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The flow of energy and matter between trophic levels (with special reference to the higher levels)

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Introduction

The interrelationships between producers and consumers are determined by their numbers, by the effectiveness with which energy is harnessed by the lower trophic levels, by the speed of renewal of dominant populations, by the ability of producers to renew consumed production, and by the relationship between energy required for maintainance and that available for production in the dominant species of different food chains. Such interrelationships determine the productivity and stability of the biogeocoenoses (BGC) and the peculiarities of energy and matter transfer. International Biological Programme investigations published recently have provided many data on the structure of BGC. Special attention is therefore paid in this paper to the functional characteristics of ecosystems.

Differences between biomes

Even rough calculations show that there are fundamental differences in biogeocoenotic indices between various biomes. In tundra the standing crop of the plants exceeds that of the zoomass by 15 times, in meadow steppes by 40 times, in cereal steppes by 50 times, in deciduous forests by 300 times, and in coniferous forests by 1200 times. The annual production of the phytomass compared with that of the zoomass also shows great differences: this index is 3 for deciduous forest, 5 for cereal steppes, 15 for meadow steppes, and 20 for coniferous forests (Isakov and Panfilov, 1969).

The consumer structure is also different. The proportions of saprophages: phytophages: predators is 20:2:1 in coniferous forests, 250:30:1 in oak woodlands, 20:5:1 in dry steppes. These rough calculations, based on data derived from various sources, demonstrate clearly the distinctions in character and the influence of biogeocoenotic processes on different trophic levels and in different biomes. The structure and function of the BGC inevitably changes sharply with alteration of the dominant species. For instance, in tundra the total biomass of phytophages exceeds that of the predators by about 10 times during quiescent years and more than 1000 times during lemming population peaks. Everyone is familiar with local changes in biogeocoenotic structure. Despite the relatively low productive processes in tundra, there are regions of *Calamagrostis* herb associations that produce a crop of up to 300–800 kg/ha of unconsumed green material during a two month growing season.

Great differences are also revealed in the structure of geographically and functionally related BGC. This can be illustrated by the biomass proportions of invertebrates in tundra with different types of ground (Fig. 1). The harmonious development of the interacting BGC of different structures is maintained by special mechanisms of coadaptation between the production processes in different ecosystems within the same BGC.

In this connection let us analyse the development of an amphibian. The biomass of eggs laid by a population of *Rana arvalis* in a given lake coincides with the biomass of young frogs leaving the water (Fig. 2). Of course, some divergences from this general rule may be observed, but there can be no doubt that this has an important role in the coordination of terrestial and aquatic subsystems of one BGC. For instance, the zoomass of arthropods inhabiting shallow basins in tundra (20% of the investigated territory) approaches 70 kg/ha (N. Olshwang, *in litt.*); up to 1.5 kg/ha of the zoomass is withdrawn from ponds by insects completing their metamorphosis, and this represents 20% of the zoomass of the terrestrial tundra BGC. Even when terrestrial ecosystems predominate, their biogeocenotic structure is determined by conditions in aquatic ecosystems where the larvae of the dominant species develop. For example, the biomass of larval *Aedes communis* mosquitoes in forest ponds was calculated to be 17 kg/ha; the imagines withdraw some 16 kg/ha from the ponds (which, if distributed randomly, would add approximately 1 kg/ha zoomass to the terrestial ecosystem, N. Nikolaeva, *in litt.*).

The development of species in adjacent ecosystems must naturally be well coordinated. Otherwise a sharp increase of a certain phase developed at the expense of one system might cause disturbances in another one characterized by a tighter energy budget. Mechanisms regulating this process revealed in *Rana arvalis* merit careful study.

