

CONSUMERS AS REGULATORS OF ECOSYSTEMS: AN ALTERNATIVE TO ENERGETICS¹

ROBERT M. CHEW

Department of Biological Sciences, University of Southern California, Los Angeles, California 90007

ABSTRACT

Little is known about consumers as regulators of ecosystem functioning. The evidence reviewed here suggests that consumers are beneficial to ecosystems as regulators rather than energy movers. In order to predict ecosystem behavior, it is essential to know how consumers cause departures from the linear transfers of energy depicted in most models. The complexity of population ecologies in nature greatly confounds generalizations based on circumstantial evidence, hence experimentation seems essential. More boldness and unconventionality is needed in experimentation. For example, diversity can be manipulated to extremes, important categories of consumers can be removed, entire fauna can be temporarily held back. Such experimentation has technical and time-span difficulties and the expense per experiment may be high, but the knowledge gained per dollar can be much more than the gains resulting from the traditional search for correlations in the accretions of field observations.

The concepts of energy flow and material transfer have stimulated much of the recent work in ecology. The first surge of studies quantified certain generalizations that should have been obvious earlier, and in general these studies were not concerned with the parts of ecosystems that are most important in energy and material transformations (table 1). Herbivores consume very little of the primary

TABLE 1
Proportion of plant production used by consumers in different ecosystems.¹

Consumer category	System	Percentage use	Source
mammals	desert, Arizona	2% total NPP ¹ 5.5% available NPP 86% seed production	Chew & Chew, 1970
mammals	oak-pine forest, Poland	0.7% available NPP	Ryszkowski, 1969
mammals	taiga forest, Alaska	13.5% available NPP	Grodzinski, 1971
leaf feeders	deciduous forest	3-8% of foliage	Reichle <i>et al.</i> , 1973
soil-litter fauna	deciduous forest	4-8% annual litter 1% litter	Witkamp, 1971 McBrayer, 1973a
insects, except ants	old-field, herbland	1% total NPP	Wiegert & Evans, 1967
ungulates	grassland, Africa	28-60% total NPP	Wiegert & Evans, 1967
domestic animals	rangeland	30-45% for maximum sustained yield	Wiegert & Evans, 1967
lemming	tundra monocots	93% NPP	Batzli, 1974
zooplankton	English Channel	98.5% phytoplankton	Macfadyen, 1964
seed predators	general	10-90% predispersal seed crop	Hanzen, 1971b

¹Net primary production (NPP) limited to above ground production only.

production of most systems; the major pathway of consumption is usually through feeding sequences beginning with saprophages. In many systems most of the energy dissipation and organic decomposition is by microorganisms, so that consumers—animals that ingest their food and digest it internally—biophages and saprophages alike, move relatively little energy and matter (see table 1).

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These observations suggest questions one scarcely ever hears: "What are the values of animals to ecosystems? Do consumers exist at the courtesy of the basic system of plants and microorganisms, or do consumers exist because they are of benefit to or necessary for the existence of ecosystems based upon complicated advanced plants?" There are few natural ecosystems of only plants (algae) and microorganisms, and they are of limited areal extent (Armstrong and Odum, 1964).

An obvious approach to answering these questions is by manipulative experimentation within natural ecosystems and laboratories. If consumers are important to ecosystems, there should be perceptible responses to the removal or other manipulation of categories of animals. In my opinion, the importance of consumers is to be found by looking beyond calories and grams of matter *per se* to the quality of the consumption of consumers and how their characteristics affect and regulate ecosystem processes.

These perceptions are not new and there is increasing interest recently in the "roles" of consumers (Golley, 1973; Petrusewicz *et al.*, 1974), but I am convinced this interest is not pervasive enough. It is high time ecologists proceed beyond circumstantial evidence to broad scale experimental testing of hypotheses regarding the regulatory roles of consumers as they facilitate (or hinder) functioning and development of ecosystems.

