ask: "IBP, what's that?" The International Biological Program ran formally from 1964 to 1974, and by 1967, when the USA joined, there were 58 participating nations. The subject of the IBP was defined as "The Biological Basis of Productivity and Human Welfare." It was organized in seven sections, three of which were concerned with productivity on land, in freshwater, and in the sea. The USA contribution took the form of a number of large, multidisciplinary studies of different biomes, and this book reports on one aspect of the US Tundra Biome Program. Much of the work done under this umbrella was published as journal articles, but the US IBP Committee has sponsored a series of synthesis volumes, of which this is number 13. Most of the book was written during summer 1974, but the loose ends were not brought together until much later, and the book finally appeared in 1980. It hit my desk late in summer 1982. Hence, the youthful may well query the relevance of such relatively ancient history.

The justification for studying a tundra biome is given in the introduction in terms of the need to study extreme environments and compare them with findings from temperate habitats in order to test hypotheses about general principles. The ponds studied were near the most northerly tip of Alaska, Point Barrow, and were small depressions, of the order of 30×40 m and up to 0.5 m deep, formed on a flat coastal plain by ice ridges arranged in a polygonal pattern. Limited data were obtained from about two dozen ponds, five were studied more intensively, and one given particular attention, including the construction of a set of subponds within it.

One of the original objectives of all US IBP biome studies was to construct predictive mathematical models of the various ecosystems. With this in mind, carbon flow was selected as the process to be modeled, and the sediment and overlying water were taken as two compartments for submodels. The dominant primary producers were the macrophytes *Carex aquatilis* and *Arctophila fulva*, and their production was supplemented by that of algae on the sediment surface. Algal photosynthesis in the water column was very low. As a result, the living biomass in the sediment was 150 times greater than that in the water. Chironomid larvae contributed the largest animal biomass, but the biomass of bacteria was even larger. Zooplankton in the water column obtained most of their carbon (and energy) from detritus. At the time of this study, it represented the best documented quantitative account of a detritus food web involving bacteria, protozoa, and micrometazoa interacting with primary producers on the one hand and invertebrate consumers on the other. The book takes us, chapter by multiauthored chapter, through the physical and chemical measurements, the studies of primary producers, zooplankton, macrobenthos, bacteria, and microbenthos, to the modeling efforts. Along the way we learn a great deal about how various parts of the system work and in many cases read of interactions and fluxes never observed or measured before.

Two ponds were used for oil spill experiments. Crude oil was added to one at a level of 1.6 liters$\cdot$m^{-2} and to another at 0.24 liter$\cdot$m^{-2}. There is an inconsistency here in the reporting, for it is said (p. 405) "At least half of the oil was lost during the first year, mostly by volatilization and chemical degradation" but on another line "After several years, at least half the oil was still present." All the *Daphnia* and fairy shrimps were killed immediately and did not return for 7 years, but *Cyclops* suffered a partial mortality and returned within a year. A consequence of this was a change in composition of the planktonic algae, and a temporary loss of productivity. Macrophytes and chironomids, the dominant producers and consumers, were only slightly affected.

The result of the modeling efforts was similar to that in several other biome studies. It was possible to construct a deterministic model that successfully simulated the seasonal cycles of biomass and production in the ponds, but it proved to be very sensitive to small changes in certain parameters. For example, the output changed drastically if the algal respiration coefficient changed from 0.25 to 0.30. Yet, as Hobbie says (p. 17) "Even if we did have a good way of measuring algal respiration, in the field it would not distinguish between these two values." When reasonable variability was incorporated in a stochastic model, the mean values of the output were quite different from those of the deterministic model. Hence it was concluded (p. 409) "It is now clear that even an ecosystem so simple and diligently studied as a tundra pond is not understood well enough for predictive modeling."

What then is the value of this volume? Probably its most important role is as a contribution to the emerging discipline of comparative ecosystem studies. Just as comparative anatomy and comparative physiology illuminated our understanding of how organisms function as systems, so, I believe, will comparative biome studies of this type pave the way for the emergence of a deep understanding of the fundamental properties of ecosystems. This, my young colleague, is the justification for the publication of this relatively ancient scientific history.