The influence of population fluctuations

Population mechanisms regulating biogeocenotic processes play a still greater role when the numbers of one of the dominant species increase sharply. Let us analyse lemming peaks. In the autumn-winter 1972/73 the population density of *Dicrostonyx torquatus* in the moss-grass tundra reached 1000 holes per hectare. Towards summer 1973 some 70% of the dominant plant species (*Carex globularis*, *Eriophorum polystachyon*, *E. russedum*) had been gnawed. By this time, however, the lemming density had fallen sharply as a result of higher mortality and a lower breeding rate, and the biomass of cotton grass regenerated to 90% of the potential biomass by July, while that of the sedges was up to 40%, the number of shoots being almost completely renewed on separate plants. The number of lemmings fell sharply though the stock of food was practically

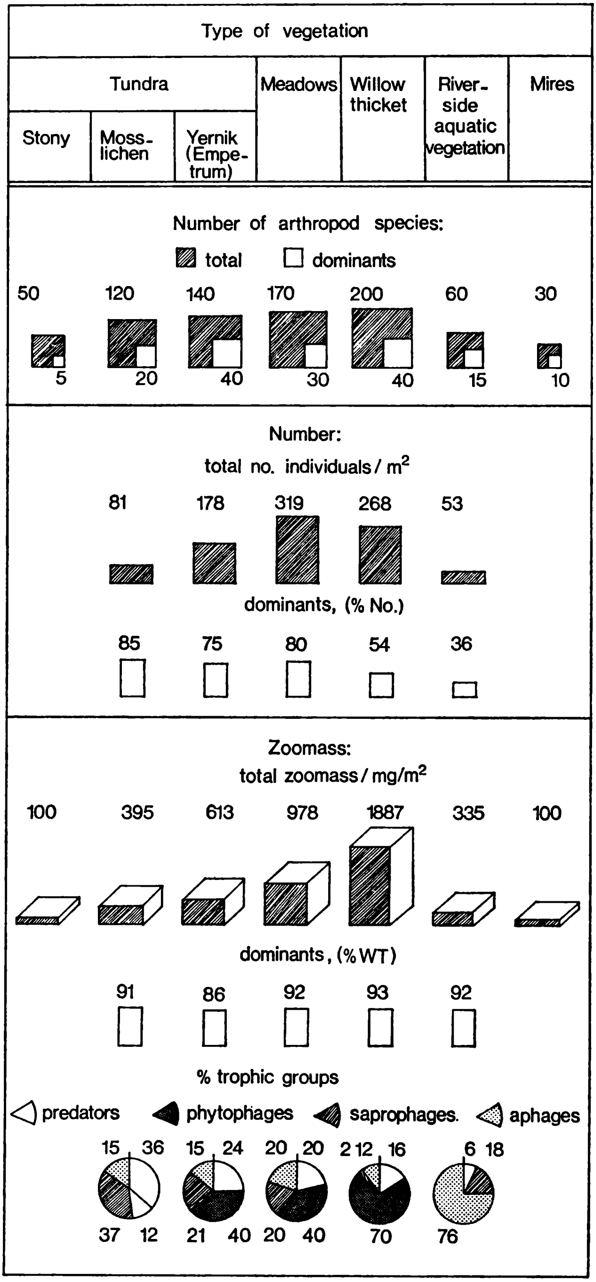

Figure 1. Biotopic spectrum of arthropods in the Polar Urals.

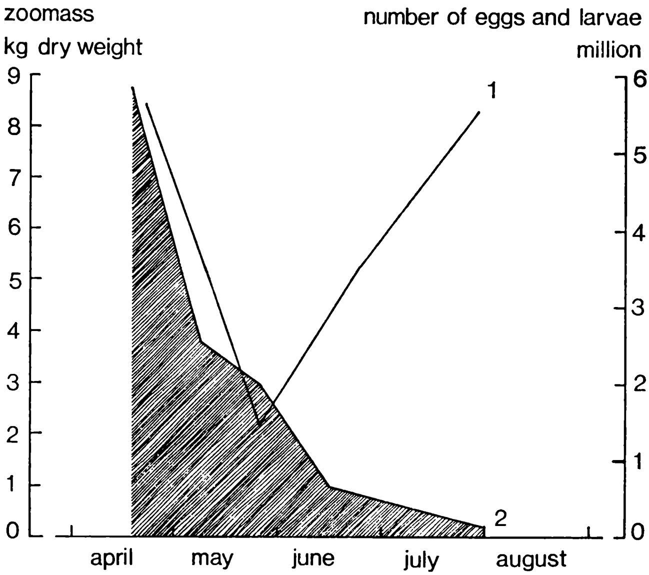

Figure 2. The relationship between zoomass (curve 1) and numbers (curve 2) of *Rana arvalis* during metamorphosis in a 1.5 ha pond in the South Urals, 1968 (after Shchupak, 1970). The overall loss of zoomass from the aquatic system was 1.2 %, compared with a mortality of 98.5 %.