This paper will review the ways in which consumers could be benefiting ecosystems, together with supporting experimental evidence and approaches. I will emphasize consumer-plant interactions and proximal rather than ultimate causes. As working criteria I propose "benefits" to be those actions of consumers that increase productivity, complexity or homeostasis of a system. Such changes are part of the "strategy of ecosystem development" (evolution through time Odum, 1969). "Benefit" as used here is not always meant strictly in Darwinian terms. An herbivore-plant interaction affects individuals of populations of a community of plants and a current benefit to the system may be at the expense of reduced fitness of certain plant populations. This disadvantage may be resolved by adaptive responses of the plants.

LITTER-SOIL INVERTEBRATES

The consumers of the litter-soil subsystem are obviously an important example. Wherever plant processes are nutrient limited, the consumers which accelerate mineralization will increase primary productivity, a benefit by my criteria. McBrayer's (1973a) detailed accounting of energy transfer and dissipation in the litter community of a deciduous forest can be simplified to show that the two major pathways of energy dissipation (and of mineralization) are the bacteria in the detritus and the fungi (fig. 1). Litter animals seem to have two roles: (a) saprophages physically change litter and thus facilitate the metabolism of microorganisms, and (b) fungivores prevent fungal overgrowth and senescence and thus maintain the fungi in vigorous exponential growth.

There is experimental evidence for the role of saprophages. When oak leaves were mechanically ground up to the same size as insect feces, they decomposed as fast as feces—seven times faster than whole leaves (Drift and Witkamp, 1960). In laboratory cultures a synergism of microbes and litter grazing mites increased decomposition rates of lignin, cellulose and xylan. In the presence of mites, microbial biomass was greater and less variable through time (Ausmus and Witkamp, 1974). Although arthropods are not necessary for decay of soft-leaved materials such as lettuce and bean leaves (Heath *et al.*, 1966), they significantly assist decomposition of grass and tree leaves. Litter in nylon bags of different mesh sizes showed increments of decomposition as microorganisms, mesofauna and macrofauna were allowed to act (fig. 2). Even in a tropical forest, leaves were 90% unaffected in a year when invertebrates were excluded by fine-mesh bags (Madge, 1965). Oak litter decayed 27% slower than normal when arthropods

were driven out by repeated applications of naphthalene (Witkamp and Crossley, 1966). Such crude experiments need to be used and interpreted with judgment (Curry, 1969; Williams and Wiegert, 1971), however, without experimentation we are limited to circumstantial evidence.

The role of fungivores in maintaining vigor of fungal metabolism is speculative as far as I can determine. However, there is experimental evidence that protozoa stimulate bacterial metabolism in just this way. Javornichy and Prokesova (1963) found that protozoa greatly reduced the numbers of bacteria, but there was a simultaneous increase in the rate of oxidation of organic substances in the water. When protozoa were removed, the numbers of bacteria rapidly increased, but oxygen consumption declined. After reintroduction of protozoa the situation reversed.

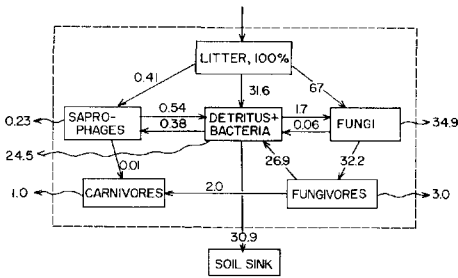


FIGURE 1. Pathways of energy transfer in a litter-detritus food web of a deciduous forest in Tennessee. Values are percentages of the litter input, after McBrayer, 1973a.

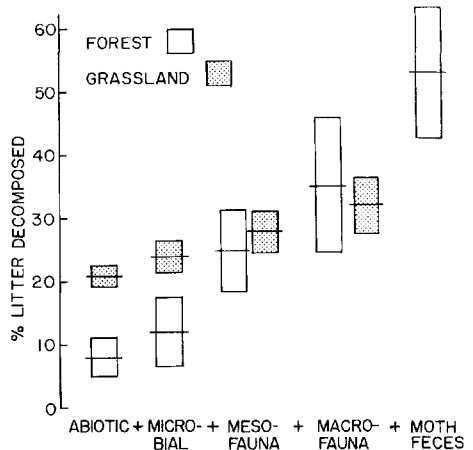


FIGURE 2. Decay of deciduous forest and grassland leaf litter, May-October, due to different agents of decomposition combined cumulatively. Treatments: abiotic decomposition, litter in 0.05 mm mesh nylon bags plus application of toluene every 7-10 days; + microbial, 0.05 mm mesh bags; +mesofauna, 1.1 mm mesh bags; +macrofauna, 10 mm mesh bags. Vertical bar is ± 2 standard errors of mean; after Zlotin, 1971.

