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Demography and Bioenergetics of Herbivorous Ants in a Desert Ecosystem as Functions of Vegetation Soil Type and Weather Variables

W. G. Whitford

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Whiteford, W.G. 1973. Demography and Bioenergetics of Herbivorous Ants in Desert Ecosystem as Functions of Vegetation Soil Type and Weather Variables. US International Biological Program, Desert Biome, Logan, UT. RM 73-29.

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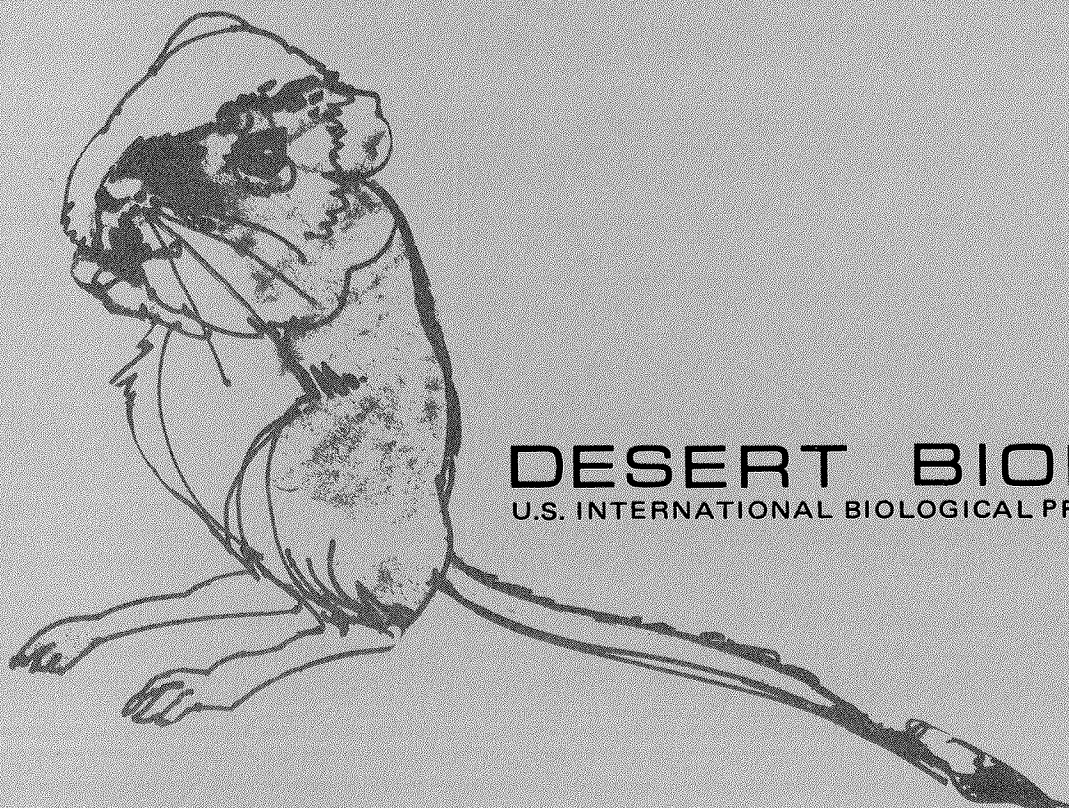


RESEARCH MEMORANDUM

RM 73-29

DEMOGRAPHY AND BIOENERGETICS OF HERBIVOROUS ANTS
IN A DESERT ECOSYSTEM AS FUNCTIONS OF VEGETATION
SOIL TYPE AND WEATHER VARIABLES

W. G. Whitford, Project Leader



DESERT BIOME
U.S. INTERNATIONAL BIOLOGICAL PROGRAM

1972 PROGRESS REPORT

DEMOGRAPHY AND BIOENERGETICS OF HERBIVOROUS ANTS IN A DESERT
ECOSYSTEM AS FUNCTIONS OF VEGETATION,
SOIL TYPE AND WEATHER VARIABLES

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New Mexico State University

Research Memorandum, RM 73-29

MAY 1973

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Report Volume 3

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ABSTRACT

Soil surface temperature (T_s) and saturation deficit (SD) combinations regulate the foraging activity of harvester ants. *Novomessor cockerelli* which is active nocturnally, was active at T_s 15-45 C with maximum activity at T_s between 20 C and 30 C and SD $<25 \text{ g/m}^3$. *Pogonomyrmex rugosus* was active at T_s 20-55 C and SD $<40 \text{ g/m}^3$ with peak activity at 45 C. *P. desertorum* was active at T_s 25-55 C and SD $<40 \text{ g/m}^3$, with peak activity at 45 C, and *P. californicus* was active at T_s 35-60 C and SD $<45 \text{ g/m}^3$, with peak activity at 45 C. There was nearly complete overlap of foraging territories between colonies of the same species and different species (*P. rugosus* and *N. cockerelli* only). Foraging effort was shown to exhibit a natural log decay function with increasing distance from the nest. Foraging effort also varied as a function of resource concentration. There was considerable overlap in the foraging preferences of the *Pogonomyrmex* species studied. In a year such as 1972 which results in high density annual forb and grass production, harvester ant foraging had a small impact on seed reserves but the seed reserves of selected plant species were significantly affected, e.g., *Eriogonum trichopes* and *Bouteloua barbata*. Regression equations were developed for predicting fruit number and biomass in several species of annual forbs and grasses.

Forager population estimates were highest coincident with maximum forage availability. Comparison with the colony sizes of excavated colonies suggested that all foragers were mobilized at that time, providing a reasonable estimate of total colony size. *P. desertorum* and *N. cockerelli* exhibited clumped distribution and *P. rugosus* colonies were randomly distributed at the Jornada Validation Site.

I N T R O D U C T I O N

Studies of ecosystems may be conducted in a number of ways and at varying levels of complexity. In the Desert Biome program, research efforts are being conducted at: 1) the whole system level, with an emphasis on models of the transfer of energy and nutrients through the components of the system, 2) parts of the system with emphasis on answering specific kinds of questions, question oriented models, and 3) synthesis and testing of ecological principles not necessarily utilizing simulation models. This study was designed to provide data for all three approaches, but with emphasis on the data requirements of a harvester ant foraging-seed reserve model produced under the direction of Dr. Kent Bridges and with the assistance of several modellers at Utah State University.

In order to predict the impact of harvester ants on the seed reserves of a given year, several behavioral parameters of harvester ant species involved must be predictable. Of these, factors affecting foraging activity and intensity must be elucidated. The literature provides few studies with information on foraging behavior in harvester ants (Tevis, 1958; Creighton, 1953; Cole, 1934; Eddy, 1970; Lavigne et al., 1971; Willard and Crowell, 1965). Of these studies, the only quantitative data on factors affecting foraging activity deal with *Pogonomyrmex occidentalis* or *P. owyheei* (Willard and Crowell, 1965; Eddy, 1970; Lavigne et al., 1971). None of these studies adequately treat climatic factors other than temperature. Therefore our studies were designed to evaluate the interrelationship between soil surface temperature and the drying power of the air (saturation deficit) as components determining foraging activity in harvester ants.

The preliminary studies demonstrated that while climatic factors were extremely important determinants of foraging activity in harvester ants, other factors probably affected foraging intensity (e.g., relative abundance and pattern of distribution of food items). No reference to papers evaluating the responses of harvester ants to variations in these parameters was found. Consequently field experiments were designed to obtain the data necessary to evaluate these parameters.

Maximum foraging distance, distribution of foraging effort as a function of distance from the nest and interactions between colonies of the same species or different species are parameters which must be measured in order to determine the reliability of uniformly applying the data provided by foraging studies to a large area. In addition, evaluation of these parameters provides data for testing hypotheses concerned with intra- and interspecific competition, niche separation etc., within natural communities. Numerous field experiments were designed to provide these data.

In addition to foraging rates, kinds and frequency of plant parts foraged as a function of availability and production must be ascertained. In desert areas, the composition of the annual plant community changes from year to year. Therefore studies of food habits of species of harvester ants at a point in time would have little predictive value unless accompanied by data on rate of production of fruits and/or seeds of various species. Data on food habits of harvester ants are also somewhat limited (Tevis, 1958; Eddy, 1970; Lavigne et al., 1971; and Willard and Crowell, 1965). Tevis (1958) presented data on material foraged by *Veromessor pergandei* as a function of seed reserves. Eddy (1970) provided data on material foraged by *P. occidentalis* in four areas in Kansas as related to seed production in the area. The other studies cited provided some data of a more qualitative nature. Our studies were designed to provide data on food preference as a function of food availability.

OBJECTIVES

1. To estimate density, biomass and population structure of harvester ants in the Jornada area. Research in 1972 concentrated on obtaining reliable data for forager populations and continued to evaluate techniques for estimating total populations.
2. To measure activity patterns as functions of temperature and season. This was accomplished for four species including saturation deficit as an independent variable.
3. To measure food-consumption rates and species of plant seeds consumed as functions of vegetation phenology, production and season.
4. To measure egestion, assimilation and metabolic rates of harvester ants. [A manuscript dealing with oxygen consumption in two species has been submitted for publication.]

In addition to the objectives stated in the original proposal (1-4) the following were added.

5. To investigate interactions between colonies of the same species and different species to provide insight into spatial relationships.
6. To identify and quantify factors in addition to climate which influence foraging activity.

METHODS

Our studies centered around four sympatric species of harvester ants which are important at the Jornada Validation Site and which are widely distributed in desert areas in the U.S. and Mexico: *Pogonomyrmex rugosus*, *P. desertorum*, *P. californicus* and *Novomessor cockerelli*. Field studies were conducted on an area adjacent to the Jornada Validation Site, 40 km NNE of Las Cruces, Dona Ana Co., N.M. and on an area 11 km east of New Mexico State University, Dona Ana Co., N.M.

Foraging activity (DSCODE A3UEE03)

Foraging activity was studied by placing a wire reference circle over a number of randomly selected nests of harvester ants. The circles were divided in eight equal areas (Fig. 1). Activity was monitored by counting the number of ants returning to the nest per unit time. The portion of reference circle counted depended on the foraging intensity (that portion that could be counted accurately). When fractions of a circle were counted at a single measurement period, several sections were counted. Sections were selected at random to eliminate the bias of a segment over a foraging trail. Foraging activity was calculated by multiplying the number of ants returning by the denominator of the reference circle fraction and dividing by the number of minutes observed. At each observation period we also measured wet and dry bulb air temperatures as close to the soil-air interface as possible with a gun psychrometer or sling psychrometer, and the soil surface temperature by laying the bulb of a mercury thermometer on the soil surface and covering it with a fine layer of sand. Foraging activity was monitored at 2 hr intervals from dawn until dusk once a week or every two weeks, depending on the season. Several all-night activity studies were conducted in mid-summer when it was obvious that some species did not cease foraging at sunset.

Variations in foraging behavior as a function of distance, colony interaction, food availability and distribution (A3UEE10)

The feasibility of using seeds dyed with vegetable dye to determine the relationships between distance and foraging behavior had previously been determined (Whitford and Ettershank, 1971). In 1972, a luxuriant growth of annuals covered the site and, as a consequence, abundance of natural food complicated such studies since the ants preferred natural seeds to the cracked milo we provided. Therefore, we selected three *Pogonomyrmex rugosus* colonies for study and completely cleared an area 15 m in radius around each nest. All vegetation was uprooted and the area swept clean with a broom. This provided us with an area essentially devoid of food in which to conduct our experiments. The experiments performed are outlined below:

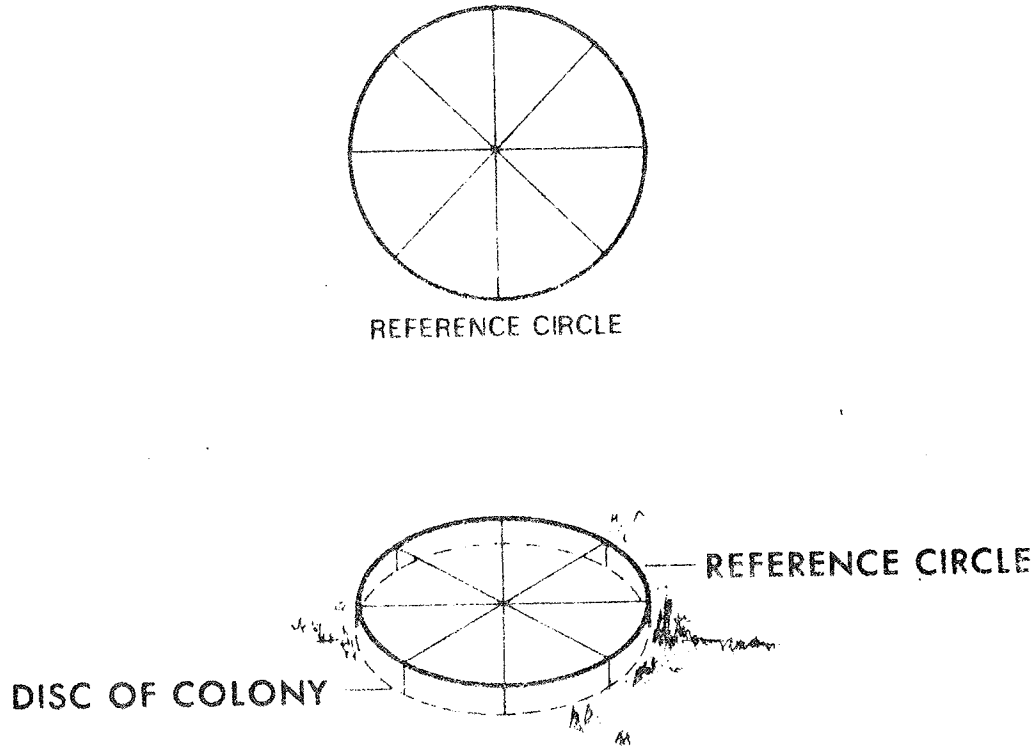


Figure 1. Diagram of the reference circle and relationship to harvester ant colony.

(1) Foraging activity; food concentration constant. Quantities of dyed milo were measured out to provide equal concentrations of food per unit area at varying distances from the reference nest. In some experiments the seeds were distributed in evenly spaced piles and in some as continuous rings (Fig. 2). Observers were stationed at colonies adjacent to the cleared area and at the reference colony to record the number of seeds of the various colors returned to the nest per unit time. Soil surface temperatures and wet and dry bulb air temperatures were recorded at the beginning of each experiment.

(2) Foraging activity; food concentration varied. To evaluate the effect of an uneven distribution of food on foraging intensity, the concentration of seeds at a selected distance was multiplied by a factor five or ten (for example, line 3 in Figure 2 might be increased to 3000 g of blue seeds). The data recorded as in (1).

2.3.3.2.-6

POSITIONS OF NOV COC COLONIES ▲
POSITION OF OTHER COLONIES PROGRUG △

COLONY INTERACTIONS
ABCD
A'BCD'

Radius - 15 m

0-REFERENCE NEST
1-100 g (red)
2-300 g (yellow)
3-600 g (blue)
4-700 g (green)

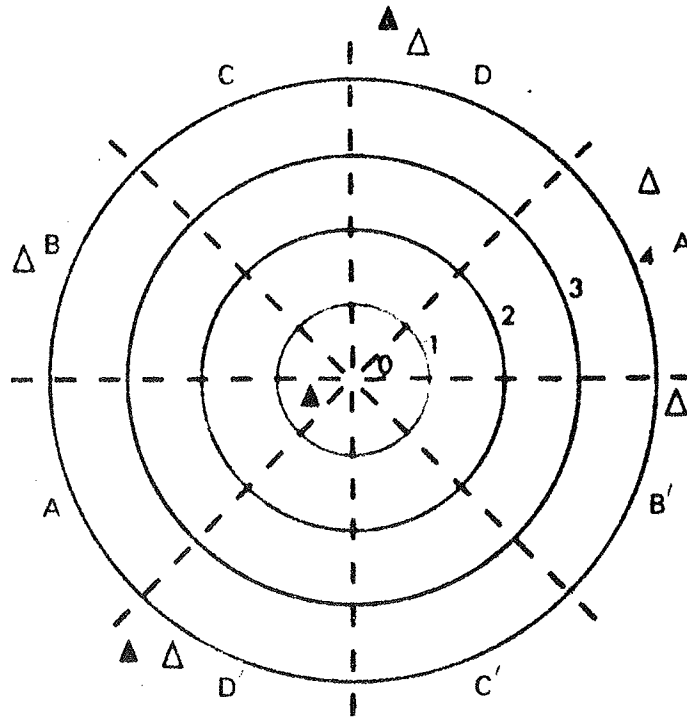


Figure 2. The relationships of harvester ant colonies and distribution of colored seeds in foraging experiments in the cleared areas. See text for details of experiments.