inexhaustible. This example shows that in natural ecosystems (not disturbed by man) even mass breedings of dominant species do not disturb the BGC balance. Furthermore, there are grounds to assert that the mass reproduction of separate species, for a long time considered to upset the balance of nature, is in reality a necessary factor in preserving the BGC productivity. In this example, the peak and crash of the lemming population caused an enrichment of the soil with organic matter and minerals. Calculations showed that no less than 300 kg/ha of organic matter assimilated by the plants originated from carcasses during the mass breedings of lemmings in the tundra, and a considerable amount of minerals (circa 1000 to 1500 kg/ha) came from the excretions of the rodents, viz: Si 6.0; Al 5.0; Fe 0.5; P 4.0; Ca 6.0; Mg 3.0; Mn 0.2; K 15.0, Na 1.8; S 1.0 kg/ha. These figures are very approximate. They were estimated from observations on the number of lemmings and on their food preferences to elucidate the chemical composition of wastes (information from various unpublished works). Some mistakes in these calculations may have arisen from inevitable mistakes in estimating the energetic and mineral turnover of rodents in nature. Nevertheless, when comparing these figures with the chemical composition of grass litter in the tundra (Table 1) it becomes apparent that population peaks do not disturb the BGC; moreover, they become an important factor in the maintenance of the BGC balance.

Table 1. The chemical composition of a grass litter of sedges and cotton grass (% of dry weight)

Element	Sedges	Cotton grasses
Si	0.03	0.25
Al	0.05	0.18
Fe	<0.01	0.03
P	0.08	0.20
Ca	0.80	0.20
Mg	0.40	0.16
Mn	0.13	0.03
K	0.60	2.40
Na	0.01	0.07
S	0.33	0.15

Similar data have been obtained by observations on insects. In the fourth year of mass reproduction of gypsy moth (*Porthetria dispar*) the amount of organic matter introduced into the soil may be as much as 5.5 t/ha, exceeding the weight of grass litter (Rafes, 1962). The temporarily disturbed phytocenotic balance is quickly re-established.

It should be emphasized that the phytocoenotic response to the population peaks of consumers is not, as it is commonly assumed, so vastly different from the biogeocoenotic processes during 'calm years'. To keep their numbers at a constant, but not high, level, many dominant species undergo a geometric increase in reproduction accompanied by an equally high mortality. In the subarctic region a pair of tundra voles *Microtus oeconomus* produces no less than four generations of voles. Only animals from the last generation survive the autumn and form a winter population. But most of these animals die off during the long Arctic winter. The offspring of only one reproducing pair consume no less than 400 kg/ha/yr of phytomass. It becomes apparent that to keep its population density at a constant, and not high, level (c. 5 pairs per ha) a population of voles consumes some 400 kg/ha of plant material, which corresponds to a high level of grass stand in northern regions. This results from the high mortality of the animals.

This conclusion was supported by field observations on *Microtus agrestis*; Figure 3 shows the total number of voles descended from a single pair, as determined by total marking. During these observations, which allowed the fates of individual animals to be traced (their birth, development and death) it was estimated that to keep the population stable one reproducing pair consumed 265 kg/ha phytomass of grass-bean-herb meadow, including no less than 1.5 kg of phosphate and 15 kg of potassium. The phytocoenosis retained its normal productivity and structure, in spite of the continuous consumption of plants produced, by the effective utilization of nutrients which are prepared for rapid consumption by the activity of the animals.