In addition to these major roles, very small arthropods such as mites and collembola may be important by inoculating litter with spores (Macfadyen, 1961). Such facilitation of microbial decomposition could occur because even the smallest mesh bags are penetrated by tiny arthropods and nematodes. The actions of litter fauna and microorganisms are mutually beneficial since chemicals in the litter can inhibit the feeding of arthropods (King and Heath, 1967; Madge, 1965). Microorganisms may remove such chemical barriers to palatability for earthworms (Satchell and Lowe, 1967). Nutritional effects are also involved, since millipedes (*Apheloria montana*) died when they were kept from reingesting their bacteria-rich feces (McBrayer, 1973b).

Earthworms are prodigious cultivators, as shown by data beginning with Darwin (Evans and Guild, 1947). When earthworms were experimentally elimi-

nated, litter accumulated at the surface and decomposition slowed (Witkamp, 1971). The growth of potted barley was stimulated by earthworms, possibly partly by the increase of vitamin B₁₂ in the pots with earthworms (Atlavinyte and Daciulyte, 1969). Dung beetles were almost as effective in enabling plants to benefit from animal dung as when dung was mechanically mixed with soil (Borne-missza and Williams, 1970). Rodents and ants are also great soil movers. Some rodents are "nutrient pumps", bringing materials onto the surface from below the root zone (Abaturov, 1972). Ants, *Atta* sp., reduced gross primary production by reducing leaf surface area, but more than made up for this by returning minerals onto the surface of the soil (Lugo *et al.*, 1973). Other kinds of ants produced intense localized increases of organic matter, Na, K, P and cations, and associated changes in bacterial and fungal densities (Czerwinski *et al.*, 1971). The specific nature of the change was related to the feeding habits of the ants. The circumstantial evidence is pervasive that consumers function to regulate the "storage" of excess plant production in the litter and soil, but there has been no experimental test of the long-term effect of litter consumers on primary production.

The litter subsystem benefits from the rain of feces from above-ground herbivores. Feces of gypsy moths significantly increased the rate of decomposition when artificially mixed into forest litter (fig. 2). In nature the rate and pathways of recycling can be greatly altered during mass insect outbreaks (table 2, Zlotin, 1971). The fall of frass from herbivores allows recycling of nutrients within the same growing season.

TABLE 2
*Effect of a gypsy moth outbreak on the production by oak and input of litter into the soil.*¹

Years	metric tons per hectare						
	1	2	3	4	5	6	7
Production of leaves in the spring	9.30	9.30	9.03	8.15	5.51	6.28	7.00
Consumption of leaves by moths	0	0.07	4.3	5.5	6.1 ²	1.9	0
Input to soil in form of moth feces	0	0.03	1.92	2.43	2.70	0.84	0

¹Data of Ilinski, as given by Rafes *et al.* (1968, fig. 43).

²Complete defoliation in spring with some regrowth of leaves.

ABOVE-GROUND HERBIVORES

It is more difficult to analyze consumer effects in the above-ground subsystem than in the litter compartment, due to the variety of reactions to herbivory (Jameson, 1963). Animal ecologists may be handicapped by a lack of appreciation of the complexity of plant responses to being fed upon. There is evidence for several ways in which herbivores could cause plants to do more for "ecosystem strategy" than they would otherwise; possibly contrary to their best interests.

Sweet and Wareing (1966) showed it is possible to experimentally increase the rate of photosynthesis in *Pinus radiata* seedlings 3-fold. They removed some or all of the fully expanded leaves, but left growing leaves in place. The increase suggests that the accumulation of photosynthate was inhibiting photosynthesis, until a sink for its use was experimentally created. One can then speculate that the removal of leaves by chewing insects and the disappearance of photosynthate into sucking insects could create a similar stimulating biological sink.