(3) Colony interaction. Interaction of colonies was studied by modifying the experimental design in experiment (1) by providing colored seeds on two sets of arcs out of the entire circle (Fig. 2). For example, the area indicated by A was supplied with arcs of red at 1, yellow at 2, blue at 3, and green at 4 while A¹ was supplied with pink at 1, brown at 2, purple at 3, and natural at 4. Arcs BB¹CC¹DD¹ received no seeds. Data were recorded as in experiment (1). Successive experiments were conducted to evaluate seed removal from areas BB¹, CC¹, and DD¹.

Forage selection: A3UEE11

Data on forage selection by species of harvester ants were obtained by collecting all of the foragers returning to a randomly selected colony over a 5 min period. Aspirators were used to collect returning foragers and their forage. Sampling by this routine was conducted monthly and at different times of the day to insure sampling at peak activity times for the species under consideration. Additional data on materials foraged were obtained during mark-recapture studies. Forage materials carried by ants collected for marking or census were collected from the foragers picked up by aspirators and stored in vials. Reference collections of fruits and seeds were made in order to classify foraged materials. Samples stored in vials were identified using a dissecting microscope and tabulated by sampling date.

Seed production -- annual and perennial forb production (A3UEE13, A3UEE14)

Analysis of food preferences of a species demands that the food preferences be expressed as a function of food availability if food habits are to have any predictive ecological significance. Since harvester ants primarily utilize the fruits of annual and perennial forbs and grasses and occasionally fruits, flowers or seeds of shrubs, a series of vegetation surveys were conducted on the ant study area adjacent to the Jornada Playa Validation Site. Initially a series of 50 m line intercept samples were run to obtain cover estimates of shrubs and perennial grasses at one point in time -- June, 1972.

At monthly intervals, density estimates were obtained of annual and perennial forbs, annual grasses and those perennial grasses such as *Tridens pulchellus* which produced fruits foraged by ants. Density estimates were obtained by the point quarter method. Randomly selected *Pogonomyrmex rugosus* colonies were used as central points. One 50 m line was laid out at a randomly selected angle in each of the four 90° quadrats. Random points within each 5 m interval were used as the center points for the point quarter. The distance to the nearest plant in each quadrat, mean canopy diameter, height, and phenology and species were recorded for each plant. More than 40 points were measured in each sampling period.

2.3.3.2.-8

In order to estimate seed (fruit) production and hence availability, it was necessary to calculate seed production from the density and size distribution estimates obtained by monthly point quarter samples. Therefore, as species of forbs or grasses attained maximum fruiting as determined by continuous observation at the study site, individual plants of varying sizes were carefully excavated, bagged and returned to the laboratory, where they were dried at 60 C. Prior to excavation the mean canopy diameter and height of each plant was recorded. The dried plants were separated by parts: seeds and fruits, leaves, stem, and roots, and the weights of the parts determined with a Mettler balance to $\pm .001$ g. Subsamples of reproductive units (seeds and fruits) were counted and weighed. Total number of reproductive units was obtained by relating number to weight.

Forager population estimates (A3UEE15)

Estimates of forager populations were obtained by the Lincoln Index. Foragers were collected with an aspirator as they returned to the nest. The aspirator jar containing the ants was placed in an iced container to immobilize them. Immobilized ants were marked with a dot of airplane dope on the gaster. Colonies had to be censused within 48 hr since ant grooming tends to eliminate these marks (Brian, 1971).

Colony distribution (A3UEE12)

In order to determine the role of harvester ants in an ecosystem, it is necessary to determine if colony density estimates have general applicability (i.e., if colonies are randomly dispersed) or if there is a degree of clumping or evenness in the pattern of distribution. Distribution of colonies and density was determined by the nearest-neighbor method. The distance from random points in the study area to the nearest nest in each quarter was measured (this provided point-quarter distances for density estimates). The distance from each nest to its nearest neighbor of the same species was measured.

RESULTS

Foraging activity (A3UEE03)

Prediction of foraging activity requires the prediction of seasonal initiation and cessation of foraging, as well as foraging intensity during the summer. Weekly observations during March, 1972 showed that while soil surface temperatures reached 37-43 C, harvester ants were not active. By mid-April, 50% of the *Novomessor cockerelli* colonies were active in the middle of the day. Soil temperatures varied from 15-24 C

at 10 cm and between 15-18 C at 50 cm between mid-April and early May. *Pogonomyrma rugosus* also initiated activity in mid-April. *Pogonomyrma desertorum* and *P. californicus* did not initiate activity until the last week in May, when soil temperatures were 19-30 C at 10 cm and 19-21 C at 50 cm. Soil temperatures resulting in cessation of foraging activity in the fall were much below the spring temperatures at the initiation of activity. *P. rugosus* and *N. cockerelli* were still foraging in mid-November when soil temperatures at 10 cm ranged between 4-10 C and at 50 cm ranged between 7-10 C. *P. desertorum* and *P. californicus* did not cease activity until early November when soil temperatures were 5-10 C at 10 cm and 8-10 C at 50 cm.

The data on the effects of soil surface temperature and saturation deficit on the foraging activity of the four species of harvester ants are summarized in Figures 3-7. In mid-summer *N. cockerelli* was primarily nocturnal, ceasing foraging activity about two hours after sunrise and beginning again approximately one hr prior to sunset. Peak foraging activity was at soil surface temperatures between 5-25 C and at saturation deficits below 20 g/m³ (Fig. 3).

The foraging patterns of the *Pogonomyrma* species differed in intensity of foraging effort per unit time and the range of environmental conditions over which they were active (Figs. 4-6). Surprisingly, all three species exhibited peak activity at 45 C (Fig. 7). *P. californicus* was the only species foraging at mid-day. Some *P. californicus* were observed foraging at soil surface temperatures between 60-62 C but no data on foraging rate were obtained under these conditions. In mid-summer, *P. rugosus* exhibited nocturnal foraging but *P. desertorum* and *P. californicus* ceased foraging at sundown. All the *Pogonomyrma* exhibited some activity at saturation deficits as high as 36 g/m³. However, saturation deficits greater than 27 g/m³ resulted in a larger reduction in foraging rate in *P. desertorum* and *P. rugosus* (Figs. 4 and 5) than in *P. californicus* (Fig. 6).

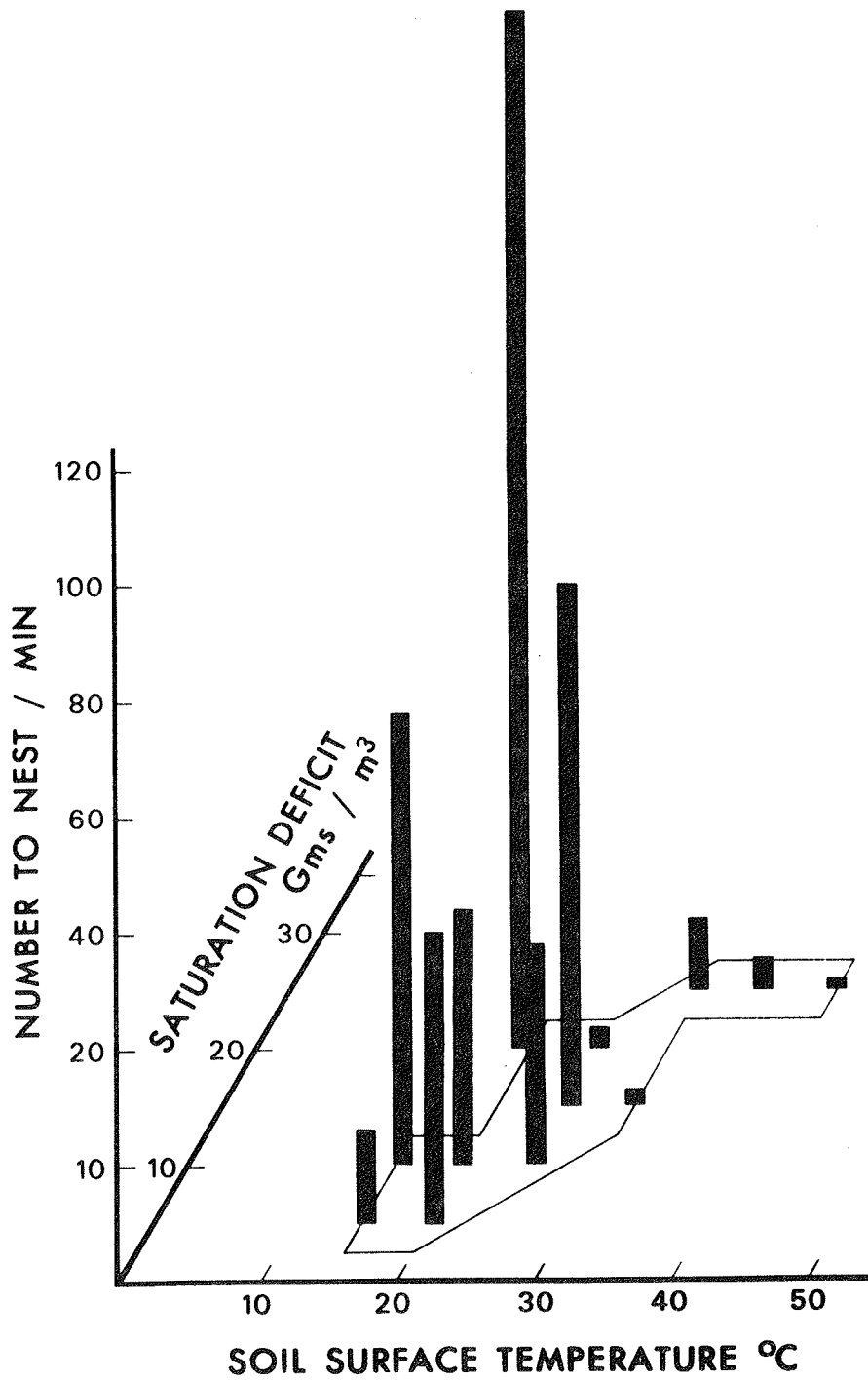


Figure 3. The effect of saturation deficit and soil surface temperature on foraging activity in *Novomessor cockerelli*. The scale for foraging activity on the ordinate applies to the length of the bars.

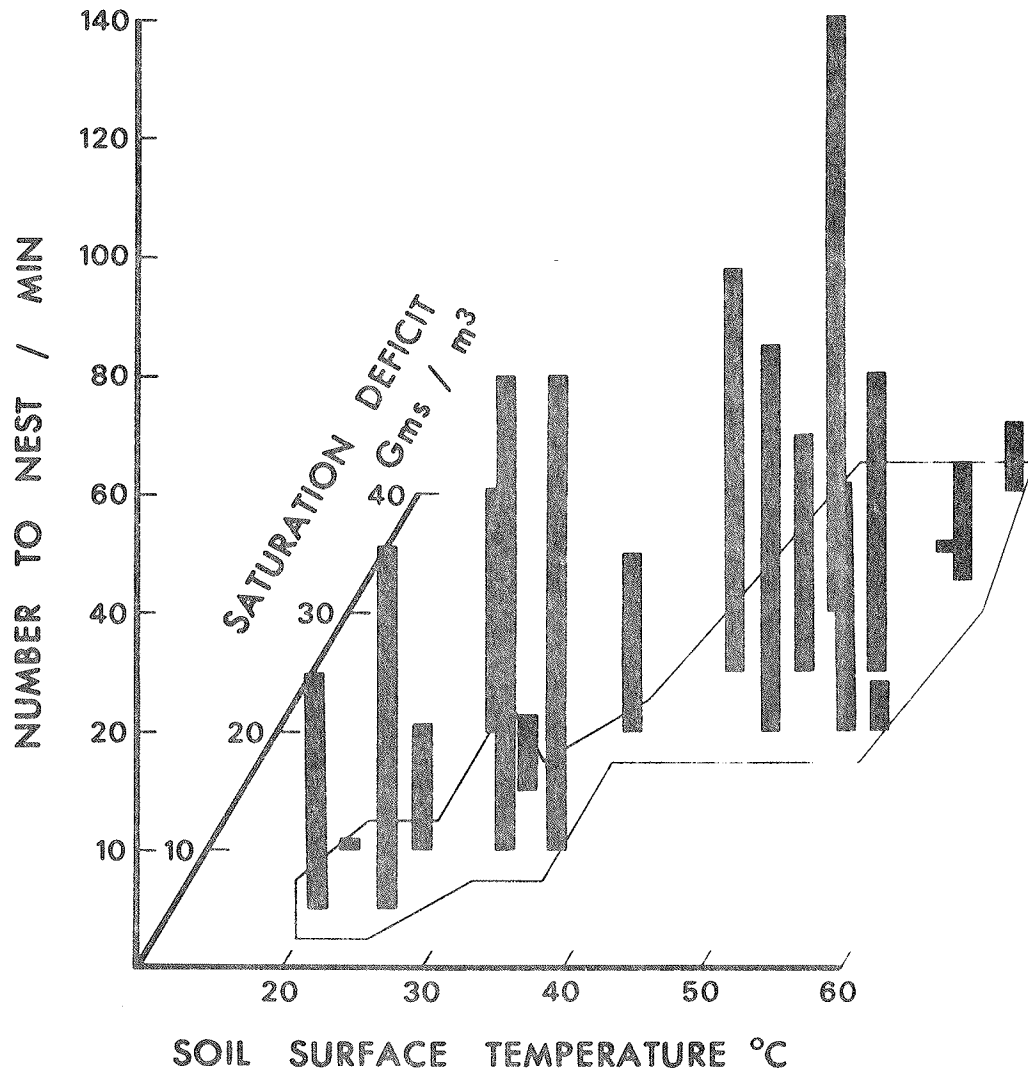


Figure 4. The effect of saturation deficit and soil surface temperature on foraging activity in *Pogonomyrmex rugosus*. Presentation is the same as in Figure 3.

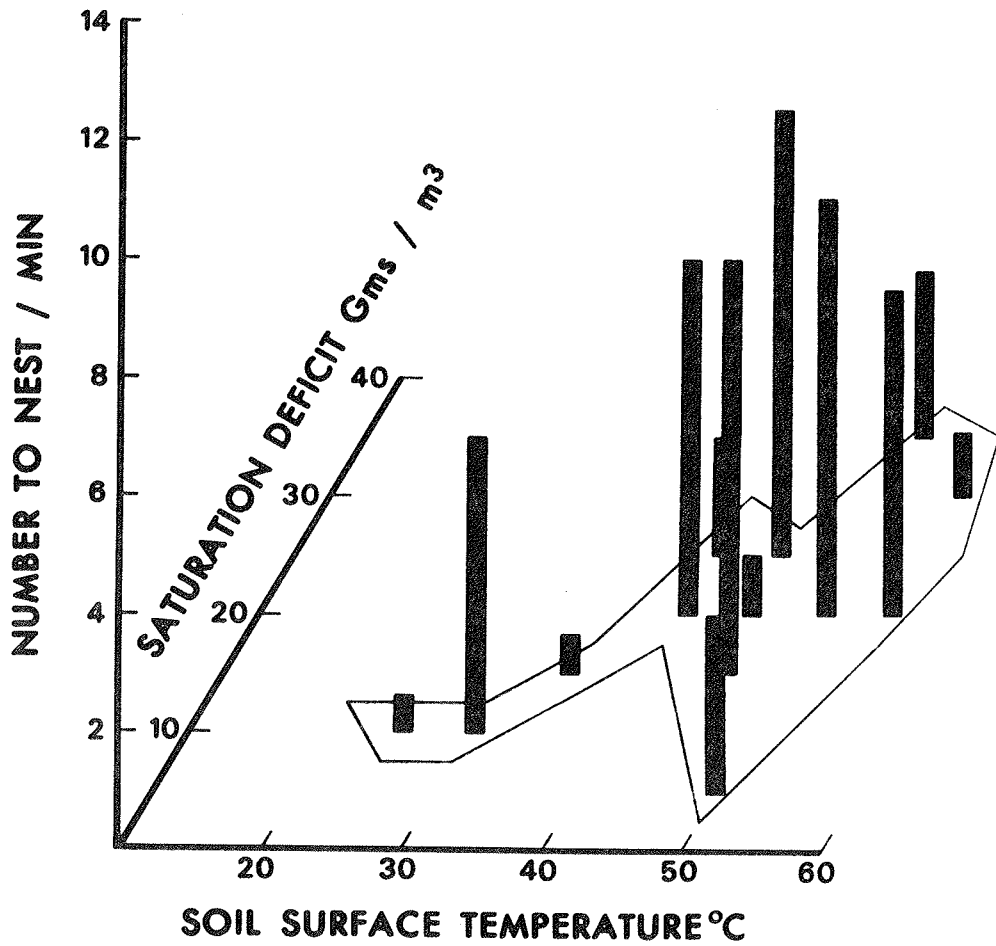


Figure 5. The effect of saturation deficit and soil surface temperature on the foraging activity of *Pogonomyrmex desertorum*. Presentation is the same as in Figure 3.

