from Great Britain and South Georgia (these two sites are located at more or less the same distance from the equator but in climatically contrasting latitudes) were cultured under controlled environmental conditions to investigate their reproductive performance in different temperatures and day-length. The results proved that British plants of both species were able to complete gametangial maturation in long or short days, but South Georgian plants matured only in long days. There was also evidence of a lower temperature optimum for maturation in South Georgian than in British plants. This implies different types of adaptation in local population to climatic conditions at their site of origin. The reason for the difference of photoperiodism in both species between Great Britain and South Georgia where the photoperiodic regime is almost the same, is not clear, but they suggested that in plants from South Georgia with low and much less fluctuating yearly temperature range, control of maturation by day-length may be more advantageous than control by temperature.

3. *Bryum argenteum*

LONGTON (1975) and LONGTON and MACIVER (1977) investigated climatic relationships in Antarctic (Ross Island and Victoria Land) and North American populations of this cosmopolitan moss, involving analysis of microclimate, growth and reproduction, as well as comparison of the behavior of plants from these populations under a range of controlled conditions. The field observations showed that sexual reproduction failed in severe Antarctic climate, but the plants produced several types of asexual propagules, which are, however, also common in temperate populations and not specific to Antarctic plants.

The experimental results suggest that each population of *B. argenteum* studied shows a broad tolerance of a range of temperatures and there is little evidence that the Antarctic plants are particularly adapted to their severe environment. Antarctic cultures, however, consistently developed shoots more rapidly than those of other provenances while, in general, shoot production was also more prolific in the Antarctic cultures. These features may be regarded as adaptations which would faciliate the establishment of *B. argenteum* colonies during the short growing season of the Antarctic.

4. Other studies were made by RASTORFER (1971) on *Bryum antarcticum*, in which vegetative regeneration and sporophyte development in artificial environment were analyzed, and by LONGTON (1972a) with three species of *Polytrichum* other than *P. alpestre* and *Psilopilum antarcticum*.

4.2. *Productivity*

Productivity of Antarctic mosses was investigated by HOLDGATE (1967), LONGTON (1970, 1972b, c, 1974a), CLARKE *et al.* (1971), BAKER (1972), COLLINS (1973, 1977), and SMITH and WALTON (1973). These studies show that figures of productivity become lower with increasing latitude, but locally situations with favorable microclimate may sometimes distort this tendency. LONGTON (1970) gave the following figures for mean annual net productivity in colonies of *Polytrichum alpestre*: South Georgia (54°17′S) 462 g/m^2, Signy Island (64°43′S) 342 g/m^2 and Argentine Islands (65°15′S) 385 and 421 g/m^2. Higher values were recorded at the Argentine Islands than the more northerly Signy Island, and this feature was considered to be due to the warmer summer microclimate at the former station.

According to CLARKE *et al.* (1971), the productivity of the three moss species, which they studies on South Georgia, varied considerably with sites where they grew, the water and light regimes being considered the most important environmental factors.

GODWIN and SWITSUR (1966) estimated the age of *Polytrichum alpestre–Chorisodontium aciphyllum* peats from Signy Island *ca.* 5 feet below the surface to be 1843±96 yr. B.P., which suggests about 1 in./30 yr. as the mean rate of growth of the moss bank.

4.3. Nutrients

ALLEN *et al.* (1967) analyzed the nutrient content of plants and soils from moss communities on Signy Island and investigated factors affecting the availability of plant nutrients. They indicated that there are three sources of nutrient supply: from rock breakdown, from the sea mainly in the form of precipitation or blown spray and from the droppings of birds and mammals, and that the major sources of the principal nutrient elements are complementary, namely, sodium and magnesium have a largely marine origin, potassium and some of the calcium come from the rocks whilst the fauna provides phosphorus and nitrogen.

SCHOFIELD and RUDOLPH (1968) in a preliminary report noted factors, including nitrogen, which determine the distribution of terrestrial plants in the area near McMurdo Station. More detailed field observations and laboratory studies made by SCHOFIELD and AHMADJIAN (1972) suggested that it was the type of nitrogen compounds and the concentration of water-soluble salts that determined the distribution of terrestrial cryptogams (algae, mosses and lichens) in continental Antarctica. In laboratory experiments, isolated mycobiont and algae of lichen and *Prasiola crispa* grew best on specific nitrogen compounds, but a moss (*Bryum algens*) grew well in pure culture on all nitrogen compounds tested, although ammonium salts gave somewhat superior results.

