

Apparently, extreme drought stress is not sufficient to prevent these pine seedlings from responding to added CO₂. Photorespiration may be involved in this response. If pines possess only the Calvin-Benson pathway of CO₂ fixation, they should be susceptible to photorespiration (Marx, 1973). Increasing CO₂ causes photorespiration to diminish as ribulose diphosphate carboxylase promotes the Calvin-Benson cycle over photorespiration. Raising CO₂ may thus remove two limitations: the limiting supply of carbon for fixation and the limitation of photorespiration. Thus, not even severe drought is enough to entirely prevent the plants from responding to increased CO₂.

Atmospheric CO₂ increase of considerable magnitude is a virtual certainty in coming years. Our work suggests that the consequent increase in net photosynthesis may be equally certain, even in dry climates.

LITERATURE CITED

- FUNSGH, R. W., R. H. MATTSOA AND G. R. MOWRY. 1970. CO₂-supplemented atmosphere increases growth of *Pinus strobus* seedlings. *For. Sci.*, **16**:459-460.
- GORDON, J. C. AND G. E. GATHERUM. 1969. Effect of environmental factors and seed source on CO₂ exchange of scotch pine seedlings. *Bot. Gaz.*, **130**:5-9.
- KEELING, C. D. 1970. Is carbon dioxide from fossil fuel changing man's environment? *Proc. Am. Philos. Soc.*, **114**:10-17.
- MARX, J. L. 1973. Photorespiration: key to increasing plant productivity? *Science*, **179**:365-367.
- MOSS, D. N., R. B. MUSGRAVE AND E. R. LEMON. 1961. Photosynthesis under field conditions. III. Some effects of light, carbon dioxide, temperature, and soil moisture on photosynthesis, respiration, and transpiration of corn. *Crop Sci.*, **1**:83-87.
- PETERSON, E. K. 1969. Carbon dioxide affects global ecology. *Environ. Sci. and Technol.*, **3**:1162-1169.
- WRIGHT, R. D. 1968. Lower elevational limits of montane trees. *Bot. Gaz.*, **129**:219-226.
- . 1970. CO₂ exchange of seedling pines in the laboratory as related to lower elevational limits. *Am. Midl. Nat.*, **83**:291-300.
- . 1974. Rising atmospheric CO₂ and photosynthesis of San Bernardino Mountain plants. *Ibid.*, **91**:360-370.
- PAUL HURT AND ROBERT WRIGHT, Department of Biology, University of Redlands, Redlands, Calif. 92373. Submitted 10 June 1974; accepted 1 October 1974.

Foraging Behavior of Chihuahuan Desert Harvester Ants

ABSTRACT: Foraging behavior was studied on a desert grassland site 40 km NNE of Las Cruces, New Mexico. The number of workers foraging decreased logarithmically with distance from colony when individual seeds were evenly distributed and varied directly with seed density. Some colonies of *Pogonomyrmex rugosus* exhibited group foraging while others did not. Foraging territories of individual colonies of *P. rugosus* were irregular in shape and overlapped considerably with foraging territories of adjacent colonies of *P. rugosus*.

INTRODUCTION

Harvester ants of the genera *Pogonomyrmex* and *Novomessor* occur at high

densities (over 175 colonies \cdot ha $^{-1}$) in some Chihuahuan Desert communities in southern New Mexico. Since these species share a common food resource, seeds (Cole, 1943; Sudd, 1966; Wheeler and Creighton, 1934), studies of foraging patterns of adjacent colonies provide data on intra- and interspecific colony interactions. Such studies provide the basis for evaluating resource partitioning in these animals and also insights into the evaluation of foraging strategies in social insects.

METHODS

Foraging patterns of individual colonies were studied in cleared arenas 15 m in radius by distributing cracked milo dyed with vegetable dye in selected patterns (Willard and Crowell, 1965). Foraging intensity, measured by the number of colored seeds returned per worker minute, was studied by placing piles of colored seeds containing nearly equal numbers of seeds in concentric rings at varying distances from the central colony, or by scattering individual seeds as evenly as possible in concentric rings at varying distances from the central colony. Piles of seeds were spaced at 0.5-m intervals in each concentric ring and the rings were spaced at 2-m intervals from the center nest. Concentric rings made up of evenly scattered seeds were also spaced at 2-m intervals from the center nest.