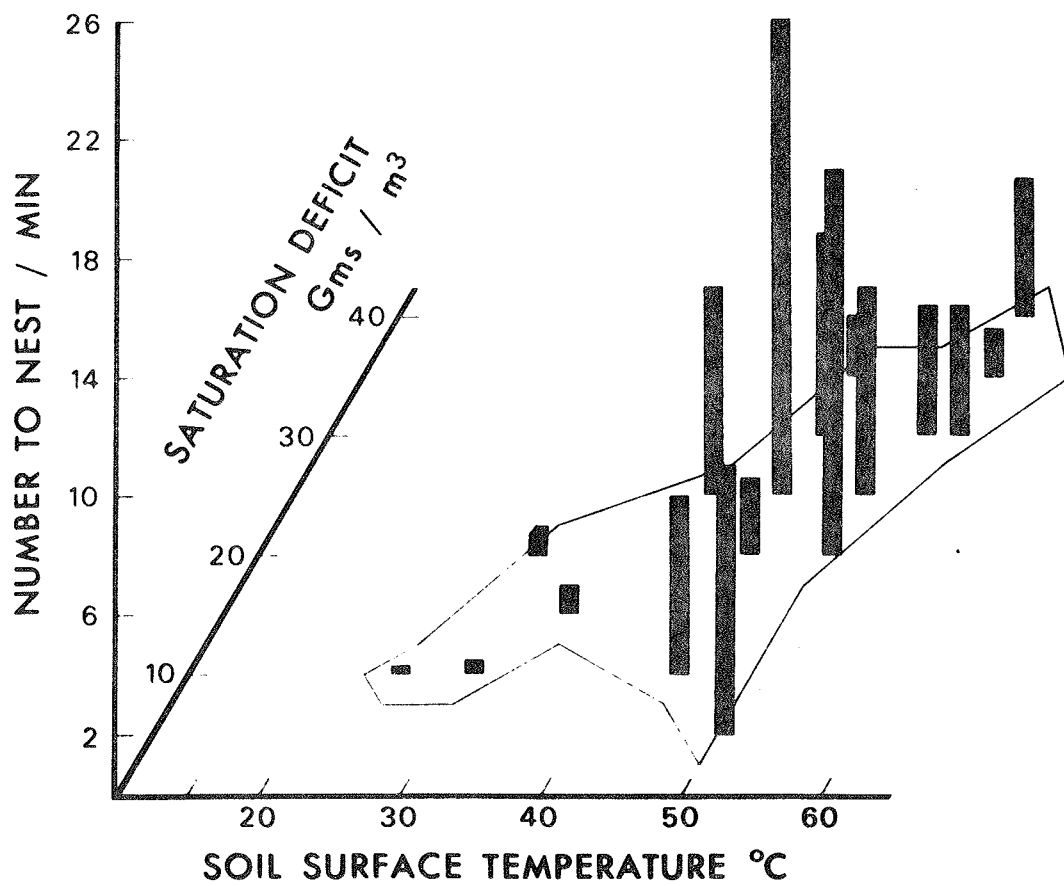


Figure 6. The effect of saturation deficit and soil surface temperature on the foraging activity of *Pogonomyrmex californicus*. Presentation is the same as in Figure 3.

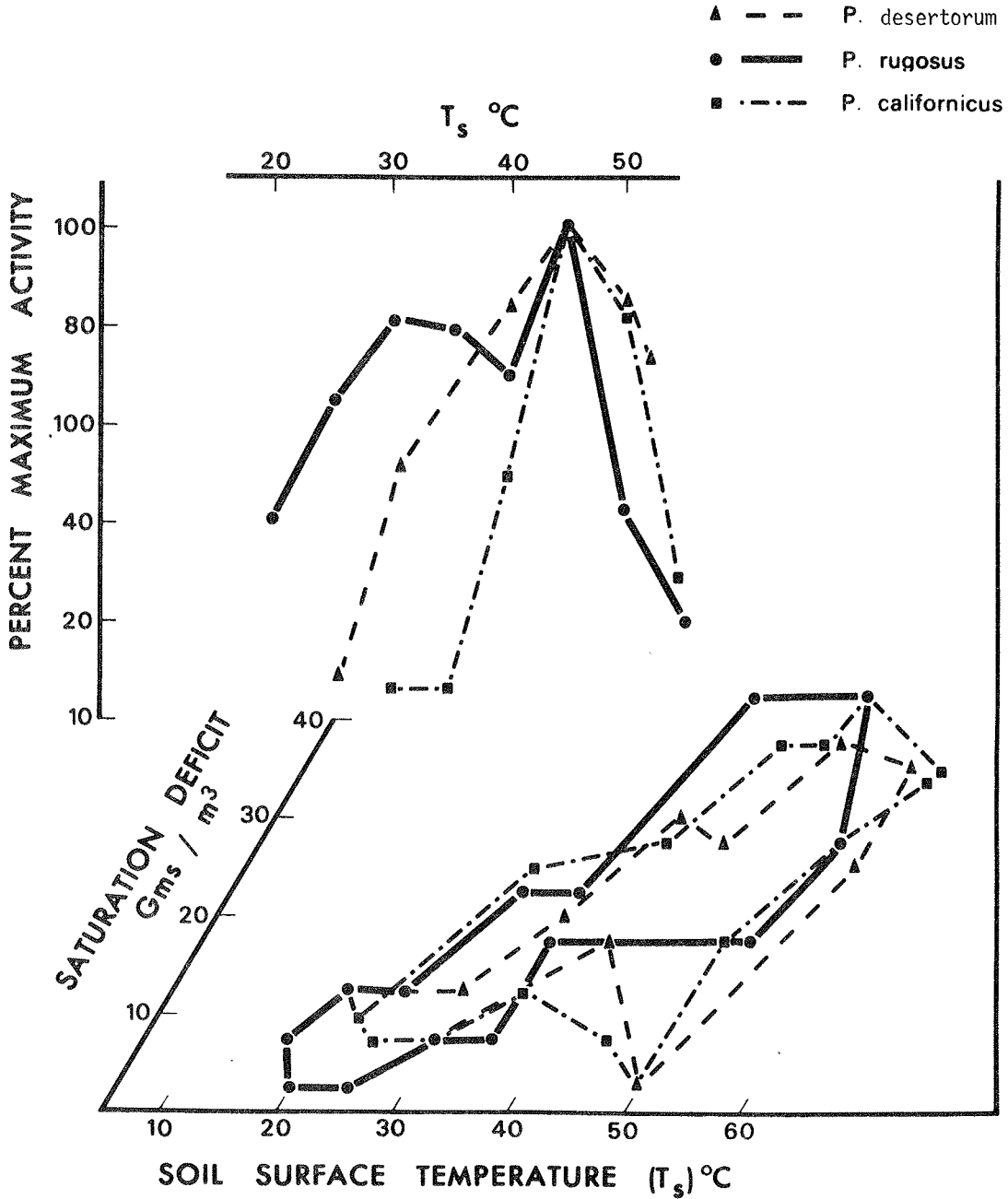


Figure 7. Comparison of effects of saturation deficit (presented as planes of activity) and soil surface temperature (T_s) on foraging activity in *Pogonomyrmex* species.

Foraging intensity, distribution of effort and colony interactions (A3UEE10)

The studies with dyed seeds provided data on the effects of food resource distribution pattern on the distribution of foraging effort and intensity of foraging in the two larger species of harvester ants, *N. cockerelli* and *P. rugosus*. In experiments where the density of food items per unit area was held constant, foraging effort exhibited a log decay with increasing distance from the colony (Fig. 8). Regression analysis of ln number to the nest per minute on distance from the colony in meters (D) gave an r^2 of 0.71. This relationship is expressed by the equation $\ln \text{Num} = 1.6 + (-.19D)$. The data were adjusted to eliminate variance due to intrinsic differences in levels of foraging activity between colonies.

Under natural conditions, it is unlikely that the distribution of food resources would remain regular. Additional observations on the constant density experiments without grain supplement showed that intense foraging near the colony quickly depleted the "close in" resources which resulted in a more even distribution of foraging effort at varying distances from the colony (Fig. 9). In the vegetation survey, it was noted that annuals, particularly *Eriogonum* spp., tended to be clumped, providing dense clumps of food items for the harvester ants. In order to examine the effect of clumped resources on foraging effort, experiments were conducted in which the ants were provided seeds in widely scattered piles; at a distance from the colony greater than the distance to the piles, we placed a dense ring of seeds (Fig. 10). These experiments demonstrated that high concentrations of food items resulted in greater forager effort at that location than would be predicted on the basis of distance from the colony. However, a solid circle of food items did not result in the cessation of foraging activity at a distance greater than the dense line, because some foragers crossed the dense line and returned with seeds from the less concentrated sources at an even greater distance from the colony.

In 60% of the experiments for which we have baseline data, addition of seed material appeared to stimulate activity (Table 1). In one of the experiments where the intensity of foraging decreased after addition of seeds, the ants were not foraging on the seeds we supplied. Although it is tempting to assume that seed supplementation stimulated an increase in foraging activity, additional experiments designed to evaluate this hypothesis using paired colonies, treated and untreated, are necessary.

Foragers returning to the colony often appeared to have been unsuccessful at finding a suitable food item. In a number of the experiments with colored seeds, the number of successful and unsuccessful returning foragers (28 experiments with *P. rugosus* and 13 experiments with *N. cockerelli*) were tallied. Percent foraging success was

2.3.3.2.-16

regressed on soil temperature, saturation deficit and hour of the day, all of which gave $r^2 < 0.1$. The range of percent success was between 0 and 96% with a mean of 48% in *P. rugosus*, and between 15 and 19% with a mean of 59% in *N. cockerelli*. Observations of returning foragers in other parts of the study and in samples of foraged materials support the 50% estimate of foraging success in these two species.

Table 1. The effect of seed addition on foraging activity (Novcoc = *Novomessor cockerelli*, Pogrug = *Pogonomyrmex rugosus*)

Colony and #	Number to nest · min ⁻¹		Number to nest · min ⁻¹	
	Baseline	Δ Time		Δ N. min ⁻¹
Pogrug 60	11.3	25	6.4	-7.3
Pogrug 61	9.3	25	12.6	+3.3
Pogrug 61	12.3	30	12.5	+ .2
Pogrug 60	14.3	30	21.0	+6.7
Pogrug 62	8.3	30	10.7	+2.4
Pogrug 50	32.6	15	18.4	-14.2
Novcoc 50	4.0	15	11.2	+7.2
Pogrug 53	30.0	15	7.4*	-22.6
Novcoc 58	4.0	60	10.8	+6.8
Pogrug 50	32.6	60	15.2	-17.4

* Not foraging on supplied seeds.

The analysis of interaction of colonies involved plotting the number of seeds of different colors returned to the colony in the cleared circle and to the adjacent colonies. The first experiments (Fig. 11) showed there was considerable overlap in foraging territory between colonies of the same species and between *P. rugosus* and *N. cockerelli*. *N. cockerelli* were often observed removing materials from the cleared disc of colonies of *P. rugosus*. The foraging territories of two *P. rugosus* colonies in relation to their associated colonies were mapped (Figs. 12 and 13). The interaction between *P. rugosus* colony 18 and *P. rugosus* 50 was selected for further study since there was considerable overlap in foraging range of these colonies (Figs. 11 and 12) and distortion in the foraging range of *P. rugosus* 50 which might have been caused by interactions with other *P. rugosus* colonies.

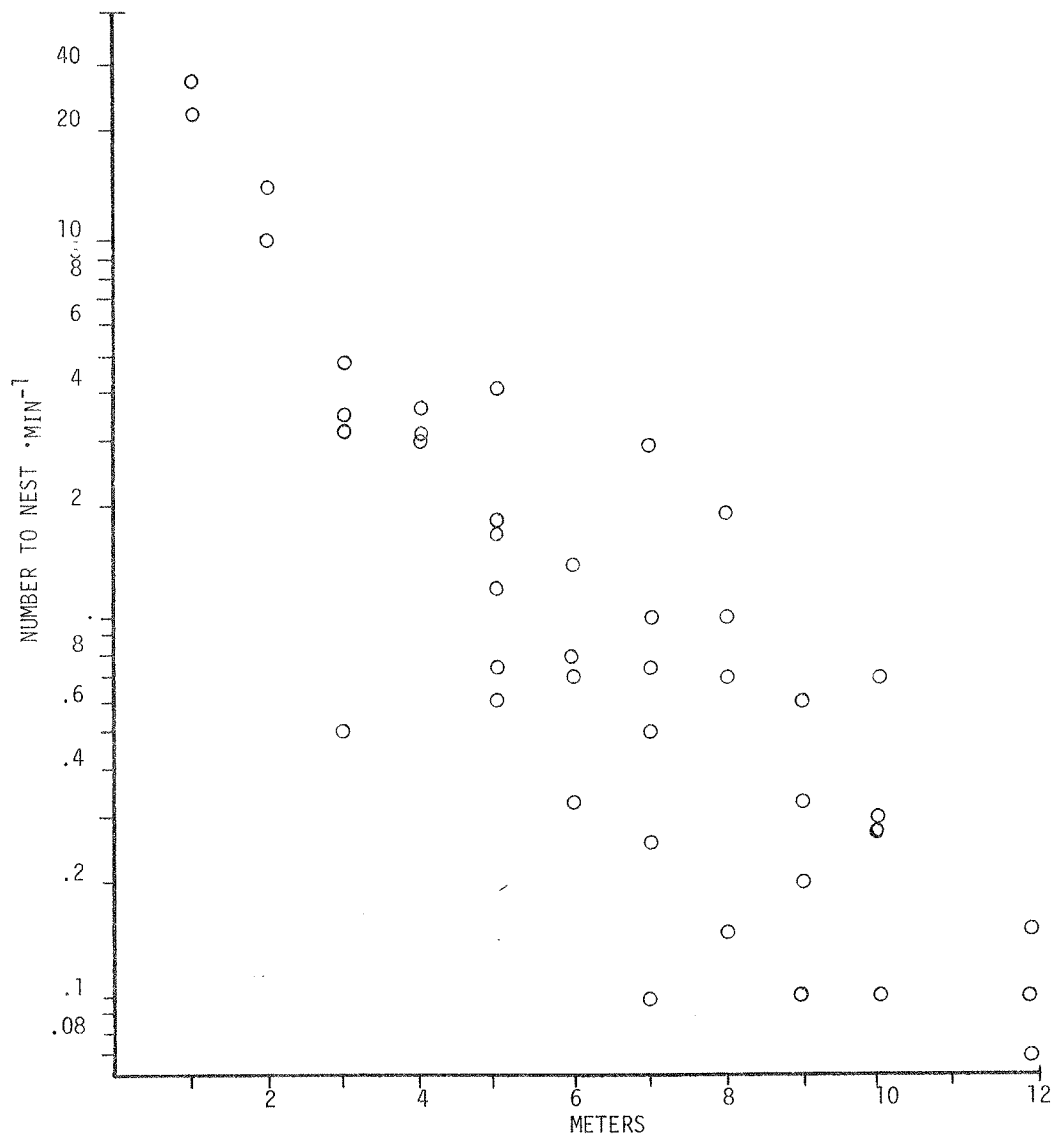


Figure 8. The effect of distance on foraging intensity of *Pogonomyrmex rugosus* and *Novomessor cockerelli* when forage distribution was even.