K. H. Mann

Marine Ecology Laboratory
Bedford Institute of Oceanography
P.O. Box 1006
Dartmouth, Nova Scotia B2Y 4A2

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TILMAN, D. 1982. **Resource competition and community structure.** Monogr. Pop. Biol. 17. Princeton University Press, Princeton, N.J. 296 p. $27.50.

Since so much has been, and still is being, written about competition and community structure is it possible to say much that is innovative about this topic? Tilman shows the answer to be "yes." Like other monographs in the Princeton series, this one is not always complete or exhaustive in its development but is exciting and creative and likely to stimulate new work. Tilman has appreciated the need for competition theory to be more mechanistic and less phenomenological. He concentrates on competition for resources: nutrients, light, space; this leads him to consider plants and sessile animals—organisms much current theory neglects. If the examples in the book will appeal most to the aquatic or plant ecologist, terrestrial animal ecologists (like myself) will ignore the book only to their cost.

After an introductory chapter comes a graphical and wide ranging "cost-benefit" analysis of how a single species might exploit a pair of resources. A pair of resources may benefit a species in a variety of ways. The resources may be perfectly substitutable—one resource may be worth a fixed fraction of the other, so a lack of one resource can always be made up by consuming enough of the other. Or the resources may interact in a variety of ways: one is if they are both *essential*—a minimum of each resource is necessary and any amount of one resource cannot make up for an insufficiency of the other. There are also several possible functional forms for the "cost" side of the equation. The costs of exploiting two resources may be linearly related; concave—when exploiting one resource makes the other more expensive—or convex—when exploiting one resource makes the other less expensive (perhaps because both resources occur together in the same place). Determination of the optimal diet requires the combination of a cost and of a benefit curve—and there are lots of possible combinations. However, from examining these combinations some generalizations emerge. For essential resources, the optimal diet does not depend on the shape of the cost curve: essential resources should always be consumed in the proportion at which growth is equally limited by both resources. It is this simplification that permits much of the theoretical development in subsequent chapters.

Dynamics are added to the models of exploiting essential resources, first for a single species (chapter 3) and then for two-species competition models (chapter 4). For the latter, conditions are derived that ensure both species coexist: at equilibrium, each species must consume relatively more of the resource that limits its own growth. This supposes that the two competing species can be limited by different nutrients and that the habitat supplies these nutrients at rates within certain bounds. Too fast a supply of one nutrient will favor one species and enable it to remove its competitor. Tilman reviews his and others' work which shows that these models can be convincing descriptions of such systems as competing freshwater algae.

Now in a homogeneous environment, at most two species can coexist on the same two essential resources. For many species with the same two essential nutrients, which two species coexist will depend on the rates at which the two nutrients are supplied by the habitat. If we imagine isolated habitats supplying nutrients at different rates, different species pairs may coexist in each and over all the habitats many species may be present. It emerges from the graphical models that a given range of nutrient supplies will contain more pairs of coexisting species when nutrient supply rates are low than when they are high. Thus, travelling along a gradient of increasing mean nutrient supply and fixed, yet finite variance of supply, one would encounter first, few species (there are not enough nutrients). Then there would be a rapid increase in diversity in the ranges of nutrients where many species pairs can coexist and finally a slow but relentless reduction in diversity (as the range of nutrient supplies required to support many species becomes ever larger relative to the range of nutrient supplies encountered). This gives possible answers to two well known paradoxes: Hutchinson's (1961) "paradox of the plankton" (how can so many species coexist on so few limiting resources?) and Rosenzweig's (1971) "paradox of enrichment" (why does species diversity often decrease when systems are enriched with energy or nutrients?)

Tilman maintains his format in following these theoretical investigations by considering how well the models explain the limited data on the effects of enrichment on diversity. Several experiments are considered and the Park Grass Experiments at Rothamsted, England, in detail. I applaud Tilman for considering these remarkable experiments: they began in 1856, continue to this day, and involve 20 plots receiving different fertilizer treatments. Fertilized plots do indeed show a steady reduction in diversity and this continued for at least the first 90 years of the study.

Chapter 6 pursues these community-level ideas in more detail. Tilman considers which nutrients are likely to be more limiting to which species and whether the species show trade-offs by having different optimal ratios of the supply of two nutrients. From such information, the changes in nutrient balance over space and time make predictions not only about how species diversity changes but also which species should be present. Tilman shows striking consistencies between the optimal resource ratio of a species as determined in the laboratory and the ratio at which that species dominates in natural communities. And the models nicely explain details of both the changes in algal composition in freshwater systems and plant composition in the Rothamsted plots.

