(hydrogen evolution) the components of the electron transport chain linking photosystem I and photosystem II are fully reduced (*8*). Consequently, oxygen evolution is not observed for anaerobically adapted algae in the absence of chemical oxidants. If *p*-benzoquinone is added to the anaerobic *Chlorella* suspension, the same experimental procedure measures the oxygen yield per flash. Under these oxidizing conditions (although still strictly anaerobic at an oxygen concentration of 10 parts per million) there is no evidence for evolution of hydrogen. This dichotomy in the local chemical conditions required for hydrogen or oxygen evolution lies at the heart of the problem of biophotolysis of water (*9, 10*).

Returning to the oxygen curve of Fig. 1, we see that the yield of oxygen on the first flash, unlike the corresponding observation for hydrogen, is zero. There is a small yield of oxygen on the second flash, which can be increased by adding ionic oxidants or increasing the flash frequency (*5*). The third flash produces the maximum oxygen yield, and the subsequent yields can be described as a damped oscillation with period 4. Oxygen oscillations have formed the experimental underpinning of the theories concerning the molecular mechanism of oxygen evolution (*3–6*). These oscillations indicate a role for photoproduced, sequential, metastable intermediates which are serially involved in the formation of oxygen. Apparently, the four oxidizing equivalents necessary to produce a molecule of oxygen from water cannot be produced in a single flash. It requires at least two flashes to produce some oxygen. This is not the case for hydrogen: one flash is sufficient. Thus, the molecular mechanism of hydrogen evolution must be such that no photoproduced, metastable intermediates are serially involved as they are in the case of oxygen evolution. Moreover, since two reducing equivalents are required to make one molecule of hydrogen, it follows that in the photoproduction of molecular hydrogen the reducing equivalents from at least two photosystems are fed into a common pool (probably ferredoxin), following the common assumption that the photosystems form one equivalent per single-turnover flash. Once in the pool, the two equivalents combine in the dark to produce hydrogen through hydrogenase. An alternate, although less probable, mechanism is one in which the first reducing equivalent is supplied by a dark reaction and the second by a light reaction (or vice versa). The sensitivity of the detection apparatus is sufficient to determine that less than 10 percent of the reaction centers are evolving hydrogen between flashes in a dark reaction.

The size of the photosynthetic unit for hydrogen evolution in *Chlorella* is chlorophyll : $H_2 \approx 1400 : 1$. The photosynthetic unit size for oxygen evolution (the Emerson and Arnold unit) for *Chlorella* coupled to benzoquinone is chlorophyll : $O_2 \approx 1700 : 1$. These data allow a determination of the ratio of hydrogen to oxygen, both normalized to the chlorophyll content of the algae. The ratio of H_2 to O_2 is 1.2. Were the movement of electrons by chlorophyll as efficient for hydrogen as for oxygen, the stoichiometric ratio would be 2. These data indicate that with regard to the photophysical apparatus of photosynthesis, the ability to utilize absorbed visible quanta for the light-driven reaction is at least 60 percent as efficient for photosynthetic hydrogen evolution as for photosynthetic oxygen evolution. One can think of several reasons why the ratio of H_2 to O_2 is only 1.2 rather than 2. One possibility is that not all the reducing equivalents are captured by the hydrogenase. Measurements on *Scenedesmus* D_3 give a unit size of chlorophyll : $H_2 \approx 800 : 1$. However, attempts to measure the oxygen unit size have resulted in a very low yield of O_2, most likely caused by losses of intermediates.

The concept of photosynthetic unit stems from the pioneering work of Emerson and Arnold (*1*). The experiments described in this report are, to my knowledge, the first determination of the photosynthetic unit size based on hydrogen evolution. This unit size is comparable to the size based on oxygen evolution.

Note added in proof: Since the initial submission of this report flash experiments identical to those performed on *Chlorella* as described above have been performed on *Chlamydomonas reinhardtii*. For *Chlamydomonas* the O_2 oscillations are essentially the same as for *Chlorella*. However, the H_2 yield is larger, such that the ratio of H_2 to O_2 is 1.9. This is close to the theoretical maximum.