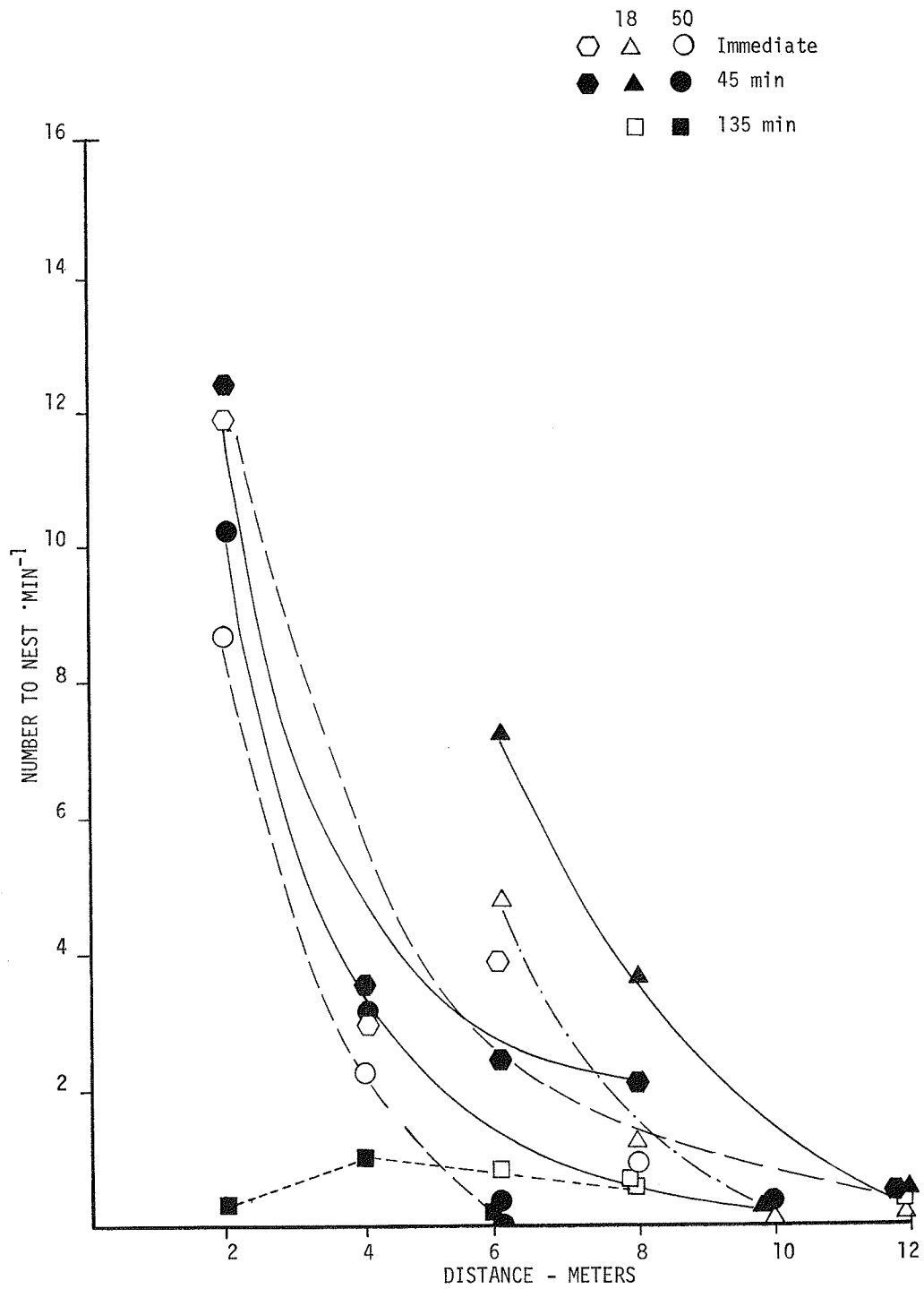


Figure 9. Effect of foraging time and distance on foraging in *Pogonomyrmex rugosus*.

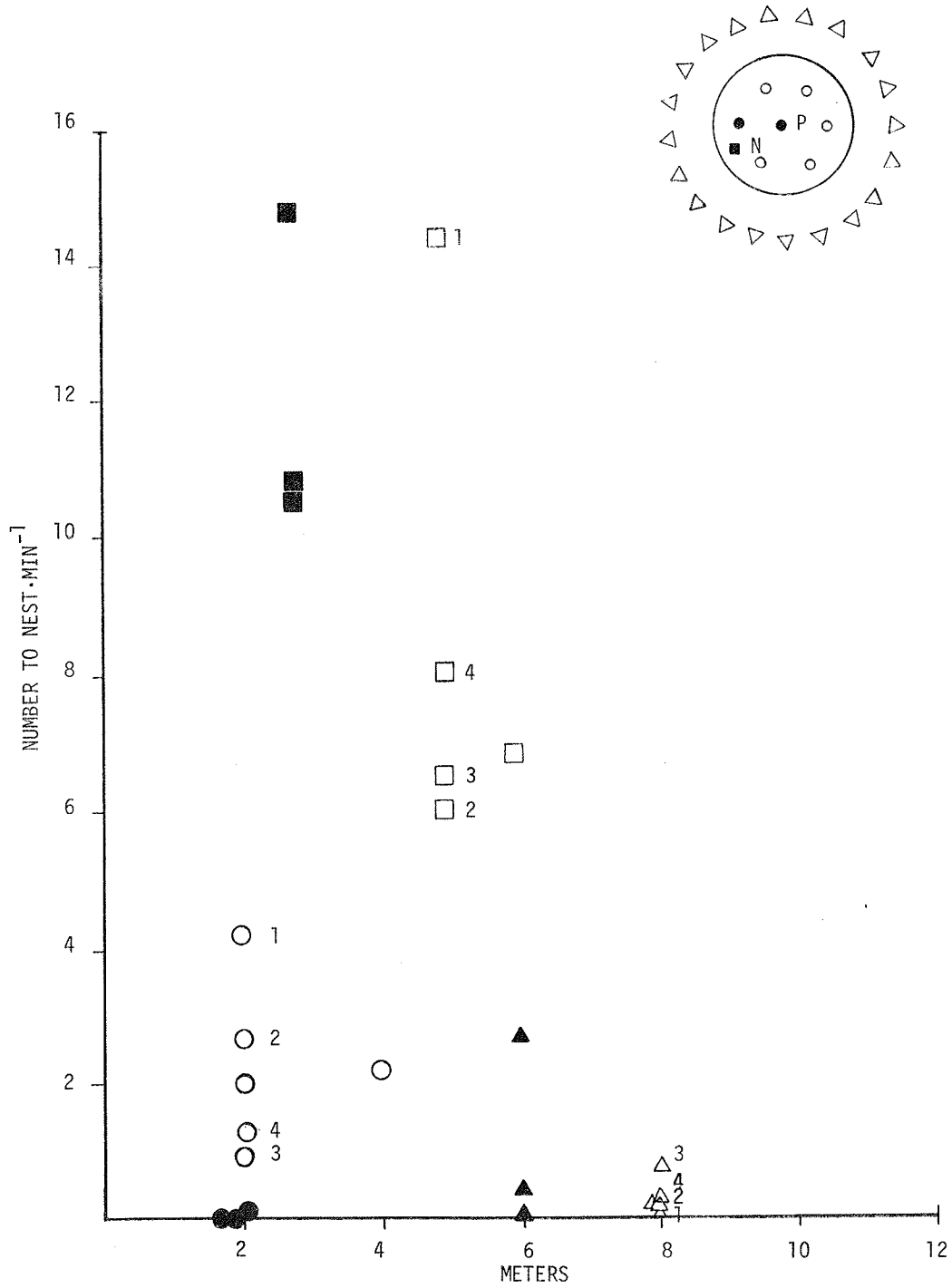


Figure 10. Effect of seed concentration and distance on foraging intensity. The diagram in the upper right shows the distribution of seed piles and ring in the experimental design. The numbers identify points in the same experiment period. Open symbols are *Pogonomyrma rugosus* and solid symbols are *Novomessor cockerelli*. Squares represent data from dense time and the other symbols represent piles of grain.

2.3.3.2.-20

On 4 October 1972, the experiments were repeated to test the response of *P. rugosus* colony 50 to the removal of *P. rugosus* colony 18, which had been completely excavated by 15 September 1972. These data are summarized in Figure 14. Comparison of Figures 11 and 14 shows that the removal of colony 18 had no effect on the foraging pattern of *P. rugosus* colony 50. In this experiment 45% of the returning foragers were carrying native fruits of *Eriogonum abertianum* and *Tridens pulchellus*. Foragers passed over the cracked milo piles to forage in the native vegetation 15 m away from the colony. No foragers were observed around the colored grain 5 m from *P. rugosus* 50 in the direction of the excavated colony.

Forage selection (A3UEE11) and seed production (A3UEE13 and A3UEE14)

There was considerable overlap in forage selection in the three species of *Pogonomyrmex* studied (Table 2). Seasonal changes in forage preference were related to the phenology of the annuals and their relative densities (Table 3). The fruits of the buckwheats, *Eriogonum abertianum* and *Eriogonum trichopes*, accounted for approximately half of the foraged materials from June through August in these species. *Chenopodium incanum*, which exhibited rapid growth in June and ripened in July, was selected by *P. rugosus* but was of much lower importance to *P. californicus* and *P. desertorum*. The composites, *Bahia* and *Baileya*, which had a high fruit production, were of low importance as forage items. *P. desertorum* foraged heavily on grass seeds when these were available; at the end of the growing season, piles of the feathery fruits of *Tridens pulchellus* and *Bouteloua barbata* ringed the mounds of this species.

Forage selection in *Novomessor cockerelli* is summarized in Table 4. In this species over half of the forage consisted of termites and other insects and miscellaneous plant parts. Forage preferences for fruits were similar to the *Pogonomyrmex* species, with the buckwheats, *Eriogonum* spp., ranking as the most frequent fruits foraged.

The data on the relationship of plant parts and seed numbers to either canopy area or canopy volume estimate for several species of forbs and grasses are summarized in Figures 15-33. The regression equations are provided below: Other data sets are currently being processed and analyzed.

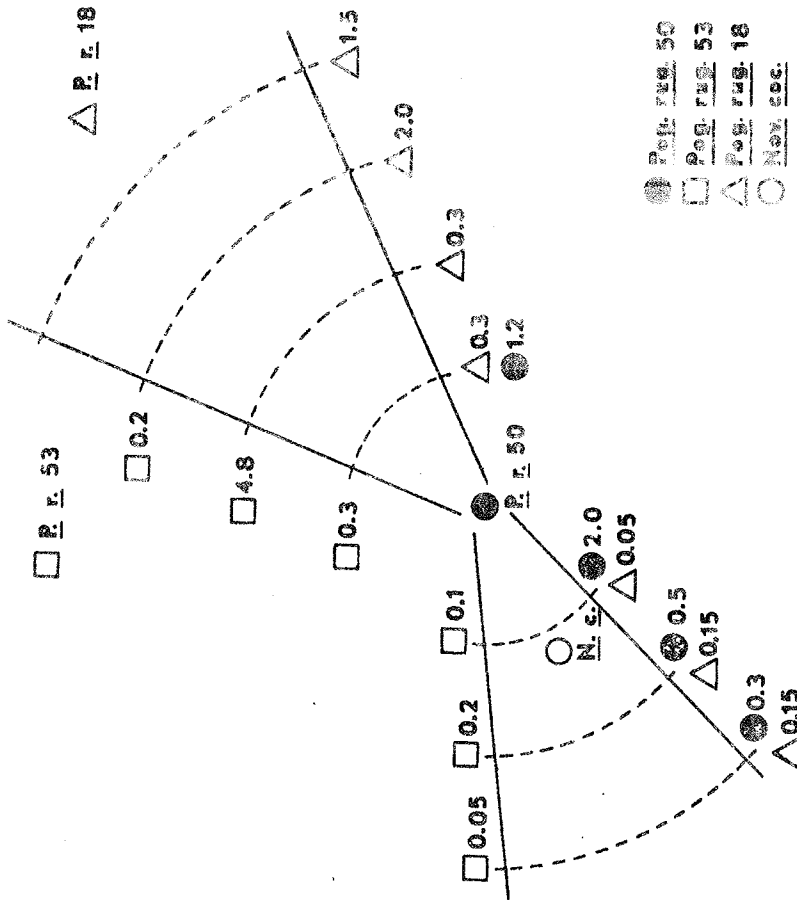
Chenopodium incanum

$$\begin{array}{ll} \text{No. Fruit} = 963 + .45 \text{ CV} & r^2 = .69 \\ \text{Biomass} = 32.5 + .00036 \text{ CV} & r^2 = .44 \end{array}$$

Eriogonum abertianum var. *ruberrimum*

$$\begin{array}{ll} \text{Root wt.} = .11 + 3.9E^{-5} * \text{ CV (CA} \times \text{CH} \div 3) & r^2 = .78 \\ \text{Biomass} = 3.27 + 7.5E^{-4} \text{ CV} & r^2 = .80 \\ \text{No. Fruit} = 1348 + 6.5E^{-1} \text{ CV} & r^2 = .81 \end{array}$$

* E = Exponentiation: eg. $3.E^{-5} = 3 \times 10^5$



● Feb. Feb. 50
 □ Feb. Feb. 53
 △ Feb. Feb. 18
 ○ Nov. coc.

FORAGING PATTERNS

Figure 11. The interaction of foraging activity in colonies of *Pogonomyza rugosus* (Pog rug) and *Novomessor cockerelli* (Nov coc). Symbols refer to colonies in the area. Numbers are numbers of seeds/minute to the colony indicated from the area shown.

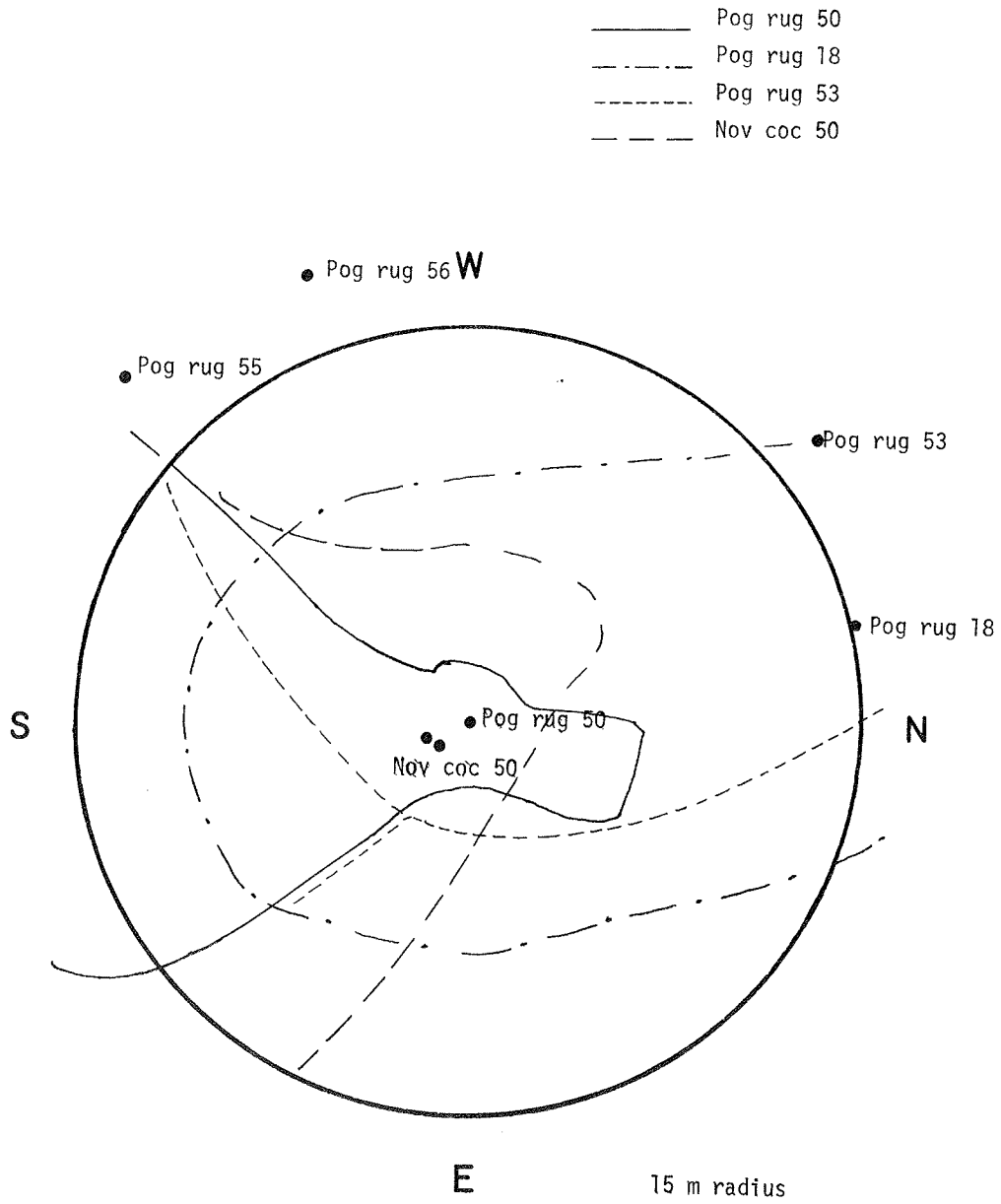


Figure 12. Map of the foraging territories of *Pogonomyrmex rugosus* and *Novomessor cockerelli* as mapped in colored seed experiments, example 1.