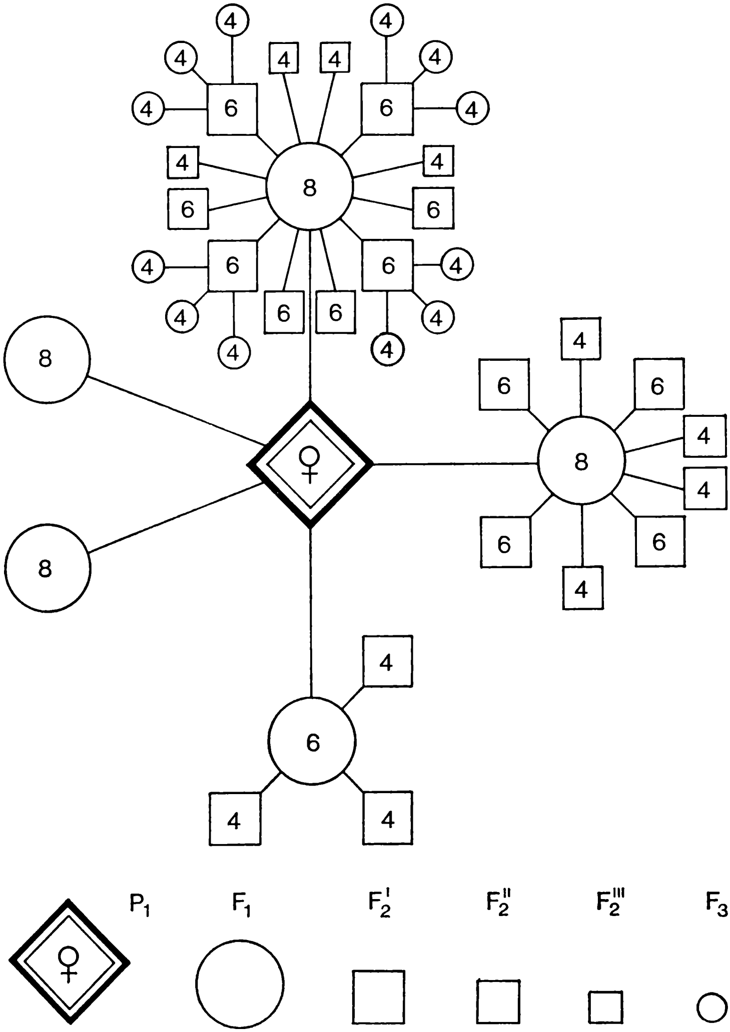

Figure 3. Reproduction in *Microtus agrestis*: P_1 overwintered female, F_1 its offspring; F_2^{i} F_2^{ii}, F_2^{iii}, the first, second and third litters of the F_2 generation; F_3 offspring of the first F_2 litter. Figures inside symbols indicate the number of animals in the litter. Mean litter size was 6.2. The total number of voles in the progeny was 196, with a sex ratio of 1:1.

The influence of the consumers on primary production

The essence of the population mechanisms regulating biogeocoenotic processes is based on the general fact that the population peak is generally followed by the population crash before the equilibrium of the BGC is disturbed on different trophic levels. Naturally these mechanisms play an important role in the life of the BGC only with regard to dominant species. Therefore it is necessary to show that a typical BGC structure is characterized by a small number of dominant species, which form the main basis of the trophic levels, and satellite species whose function is to ensure the normal activity of the dominants (Fig. 1). Irrespective of great differences in the total number and biomass of insects in various types of tundra BGC, and of differences in proportions of species belonging to different trophic levels, the role of dominants in creating biological production appears to be practically the same. Many similar examples could be given. It is important to stress, however, that the dominant producer in many BGC lies outside the control of the consumers. One can observe this on subarctic willows. In the Yamal peninsula these are damaged by 42 species of insect, especially by the sawflies *Amauronematus harpicola* and *Phytodecta pallidus* and by a leaf-eating beetle. The biomass of these species is up to 320 mg (80 mg dry weight) per m^2 (80–90% of the total insect biomass). The productivity of the willows ranges from 24 to 235 g/m^2; consumers eat no more than 7% of their potential food supply (Bogachova, *in litt.*). Similar relationships are typical for young BGC.