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Competition Between Seed-Eating Rodents and Ants in Desert Ecosystems

Abstract. *Three kinds of evidence indicate that desert rodents and ants compete for seeds: (i) extensive overlaps in diet, (ii) reciprocal increases when one taxon is experimentally excluded, and (iii) complementary patterns of diversity and biomass in geographic gradients of productivity. The effect on seed resources and annual plants seems to be similar whether rodents, ants, or both are foraging.*

A primary challenge of contemporary ecology is to understand the processes that determine the diversity, organization, and stability of natural ecosystems. Competition between species for food and other resources is thought to be an important determinant of ecosystem structure and dynamics. Empirical support for this conclusion comes almost exclusively from field and laboratory studies of a small number of closely related species (*1*). Taxonomic specialization has prevented most ecologists from recognizing and investigating the significance of competition among distantly related organisms. Several recent studies indicate that such distantly related taxa as insects, birds, and mammals eat similar foods and are potentially important competitors (*2–4*). We now report competition between seed-eating desert rodents and ants that affects the structure and dynamics of ecosystems.

Seeds play a major role in the ecology

of desert regions. They constitute dormant, resistant life-history stages that maintain large populations of annual plants for the long, unpredictable intervals between short periods of vegetative growth. Seeds of annuals are the primary food of several distantly related taxa of specialized granivores such as rodents, birds, ants, and other insects (for example, bruchid and curculionid beetles).

Rodents and ants are similar in their utilization of seed resources. Experiments in which domestic seeds were distributed in desert habitats demonstrated that these two taxa took most of the seeds, harvested the same sizes and species, and collected them from the same microhabitats (*3*). Foraging rodents and ants select overlapping sizes and species of native seeds (Fig. 1) (*5*). The overlaps provide the potential for strong competition between rodents and ants, but other evidence is required to demonstrate whether they actually compete and to assess the magnitude of interaction and its impact on the ecosystem.

Since 1973, we have performed a set of exclusion experiments to test directly for competition between rodents and ants. Replicated, circular plots, each 36 m in diameter, were established in relatively level, homogeneous desert scrub (*Larrea-Franseria*) habitat on the Silverbell Bajada, approximately 60 km northwest of Tucson, Arizona. Two plots were subjected to each of the following treatments. (i) Plots were fenced with ¼-inch wire mesh to exclude seed-eating rodents, and those present were removed by trapping; (ii) granivorous ants were removed by repeated application of insecticide (mirex or chlordane) to individual colonies; (iii) both rodents and ants were excluded by fencing, trapping, and applying insecticide; and (iv) two plots were reserved as unmanipulated controls. We censused rodent and ant populations periodically. Rodent numbers were assessed by simultaneously live-trapping all of the plots with equal trapping effort and standardized grids. Ant colonies were counted directly once or twice each year during periods when most species were most active. In late summer of 1976, we used a photographic technique to sample populations of annual plants that had germinated in response to rain. An independent investigator (*6*) analyzed seed content of soils on our plots.

Relative to populations on unmanipulated control plots, the number of ant colonies increased 71 percent on plots from which rodents had been excluded, and rodents increased 18 percent in number of individuals and 24 percent in biomass on plots where ants had been removed (Wilcoxon matched-pairs signed-ranks tests, $P < .01$) (Table 1). These results constitute direct evidence for strong competitive interactions. Our relatively short-term experiments measured competition only in contemporary ecological time. Since seed-eating rodents and ants probably have coexisted in arid habitats for at least 2 million years, evolutionary adaptations may reduce competition between the two groups; these would limit their potential numerical responses to the sudden artificial removal of competitors.