Chapter 7 is a theoretical exercise relating the models to classical competition theory.

Chapter 8 argues that the effect of disturbance is to supply space in the same way that a nutrient may be supplied. This interesting view enables Tilman's models and their subsequent development to be applied to such systems as sessile organisms in rocky intertidal habitats or a forest with wind-caused tree falls. Different trade-offs between rates of exploiting food and space, and an environment heterogeneous in the supply of these resources, permit many species to coexist and suggest that moderate levels of the supply of disturbances facilitate the highest diversity.

Chapter 9 tackles some "concluding remarks and speculations," and it includes some discussions of how species composition and diversity should change during succession.

Though interesting, the book is not without problems. The theoretical development, particularly that in chapters 5 and 9, seems incomplete and highly dependent on fragile assumptions. Substantial portions of the book often seem unnecessarily distracting from the main thrust, perhaps because the issues are, at present, only investigated in a preliminary way. And, Tilman seems almost naively to believe he has solved certain problems in community ecology, whereas his models have only brought him to the starting point of theory 15 years old.

Tilman gives considerable attention to his question (p. 4): "what limits does resource competition place on the diversity of a community?" We are constantly led to believe that finding more than two species coexisting on two resources and the potential to pack unlimited species into an environment heterogeneous in supply rates is a considerable advance. This is not so. There is an extensive literature on species packing which examines how many species can fit along one or more resource axes. There are various limits to packing imposed by finite densities or stochastic effects and largely unresolved problems about how generalized species should be. Tilman does not seem to recognize his gradients (in say N:P supply) as equivalent to a resource axis and so treats subsequent topics casually and integrates them poorly with known ideas. The often preliminary investigations of topics already well studied does not really diminish the book's value, but it would have been easier to read and more persuasive had it been subjected to more brutal editing.

The assumptions required to get a peak in diversity and then a decrease with increasing nutrient supplies require very special arrangements of how species are limited by resources and of environmental variation. The variance of nutrient heterogeneity, in particular, must either not increase, or increase slowly and linearly with the mean level of the nutrients supplied. Other scenarios are not only possible, but perhaps more likely—such as the standard deviation increasing linearly with the mean (and the variance as its square) in order to maintain a constant coefficient of variation. Such relationships are certainly possible to investigate empirically (Tilman presents data that would permit this). One wonders whether, if this is true, diversity might continue to increase with increasing nutrient supply—or at least be insensitive to its variation.

The question then, is that given the special assumptions (1. of resource use—resources are strictly "essential"; 2. geometric arrangements of resource use; 3. form of coexistence—each habitat contains a pair of species dynamically isolated from all other species pairs; 4. patterns of resource heterogeneity) are Tilman's hypotheses and his interpretations of field results useful? Indeed, Tilman's models may finally be replaced by models which accord better with field data. But I would not agree with those who see the simplicity of any theory, and the necessity of sometimes marginally realistic assumptions, as justification for ignoring theory altogether. The research program Tilman establishes is compelling. His models explain a wide variety of ecological patterns at many different levels with a minimum of assumptions. I am less happy with his approach of showing that field and laboratory data can be interpreted in terms of his models—rather than showing that his models predict reality any better than alternatives: if these exist, they are not mentioned. This process can be all too seductive. We are led to believe the theory because nothing else is available: I prefer Lakatos' (1970) view that progress in science comes when data adjudicate two or more rival hypotheses.

Tilman's ideas are a challenge to field biologists and theoreticians, alike. In developing a momentum of ideas the book is at its strongest; it is only weak when its author becomes sidetracked into issues his models are not designed to answer.

Stuart L. Pimm

Graduate Program in Ecology
The University of Tennessee
Knoxville 37916

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Using remote sensing from various types of satellite and sometimes aircraft is very much in its infancy in aquatic systems. In this it contrasts with the regular, detailed use made of remote sensing in agriculture and forestry. Part of the slow development is the classic aquatic problem: unlike a tree or a cornfield, water will not stay still and be analyzed! The crux of aquatic remote sensing is thus simultaneous "water truth" calibration while the satellite senses from afar. Although this is regularly possible, with effort, in lakes, it is costly or impossible as a regular method in the huge oceans.