To evaluate such data the characteristic response of the plant to damage needs to be taken into account. It is known that even during mass breedings of leaf-eating insects the weight of leaves changes little for a long time because the hyperfunction of the chloroplasts compensates for this. In cases where losses exceed the ability of the compensating reactions, the decrease in leaf weight exceeding the weight of consumed food points to a pathological process. There is convincing evidence that reactions are specific for different species in the producer-consumer system. When the population of specialized consumers increases, the productivity of the foodplants decreases, but the productivity of other producers rises. Following a four-year increase in the number of the moth *Tortrix viridana* the accretion of oak declined by 21%, but that of the ash rose by 58%, and the total increment of the first trophic layer remained unchanged (Rafes, 1968). Similar phenomena have been noticed when sharp changes in population were caused by changes in climate. Numerous investigations made by N. N. Danilov in the southern tundra have shown that within related groups (*Anthus*, pipits, for example) northern species stay to nest if spring is late, but mostly southern ones nest here if spring comes early. On the whole the total number of animals playing similar roles in the ecosystem varies little. A change of dominant species within one trophic level is of great importance. The specific role of a particular species should not be underestimated, but neither should it be exaggerated when the question concerns general biological characteristics. Five amphibian species were studied in connection with this problem (*Rana arvalis*, *R. temporaria*, *R. macrocnemis*, *R. camerani*, *Pelobates syriacus*). It was found that the tadpoles of all these species utilized their food with almost equal efficiency (9.0 to 13.1% of the food consumed being converted into animal biomass), despite great differences in growth and development rates when these were regulated experimentally.

This type of information permits the evaluation of the intensity of energy balances on different trophic levels without concrete measurements.

Differences between the actions of homeotherm and poikilotherm consumers

Animals of entirely different metabolic types play different roles in the BGC. This may be proved by comparing a frog and a bird of about the same body weight and food regime. The activity of the homeotherm animal is impaired if the quantity of prey is unlimited but its population density is low, because this makes its search for prey energetically disadvantageous. A poikilotherm frog reduces its activity when it lacks food, but it continues to influence the number of prey whatever the number. The biogeocoenotic consequences of this are exceptionally important (in spite of the relatively few insects, populations of frogs numbering 1000 per ha were observed). Such observations help to explain the appearance of paradox ecosystems in which the biomass of predatory insects greatly exceeds that of phytophages, giving an erroneous impression of the intensity of energy balances within separate links of trophic chains. The potential omnivorousness of any predators (including snakes) must play a significant role in the formation of such ecosystems. This was proved by our physiological experiments more than twenty years ago (Schwarz, 1954).

The different types of adaptation of homeotherm and poikilotherm animals to their media have other biogeocoenotic consequences. To retain a body weight of some 20 g, a pair of insectivorous birds needs to consume 9 kg of food. Under the same conditions a reproducing pair of frogs consumes no less than 20 kg of insects. Similar differences exist between closely related but ecologically dissimilar species. A combination of animals, differing in the energy required to preserve their average population size, and differing in their influence on the lower trophic levels within one BGC, ensures the dynamic equilibrium of ecosystems.

Intra-and interspecific interference

A stable biogeocoenotic balance depends not only on optimal structures of BGC and separate links of food chains, nor on the number of individual species, but also on population regulation based on the specific action of animal metabolites. Studies on the larvae of amphibians and insects have shown that metabolites regulating the development and growth of animals accumulate in the media as the population density increases (Schwarz, 1972). As a result, the population becomes divided into groups of individuals developing at different rates. At any one time relatively few animals in the population grow rapidly and consume food. Influenced by the metabolites of the youngsters, these quickly complete their metamorphosis and leave the water. Vital resources are thus released for the next batch of individuals to develop. Thus food resources are used by the population with maximum effectiveness.

Interactions between organisms forming different trophic levels depend on many factors. Experiments were designed to determine the integrated effect of consumers on producer associations. Different population densities of rodents were created experimentally on confined tundra sites and on herb meadows in the South Urals, and the response of the vegetation was then observed. Detailed results of this work are published elsewhere (Smirnov & Tokmakova, 1972; Dobrynsky, 1974, in press), but the logic of the investigations and general results are given here.

