The Changing Pattern of Antarctic Botanical Studies

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Abstract: Some of the major changes which have characterized the study of botany within the Antarctic Botanical Zone are briefly reviewed. Almost all the work in the pre-IGY phase was of a taxonomic or distributional nature, being based principally on preserved material. Since the IGY however, an increasing emphasis is being placed on the study of living material, one result being the rapid development of ecological programmes which so far, have concentrated on problems of vegetation description, environmental analysis and experimental autecology.

Thus, a classification of the vegetation in the vicinity of the Antarctic Peninsula, based primarily on physiognomic criteria has recently been proposed. Environmental studies have been concentrated on descriptions of the microclimatic conditions occurring at plant level and have revealed aspects of the widely fluctuating conditions which prevail in the summer, in contrast to the remarkably uniform conditions that exist under the winter snow blanket. Studies on water availability in Antarctic mosses have also been reviewed. The experimental autecological work to date, has been concerned with the effects of microclimate on the growth and reproductive behaviour of various mosses as well as the two native Antarctic flowering plants, and attempts have been made to interpret the data from field studies by growing representatives of the field populations under controlled conditions in a phytotron.

Introduction

Although the study of botany within what is now known as the Antarctic Botanical Zone (GREENE, 1964) began over 130 years ago with the observations of J. WEDDELL (1825) and J. EIGHTS (1833), it is only in the last 10 years — in fact since the IGY — that there has been noticeable change in the nature of research. It is not necessary to look far to understand the paucity and uniformity of most of the early work, since a desire to study plants rarely, if ever, secured a place on a pioneering expedition. Neither is it difficult to understand the timing or the speed of the change which coincided with the provision of the spectacular logistic facilities that became available to botanists during the IGY.

Currently, discussions are taking place between SCAR and SCIBP (IBP News, 1965, 1966) and if these result in the initiation of programmes in Antarctic regions, as part of the IBP, a further period of rapid change is predictable.

My purpose then, in this short paper, is to review briefly what seem to me to be some of the most significant changes which are taking place in the study of terrestrial botany within the Antarctic Botanical Zone.

Taxonomy

If a name had to be found to characterize the work of the pre-IGY period, it could well be called the taxonomic phase, since this type of work predominated. The methods used were the collection, preservation and description of specimens with the object of compiling a descriptive catalogue of the flora and determining the distribution patterns of its species. The material available for study was collected as circumstances allowed, and as it was handed over for description and publication to specialists who had not worked in the south, much of the botanical literature suffered from the customary deficiencies of what may be called "second-hand" publications. There were, of course, notable exceptions as in the case of J. D. HOOKER and C. SKOTTSBERG, and it cannot be doubted that the quality of their work on Antarctic botany owed much to the observations and collections they themselves made in the south.

Owing to the high percentage of cryptogams in the Antarctic flora, this "second-hand" approach was less successful here than in other parts of the world. Indeed it was not until the recent advent of cryptogamic specialists into the south that the first adequate collections became available for study. The position at the beginning of the IGY was well portrayed in papers by LLANO (1956, 1961) and STEERE (1961).

In spite of these difficulties, some of the characteristics of the Antarctic flora were recognized at an early stage. For example, it soon became clear through the work of HOOKER (1844–47), CARDOT (1908), and DARBISHIRE (1912), that the flora was not homogeneous but comprised a variety of phytogeographical elements, facts which raised a number of serious distributional problems. But notwithstanding the increasing clarification of these distribution patterns (LAMB, 1964; GREENE, in press) we are really little nearer the solution of such fundamental problems as the age and origins of the Antarctic flora. Neither will we get any closer until fresh evidence is available from new lines of botanical research, such as can be expected, for example, from cytological studies and the various disciplines included in the field of quaternary studies.

Some new taxonomic approaches have been introduced during the post-IGY period, the most notable resulting in the publication by TATUNO (1963) of the first chromosome counts for any Antarctic cryptogams. The establishment of living collections of cryptogams in some research centres, as at Birmingham, is also of importance since it provides opportunities for extended studies of such problems as variability, depauperation and sterility.

Ecology

If the development of botanical studies in the pre-IGY period was slow, this is certainly not true of the post-IGY phase.