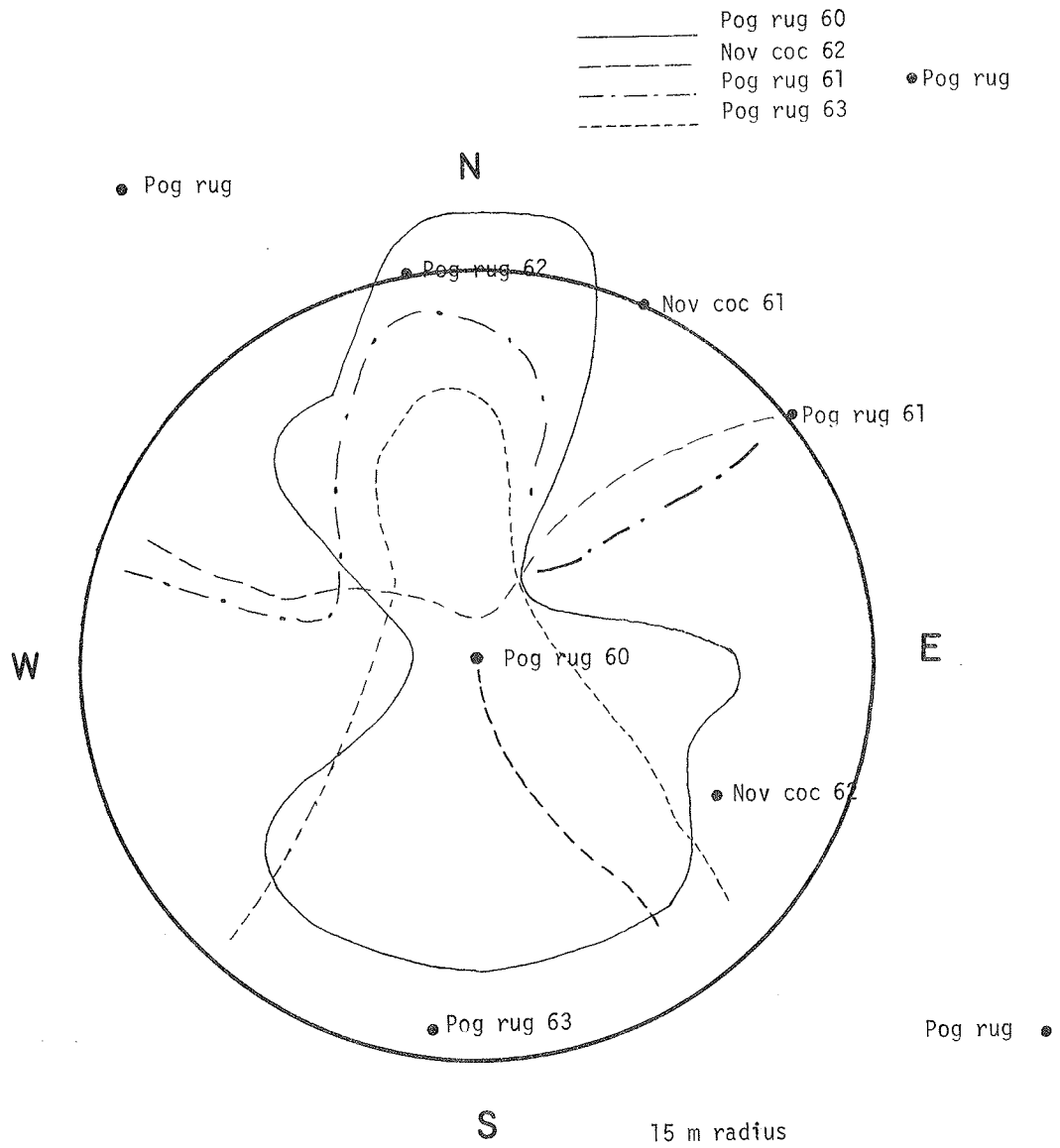


Figure 13. Map of foraging territories of *Pogonomyrmex rugosus* and *Novomessor cockerelli* colonies as mapped in colored seed experiments, example 2.

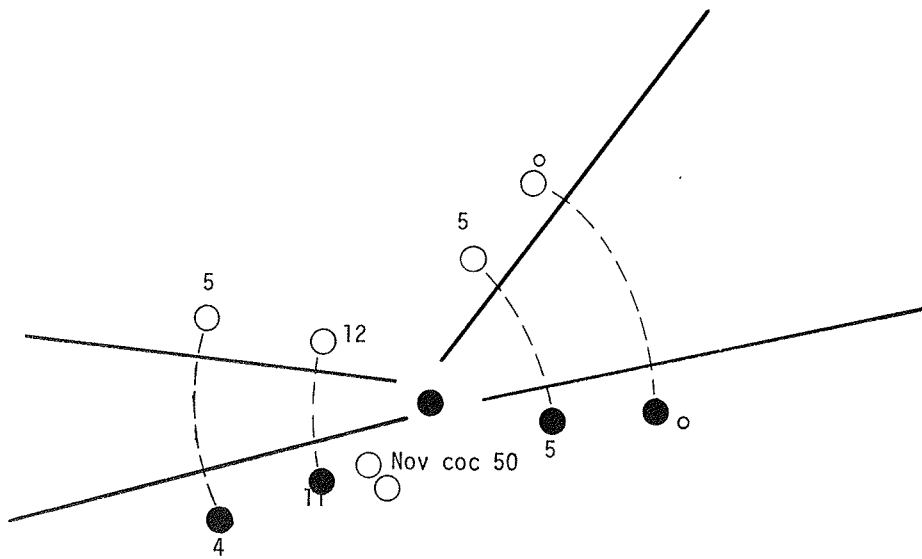


Figure 14. The results of the repeat of the experiment summarized in Figure 11 after the removal of Pog rug 18 by excavation.

Eriogonum abertianum var. *abertianum*

Biomass = $1.8 + 4.64E^{-3}$ CV (CA x CH ÷ 3)	$r^2 = .64$
No. Fruit = $2388 + 1.8$ CV	$r^2 = .13$
Foot wt. = $.21 + 6.3E^{-4}$ CV	$r^2 = .31$
\bar{x} seed number = 3095	

Bahia absinthifolia

No. Fruit = $378 + 8.4$ CA	$r^2 = .73$
Biomass = $-0.0106 + .011$ CA	$r^2 = .84$
Root wt. = $.36 + .00062$ CA	$r^2 = .48$

Baileya multiradiata

No. Fruit = $-351 + 3.77$ CA	$r^2 = .88$
Root wt. = $.57 + 1.56E^{-5}$ CV (CH x CA ÷ 3)	$r^2 = .41$
Biomass = $5.32 + 6.5E^{-4}$ CV	$r^2 = .87$
Biomass = $-.56 + .0115$ CA	$r^2 = .89$
No Fruit = $1158 + -.04$ CV	$r^2 = .19$

Bouteloua barbata

No. Fruit = $.89 + .17$ CV (CH x CA ÷ 3)	$r^2 = .54$
Biomass = $.077 + .0026$ CA	$r^2 = .49$
No. Fruit = $.135 + .94$ CA	$r^2 = .48$

Eriogonum trichopes

No. Fruit = $209 + .028$ CV (CH x CA ÷ 3)	$r^2 = .08$
Biomass = $1.2 + 0.00034$ CV	$r^2 = .53$
Stem wt. = $.92 + .0003$ CV	$r^2 = .52$
\bar{x} FFN = 278/plant	

With data on seed production, foraging behavior of species of harvester ants, and density estimates, we were able to estimate the impact of the harvester ant population on the potential seed reserves (Table 5). Harvester ants had the greatest impact on the potential seed reserve of *Eriogonum trichopes*, removing more than 90% of the total estimated production. In contrast, the foraging activities of these species removed only an estimated 8% of the fruit production of *Eriogonum abertianum* var. *abertianum*. *Bouteloua barbata* was also hit hard by foraging, which accounted for approximately 71% of its seed production.

Table 2. Food items foraged by harvester ants of the genus *Pogonomyrma* at different times during the active foraging season*

	Early June		June		July		August		Sept		October	
	rug	cal	rug	cal	rug	cal	rug	cal	rug	cal	rug	cal
<i>Eriogonum abertianum</i>	14	<1	32		14	27	17	46	21	56	11	35
<i>Eriogonum trichopes</i>	3	74	59		73	47	19	32	4	5	0	20
<i>Baileya multiradiata</i>		3			2	1	5	10	3		17	20
<i>Euphorbia</i> sp.					11	11	2	<1	21	12	29	12
<i>Chenopodium incanum</i>		1			2	1	29	1		6	9	0
<i>Eriogonum rotundifolium</i>	<1	<1			3	0	<1	5	1	3	4	0
<i>Allionia incarnata</i>							<1		1	1		
<i>Bahia absinthifolia</i>							<1	7	7	<1	<1	
<i>Bahia pedata</i>							<1					
<i>Bouteloua barbata</i>							9		10		57	3
<i>Boerhaavia spicata</i>									2		4	
<i>Cassia bauhinioides</i>												
<i>Croton pottsi</i>	<1											
<i>Cryptantha</i> sp.	40	5				<1						
<i>Descurainia pinnata</i>	10											
<i>Kallstroemia parviflora</i>												
<i>Larrea divaricata</i>	8	2					<1					
<i>Muhlenbergia porteri</i>	14								14			
<i>Salsola kali</i>												
<i>Tridens pulchellus</i>	1						<1	<1	6		12	7
Annual parts	2	<1	<1				<1	<1	<1	3		
Plant parts	2	3	<1		<1	4	4	1	<1	6	5	5
Termites	1	12	3		<1		<1	3	2		<1	1
Other seeds	5	4	<1		<1	5	2	<1	0	6	<1	1

* Species of *Pogonomyrma* represented as follows: rug - *P. rugosus*, des - *P. desertorum*, cal - *P. californicus*. Foraged items are expressed as percent to total items foraged.

Table 3. Density of annual grasses and forbs on the study area south of the Jornada Playa Validation Site

	June 16			July 25			Aug. 31			Oct. 5		
	PC	REL	DEN	PC	REL	DEN	PC	REL	DEN	PC	REL	DEN
<i>Bahia absinthifolia</i>	1			1	1.3	5,407	2			3		
<i>Baileya multiradiata</i>	1	8.3	8,567	2	6.3	26,201	2	7.0	15,895	3	4.4	9,331
<i>Bouteloua aristata</i>	0			0			3			4	5.5	11,665
<i>Bouteloua barbata</i>	0			1	2.1	8,734	3	.5	1,135	4		
<i>Boerhaavia spicata</i>	1			1	2.5	10,397	3	4.5	15,895	0		
<i>Cassia bahinioides</i>	1			1			3	28.5	65,853	3	13.2	27,995
<i>Chenopodium incanum</i>	1	31.2	32,166	3	33.3	137,245	3	4.0	9,083	4	5.5	11,665
<i>Croton pottsi</i>	2	9.3	9,601	2	6.3	26,201	3	15.0	34,062	3-4	23.4	26,795
<i>Eriogonum abertianum</i>	1	7.0	7,201	3	14.7	62,397	3	9.5	22,708	4	2.1	2,478
<i>Eriogonum trichopes</i>	2	11.2	11,522	3	6.3	26,201	3	18.0	40,875	3		
<i>Euphorbia</i> spp.	1			1	15.6	66,543	2	6.0	13,625	0		
<i>Kalistroemia parviflora</i>	1			1	6.3	26,201	1			3	13.2	27,995
<i>Tridens pulchellus</i>	1			1	5.5	22,874	1			3		
Total density estimates: forbs and grasses/hectare												
		June 16, 1972	103,220									
		July 25, 1972	415,893									
		August 31, 1972	227,082									
		October 5, 1972	212,299									
		*	116,500									

PC indicates the phenology code: 1 = green vegetative; 2 = flowering; 3 = flowering and fruiting; 4 = stem cured.
 REL indicates relative density in percent and DEN indicates computed densities in numbers per hectare.
 Columns and data marked with an asterisk indicate sampling of selected forbs and grasses which appeared to be important to the ants.

Table 4. Forage selection by *Novomessor cockerelli* during the growing season 1972

Forage Item	Percent of Total			
	June	July*	August	Sept.*
<i>Eriogonum abertianum</i>	20	6	29	22
<i>Eriogonum trichopes</i>	6	4	0	2
<i>Eriogonum rotundifolium</i>	6		1	
<i>Baileya multiradiata</i>	1			
<i>Bahia absinthifolia</i>			4	
<i>Allionia incarnata</i>			<1	33
<i>Euphorbia</i> sp.			4	8
<i>Chenopodium incanum</i>			2	
<i>Croton pottsii</i>			4	
Insect and insect parts	29	25	2	
Termites	17	11	47	25
Plant parts	13	52	1	8
Miscellaneous fruits	5		2	
\bar{x} Fruits	38	10	49	65
\bar{x} Animal	46	36	49	25
\bar{x} Plant parts	13	52	2	8

* small sample size collection from one or two colonies only.

Table 5. Analysis of impact of harvester ant activity on seed reserves**

	Estimated total number of seeds foraged per month per ant species											
	June			July			August			September		
	P. rug	P. des	P. cal	P. rug	P. des	P. cal	P. rug	P. des	P. cal	*P. rug	P. des	P. cal
	33.6E6	14.5E6	5E6	16.8E6	7.15E6	2.5E5	15.1E6	8.25E6	3E6	15.1E6	6.2E6	2.25E5
Estimated number of seeds of important forage plant species per month per ant species												
<i>Eriogonum abertianum</i>	7.2E6		8E4	9.2E6	1E6	6.75E4	2.56E6	2.2E6	1.38E5	1.79E6	1.3E6	12.6E4
<i>Eriogonum trichopes</i>	6.2E6	5.4E6	1.4E5	5E5	5.3E6	1.2E5	2.85E6	2.4E6	9.6E4	1.42E6	2.4E5	1.13E4
<i>Chenopodium incanum</i>				4E6	1.4E5	2.75E4	4.4E6	7.4E5	3E3	3.57E6		2.7E4
<i>Baileya multiradiata</i>	2.1E5			5E5	1.4E5		7.5E5	1.4E6	3E4	3.75E5	1.8E5	
<i>Bouteloua barbata</i>							1.35E5			7E4	6.2E5	

*by extrap.

Production vs. forage impact[†]

	Totals											
	PROD	FOR	%	PROD	FOR	%	PROD	FOR	%	PROD	FOR	%
<i>E. abertianum</i>	2.23E7	7.28E6	32%	1.9E8	1.7E7	8.8%	1.06E8	4.9E6	4.6%	7.1E7	3.2E6	4.5%
<i>E. trichopes</i>	3.2E6	13E6	400% [†]	7.3E6	1.57E6	21%	6.3E6	5.35E6	84%	3.15E6	1.7E6	53%
<i>B. multiradiata</i>				4.96E7	6.4E5	1.2%	20.6E6	17.8E5	8.6%	3.15E6	5.6E6	1.6%
<i>C. incanum</i>				2.2E8	4.17E6	0.2%	4.1E8	5.14E6	1.3%	7.5E7	4.2E6	.5%
<i>B. barbata</i>							1.8E6	2.09E6	100%	2.1E6	6.9E5	32%

[†] if rather than average production maximum seed production assumed (eg. 70%/plant) for June, the foraging in past on *E. trichopes* is reduced to 20%.

**Fruit production based on plant densities, regressions for fruit number on canopy volume or canopy area, and mean plant volumes or canopy areas for one month indicated. Foraging was calculated on the number of hours per month suitable for foraging for each species x a 50% success factor x the percent of foraged materials by ant species for each plant species represented, x the density per hectare for each species.

