PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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The I.B.P. Bipolar Botanical Project

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A summary is given of comparative work carried out within the I.B.P. Tundra Biome at an Arctic station (Greenland) and a sub-Antarctic station (South Georgia). The investigations covered many aspects of plant ecology, primary production and adaptation to polar environments. The work was extended by an international synthesis of results. General conclusions are reported and the current continuation of the studies is discussed.

Introduction

The Bipolar Botanical Project was conceived by Drs M. C. Lewis & S. W. Greene, formerly of Birmingham University, as a comparative study of the processes of primary production in a polar region of each hemisphere. The project was initially planned to run from 1967 to 1973 (Lewis 1968) with field sites at Disko Island, West Greenland (lat. 69° 15′ N, long. 53° 30′ W) and Grytviken, South Georgia (lat. 54° 17′ S, long. 36° 31′ W) which could be compared with other Tundra Biome sites. The Arctic programme was financed by the Royal Society while the Antarctic work was supported mainly by the British Antarctic Survey.

The main objective comprised three areas of research (Lewis 1968):

(*a*) an investigation of the different environments on each island;

(*b*) estimations of primary productivity in ecologically important plants and communities;

(*c*) investigations of adaptations in the indigenous flora to the various environments.

This undertaking resulted in a reconnaissance visit to each island (1967–8) followed by longer periods of intensive field-work during 1969–71 (Lewis & Callaghan 1971; Smith 1971).

At the conclusion of the bipolar comparisons the synthesis was extended to a much broader tundra basis as a result of the Royal Society Tundra Biome Visiting Research Fellowship granted to one of us (T.V.C.). This enabled visits to be made to most of the other I.B.P. tundra sites during 1972. The main objective was a comparison of strategies of growth and population dynamics in tundra plants. N. J. Collins, Institute of Terrestrial Ecology Bryophyte Project Group, was invited to participate and include his work on bryophytes.

This condensed project summary serves only to exemplify the more important results on particular species. Within the project lines of research and species studied were very diverse.

South Georgia and Greenland

Environmental investigations

During the reconnaissance phase sites were selected which, while representing a range of environmental severity on each island, provided analogous habitats for between-island comparisons. At each site the local environment was recorded by continuous automatic monitoring of soil and air temperatures, solar radiation, wind speed and humidity, and the soils at each site were sampled and analysed. The relevance of environmental site differences to growth was revealed by growing a standard genotype of a given plant under either standard edaphic conditions (fertilized vermiculite) at different sites or in different native soils at one site. Crop plants, e.g. oats, barley, radish, were used as phytometers in addition to some native species. An initial trial showed considerable differences between sites and generally greater growth rates at the Greenland sites (Lewis & Greene 1970) but soil conditions usually limited growth more than microclimate (Callaghan & Lewis 1971 *a*). Multiple trials within a growing season ndicated that growth rates and dry mass production varied more with time of season than between sites, with site differences only assuming maximum expression when the weather was most severe (Smith & Walton 1975 *a*; Walton & Smith 1976).

Energy values obtained for much of the South Georgian flora compared more closely with Alpine rather than Arctic data (Smith & Walton 1973). Determinations of plant mineral content showed similar seasonal trends to those in northern temperate regions. There were however very marked differences in the rates of mineral cycling within different ecosystems (Walton & Smith, in press).

Primary production of native species

Production studies were carried out at community level by area sampling techniques, and at species level by various methods. The productivity of dominant communities on South Georgia proved to be very high compared with other tundra communities and the rates and components of production showed great affinities to alpine areas (Greene, Walton & Callaghan 1973; Smith & Stephenson 1975; Walton *et al.* 1975). Similarly, the production values for individual species of mosses, e.g. *Pohlia wahlenbergii* (Clarke, Greene & Greene 1971), dwarf shrubs, e.g. *Acaena magellanica* (Walton 1973) and grasses, e.g. *Phleum alpinum* (Callaghan 1973) proved high on both islands when compared with data from other tundra locations. In general, productivity for each growth form was greater on Disko Island than on South Georgia. The factors underlying the primary production were investigated by detailed autecological studies.