Perhaps the greatest single change has been the shift in emphasis from the study of preserved material to that of living plants. Associated with this has been the purposeful nature of field activities, *i. e.* a change from haphazard observations and collections to the disciplined pursuit of specific objectives. Lastly, I attach great significance to the appearance of a literature stamped with the authority of authors who have had first hand experience of their subject in the field. Of course it must not be overlooked that these developments really owe as much to changing ideas in the Science of Botany as they do to the provision of excellent field facilities in the South, since I have little doubt that if the facilities had been available earlier, the present phase of expansion would have begun sooner and at a slower rate.

The majority of the new topics are concerned, one way or another, with the performance of living plants in their natural environment and so fall within the compass of ecology. For convenience they may be considered under three subheadings: Vegetation Description; Environmental Analysis and Experimental Autecology.

Vegetation Description

In spite of taxonomic difficulties, an outline scheme describing the vegetation of part of the Scotia Ridge — Antarctic Peninsula Sector has already been proposed by LONGTON (in press). This scheme is a development of HOLDGATE's (1964) account of the vegetation of Signy I., and recognizes two formations — the Antarctic Cryptogam Formation and the Antarctic Phanerogam formation, the former with six and the latter with one sub-formation.

These units are based on physiognomic criteria and so remain recognizable in spite of variation in floristic composition from site to site. It was suggested by LONGTON that edaphic factors such as water availability are of great importance in determining local distribution patterns, but that climatic factors may be of greater importance in determining the character of the vegetation over the region as a whole. Although the formal definition of categories below the level of the sub-formation was not attempted, this scheme reveals a floristic variety and a complexity of structure in the vegetation units of this part of Antarctica.

GIMINGHAM (in press), working on Signy I., attempted a detailed floristic assessment of part of the island's vegetation, basing his conclusions on the results of a computer analysis of his field data using the "Normal association" analysis of WILLIAMS and LAMBERT. The results so far available confirm the existance of a variety of associations below the sub-formation level, and it is even possible to recognize still smaller units characterized by the local dominance of particular species in specific habitats.

So far no attempt has been made to define formally any of the vegetation units of continental Antarctica, but from the accounts of RUDOLPH (1963) and MATSUDA (1964), as well as what I have seen myself in various parts of Victoria Land, it seems clear that the continental communities are normally very much simpler than most of those noted by LONGTON. In Victoria Land at least, they are often little more than isolated populations of single species, which may at times coalesce to give a reasonable cover. Less commonly, two or more species are involved but owing to the scattered nature of the populations, competition is slight or absent, so that the response of a species to the environment is often the sole factor determining its establishment and survival.

Environmental Analysis

Temperature has long been considered to be the prime environmental factor limiting plant growth in the South. The assumption that few plants can withstand the harsh cold summers, was well summarized by BROWN (1912) when he remarked that "the Antarctic summer is but an astronomical conception". These considerations, of course, were based on the results of air temperatures taken approximately 1.5 m above the ground. While the prevailing summer temperature regimes at plant level may indeed be too harsh for many species, it has recently become clear that some of these regimes are considerably less severe than the standard meteorological data suggest.

SIPLE (1938) was one of the first to draw attention to the fact that summer temperatures at plant level may be far in excess of air temperatures and he attributed the greater number of lichens on dark as opposed to light coloured rocks in Marie Byrd Land to the fact that the former will absorb more radiant heat in clear sunny periods. HOLDGATE (1964) presented more extensive data from Signy I. which showed that, in a *Polytrichum - Dicranum* turf, temperatures well in excess of air temperature occur regularly on clear sunny days when the diurnal amplitude may reach as high as 15°C, while MATSUDA (1964) recorded a maximum temperature of 19°C in a cushion of *Bryum argenteum* on the Ongul Is. Also under clear conditions, RUDOLPH (1965) found the amplitude on lichen surfaces on rocks at Cape Hallett to be as much as 30°C, with temperatures of 32°C being attained briefly.

Recent data from within a *Polytrichum alpestre* turf on the Subantarctic island of South Georgia, also showed fluctuating summer temperatures with a regular diurnal amplitude of 20°–30°C on clear days in high summer, when the entire range was normally above freezing: temperatures as high as 35°C were recorded briefly (LONGTON and GREENE, in press).

The aspect, or orientation of a habitat to the sun's rays, may be expected to affect the amplitude of the diurnal rhythm. Thus LONGTON and HOLDGATE (in press) reported that in a cushion of a species of *Grimmia* on Deception I., when the summer air temperature was 0.4°C, the mean temperature in cushions on north-facing rocks was 11.2°C, while comparable cushions on south-facing rocks gave a mean value of 0°C.