In the absence of either rodents or ants, the species of the remaining taxon that showed the greatest increase were those that tend to specialize on densely distributed seed resources. Thus, rodent biomass was enhanced more than the number of individuals because of increases in the relative abundance of the largest species, *Dipodomys merriami*, which specializes in harvesting dense clumps of seeds (*7*). Similarly, ant species of the genus *Pheidole* that forage in coordinated

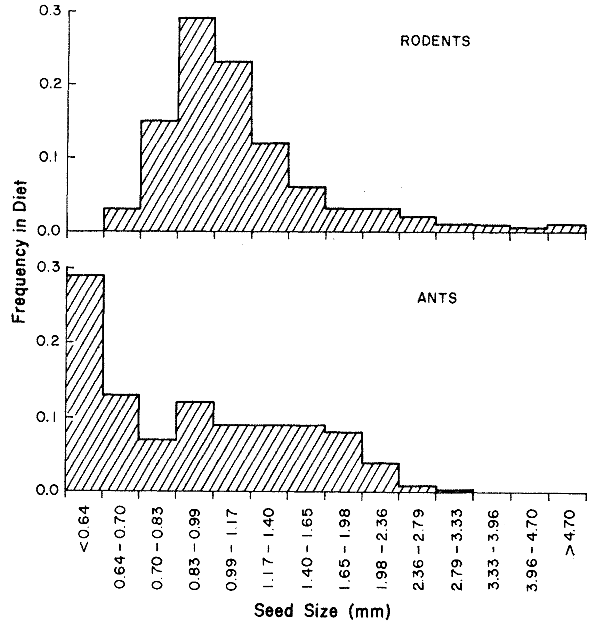

Fig. 1. Sizes of native seeds harvested by coexisting ants and rodents near Portal, Arizona. A total of 11,518 seeds were collected from the cheek pouches of 134 rodents representing five species, and 1052 seeds were collected singly from ants representing seven species. These were sized by passing them through a graded series of sieves (Tyler). Although ants take some seeds smaller than those utilized by rodents, there is extensive overlap (*5*).

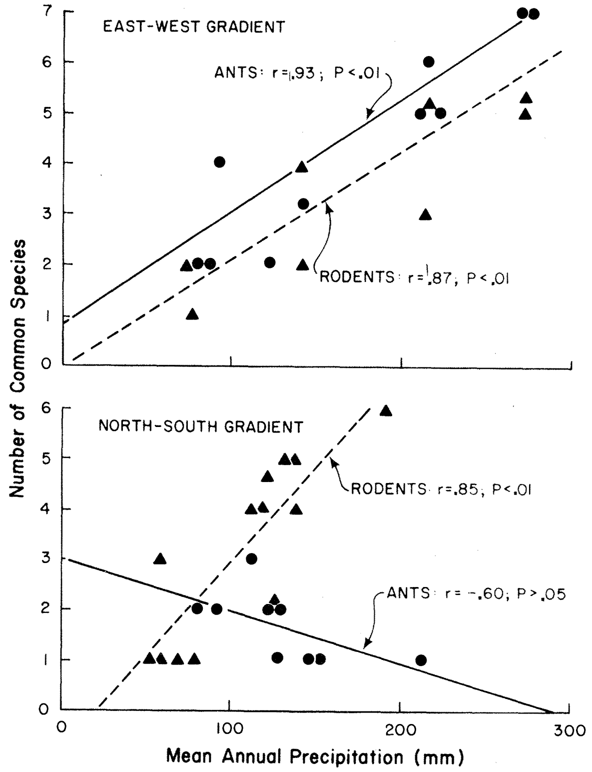

Fig. 2. Patterns of species diversity of seed-eating rodents (triangles) and ants (circles) inhabitating sandy soils in geographic gradients of precipitation and productivity. Correlation coefficients and significance levels for the fitted linear regressions are indicated. In the north-south gradient, where ant diversity does not vary significantly, rodent diversity increases more rapidly with precipitation than in the east-west gradient, where the slopes for the two taxa are similar.

Table 1. Summary of the results of experiments in which ants or rodents were eliminated from plots and the unmanipulated taxon was repeatedly censused. Values in first three columns are totals of all censuses. Ants were censused five times, and there were two replicates of each treatment for a total of ten comparisons. There were 25 comparisons of rodent censuses: 13 censuses of the first replicated set of plots (established in August 1973) and 12 censuses of the second set (established in December 1973). The last column gives the fraction of the comparisons in which the experimental census exceeded the control census.