[†]PROD = seeds produced, FOR = seeds foraged, % = % total production removed

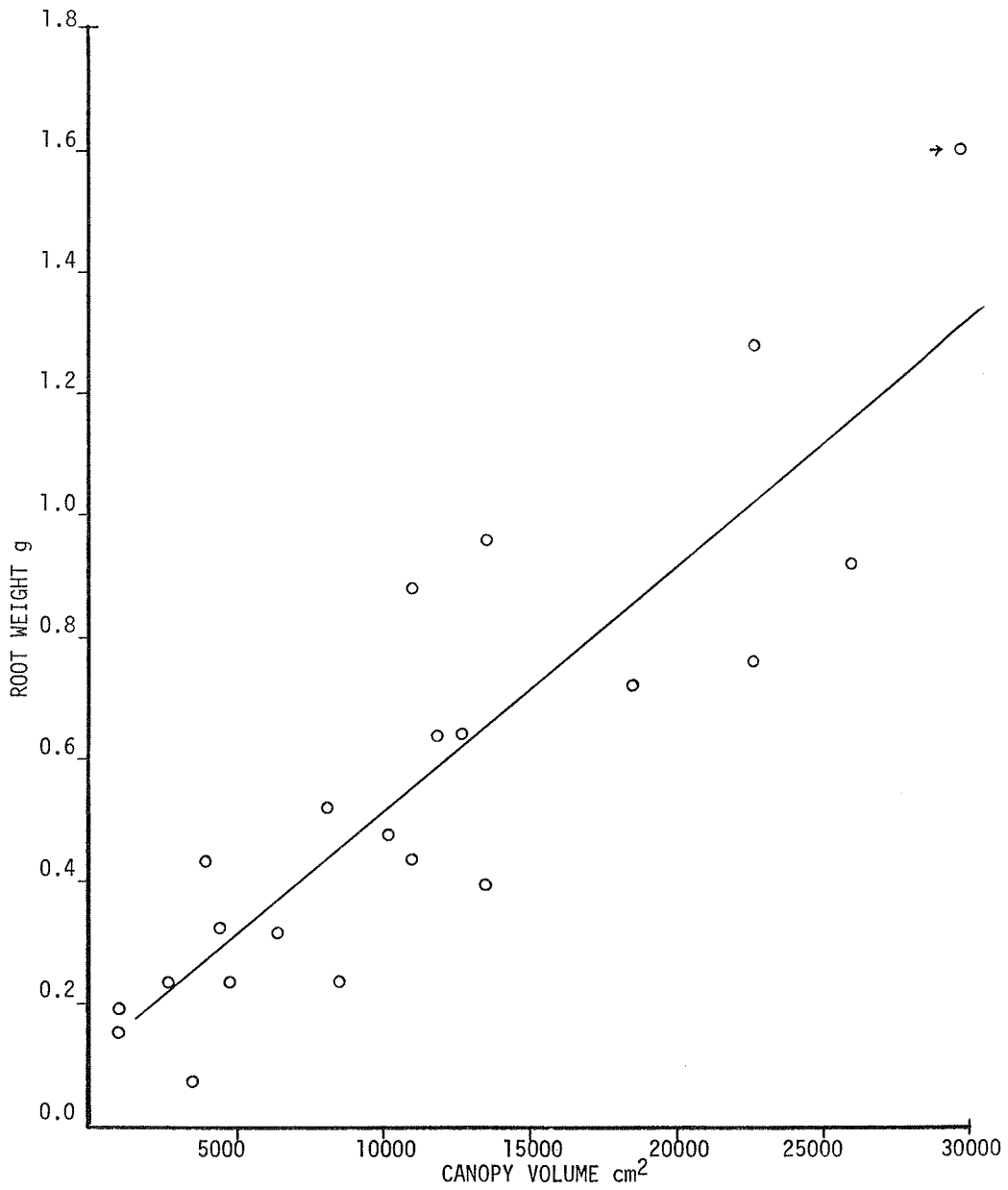


Figure 15. The relationship between root weight and canopy volume in *Eriogonum abertianum* var. *ruberrimum*. (DSCODE A3UEE14)

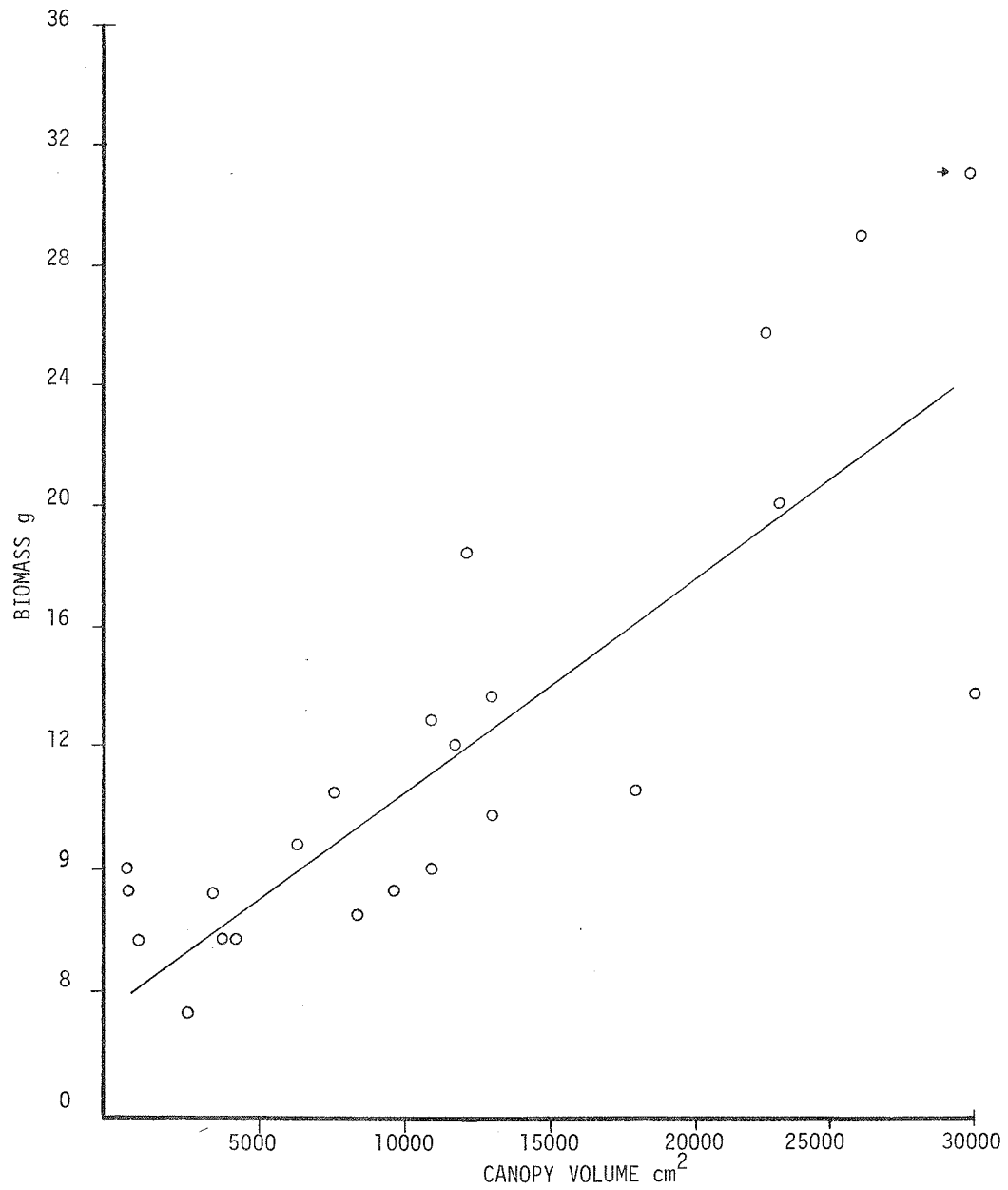


Figure 16. The relationship between total above-ground dry weight biomass and canopy volume in *Eriogonum abertianum* var. *ruberrimum*. (DSCODE A3UEE14)

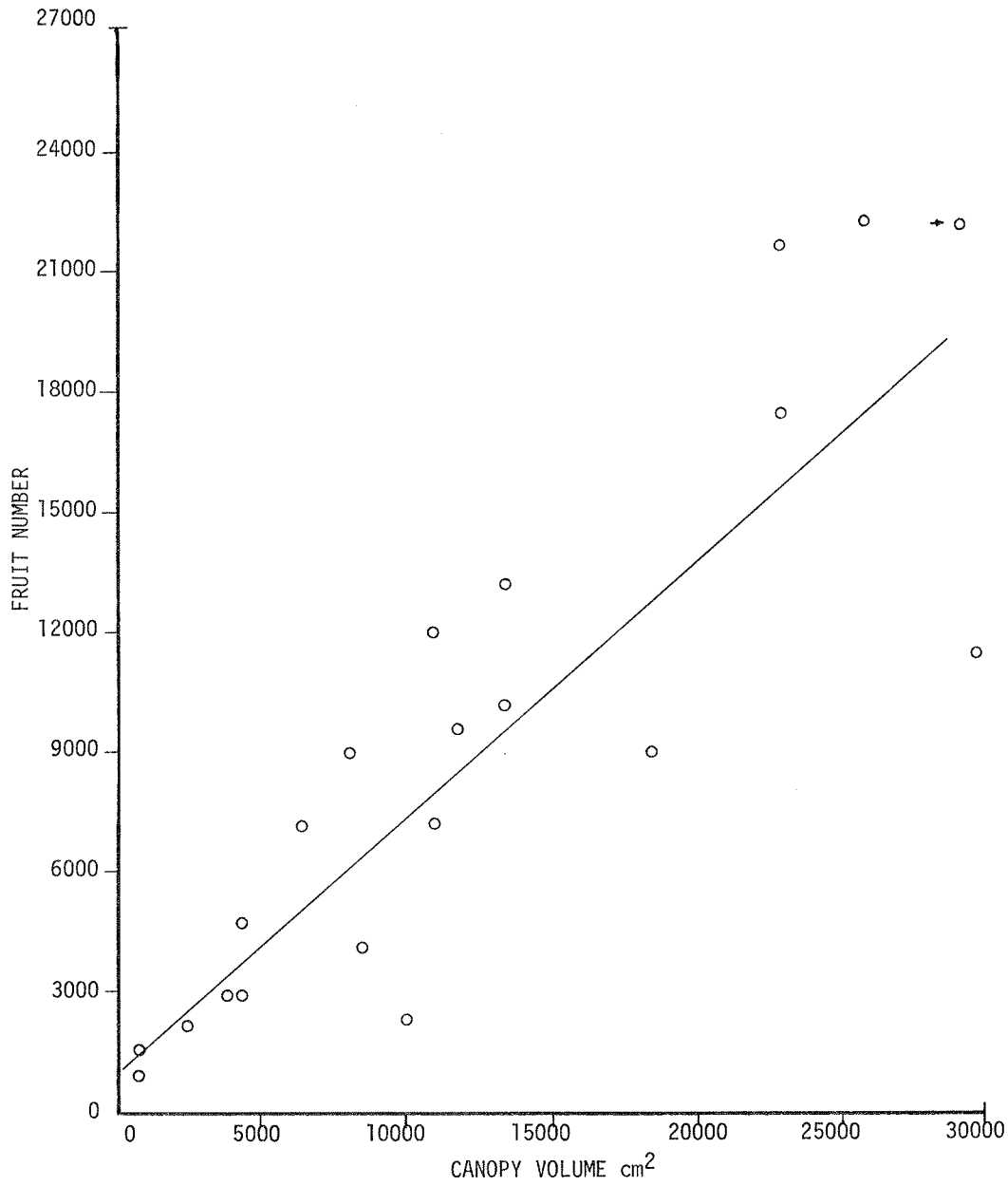


Figure 17. The relationship between fruit number and canopy volume in *Eriogonum abertianum* var. *ruberrimum*. (DSCODE A3UEE14)

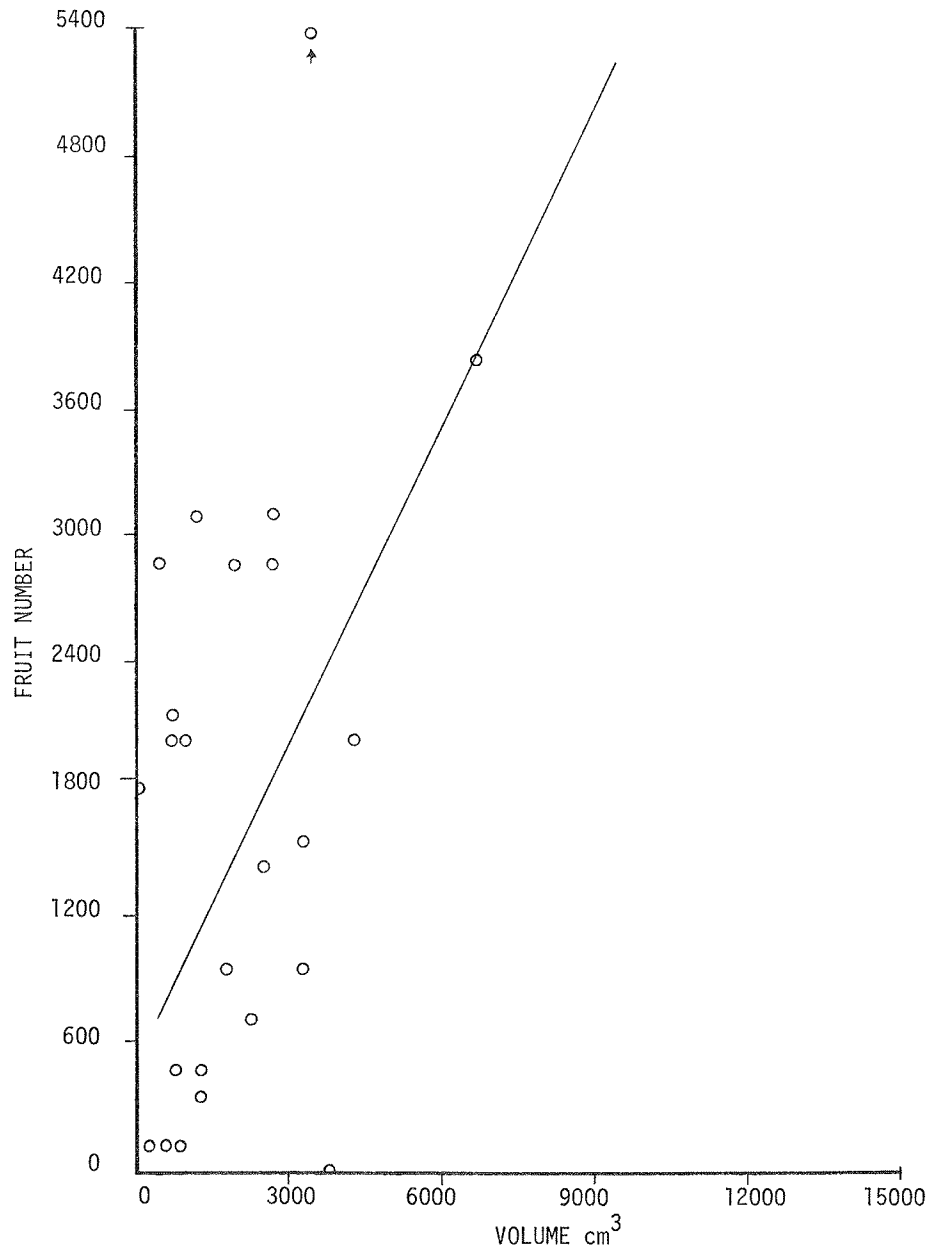


Figure 18. The relationship between fruit number and canopy volume in *Chenopodium incarum*. (DSCODE A3UEE14)

