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)].

life of 27.7 years gives ample time for solvation and precipitation processes to act selectively on Ac^{227} and effect a separation of it from its parent Pa^{231}, I thought that a direct determination of Pa^{231} in ocean water was necessary.

The procedure, a modification of one developed by Potratz and Bonner (*2*), was as follows. A known activity of Pa^{233} (a beta emitter which results from the decay of Th^{233} produced by the thermal neutron irradiation of Th^{232}), Fe^{3+} solution, and acid were added to portions of ocean water filtered through Whatman 41H paper. Naturally occurring Pa^{231} and the added Pa^{233} were concentrated by co-precipitation with $Fe(OH)_3$ upon the addition of NH_4OH and then separated from the iron by two co-precipitations on $ZrO(IO_3)_2$ from 4*M* HNO_3 solutions. Further purification of the protactinium isotopes was obtained by their extraction from a 6*M* HCl solution into diisobutylcarbinol. After washing the organic phase with several portions of 6*M* HCl, protactinium was back-extracted into a dilute HF solution which was washed with several portions of fresh diisobutylcarbinol and evaporated to dryness on a platinum plate. After these operations, the yield of protactinium was determined by comparing the Pa^{233} beta activity with that of an aliquot of the original tracer solution mounted and counted in the same manner. Counts of the total alpha activity gave a measure of Pa^{231}, since this is the only naturally occurring alpha-emitting isotope of protactinium.

For sediments, 2-g samples were digested with H_2SO_4 and addition of HF was repeated until no silica remained. After the last traces of HF had been removed by fuming with H_2SO_4, the solution was cooled and diluted, and the procedure described above was followed, starting with the precipitation of $Fe(OH)_3$.

In order to test the validity of the foregoing methods, several Pa^{231} determinations were made on material which had a known amount of uranium and the equilibrium quantity of daughter elements. The results are listed in Table 1. There is rather good agreement between experimental and theoretical values, and the experimental alpha activity did not change with time—a finding which indicated the absence of short-lived radioactive species or long-lived species with short-lived daughter elements.

On the assumption that the foregoing procedures are valid, determinations were made on two 76-lit. samples of Pacific Ocean water collected from the end of the pier of the Scripps Institution of Oceanography at La Jolla, Calif., and the results in Table 2 were obtained.

It appears that one may safely state that the Pa^{231} alpha activity in 76 lit. of ocean water is less than 0.2 disintegration/min, which is less than 3 percent of the amount which could be in equilibrium with a uranium content of 3 μg/lit. (*3*).

The deficiency of Pa^{231} in ocean water indicates that Pa^{231} is removed as it is formed from the radioactive decay of U^{235} in a time much shorter than its half-life; this behavior is similar to that of ionium (Th^{230}). Therefore, as in the case of ionium, one may expect to find quantities of unsupported protactinium in ocean sediments. This was experimentally verified for the six samples listed in Table 3.

The data indicate that there is unsupported Pa^{231} in the top layers of equatorial Pacific deep-sea sediments and that there is also the expected decrease with depth. Apparent protactinium-ionium ages for the two sections for which ionium values were obtained agree with estimates based on productivity studies and extrapolated C^{14} ages (*4*). Protactinium-ionium dating promises to be a valuable tool in the geochronological study of deep-sea sediments (*6*).

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Table 1. Protactinium-231 content of New Brunswick Laboratories AEC counter calibration sample, which contained 0.5 percent of uranium.

Sample size (g)	Yield (%)	Pa^{231} (disintegration/min)	
		Experimental	Theoretical
0.200	96 ± 4	31.6 ± 1.3	33.8
0.200	75 ± 3	28.3 ± 1.1	33.8
0.400	66 ± 2	65.0 ± 2.0	67.6
0.400	80 ± 2	64.5 ± 2.0	67.6

Table 2. Protactinium-231 content of ocean water.

Sample	Tracer yield	Total alpha activity corrected for yield and geometry (disintegration/min)
Reagent blank	72 ± 3	0.22 ± 0.06
No. 1, 76 lit.	57 ± 2	0.22 ± 0.08
No. 2, 76 lit.	36 ± 1	0.24 ± 0.10

Table 3. Protactinium content of deep-sea sediments. Ppm, parts per million; *A*, activity.

Core No.	$CaCO_3$* (%)	Total uranium (ppm)	Pa^{231} uranium equivalents† (ppm)	Th^{230} uranium equivalents (ppm)	$A_{Th^{230}}/A_{Pa^{231}}$	Apparent age (yr)
Scripps						
Capricorn 33HG 1 cm	86		342 ± 17			
Capricorn 42HG 0 cm	85		447 ± 33			
Capricorn 50HG 0 cm	76		123 ± 9			
Swedish deep-sea expedition						
Core 61, surface	65	1.5	216 ± 11	86 ± 9	9 ± 1	(0 ± 10) × 1000
Core 61, 161 cm	87		133 ± 30			
Core 61, 232–240 cm	67	1.0	86 ± 9	111 ± 11	28 ± 4	(95 ± 13) × 1000

* Cores with a high calcium carbonate content and thus with a comparatively high rate of deposition were selected for analysis in order to minimize the effect of mixing by organisms at the sediment surface on the resolution of time (*4*, *5*). Protactinium and ionium values are listed on a carbonate-free basis. † Uranium equivalents are defined as that concentration of uranium which is necessary to support the protactinium or ionium activity found, or both.

References and Notes

1. F. F. Koczy, E. Picciotto, G. Poulaert, S. Wilgain, *Geochim. et Cosmochim. Acta* **11**, 103 (1957); W. M. Sackett, H. A. Potratz, E. D. Goldberg, *Science* **128**, 204 (1958).
2. H. A. Potratz and N. A. Bonner, *U.S. Atomic Energy Comm. Rept. No. La-1721* (1958).
3. M. Nakaneshi, *Bull. Chem. Soc. Japan* **24**, 36 (1951).
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5. ———, *Researches in Geochemistry*, P. H. Abelson, Ed. (Wiley, New York, 1959), p. 22.
6. This is a Scripps Institution of Oceanography contribution, new series. The research was carried out under contract with the U.S. Atomic Energy Commission [contract No. AT (11-1)-34, project 44], whose support is gratefully acknowledged. I am indebted to Dr. Gustaf Arrhenius for making this work possible through his invaluable advice and encouragement, and I also acknowledge the personal communications of Dr. Edward D. Goldberg and Dr. Hans Korkisch regarding the ionium and the uranium analyses, respectively. Some of the equipment and materials were kindly furnished by Dr. James R. Arnold and Dr. William H. Thomas, and I wish to express my gratitude for this help.

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Some Effects of Ionizing Radiation on Translocation in Plants

Abstract. Petioles and apical regions of *Phaseolus vulgaris* var. Black Valentine were subjected to ionizing radiation to study the effect on the translocation process. Petiole irradiation produced no discernible effect. Inhibition of translocation to the irradiated meristems was reversed by application of the auxin naphthaleneacetic acid.

The tissue generally accepted as the locus of translocation of organic material and minerals from leaves is the phloem. More specifically, the cytological evidence would implicate the sieve