A further interesting fact shown by SCHOFIELD and AHMADJIAN (1972) was that the type of nitrogen source affected the gross morphology of the moss, which suggests that some so-called subspecies and even species may be no more than ecophenes attributable to the type of nitrogen sources in the habitat. For example, *Bryum siplei* BARTRAM, which is distinguished from *B. argenteum* only by the presence of axillary gemmae, seems to be found almost without exception where birds occur, while *B. argenteum* is not always restricted to such a habitat.

Recently YAMANAKA and SATO (1977) analyzed soils of moss and algal communities developed near Syowa Station, in regard to pH, total N and C, available P_2O_5 and exchangeable Ca, Mg, K and Na. It is of interest that they observed well-developed moss communities on some sites in which nitrogenous nutrients were considered to have been supplied from blue-green algae growing on or around the mosses.

4.4. Photosynthesis and respiration

Physiological studies on Antarctic mosses carried out by RASTORFER (1968, 1970a, b, 1972), RASTORFER and GNAU (1969) and COLLINS (1977) are remarkable. Some interesting facts exhibited in these studies are summarized as follows:

1. Optimal temperatures for net photosynthesis were 25–30°C and 15–20°C with maximal rates of 117 and 27–37 μliters O_2 evolved hr^{-1} cm^{-2} for *Bryum argenteum* and *B. antarcticum*, respectively, whereas the respiratory rates increased with increasing temperatures throughout the range of temperatures tested. Apparently, these mosses do not require low temperatures or high light intensities to survive the harsh Antarctic environment, but have a capacity to endure these conditions. It is evident that the photosynthetic and respiratory responses of *Bryum argenteum* and *B. antarcticum* to temperature and light intensity are scarcely different from those in temperate zone mosses. (RASTORFER, 1968, 1970b).

2. Photosynthesis and other physiological characters are different between morphologically different forms, namely, pleurocarpous forms, such as *Calliergidium austro-stramineum* and *Drepanocladus uncinatus*, are physiologically quite different from acrocarpous forms, such as *Polytrichum alpestre* and *Pohlia nutans*. For example, chlorophyll content is higher in the *Calliergidium* and *Drepanocladus* (888–900 μg) than in the *Polytrichum* and *Pohlia* (313–486 μg), and both light compensation and light saturation points are higher by nearly a factor of 2 in the *Polytrichum* and *Pohlia* than in the *Calliergidium* and *Drepanocladus*. These four moss species do not appear to require a cold temperature for survival, but can endure freezing temperature for long periods. (RASTORFER, 1970a, 1972).

3. Material of *Polytrichum alpestre* from Signy Island, grown under a temperature regime similar to that experienced in the field (—5°C night/+5°C day) has an optimal temperature for net photosynthesis of 5°–10°C, whereas *Drepanocladus uncinatus* has the optimal temperature of about 15°C. When grown at higher temperatures (0–5°C night/10–15°C day), similar to those experienced on South Georgia, the optimul temperature for *Drepanocladus uncinatus* remains the same, but for *Polytrichum alpestre* it changed to between 10° and 15°C. *Polytrichum alpestre*, thus, has an ability to acclimate to changing growth period, and this ability is evidently of adaptive significance when there is an extended warm period in the field. (COLLINS, 1977).

5. Problems for Future Studies

Antarctic terrestrial vegetation, although it is composed principally of cryptogamic plants only in a single layer, provides a unique opportunity to study several biotic problems of ecosystem and vital functions of plants in marginal environmental conditions (RUDOLPH, 1971). Recent active investigations by various authors have greatly contributed to clarifying the ecology of Antarctic plants and vegetation, but many difficulties and unsolved or imperfectly resolved problems remain for future studies.