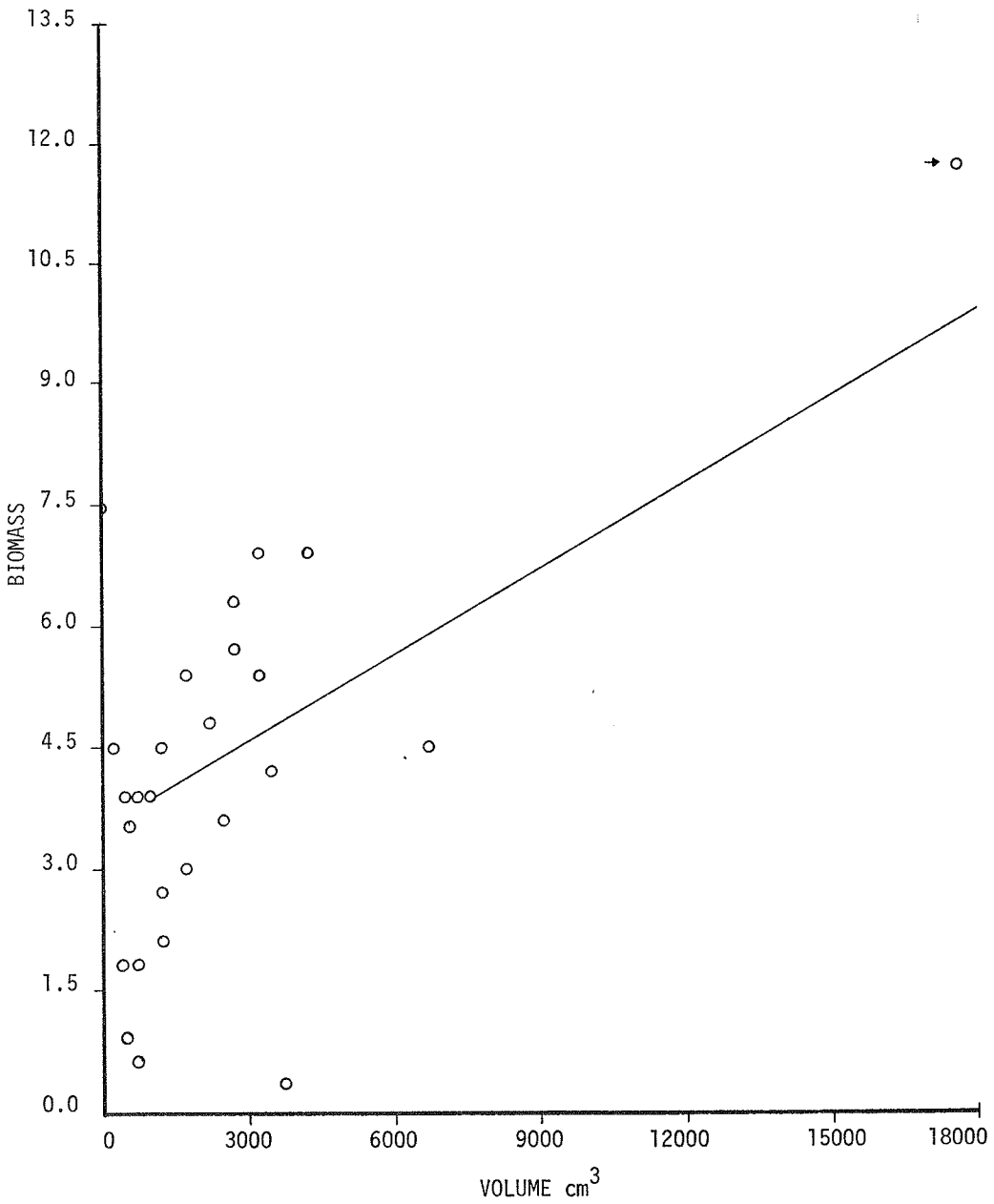


Figure 19. The relationship between above-ground biomass and plant volume in *Chenopodium incanum*. (DSCODE A3UEE14)

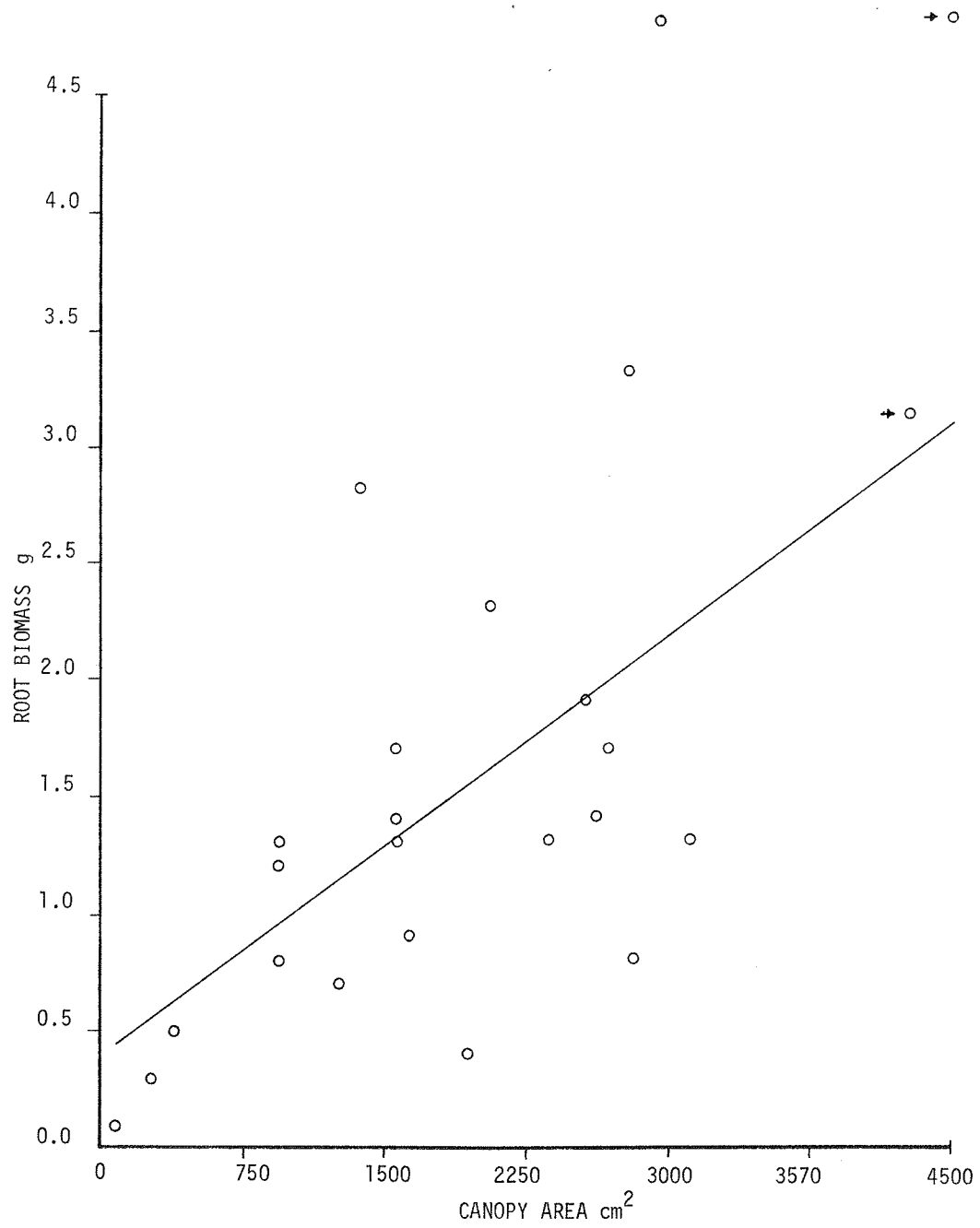


Figure 20. The relationship of root biomass to canopy area in *Bahia absinthifolia*. (DSCODE A3UEE14)

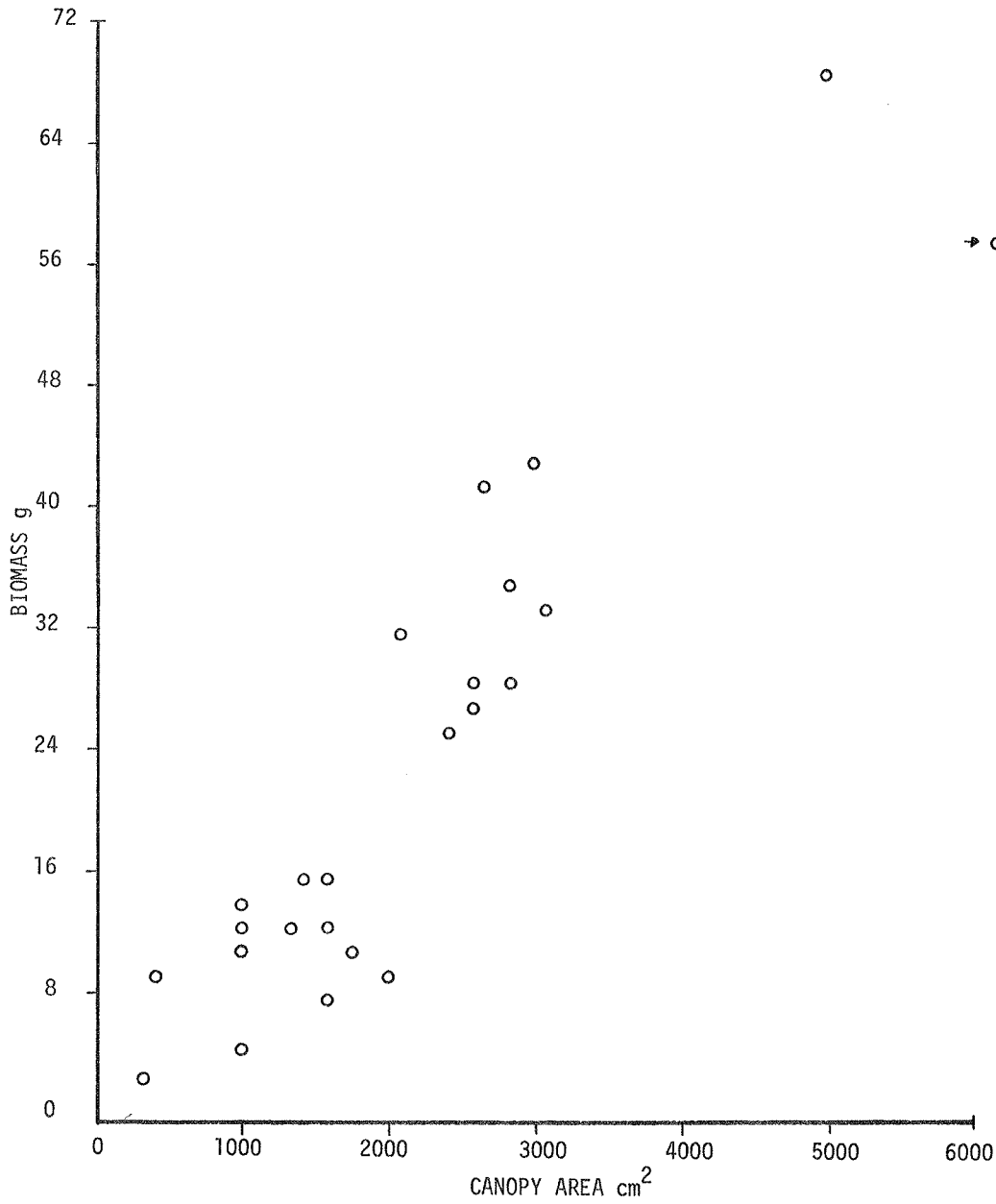


Figure 21. The relationship between above-ground biomass and canopy area in *Bahia absinthifolia*. (DSCODE A3UEE14)

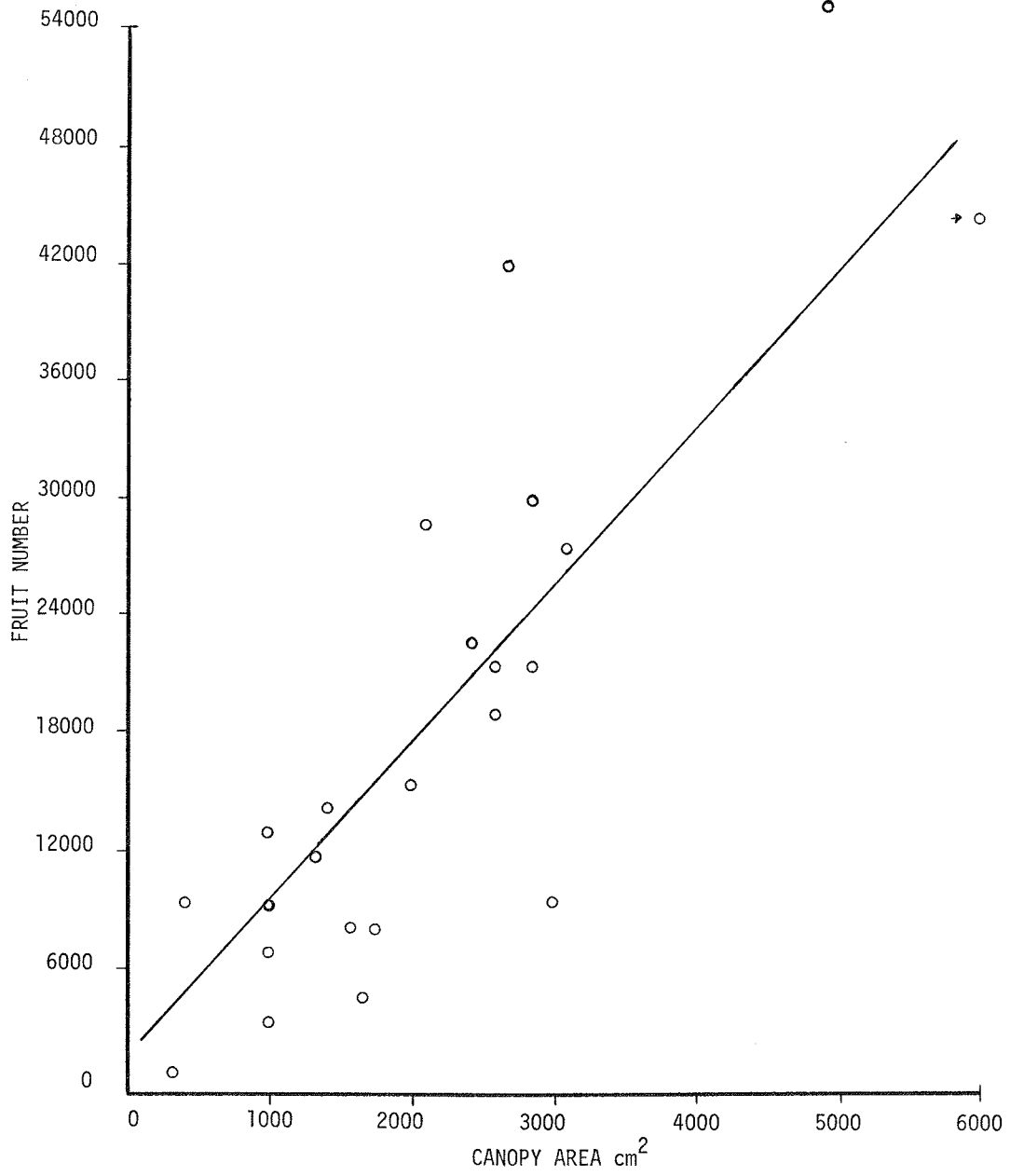


Figure 22. The relationship between fruit number and canopy area in *Bahia absinthifolia*. (DSCODE A3UEE14)

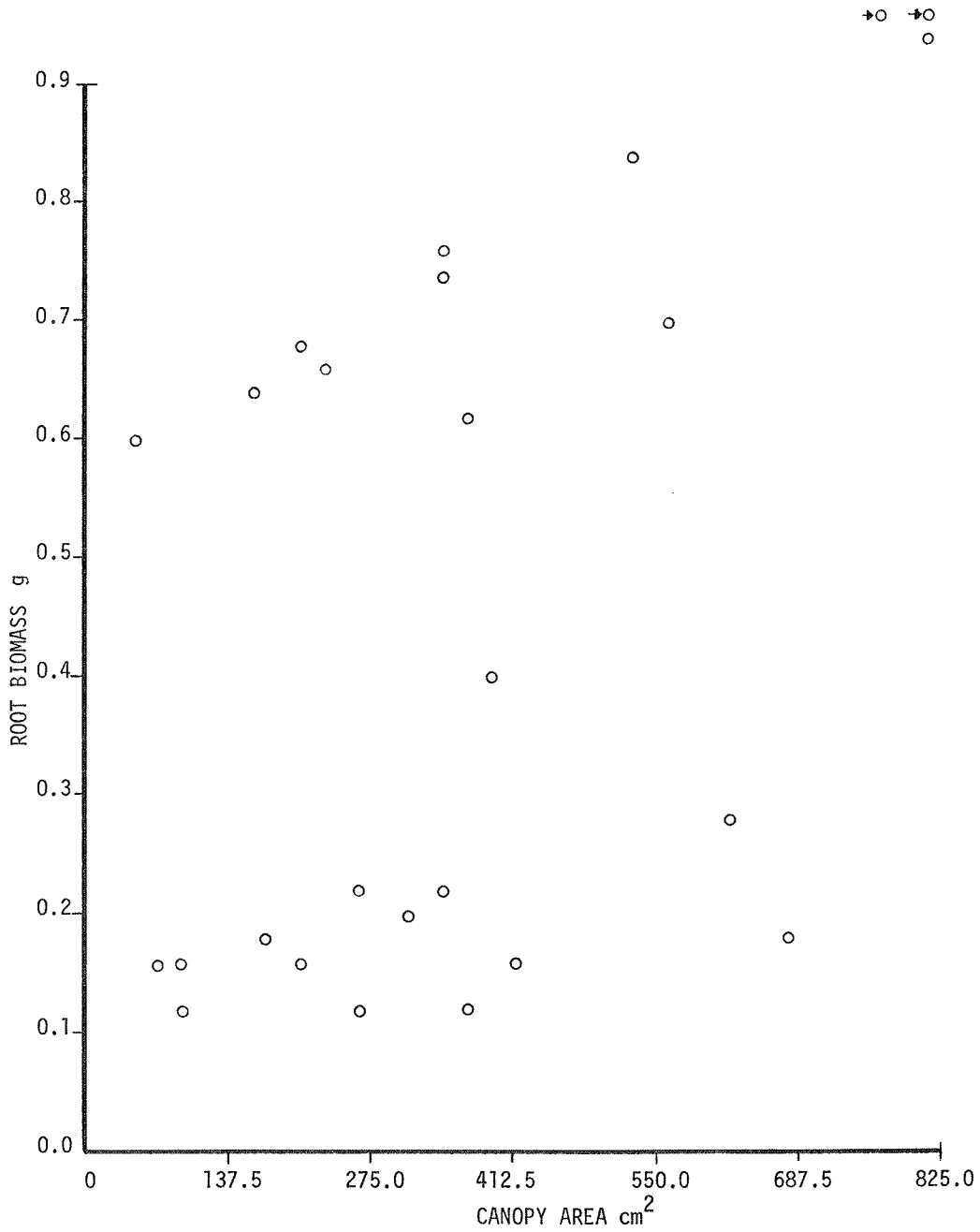


Figure 23. The relationship between root biomass and canopy volume in *Eriogonum abertianum* var. *abertianum*. (DSCODE A3UEE14)