Adaptive strategies of indigenous species

Ecologically important species at each station and bipolar species were intensively studied *in situ*. In Greenland *Phleum alpinum*, *Salix glauca* and *Alchemilla glomerulans* were aged and dry mass accumulation and partitioning followed throughout their life cycles. Their phenology and rates of development were also monitored. Between-species comparisons pointed to general tundra-adaptive strategies such as longevity, the predominance of vegetative reproduction and the acceleration of sexual reproductive processes (Clarke & Greene 1970; Callaghan 1973). Between habitat comparisons revealed specific adaptations such as increased photosynthetic efficiency to compensate for low leaf area ratios reduced by site severity (Callaghan & Lewis 1971 *a*). Comparisons between the islands revealed that the annual reproductive cycle of *Phleum alpinum* on South Georgia allows population stability (Callaghan & Lewis 1971 *b*) whereas occasional seed set on Disko Island, although compensated for by higher reproductive capacities, results in precarious population fluctuations (Callaghan 1974). The genetic nature of these inferred adaptations was demonstrated by growing different populations under standard conditions in the field in reciprocal transplant experiments (Callaghan 1974) or under controlled conditions in the laboratory (Clarke & Greene 1971). Ecological limitations in the South Georgian taxa of *Acaena* were related both to genetically determined aspects of development and morphology, and to phenotypic responses to environmental constraints (Walton 1974, 1976).

Conclusions

The general conclusions from all the bipolar work are that the short, although favourable, Greenland summers restrict development and reproduction while the long, cool and wet South Georgian growing seasons limit vegetative growth. The Arctic climate has selected species capable of short periods of fast growth and opportunistic reproduction or rapid reproductive development. Alternatively, the South Georgian climate has favoured species with slow but consistent rates of reproduction and growth. The higher incidence of sexual reproduction on South Georgia has allowed considerable genotypic differentiation although some species with wide ecological tolerances show instead a high degree of plasticity. It would appear that the impoverished flora of South Georgia is primarily due to its geographical isolation rather than to environmental constraints.

International synthesis

The visits to most of the other I.B.P. tundra sites enabled direct comparisons to be made between sites both for individual widespread species and for different species occupying analogous niches (Callaghan & Collins, in press) by using methods and experience obtained in the Bipolar Project. The estimation of production from the interaction between population dynamics and growth allowed both detailed comparisons at various stages of the life cycle and overall comparisons. The detailed comparisons have revealed important adaptations such as the differentiation of tillers in graminoids and a system of non-genetic variation (Callaghan & Collins 1976; Callaghan 1976) while the broad comparisons have resulted in a site classification complementary to that based on the physical environment. These methods have enabled the construction of computer models which simulate plant growth throughout the life cycle. From their predictions of future age class structures and densities the models also estimate future biomass and dry matter production.

Synthesis work is also being carried out by M. C. Lewis on more physiological production processes.

Continuation and extension

The experimental work initiated as a result of this I.B.P. project enabled additional studies during the visits to South Georgia. A survey of the island's natural and alien vegetation was carried out (Walton & Smith 1973) together with phytosociological and ecological studies. To complement phytometric work on the island's climate, phenological observations were made on Falkland Island plants transplanted to South Georgia (Edwards & Greene 1973).

Although the I.B.P. is officially concluded, there are still some continuing projects. Work is continuing on the synthetic and comparative aspects of the life cycles of tundra species, while further analysis of microclimate data should allow the study of detailed plant-energy relationships.

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Much work has been synthesized and Smith & Walton (1975*b*) have attempted to bring together all the available information on South Georgia. This has resulted in a recognition of the various areas in which knowledge is severely lacking and has provided a basis for the forward planning of South Georgian studies, some of which are now in progress. The results of the Arctic phase have shown tundra ecosystems and plants to be amenable to some detailed autecological studies almost impossible in other regions because of increased community complexity and higher rates of decomposition (Callaghan & Collins 1976). The international synthesis at a broad level of resolution has revealed important sites for the continuation of specific detailed research; this is currently being carried out within the Institute of Terrestrial Ecology.

Both the completed and continuing studies have considerable relevance to our understanding of natural and exploited ecosystems. While plant density and production can be predicted in a long term context, an increased understanding of the constraints on plants and their adaptive responses in a range of tundra habitats may prove useful in the breeding of crop species for higher latitudes. On the other hand, the adaptations by which some species overcome the constraints of fell-fields may well be of relevance in the revegetation of the analogous habitat of the temperate regions – the spoil heaps of our extractive industries.

It is impossible to give adequate acknowledgement to the many people who have helped this project in various ways since its inception. We must, however, offer our grateful thanks to those who initiated the projects – M. C. Lewis, S. W. Greene and O. W. Heal and those who took part directly – D. M. Greene, G. C. S. Clarke, C. Stephenson, J. R. B. Tallowin, N. J. Collins, B. J. Phillips, G. E. Jones and R. Law. We are indebted to the Universities of Birmingham, York, Manchester and Copenhagen and the Institute of Terrestrial Ecology Merlewood Research Station for their generous provision of facilities and, especially, to the Royal Society and the British Antarctic Survey for their financial support of the whole project. To our many other colleagues in Britain, Greenland, South Georgia and the Tundra Biome in general, we are indebted in many ways for advice, assistance and support.

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