Taxon	Total			Increase relative to control (%)	Experimental > control
	Rodents removed	Ants removed	Control		
Ant colonies	543	—	318	70.8	9/10
Rodents					
Number	—	144	122	18.0	15/25*
Biomass (kg)	—	5.12	4.13	24.0	16/25†

*In five comparisons, the experimental equalled the control census. †In three comparisons, the experimental equalled the control census.

columns for dense aggregates of seeds (*8*) showed the greatest numerical response to removal of rodents. This result suggests that exclusion of either rodents or ants enhanced the density of seeds available to the other taxon and corroborates competition.

Comparative studies of associations of seed-eating rodent and ant species over geographic gradients of productivity suggest that competition between these two taxa affects the organization and function of desert ecosystems. In an east-west gradient, where latitude and environmental temperature were relatively constant, the numbers of coexisting species of both rodents and ants increased at almost identical rates (Fig. 2) with enhanced precipitation, a measure of productivity in arid regions (*8, 9*). In contrast, in a north-south gradient, where declining environmental temperatures accompany greater mean rainfall at higher latitudes, there was no significant change in the number of ant species, but rodent species diversity increased more rapidly with productivity than in the east-west gradient (*10*). Although data are less complete, the same patterns characterize biomass and population densities of the two groups (*8–10*). These data are consistent with the hypothesis that the two taxa compete for limited food resources. When other environmental conditions remained relatively constant, the two taxa responded similarly to the increasing availability of seeds. However, when one taxon was unable to respond to increased productivity [in this case, presumably because low temperatures inhibit ant activity (*11*)], the other increased in density, biomass, and diversity. Since distributions of rodents and ants are limited by different environmental constraints and geographic barriers, this ability to compensate for the absence of competitors may result in the evolution of taxonomically divergent but functionally similar granivore communities in geographically isolated deserts.

Preliminary data from our exclusion experiments indicate that the increase of rodents or ants in response to the absence of the other taxon may have a compensatory impact on seed resources and plant populations. Analyses of annual plants and seeds in the soil revealed 5.5 times greater densities of seeds and 2.0 times greater densities of annual grasses (*Bouteloua barbata* and *B. aristidoides*) on plots from which both rodents and ants were absent than on any others; there were no significant differences among plots in which rodents, ants, or both were present. This finding suggests that rodents and ants are the primary granivores in this ecosystem and that their competitive interaction results in a compensatory reduction of seed resources when one taxon is removed. Additional field work is required to document the effects of these and other seed eaters on the diversity, stability, and productivity of desert plant communities (*12*).

Strong competitive interactions among distantly related organisms such as we have demonstrated here are probably widespread and important in natural ecosystems. In most habitats the important kinds of food resources are used by several major taxa of potentially competing consumers. Obvious examples include phytophagous insects and grazing mammals in temperate and tropical grasslands (*2*), frugivorous insects, birds and mammals in tropical forests (*4*), insect and avian nectar feeders in many habitats, and even insectivorous plants, arthropods (spiders), and vertebrates in areas of acid soils. Competition among distantly related taxa may account in part for the higher density of some populations of birds (*13*) and lizards (*14*) on some oceanic islands compared to that in similar habitats on nearby continents. These insular populations may attain high densities by consuming food resources which, in continental habitats, are utilized by competitors that disperse poorly across bodies of water. Additional fieldwork will be required to assess the general significance of competition between unrelated taxa, to determine the effects of such interactions on ecosystems, and to produce realistic models of these processes.

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$$\alpha_{ij} = \frac{\Sigma\, p_i p_j}{\Sigma\, p_i^2}$$
where α_{ij} is the overlap of taxon j on taxon i, and p_i is the unweighted utilization of a particular seed size category by species i relative to its utilization of the other size categories [R. H. MacArthur and R. Levins, *Am. Nat.* **101**, 377 (1967)]. When this is done, the overlap of rodents on ants is 0.59 and the overlap of ants on rodents is 0.50.
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