5.1. Taxonomical problems to be revised

The greatest single change in Antarctic botanical studies after the IGY has been the shift in emphasis from the study of preserved material to that of living plants (GREENE, 1967). In other words, the taxonomical and geographical studies on the basis of dried specimens brought back by early expeditions, which were the prime source of knowledges of Antarctic plants in the pre-IGY period, has changed to ecological and physiological studies by field observations and laboratory experiments based on living plants. However, it must always be borne in mind that correct taxonomical treatment of plants is of fundamental importance for ecological studies. Consequently, it is necessary to develop further taxonomical studies and to solve problems of taxa whose identity is even now in difficulty or confusion. A few examples of mosses which require taxonomical revision are given as follows:

1. *Bryum algens* CARD. seems to be a common species in the maritime Antarctic, being frequently seen in phytosociological data from this region. SAVICZ-LJUBITZKAJA and SMIRNOVA (1972) noted *B. algens* as the most wide spread moss of East Antarctica and discussed in detail its morphology and ecology. In this study they reduced *Bryum ongulense* HORIKAWA et ANDO, described from the Ongul Islands, to a synonym of *B. algens*, but without any comment about the relationship between *B. algens* and *B. inconnexum* CARD.; the latter species having been recorded by HORIKAWA and ANDO (1961, 1967) and subsequent Japanese authors from the Ongul region, East Antarctica. HORIKAWA and ANDO (1967) stated that their species *B. ongulense*, which SAVICZ-LJUBITZKAJA and SMIRNOVA (1972) later treated as a synonym of *B. algens*, is only an extremely modified form of *B. inconnexum*. Thus the question arises: Is *Bryum algens* identical to or different from *B. inconnexum*? OCHI (1976) considered *B. algens* to be possibly a distinct species, being related to *B. caespiticium* HEDW., while KANDA (personal communication), who studied both the type specimens, admits the specific identity of the two species, and the present author is inclined to agree with KANDA. OCHI (1976) has treated *B. inconnexum* as a form of *B. pseudotriquetrum* (HEDW.) GAERTN., and SHIMIZU (1977), following OCHI, employed the latter name in his paper on the moss vegetation on West Ongul Island and Teöya. Thus, the most common and important moss of the genus *Bryum* is now appearing in literature under three different names.

2. DIXON and WATTS (1918) suggested that *Bryum antarcticum* HOOK. f. et WILS. showed an extraordinary variability and that *B. gerlachei* CARD., *B. inconnexum* CARD., *B. austro-polare* CARD., *B. filicaule* BROTH. and probably *B. algens* CARD., all described from the Antarctic, might be considered synonymous with *B. antarcticum*. This opinion, although followed by some subsequent authors, seems unreasonable, because several leaf characters of *B. antarcticum* are considerably different from the other species of *Bryum* (HORIKAWA and ANDO, 1967; GREENE, 1968). Recently INOUE (1976) proved that the chromosome number of *B. antarcticum* (material from Skarvsnes, near Syowa Station) is $n=26+2$ acc. The chromosome numbers of the genus *Bryum* have been known to be $n=10$, 20 and 30, with a few exceptions. Thus, INOUE concluded, it seems probable that *B. antarcticum* is not a *Bryum* but belongs to the family Pottiaceae, in which the basic number is known to be $X=13$. This result suggests that cytological studies on Antarctic bryophytes will provide a valuable clue to clarify the identity of doubtful species.

NAKANISHI (1977) observed that sporophytes of *B. antarcticum* in his collection from Skarvsnes showed characters of the genus *Pottia* rather than *Bryum*.

Bryum antarcticum is an important element of the moss vegetation in the continental Antarctic and it is highly desirable that its status can be decided and generally accepted.

3. *Sarconeurum glaciale* (C. MUELL.) CARD. et BRYHN had been known as a species of the only moss genus endemic to the Antarctic botanical zone, but recently GREENE (1975) proved that *Tortula lithophila* DUS. and *T. pygmaea* DUS., both described from southern South America, are conspecific with *S. glaciale*, thus extending the known range of the latter into southern South America. This important finding suggests that taxonomy of Antarctic bryophytes should be reviewed in comparison with those of neighboring Subantarctic areas, especially of southern South America. Such studies should give a lead for tracing the origin and evolution of Antarctic bryophytes and hence, the history of the vegetation in the Antarctic.

5.2. Classification scheme of the terrestrial vegetation covering all the Antarctic botanical zone

Vegetation units can be considered as comparable to "taxa" in plant taxonomy, and it is desirable that the process of community classification and the nomenclature of units is made uniform at least in treating formations of the same type within a certain limited section of the earth.