Sucking Insects. A sink effect has been demonstrated for aphids (*Brevicoryne brassicae*) on brussel sprouts. Aphids in groups grew larger than single aphids, due to an increase in the flow of plant juices to the infected area. When 500 aphids were put on one leaf, the flow of sucrose to the infested leaf increased 75-

fold, so aphid infestation increased assimilation rate of old leaves (Way and Cammell, 1970). However, the net productivity of host plants was probably decreased. Llewellyn (1972) estimated that aphids sucked the equivalent of 41,900 kcal from a lime tree in one year, but about 91% of this went into feces and urine, *i.e.* aphid honey dew. This 41,900 kcal is what I call an "old-fashioned" measure of the impact of an herbivore; it is simply how much was ingested. The "new-fashioned" measure is of consequences for the plants, and the limited evidence to date shows a negative impact. Lime and maple saplings responded differently to aphids (Dixon; 1971a, 1971b). Infested lime saplings had normal stem and leaf growth; but root growth was severely reduced, and the leaves aged and fell earlier. Maple saplings showed a reduction in wood, leaf and root growth, and the leaves had a much higher than normal nitrogen content when they fell. The reduction in leaf growth was six times greater than the energy lost in ingested plant juice. Dixon believed the loss was due to substances injected in the saliva of the aphids rather than the materials removed from the plant. This idea is consistent with the observation that the photosynthetic capacity of spruce needles was permanently reduced by one period of aphid feeding (Kloft and Ehrhardt, 1959), and that the feeding of leafhoppers reduced growth and water balance of pasture grasses even in hydroponic culture (Andrzejewska, 1967). Aphids feed from phloem, but other insects suck xylem juice, in which case plant growth may be reduced by protein deprivation. The organic content of xylem sap of tomato plants is 98% amino acids, and spittlebugs can assimilate all the amino acids they ingest (Wiegert, 1964). So, Wiegert reasoned that each gram of amino acid removed by spittlebugs would cause a loss of five grams of dry weight production by alfalfa, since alfalfa is 20% protein.

Leaf Feeders. The effects of leaf loss can be studied by regulating the densities of grazers and simulating their feeding. Most studies have measured effects on herbage yield, *i.e.* the amount of dry matter that can be harvested at specific times (Ellison, 1960). A difficulty with this viewpoint is that yield is less than net production, because part of the growth dies and disintegrates before harvest and part is removed by consumers. To correct for these losses of production requires a much more complicated procedure than a clipping schedule (Wiegert and Evans, 1964), or the direct measurement of gaseous exchanges. Vickery (1972) measured gaseous exchanges of cores of grasses taken from pastures that had been grazed by sheep at different levels for 5 years. Net productivity was maximum at the level of 20 sheep per hectare; it was significantly less for pastures with 10 or 30 sheep per hectare. Little other experimental evidence supports an optimum grazing pressure for extracting yield from a pasture. Controlled moderate grazing by voles, *Microtus* spp., increased production of tundra herbs by stimulating new shoot growth (Smirnov and Tokmakova, 1972). In the simple ecosystems of thermal springs, the feeding of fly larvae stimulates productivity of the algal-bacterial mat (Wiegert, 1974).

In almost all other reports, leaf removal reduced yield of herbs, possibly because the intensity of removal was almost always greater than the optimum for stimulation of growth. The exceptions merit attention. Yield of several native grasses increased during several years of clipping, but then declined (Albertson *et al.*, 1953). The yield of tobosa grass, *Hilaria mutica*, increased through 11 years of clipping (Canfield, 1939). Primary production was 12% greater on grazed than ungrazed desert grassland (Pearson, 1965). Clipping part of the current growth stimulated some shrubs (Ellison, 1960). Grazing by free-roaming animals, which is spotty in space and time, can possibly stimulate productivity of native vegetation. Desert herbs may respond positively to loss of leaves if production is normally much below potential, whereas vegetation nearer maximum performance responds negatively.

Apparently herbivores can increase productivity by increasing the production:

respiration ratio of plants. Brougham (1956) found an increase in the yield per cm^2 of leaf of clipped legume-grass pasture in proportion to intensity of cutting. He suggested maximum yield would occur when grazers were regulated so they left enough leaf surface to intercept 100% of the light, a leaf-area index (LAI) of 5 in this case. Unclipped plants grew to an LAI of 8 to 9. Consumers possibly increased the primary production by removing the leaf area in excess of optimum, and also hastened the death of old and shaded leaves.