To study the effect of densely clumped seeds on the pattern of foraging by colonies, I provided colonies with piles of seeds at distances less than 10 m from the center colony and at 10 m placed a solid ring of seeds.

Foraging territories were mapped by plotting the number of seeds of various colors returned to the colony in the center and to colonies on the periphery of cleared arenas.

RESULTS AND DISCUSSION

In experiments where seeds were distributed in evenly spaced piles or as individual seeds dispersed in concentric rings at varying distances from the central colony, the number of seeds returned per worker minute in *Pogonomyrmex rugosus* and *Novomessor cockerelli* exhibited a log decay with increasing distances from the colony expressed by: $\log N = 1.2 - 0.19D$ ($r^2 = 0.71$); where N = number of foragers returning to the colony per unit time and D = distance in meters. Intense foraging rapidly depleted the seeds close to the colony; within 30 min of the initiation of an experiment there was a relatively even distribution of the number of seeds returned per worker minute at varying distances from the colony.

The logarithmic decrease in foraging effort as a function of distance from the colony suggested that colonies of *Pogonomyrmex rugosus* employ a random search pattern. In these experiments, 10 colonies of *P. rugosus*, three colonies of *Novomessor cockerelli* and eight colonies of *P. desertorum* foraged in the cleared arenas. Of these, two *P. rugosus* and one *N. cockerelli* colonies were in the center of the arena with the remaining colonies at the periphery. Three of the *P. rugosus* colonies at the periphery exhibited group foraging forming distinct foraging trails to piles of colored seeds; the remaining colonies of *P. rugosus*, and the *N. cockerelli* and *P. desertorum* colonies exhibited random search.

In the initial experiments, the number of seeds returned to the nest \cdot min $^{-1}$ ($\bar{x} \pm SD$) in colonies using group foraging was 32.9 ± 12.4 and in other colonies was 4.5 ± 4.3 . After 2 days of experiments in which the group-foraging colonies had removed an estimated 160 g of seeds, the group-foraging colonies ceased activity while the other colonies continued foraging, collecting 4.4 ± 3.4 seeds \cdot min $^{-1}$. Twenty-two days after the initial experiments, group-foraging

colonies resumed activity collecting 2.2 ± 0.3 seeds \cdot min⁻¹, and the other colonies collected forage at a rate of 10.9 ± 3.8 seeds \cdot min⁻¹.

These data provide a basis for evaluating the problem of group-foraging behavior in laboratory colonies of *Pogonomyrmex* and the reported absence of group-foraging behavior in the field (Carroll and Janzen, 1973). Some colonies of *P. rugosus* responded to seed amendment in cleared arenas by group foraging but other colonies of *P. rugosus* did not. I suggest that group foraging in *P. rugosus* may be a genetic characteristic of a fraction of the colonies of this species in the Chihuahuan Desert. Group foraging should be selected for in an environment where the resources are reliably present, but in clumps of unpredictable location, on a microscale. In the stochastic environment of the Chihuahuan Desert, examination of past rainfall data (Houghton, 1972) indicates that high densities of the annual plants which are the preferred forage of ant colonies in any one area are available less than 33% of the years. High productivity of these annual plants may occur for several successive years, or may be absent for as long as 5 successive years. Thus, group foraging appears to be of marginal value in the environment where forage items are scattered, the more typical situation in the Chihuahuan Desert. This strategy is characteristic of *P. desertorum*, *P. californicus*, *N. cockerelli* and most *P. rugosus* in the area.

The complete cessation of foraging in group-foraging colonies and the large variance in foraging activities of other colonies are attributed to colony satiation. Wallis (1964) presented evidence that the degree of hunger or satiation of a colony had a direct effect on the foraging intensity of *Formica fusca*.

The decrease in foraging activity after 6 successive days of experiments (2.0 ± 0.4 seeds \cdot min⁻¹) and the increase in foraging of both group- and nongroup-foraging colonies after the 16 days of no-seed amendment support this idea. I dug into the surface storage chambers of two colonies which had ceased foraging after 2 days and found the storage chambers filled with dyed grain.

The foraging rate was greater at the distant concentrated food source than at the scattered piles closer to the colony. Some foragers from the center colony returned with seeds which were placed 3 m beyond the solid ring. Thus, the presence of a continuous, dense source of seeds did not cause all workers to stop at that location. This indicates either that some workers in a harvester ant colony may search at fixed distances from the colony regardless of this distribution of suitable forage closer to the colony or that these workers are searching for other kinds of food items.