These authors (LONGTON and HOLDGATE, in press), in their recent review of temperature relationships of Antarctic vegetation, summarized present knowledge of summer conditions as follows: "During summer solar radiation frequently heats the surface of soil and bryophyte colonies to levels greatly above air temperatures by day, but at night loss by convection may cause an inversion so that soil and vegetation surfaces are cooler than the surrounding air. Wide and rapid diurnal fluctuations in temperature thus occur, particularly in clear weather, and considerable warming of the plants also takes place at times during light overcast conditions. On cloudy days however, temperatures near the surface of the vegetation may differ little from air temperature".

Winter data have been provided by MATSUDA (1964) from the Ongul Islands and by LONGTON and GREENE (in press) from South Georgia, all of whom commented on the total absence of a diurnal rhythm under snow cover. On South Georgia, once the snow cover had been established, the temperature remained at or slightly above zero for almost the whole of the winter, $-0.4°C$ being the lowest temperature recorded during this period. In passing, it may be noted that this was not the absolute minimum temperature recorded in the moss turf, $-4°C$ being noted in spring when the plants lacked snow cover. On the Ongul Is., the temperature under snow showed a gradual fall to a monthly mean of $-16°C$ in August, with $-20°C$ the lowest temperature recorded, occurring in this month, *i.e.* during winter. But MATSUDA also noted a winter temperature of $-29°C$ in dry uncovered moss cushions in May.

Too few data are yet available to allow satisfactory comparisons, but it is already clear that plants from different localities experience a variety of temperature regimes and indeed at one site the temperatures at plant level may vary greatly depending upon the substrate and the aspect. It is also true to say that for successful growth and reproduction in Antarctica, plants have to withstand summer temperature regimes characterized by normally rapid and irregular diurnal changes while winter temperatures are low and under snow cover lack a diurnal fluctuation. Indeed the capacity to withstand summer conditions, rather than an ability to sustain low winter temperatures, may provide the greatest selection presssure determining which plants can grow on or near the Antarctic continent.

Water availability is another important environmental factor, but under field conditions it is sometimes difficult to isolate its influence from that of temperature. For instance, in the South Sandwich Is., on otherwise almost barren areas, luxuriant cryptogamic vegetation is developed locally around fumaroles where the ground is warmer and also moister (LONGTON and HOLDGATE, in press). But it is uncertain whether the marked zonation existing within this fumarole vegetation has developed as a response to a temperature or moisture gradient, or to a combination of both.

In Marguerite Bay however, LONGTON (in press) noted that wherever the prevailing dry slopes were irrigated by melt water, cryptogamic vegetation developed, a situation comparable to what I have seen in Victoria Land. So it seems safe to conclude that in these cases it is the lack of water, rather than an unfavourable temperature regime, which is the limiting factor.

RUDOLPH (1963) reached a similar conclusion about the factors most affecting plant distribution at Cape Hallett, while LONGTON (in press) stressed the relationship between growth form and moistness of the habitat in his account of Antarctic vegetation. Consequently GIMINGHAM's (in press) studies on the rate of water loss and rehydration of certain mosses on Signy I. are of interest as he demonstrated strong positive correlations between the water holding capacity of certain species and the moisture level of their habitats.

Loss of water from moist samples consisting of isolated shoots and small portions of the intact colony, was followed in controlled conditions of relative humidities of 93%, 70%, and 45%, at room temperature, thus simulating mild to severe evaporation stresses. Rehydration, or water uptake, was studied using samples from which free water had been spun off by slow (=250 g) centrifuging. A centrifuge was also used to estimate the amount of water held externally in samples from the field.

The results showed that plants of wet ground such as species of *Acrocladium* and *Brachythecium* hold most of their water externally and that it is lost rapidly under conditions of high evaporation stress, but rehydration was also fast. In the case of species of *Andreaea* which grow in drier conditions, far less water was held externally, and water loss, although rapid, was much slower than in the case of *Acrocladium* and *Brachythecium*, intact portions of the colony losing water more slowly than isolated shoots. Rehydration was also fast but it involved the uptake of less water than in *Acrocladium*. Taken together these and the other results given by GIMINGHAM demonstrate that species with little or no mechanism for preventing water loss are confined to the wetter sites whereas those which hold less water externally and lose it more slowly are able to grow in the drier situations. Much more analyses of this sort are essential before we can understand the effects of the different environmental factors on plants in the field.