In the maritime Antarctic, the vegetation has been systematically studied and classified by British botanists and a fine hierarchical scheme of classification has been established, in which the criteria of physiognomy for formation, of growth form for sub-formation, and of floristic composition assessed by constancy and dominancy for association and sociation respectively. FOLLMANN (1965) attempted to classify lichen communities in the Antarctic by BRAUN-BLANQUET's methods, but such methods are not considered appropriate for Antarctic moss communities.

In the floristically simple Antarctic moss community consisting of a single layer, dominancy of certain species is distinct and easily recognized, but associated species of small quantity are apt to be overlooked in field observation, especially in continental Antarctica, where moss communities are formed only with short turf (small acrocarpous) species in compact turfs or cushions with uniform aspect. Dominant species are here usually confined to particular habitats, and play a role as character or differential species, thus being meaningful in classifying the communities.

Classification of the vegetation units by a system comparable to that in the maritime Antarctic was attempted for continental Antarctica by LONGTON (1973a) and by NAKANISHI (1977). The units described by them, however, are concerned only with local vegetation types and it is to be desired that phytosociological studies on the vegetation of continental Antarctica will be further expanded so that a more broadly based scheme of classification can be established and incorporate the terrestrial vegetation covering both the maritime and the continental Antarctic.

5.3. Autecological studies on the world-wide basis

Autecological studies by field observations and laboratory experiments of certain species such as *Bryum argenteum* and *Polytrichum alpestre* from the Antarctic have been carried out by several authors based on comparison of material of the same species from other regions of the Northern Hemisphere. The Antarctic bryophyte flora includes a considerable number of species which are widely distributed over the earth and their biological problems, such as the adaptations to extreme and unusual conditions, will be the better understood if during these investigations they are compared with plants of different populations from other parts of the world.

LONGTON (1974b) proposed an investigation of the biology of widely distributed bryophytes as a possible project for the International Association of Bryologists. He emphasized that such studies would be of immense value in increasing an understanding of the environmental relationships of bryophytes as well as the intriguing question of the extent and flow of genetic variability within bryophyte species. The present author supports LONGTON's suggestion, and as examples of the suitable material suggests, beside *Bryum argenteum* and *Polytrichum alpestre*, the following moss species: *Ceratodon purpureus, Bryum pseudotriquetrum* (OCHI, 1976, considered *Bryum inconnexum* to be a synonym of this species), *Pohlia nutans, Drepanocladus uncinatus* and *Polytrichum alpinum*.

5.4. Conservation of the Antarctic flora and vegetation

With the development of research activities in the Antarctic, man's physical and biological impact on the environment and organisms becomes more marked. Man's disturbance of plants life arises from: pollution by sewage, waste, oil, etc., trampling and crushing by men and vehicles, collection and unintentional introduction of exotic species.

The Scientific Committee on Antarctic Research (SCAR), through its Working Group on Biology, advised the establishment of "Specially Protected Areas" as well as "Sites of Special Scientific Interest" under the Antarctic Treaty by the Agreed Measures for the Conservation of Antarctic Fauna and Flora. The purpose of "Specially Protected Areas" is to preserve the natural ecosystems of areas of outstanding scientific interest. However, nature conservation must always be kept in mind not only for such special areas, but also in all other areas of the Antarctic. Biologists as well as other scientists, when they carry out their researches in the field, should take especial care that their activities never interfere needlessly with the natural life of the Antarctic.

In surveys of the vegetation, efforts to minimize the disturbance by trampling and plant collecting must be constantly borne in mind. In studies of bryophyte communities in temperate regions, gathering of all the plants within a quadrat is usually conducted for laboratory work to verify the identification and to estimate the coverage more accurately, but such a work should be strictly avoided in Antarctic field surveys. It is supposed that the re-establishment of native vegetation requires a long-term process especially in the Antarctic with severe environmental conditions. At present there are no data about the regenerative ability of Antarctic bryophyte communities once destroyed. Thus the extent of man's impact on such vegetation and how the communities once destroyed are able to recover are important problems to be clarified for this region.

I should like to conclude this paper with citing the statement of RUDOLPH (1971), "It is the duty of every person visiting this unique continent to take it upon himself to do all he can to preserve its ecosystem. Our survival in the future may depend upon the understanding of such 'simple' ecosystems existing under hostile environmental conditions".

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