The age and position of leaves affects their role in production. The lower leaves of trees contribute less to wood growth than upper leaves, and pruning lower branches can increase shoot growth (Kulman, 1971). Two examples suggest that differential feeding can enhance growth. In some species of trees early herbage removal is more easily compensated for, because early growth uses stored photosynthate while later growth depends on current photosynthate (Kulman, 1971). For some evergreen oaks the gradual accumulation of tannin in the leaves discourages late feeding by caterpillars; tannin apparently inhibits digestive enzymes (Varley, 1970). Beetle larvae and moth larvae had different effects on turnip growth (Taylor and Bardner, 1968). Beetle larvae remained on older leaves and greatly damaged them, because their rasping of leaf surfaces and severing of veins killed more leaf tissue than they ate. Moth larvae fed on leaves of all ages, eating them cleanly and leaving veins intact, so moth larvae had less effect on leaf area (table 3). The efficiency of root yield increased at all levels of beetle infestation

TABLE 3

Effect of feeding of moth larvae (Plutella maculipennis) and beetle larvae (Phaedon cochleariae) on leaf and root growth of turnips (from Taylor & Bardner 1968, table 2).

Number of leaf-feeding larvae/plant	Turnips fed on by moths			Turnips fed on by beetles		
	Leaf area % control ^{1a}	Root yield, gm	Root yield, gm/cm ² leaf	Leaf area, % control ^{1b}	Root yield, gm	Root yield, gm/cm ² leaf
0	100	1.85	0.0037	100	2.13	0.0060
5	82.8	1.99	0.0048	79.4	2.26	0.0080
10	85.2	1.91	0.0045	57.7	1.68	0.0082
15	85.8	1.71	0.0040	61.1	1.55	0.0071
20	81.8	1.83	0.0045	45.9	1.19	0.0073

¹(a) 500 cm^2 surface for control plants (b) 355 cm^2 .

and the absolute yield increased at moderate levels, and Taylor and Bardner (1968) suggested that manipulation of the potato beetle might increase crop production!

In contrast to root-crop plants, root production in other plants is depressed by defoliation or pruning. There is an almost immediate effect, sometimes prolonged, possibly due to the dependence of roots on carbohydrate or some other substance, such as thiamine, produced in the leaves (Jameson, 1963).

Wood growth is not reduced when less than 50% of leaf surface is lost (Rafes, 1970); consumers usually remove much less than this (table 1). Beyond a 75% loss, wood growth decreases in proportion to the extent of defoliation (Kulman, 1971). At least in maple trees, the reduction in xylem growth may be an hormone-regulated response to reduced leaf surface, rather than a consequence of lost photosynthate (Dixon, 1971b). Consumers may be particularly important when they react with hormone systems of plants. Phytophagy of small sites that are active in hormone production can have exaggerated consequences, for example the feeding on terminal buds which produce auxins that inhibit lateral growth. When terminal buds were removed from red maple, simulating feeding of bud

caterpillars, lateral buds became active and there was greater shoot growth than in normal branches (Kulman, 1965). However, in sugar maples the auxillary buds never assumed a "terminal" function and there was much death of debudded terminal shoots.

Possibly consumers can prolong plant growth and increase productivity by delaying plant senescence, which causes definite effects on the quality of forage. Protein concentration of leaves decreases with maturity (Jameson, 1963). Cutting generally increases the percentage of protein in future growth; with repeated cuttings there can be an increase in total protein yield, in spite of a decline in dry matter yield (Heinrichs and Clark, 1960). Protein increases will benefit consumers, but they are of uncertain consequences for the plants. Circumstantial evidence suggests that midseason cutting of grasses such as *Bouteloua gracilis* delayed senescence and increased yield, and rhizome growth of *Andropogon* spp. increased when senescence was delayed by removal of terminal buds (Jameson, 1963).