Experimental Autecology

An analytical approach seeking correlations between field behaviour and changes in environmental conditions is fundamental to the study of many autecological problems. But even when clear associations can be demonstrated it is rarely that the primary causal relationship can be confidently inferred, unless experimental methods have been used to isolate the effects of individual factors.

Such an approach forms the basis of a long term programme being organized from Birmingham, into the effects of climatic factors on the growth and reproduction of Antarctic plants. For the species selected, their behaviour at a number of widely scattered sites in the Scotia Ridge — Antarctic Peninsula Sector — where microclimatic parameters are being monitored — is compared with the responses of material from the same sites grown under a range of controlled conditions in a phytotron. Thus performance under experimentally controlled conditions is being compared with performance under known field conditions, so providing a basis for interpreting any climatic behaviour correlations suggested by field observations.

So far only preliminary results are available from two studies using this method. The first concerns several mosses belonging to the genus *Polytrichum*, while the second deals with the two native Antarctic flowering plants, *Colobanthus crassifolius* and *Deschampsia antarctica*.

The work on *Polytrichum* was initiated on South Georgia and later extended to a number of sites as far south as Marguerite Bay (LONGTON and GREENE, in press). Field observations included estimates of the duration and extent of vegetative growth, gametangial production and sporophyte development, as well as recordings of temperature and relative humidity at plant level: measurements of additional factors such as precipitation, day length and amount of sunshine were available from the standard synoptic meteorological data from the nearby bases.

The results available refer to performance on South Georgia where growth rate estimates gave a mean annual increase of 3–5 mm in stem length. Gametangia of both sexes developed regularly, with antheridia appearing in autumn but the appearance of archegonia was delayed until the beginning of the next season. Fertilization appeared to take place in early summer (December–January), with the first sporophytes being recorded soon after but, due to development being arrested during winter, the spores were not shed until the autumn (March–April) of the following season, *i.e.* 15–17 months after fertilization. Detailed results are not yet available from the sites farther south, nor from the phytotron, but the regular failure of fruit production south of South Georgia is a conspicuous feature.

In *Polytrichum alpinum* sporophyte development on South Georgia is almost identical to *P. alpestre* and, like the latter species, south of South Georgia fruit is only very rarely produced. It has been established however, that gametangia of both species develop at a number of localities near the Antarctic Peninsula in some seasons, and that bisexual populations of *P. alpinum* occur on Signy I. But why fruit is so rarely formed here or at other localities south of South Georgia is not yet clear.

The work on *Colobanthus* and *Deschampsia* has already yielded some preliminary results from experiments in the phytotron and observations in the field. It appears that both species undergo some vegetative growth and flower production in all the localities examined from South Georgia (lat. 53°50′∼55°S) southwards to their most southerly known station on Neny I. (68°12′S) in Marguerite Bay. On South Georgia, and at sites from the Argentine Is., south to Neny I. (65°15′S to 68°12′S), viable seed appears to be produced annually, but further north in the South Orkney Is., and South Shetland Is., (lat. approx. 60°S to 63°S), successful seed production occurs infrequently, for example in *Deschampsia* only once in the last five seasons on Signy I., although during the same period *Colobanthus* formed viable seed in two of the seasons.

Under experimental conditions, flowers and seeds were regularly produced in *Colobanthus*: they were also regularly produced in *Deschampsia* provided the plants had received a cold pretreatment and were grown under long day conditions. But in both species the duration of flowering and the amount of seed produced depended upon the temperature and the day length under which the plants were grown.

Summary and Conclusions

From this brief review it is clear, I think, that compared with the limited botanical achievements of the pre-IGY phase, the short period since then has been characterized by the rapid development of a range of field and laboratory programmes concentrating on the responses of living plants. These programmes include attempts to define the units of vegetation and to correlate their distribution with climatic or edaphic factors, water availability being one such factor which has been investigated experimentally. Autecological studies combining field observations with phytotron experiments have also been initiated to provide an understanding of the effects of climatic factors on the growth and reproduction of selected species. But owing to shortage of time no comments have been made on recent studies on Antarctic soils or on the metabolic activities of their microbial flora.

If during the IBP new internationally co-ordinated programmes, employing some standardization of methods and presentation of results, can be initiated and maintained for a 2–3 year period, then I think that Antarctic botanical studies could enter upon a new phase of further rapid expansion

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