The maximum production of standing crop was observed in sites where 20% of the vegetation had been consumed by *Microtus oeconomus*. This corresponds to a density of voles of about 100–200 per ha for 100 summer days, or 27–33 per ha throughout the year. As stated above, mechanisms regulating population size protect the BGC from too high densities of dominant consumers. The increase in phytomass in the study areas exceeded that of the control (Fig. 4).

The results of rodent activity were estimated by observing the growth of separate plants and changes in the structure of associations. The best index is the total photosynthetic activity of the disturbed plant community. Experiments were based on the premise that the total CO_2 consumption by all levels of the community indicates its total productivity. Different densities of *Microtus agrestis* were set up on experimental plots, and the CO_2 content of air samples was determined with an infrared gas analyser. Several days later the voles were removed and CO_2 consumption estimates were made. Subsequently regular observations on the restoration of the photosynthezising activity of the phytocoenoses were made with regard to the density of voles in experimental plots.

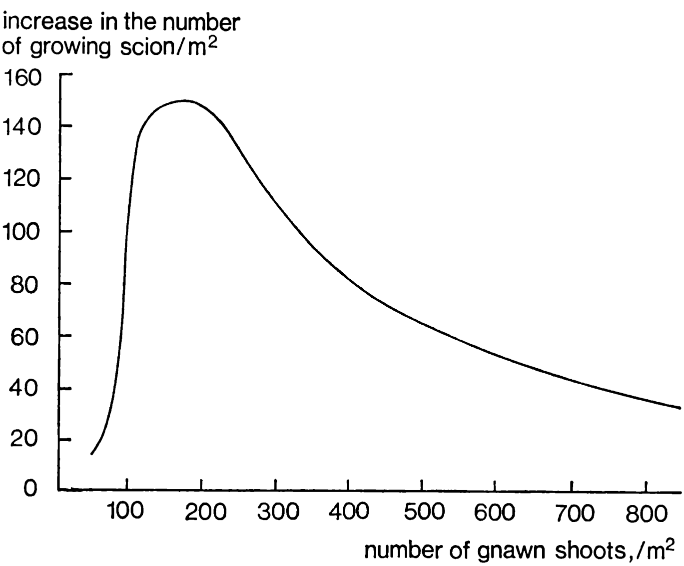

Figure 4. The response of the sedge-cotton grass-sphagnum community of producers to the influence of the consumer vole *Microtus oeconomus* in the Polar Urals, 1968–71.

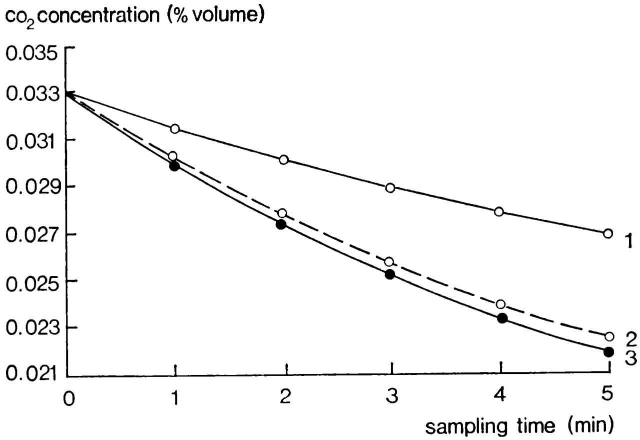

Figure 5. The ecological impact of *Microtus agrestis* voles on the total photosynthesizing activity of the phytocoenosis in 1.5 m^2 experimental plots. Curve 1 indicates the CO_2 content in air samples after one vole has been present for one week in a 1.5 m^2 plot; curve 2, the same plot a month later; curve 3, the control.

It was established that a vole population of 650/ha over one week caused some changes in the phytocoenosis which decreased the CO_2 absorption by 1.4 times. Within a month the photosynthetic activity and structure of the association was renewed (Fig. 5). But higher densities of voles (c. 1100/ha) produced such changes in the phytocoenosis that it could not be restored in one growing season.

Conclusion

The given facts all show that a harmonious development of BGC depends on population mechanisms regulating the number of dominant species, and on optimal interrelationships, fixed by evolution, between species belonging to different trophic levels.

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