Reports

Limitations of the Competitive Exclusion Principle

Abstract. Under severe conditions in the arctic the physical environment frequently overrides biological competition, allowing essentially random occurrence of plants without distinct associations and with the frequent coexistence of related species that have extremely similar requirements. Furthermore, a mixed population may be so advantageous in reducing disease incidence as to offset competition.

Biologists are indebted to Cole (*1*) for his warning against blind acceptance of the principle that two species which occupy the same ecological niche cannot coexist, and of the dangerous corollary that two species must have different ecological requirements because they do coexist.

Any botanist who has done much field work in unfavorable environments must have doubted the universal applicability of this principle, for in very poor habitats competition often seems to be of minor importance. As a result of much of my field work in recent years having been in alpine and arctic regions, I have become increasingly impressed by the inadequacy of the exclusion principle in many habitats. Cole reminds us that Skellam (*2*) has shown mathematically that in a poor habitat greater fertility may outweigh competitive ability. Reading his report just after returning from the bleakest part of the Canadian arctic archipelago (Ellef Ringnes and adjacent islands), I could fully appreciate his argument. In this region, and to a slightly lesser degree in many other nonmountainous parts of the archipelago, the plants are severely limited in both stature and variety by the short season, very low summer temperature, high winds, and low summer rainfall. A closed plant cover is seldom approached except in the relatively scarce marshes, and on many clay or gravel plains the cover may be from 1 to 10 percent of the ground surface. Under such severe physical restrictions biological competition is greatly reduced and is often negligible. In warmer arid lands a sparse ground cover is often accompanied by an extensive root system; and the ground may thus be nearly fully occupied. But in these arctic deserts the root systems generally occupy approximately the same area as the aerial parts of the plants.

In view of the suggestion by Hutchinson (*3*) that Skellam's model applies primarily to annual plants, it should be noted that very few annuals reach the arctic, where they tend to be eliminated by occasional disastrous summers, and that only perennials occur in the high arctic.

Two features of the arctic flora emphasize the reduced importance of competition. First, there is the absence of clearly defined associations in the poorer habitats. The plants that are able to survive in such habitats generally occur randomly in any combination. This point was vividly brought to my attention on a recent arctic field trip, when a botanist unfamiliar with the arctic sought my help in identifying plant associations on arid limestone gravel. The "association" changed from step to step without any regular pattern. In such regions it is advisable to describe the flora in terms of major habitats rather than by associations.

The second significant feature of the high arctic flora is the frequent coexistence in a single habitat of two or more closely related species. When the plants are severely stunted, such mixed occurrences may be exasperating to the collector, who may later find he has mixed collections of *Draba, Cerastium,* or *Potentilla* spp., when he had intended to take a long series of one species. The most striking examples of such coexistence occur in *Saxifraga,* the principal genus of the high arctic. Of eight species of *Saxifraga* at Isachsen, Ellef Ringnes Island, seven occurred in strongly overlapping to essentially identical habitats; and two to five species were often found intimately mixed on a small area of uniform habitat. Here there was no problem of identity, save for the occasional simulation of *S. tenuis* by *S. nivalis*; but I doubt whether the situation is fundamentally different from some situations in temperate regions, where we have wondered whether two plants were really distinct species rather than one being a sporadic mutant of the other, because we so often find them growing together. We surely cannot draw a sharp line between severe conditions in which competition is ineffective and benign situations in which it is omnipotent in excluding a species.

A further limitation of the competitive exclusion principle is probably to be found in the effects of diseases and pests upon a solid stand of a single species. Even closely related species with identical ecological requirements often differ significantly in their resistance to diseases. A mixed population may accordingly have a decided advantage over a pure stand of one component of the mixture. This point has been well emphasized by Elton (*4*), especially in relation to agriculture, but has perhaps been inadequately appreciated by many biologists (*5*).

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References and Notes

1. L. C. Cole, *Science* **132**, 348 (1960).
2. J. G. Skellam, *Biometrika* **38**, 196 (1951).
3. G. E. Hutchinson, *Cold Spring Harbor Symposia Quant. Biol.* **22**, 415 (1957).
4. C. S. Elton, *Ecology of Invasions by Animals and Plants* (Methuen, London, 1958).
5. This report is contribution No. 108 from the Plant Research Institute, Research Branch, Canada Department of Agriculture.

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Protactinium-231 Content of Ocean Water and Sediments

Abstract. By means of a direct method for determining the nuclide protactinium-231, a deficiency in ocean water was found to be accompanied by unsupported Pa^{231} in ocean sediments. Protactinium-ionium ratios obtained for a surface and a deep section in the same equatorial core yielded apparent ages which were in agreement with predicted ages.

In the past, workers (*1*) set maximum concentration limits for Pa^{231} in ocean water by determining an upper limit for Th^{227} and then assuming that Th^{227}, Ac^{227} and Pa^{231} were in secular equilibrium. Since the half-

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Type manuscripts double-spaced and submit one ribbon copy and one carbon copy.

Limit the report proper to the equivalent of 1200 words. This space includes that occupied by illustrative material as well as by the references and notes.

Limit illustrative material to *one* 2-column figure (that is, a figure whose width equals two columns of text) or to *one* 2-column table or to *two* 1-column illustrations, which may consist of two figures or two tables or one of each.

For further details see "Suggestions to Contributors" [*Science* **125**, 16 (1957)].