PHYTOPHAGY AND SEED PRODUCTION

Phytophagy affects the fitness (reproductive success) of plant populations. There is a threshold of no effect: less than 50% leaf loss in snap beans, 33% in sorghum, one leaf in wheat (Rockwood, 1973). Beyond the threshold, phytophagy reduces either the number or size of seeds (James, 1963; Janzen, 1973; Rockwood, 1973). Grain yield could be sensitive to differential feeding on leaves, since in one variety of barley the development of grain was 10% due to photosynthesis by awns, 16% to other parts of the grain ear, 59% to the flag leaf, and 15% to other leaves (Watson *et al.*, 1958).

Interesting compensations occur when the flowers are eaten. When all but one flower was removed from each stem of cotton, the yield of seed and fiber increased (Eaton, 1931). When all flowers were removed from heather, *Calluna* sp., photosynthesis decreased almost immediately, which suggests a hormonal interaction between flowers and leaves (Grace and Woolhouse, 1970). There was a progressive decline in seed yield as more and more flowers were removed from dock, *Rumex crispus*, but there was an increase in the average weight of seeds (Maun and Cavers, 1971). Change in seed weight has multiple consequences for survival; fewer but larger seeds might increase the fitness of dock. Effects of seed size on dormancy could be particularly important to annual plants, which must be adapted to occasional total loss of a year's seed output (Cantlon, 1969).

SEED PREDATION

When consumers eat mature seeds, the parent plants cannot sense the loss and compensate for it and the consequences can only be worked out through natural selection. Coevolution of seed production and seed predation strategies can affect major parts of a community (Smith, 1970). Loss of seeds to predators can be high even before dispersal (table 1). Many examples suggest the loss is a worthwhile tax for the dispersal of seeds to germination sites. This benefit is most probable when the predator stores seeds, since it may not use all that it caches. Kangaroo rats, *Dipodomys merriami*, don't recover all seeds they bury in small shallow caches, and they successfully plant mesquite (Reynolds, 1958). In the Siberian taiga, where most vertebrates feed on seed of *Pinus cembra*, the seeds stored by nutcrackers help in regeneration of forests; farther south jays plant hundreds of oaks per hectare each year (Rafes *et al.*, 1968). In contrast, white-footed mice, *Peromyscus leucopus*, and voles, *Clethrionomys gapperi*, are so effective in recovering caches of pine seeds that seedlings probably survive only in years when an above average crop satiates the predators (Abbott and Quink, 1970).

Successful dispersal of seeds is less likely when the predator does not cache. Roessler (1936) recovered only 7 viable seeds from the feces of linnets that he

experimentally fed 40,025 seeds of 20 different species of weeds. Although most seeds are killed in the digestive tract, the few surviving ones can be very important. Survival of pasture juniper, *Juniperus communis*, in parts of New England is greatly increased by robins that defecate juniper seeds onto rocks. The viable seeds wash into cracks and to moister soil at edges of rocks, where they have a greater survival than in pastures next to the parent junipers (Livingston, 1972).

CONSUMERS AND VEGETATION DIVERSITY

Grass-dominated communities are of special interest because they are exceptions to the rules (table 1); they endure a heavy impact by consumers (Batzli and Pitelka, 1970), and in spite of millenia of grazing, most dominants are palatable species (Ellison, 1960). Grasses are the terrestrial equivalents of phytoplankton, *i.e.* plants that have a minimum investment in maintenance structures and can thus support heavy predation (Wiegert and Owen, 1971).

Ellison (1960) reviewed the literature on the influence of grazing on herblands, to discover the evidence "ecologists . . . reasonably expect . . . of the mutual dependence of grasses on grazers" (p. 65). But, the evidence suggested the relationship is "essentially one of parasitism by the animals." Ellison concluded that "the benefits of grazing, if any, . . . accrue to the ecosystem" rather than to plant populations; grazing animals make the environment heterogeneous by their disturbance and thus encourage a more complex flora. Floral diversity may be critical in allowing grassland to maintain functional integrity during prolonged drought (Weaver and Albertson, 1944). The positive role of consumers in generating diversity was recently emphasized by others (Harper, 1969; Janzen, 1971b; Harris, 1972).

