Standing crop ≠ food

from our Animal Ecology Correspondent

THE trend towards simplifying ecosystem complexity for comparative purposes by the use of common energetic terms often causes confusion by obscuring basic principles. The 'standing crop' of an ecosystem is one such term which indicates how much energy there is in the system at any one time. But the total amount of, say, primary production in energy terms available may not be the same as the amount actually available to the herbivores which feed upon it. Thus the figure for standing crop may be a red herring to anyone wishing to determine whether food is limiting in the ecosystem. A rule of thumb guide to consumption of grassland vegetation by herbivores is that rarely is more than 10% of annual primary production actually eaten (Wiegert and Evans, in *Secondary productivity of terrestrial ecosystems*, 449 (edit. by K. Petruzewicz) (Polish Academy of Sciences, Warsaw, 1967)), and in many instances 2% is nearer the mark (Grodzinski, *Acta theriol.*, **16**, 231; 1971). On the face of it, therefore, food would not seem to be a limiting factor to herbivore populations.

The fallacy in this argument is to equate primary production standing crop with food. Food is more than just energy, and for most large ungulates a constituent of major importance is crude protein. Bredon *et al.*, among others, concluded that when the crude protein content of forage dropped to less than 4% dry weight, plant material ceased to function as food and ungulates feeding on it started to lose weight (*J. agric. Sci. Camb.*, **61**, 101; 1963). Death does not follow immediately and cattle kept on low quality grass continue to feed, but they face mounting physiological stress.

A careful demonstration of the hazards inherent in the standing crop approach to ecosystem dynamics is provided by Sinclair's recently reported studies on limiting factors in the Serengeti (*J. Anim. Ecol.*, **44**, 497; 1975). He points out that herbivores—ungulates, small mammals and grasshoppers—consume 27%, 38% and 14% of the annual primary production of tall grassland, short grassland and kopje country respectively. This leaves a large portion of the annual production for detritivores and for fuelling fires. Why is it not used to support higher populations of herbivores? The answer is that for a part of the year it is unavailable as food, much of the protein and carbohydrate in the leaves having returned to the roots. Sinclair's figures show that from a spring level of 8% crude protein, dry season grass contains between only 1% and 3%. In the tall grassland, food required by herbivores is in excess of that available for the duration of the dry period—July to September. This is associated with a drop in small mammal and grasshopper populations and hence foraging pressure, but is compensated for by an increased intake by ungulates. Monitoring bone marrow fat levels in wildebeest over the year reveals that they fall slightly during the dry season indicating some degree of physiological stress experienced at this time. In the kopje country where ungulates were seldom seen, herbivore food requirements outstripped production for a much shorter period largely because of the rapid decline in rodent and insect numbers. This strategy for accommodation to sudden unavailability of food is open only to small herbivores with fast growth and reproductive rates and is barred to ungulates who must tighten their belts and just make do.

Hairston *et al.* and other workers have suggested that since herbivore populations consume so little of the primary production they cannot be limited by lack of food, and so must be limited by parasites, predators or disease (*Am. Nat.*, **94**, 421; 1960). The available evidence simply does not support this hypothesis. Sinclair is right to point out that an important implication of Hairston's hypothesis is that interspecific competition and niche diversification is precluded. There is no evidence that this occurs and plenty that it does not. Furthermore, consideration of mean annual values hides fluctuations not only in crude protein content but perhaps also in trace elements and other specific nutrients at certain times of the year. Availability of primary production as food is also affected by the physical correlates of feeding; crushing, despoiling and dropping. It is also affected by the nutritional and other needs of different age and sex classes in the populations.

ceeding 70% in its reconstructed synchro-cyclotron.

Work on heavy-ion acceleration was reported from several laboratories. A 25 MeV Tandem Van-de-Graaff under construction at Oak Ridge National Laboratory will inject ions into an existing cyclotron and will raise its energy to 800 MeV for ions of mass 160. M. Gouttefangeas (CEA, Saclay) described a recently authorised French project in which three cyclotrons in cascade will accelerate the heaviest nuclei to 10 MeV per nucleon.

The large, split-pole cyclotrons favoured at present make for easy acceleration and extraction but require much steel and expensive buildings. Much more compact constructions can be achieved by using superconducting coils to provide fields of order 5T and the conference learnt of projects for such "superconducting" cyclotrons at the Lawrence Berkeley Laboratory and at Chalk River, Canada. Michigan State University is constructing a superconducting cyclotron magnet in order to study the problems posed by this new technique.

A tantalising project for a 100 mA 800 MeV proton cyclotron was described by Yu. N. Denisov (JINR, Dubna, USSR), but its estimated radio-frequency power of 76 MW made it seem somewhat unrealistic.

Although primarily a gathering of accelerator physicists and engineers the conference devoted several sessions to the applications of cyclotrons and the range of topics proved the cyclotron to be a maid-of-all-work. The measurement by surface activation of abrasion in slurry-carrying ducts or of railway wheels, the determination of the fluorine content of a cup of tea by charged particle activation analysis, the study of nuclear level structures and excitation functions, radiation damage in reactor materials, the production of isotopes for medicine, neutron therapy, proton radiography and surgery are only a few of the topics covered by various contributions.

M. M. Kligerman (University of New Mexico) reported on a comparative test of a treatment of skin melanoma by pions and X rays. The dramatic superiority of pions is a challenge to accelerator designers. A panel discussion on "Accelerators for Hospitals" reflected the difficulties, but tended to favour a proton-accelerator of variable energy.

The conference participants were able to visit the cyclotrons and experimental installations of SIN where a biomedical pion-channel and an eight-metre superconducting solenoid providing record fluxes of muons were of particular interest.

Professor M. S. Livingston, the co-inventor of the cyclotron, reviewed its early history in a delightful and informative after-dinner speech. Dr R. Wideroe, the inventor of resonant acceleration also attended the conference and one may hope that the two veterans were pleased with the development of their brain-child. □