By plotting the numbers of seeds of various colors returned to the colonies in the center and periphery of the cleared arenas, I was able to map the foraging territories of the colonies of *Pogonomyrmex rugosus* and *Novomessor cockerelli* (Fig. 1). Foraging territories had irregular shapes and the shapes did not vary over the 30 days of the study. There was considerable overlap of foraging territories of *P. rugosus* colonies. *N. cockerelli* foraging territories did not appear to overlap each other but did overlap almost completely the foraging territories of adjacent *P. rugosus* colonies. I hypothesized that random foraging behavior should result in nearly circular territories and that deviations from that pattern probably resulted from intraspecific interactions. To test the hypothesis that noncircular foraging territories result from colony interactions, I completely excavated a colony which overlapped and appeared to influence the foraging of one of the central colonies. Two weeks after this colony had been removed, there was no change in the foraging territory of the central colonies. This suggests that the constancy and irregular shapes of foraging territories are not the result of intraspecific interactions or at least are not responsive to the removal of one interacting colony.

I never observed direct aggressive interaction between workers of different colonies of the same species or of other species. Aggressive interaction did not occur even when foragers from one colony traversed the nest disc of another colony, and on several occasions I observed nonresident foragers remove seeds from the nest disc. These observations support the premise that the irregular shape and constancy of foraging territories in *Pogonomyrmex rugosus* are not the result of direct colony interactions.

Acknowledgments.—This research was supported by the US/IBP Desert Biome Program under Grant GB-15886 from the NSF. I thank Helen Hart, Rebecca Delson, Barry McLaughlin, Tim Cox and Ken Rall for their help and W. Brett Whitford for suggesting cleared arenas.

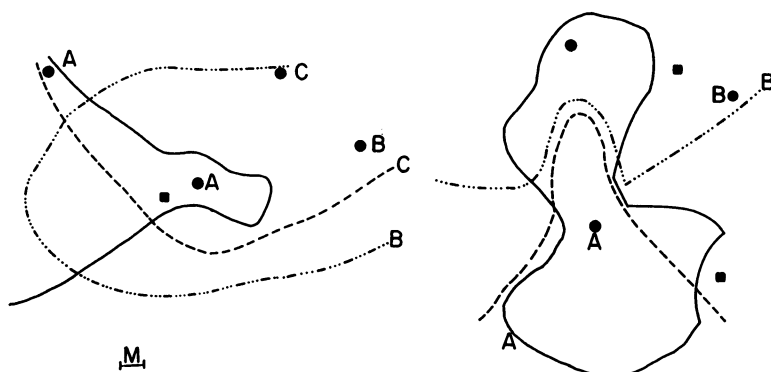


Fig. 1.—Overlap in foraging territories of colonies of *Pogonomyrmex rugosus* and *Novomessor cockerelli*. *P. rugosus* nests are represented by circles and *N. cockerelli* nests by squares. The perimeters of foraging territories for specific nests are indicated by the letters A, B, C

LITERATURE CITED

- CARROLL, C. R. AND D. H. JANZEN. 1973. Ecology of foraging by ants. *Annu. Rev. Ecol. Syst.*, **4**:231-257.
- COLE, A. C. 1943. An ecological study of the ants of the southern desert shrub region of the United States. *Ann. Entomol. Soc. Am.*, **27**:388-405.
- HOUGHTON, F. E. 1972. Climatic guide, New Mexico State University, Las Cruces, New Mexico, 1851-1971. *N.M. Agric. Exp. Stn. Res. Rep. No. 230*. 20 p.
- SUDD, J. H. 1966. An introduction to the behavior of ants. St. Martins, London. 200 p.
- WALLIS, D. I. 1964. The foraging behavior of the ant *Formica fusca*. *Behaviour*, **23**:150-176.
- WHEELER, W. M. AND W. CREIGHTON, SR. 1934. A study of the ant genera *Novomessor* and *Veromessor*. *Proc. Am. Acad. Arts Sci. Boston*, **69**:341-387.
- WILLARD, J. R. AND H. H. CROWELL. 1965. Biological activities of the harvester ant, *Pogonomyrmex owyheeii*, in central Oregon. *J. Econ. Entomol.*, **58**:484-489.
- WALTER G. WHITFORD, Department of Biology, New Mexico State University, Las Cruces 88003. Submitted 25 July 1974; accepted 13 February 1975.