Animals can impart heterogeneity to ecosystems by effects on both habitats and plant populations. Microvariation of soil topography is important to establishment of a variety of plantains, *Plantago* spp., (Harper *et al.*, 1965); digging animals cause much larger scale soil variations. In areas of southern Russia the soil from abandoned rodent burrows covers 10% of the steppe and supports 3 to 5 times the plant biomass of adjacent soil (Dinesman, 1967). Herbs flourish on the sites of abandoned harvester ant nests (Gentry and Stiritz, 1972). However, there is no experimental demonstration of any importance of heterogeneity to primary production. McNaughton (1974) did not find a significant change in productivity when the diversity of old-field vegetation was changed by application of fertilizer.

Consumers that specialize in one or a few food plants can particularly affect vegetation diversity. Janzen (1970) presented a model with much force of logic to explain how seed predators can cause the high diversity of some tropical forests. If specialized seed predators, such as a species of bruchid beetle, are concentrated in the dense seed fall under the parent tree, the probability of a seed escaping predation will increase with its distance from the tree. The predator thus forces a low, widely spaced density upon its prey. If the predator is very efficient in searching, there is no escape within the normal seed fall pattern of the tree. It may be that *Cassia grandis* requires help from vertebrate fruit feeders to get some of its seeds beyond the range of its bruchid predator (Janzen, 1971a). This model can be tested by checking its predictions in nature, but it is difficult to do experiments with seed predators. The circumstantial evidence of "natural experiments" is consistent with the model. On islands where there is a depauperate seed predator fauna, trees produce dense homogeneous stands. Introductions of seed predators to such islands have drastically reduced density of some stands (Janzen, 1971b).

Under certain conditions less specialized seed-feeders can suppress dominance of a plant. Small mammals and birds can suppress annual plants and create a bare zone around chaparral shrubs, because their activity is concentrated there (Bartholomew, 1969). More evidence is available for the effects of leaf-feeders on

plant diversity, since we have the experiments of biological control and manipulation of grazers. A specialist grazer can reduce a dominant plant to a rarity. A classical example is the reduction of Klamath weed, *Hypericum perforatum*, from millions of acres in western United States to local patches in shady microhabitats, by the beetle, *Chrysolina quadrigemina* (DeBach, 1964). The beetle larvae feed on the basal leaves of *Hypericum* and within a few years the weed fails to flower, exhausts its reserves, and dies. Without the history of the biological control, one could not guess from the current low densities of *Hypericum* and *Chrysolina* that the beetle affects the plant, much less controls it. Many similar examples probably are hidden in nature and might be uncovered by experimental removal of predators. Spring populations of an annual, *Melampyrum lineare*, increased 3-fold in four years after removal of insecticide-sensitive consumers (Cantlon, 1969). When goats were excluded, *Acacia koa* reproduced abundantly by vegetative growth (Spatz and Mueller-Dombois, 1973).

A review by Harper (1969) shows that the effects of herbivores on vegetation diversity vary according to the feeding behavior of the animal, the time of feeding and the nature of the plant dominants. If the grazer is a strict generalist, eating each species in proportion to its presence, the result is a simplification of the vegetation. Presumably this results because only plant competition then determines the outcome. If a broad-spectrum feeder prefers certain palatable dominants, then the effect depends on the timing of the feeding. If grazing is heavy for one season and then removed, the vegetation may be simplified. One plant species or another is favored according to its phenology. If the vegetation is overgrazed during part of the year and then undergrazed during the growing season, as is often the case in nature, then each species bears some impact of the herbivores and all have some respite, and a maximum diversification occurs. Simplification of vegetation has been observed when a grazer, such as the European rabbit, is removed from a system. If the dominants are not palatable and a selective generalist is allowed to graze or not, by choice, the animals will return repeatedly to suppress the minority palatable species, and thus limit the diversity of the vegetation. But, if there are alternating periods of hard grazing and rest, then the forced impact on the unpalatable species will result in some increase in diversity. Rare palatable species that tolerate heavy grazing can act as foci of grazing; this brings pressure on surrounding less palatable species and reduces them (Nicholson *et al.*, 1970). Because of the various combinations of factors it is not possible to generalize the effect of herbivores on plant diversity.

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