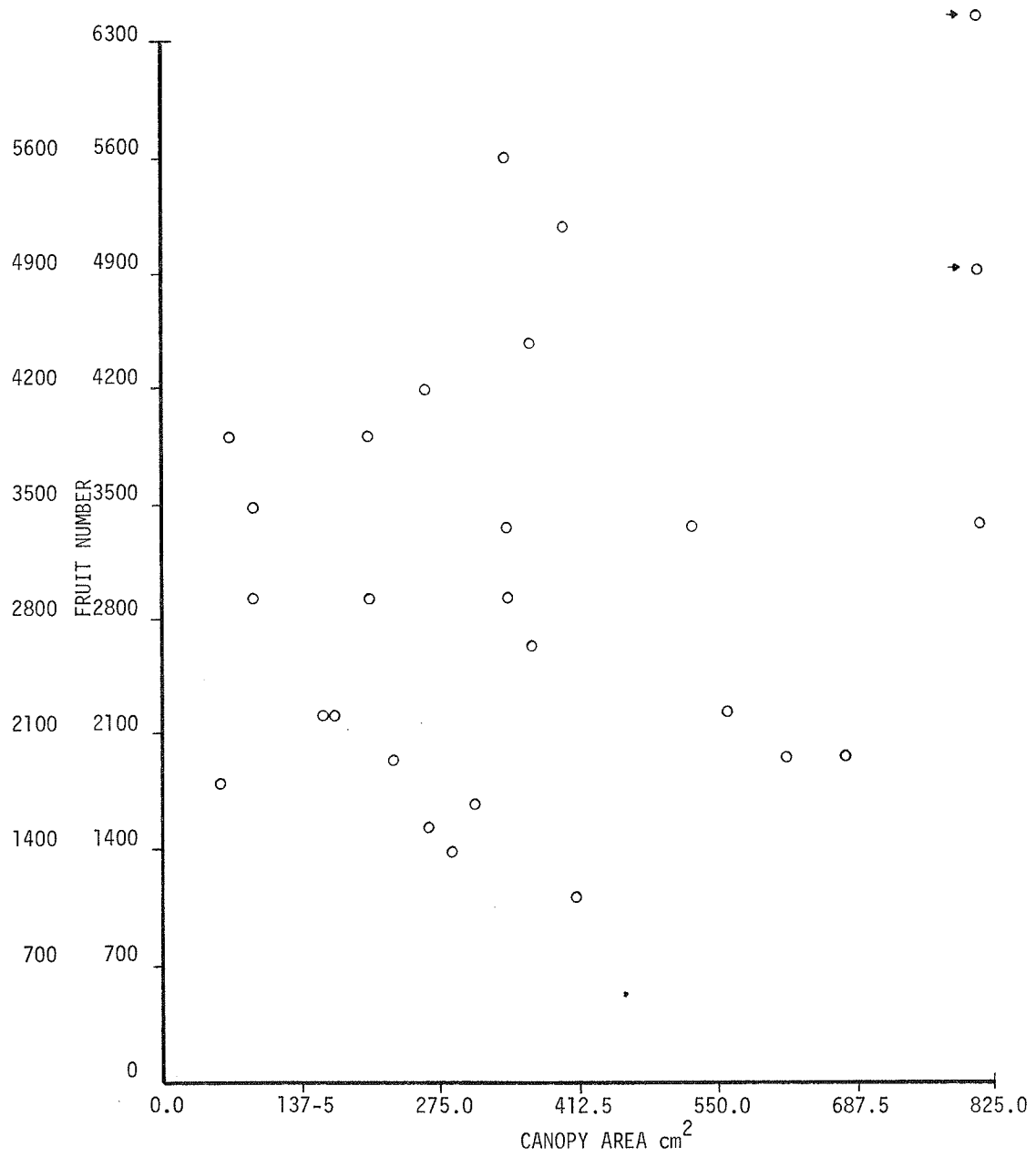


Figure 24. The relationship between number of fruits produced and plant volume in *Eriogonum abertianum* var. *abertianum*. (DSCODE A3UEE14)

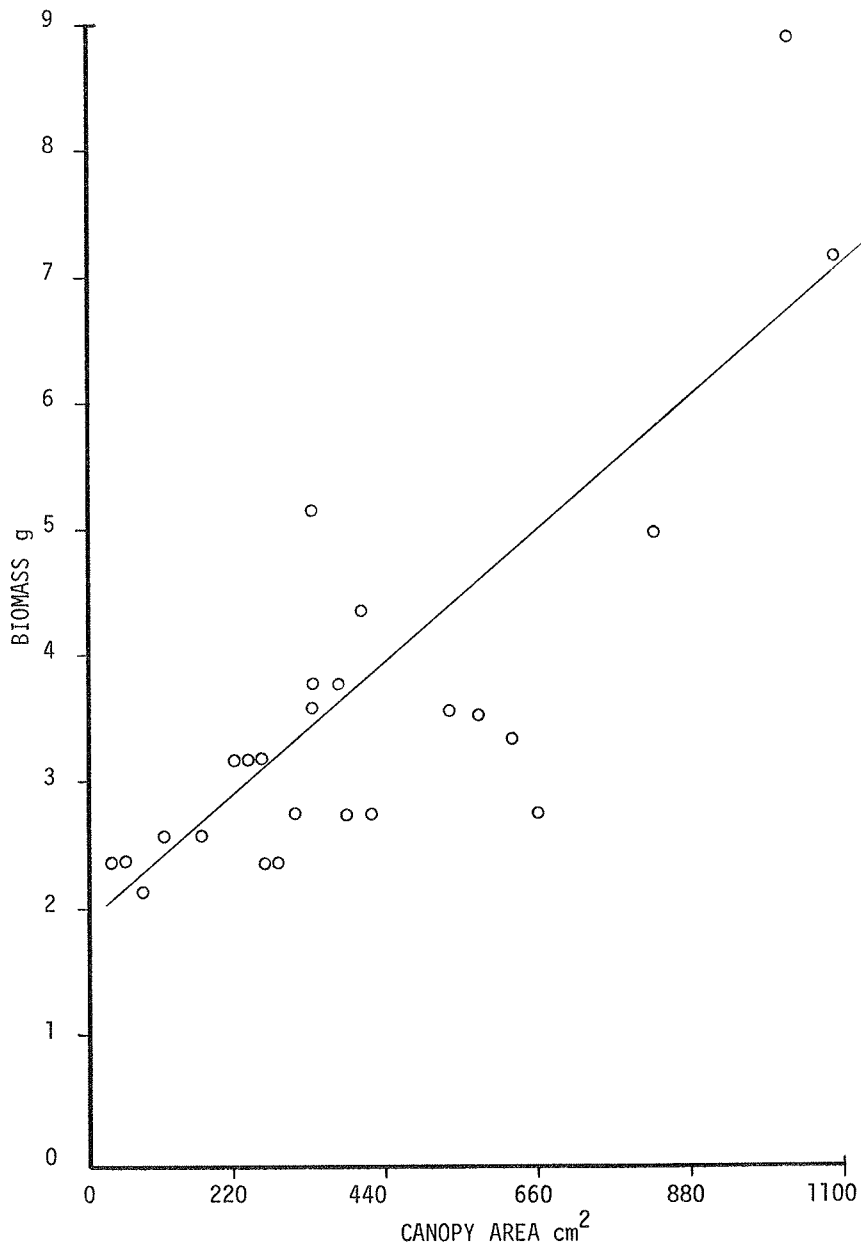


Figure 25. The relationship between above-ground biomass and canopy volume in *Eriogonum abertianum* var. *abertianum*. (DSCODE A3UEE14)

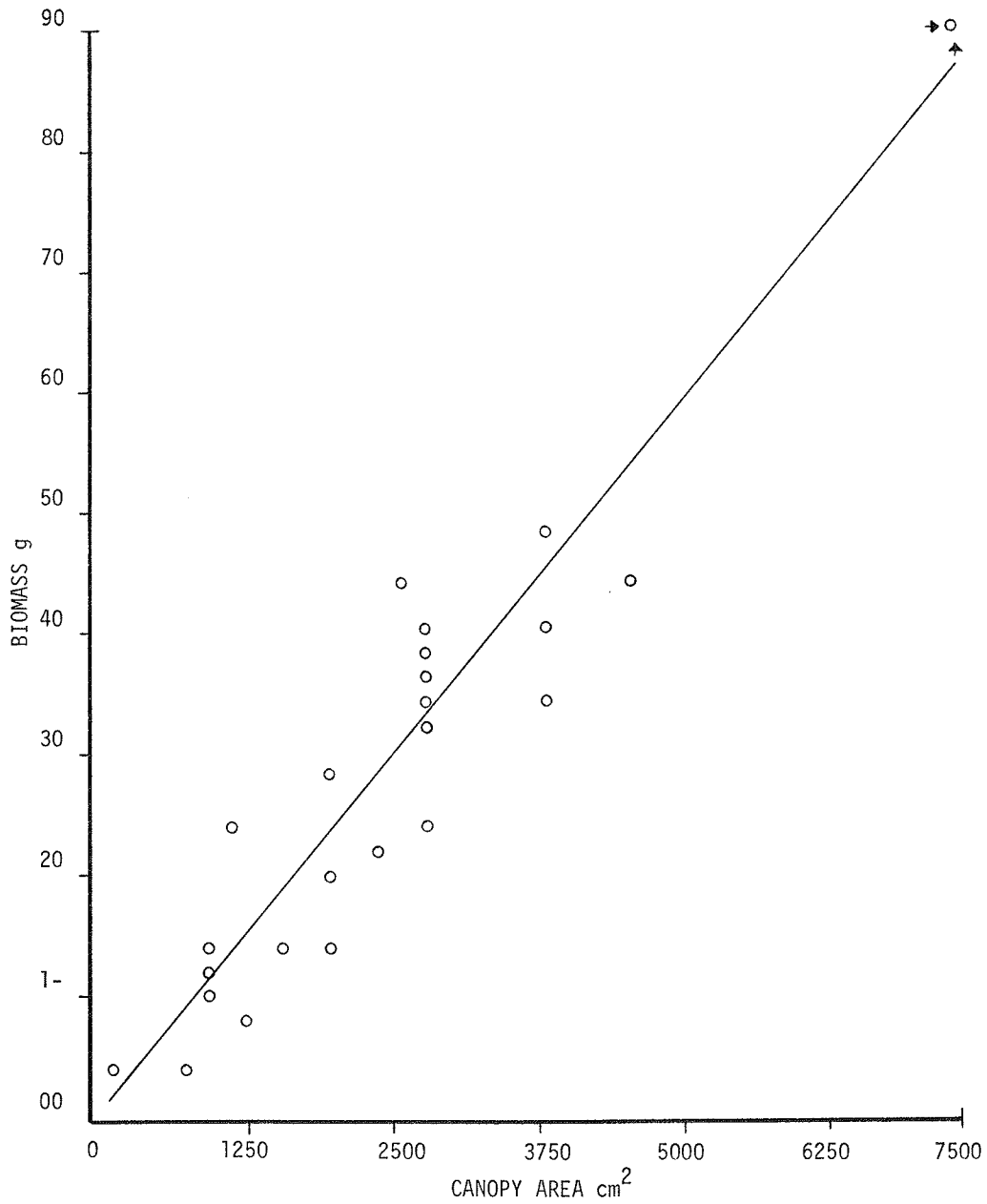


Figure 26. The relationship of above-ground biomass to canopy area in *Baileya multiradiata*. (DSCODE A3UEE14)

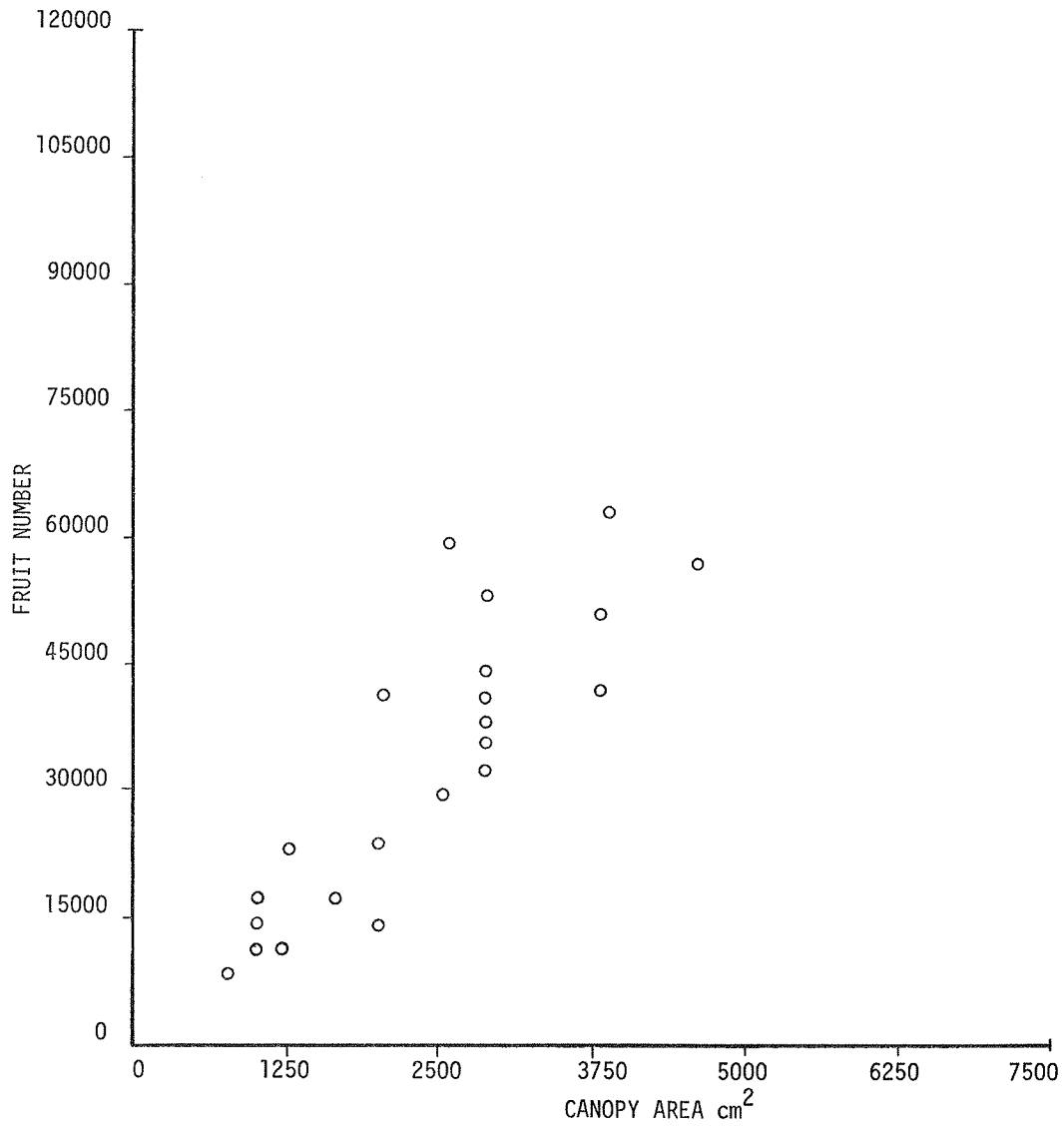


Figure 27. The relationship between number of fruits (based on total reproductive structure biomass) and canopy area in *Baileya multiradiata*. (DSCODE A3UEE14)

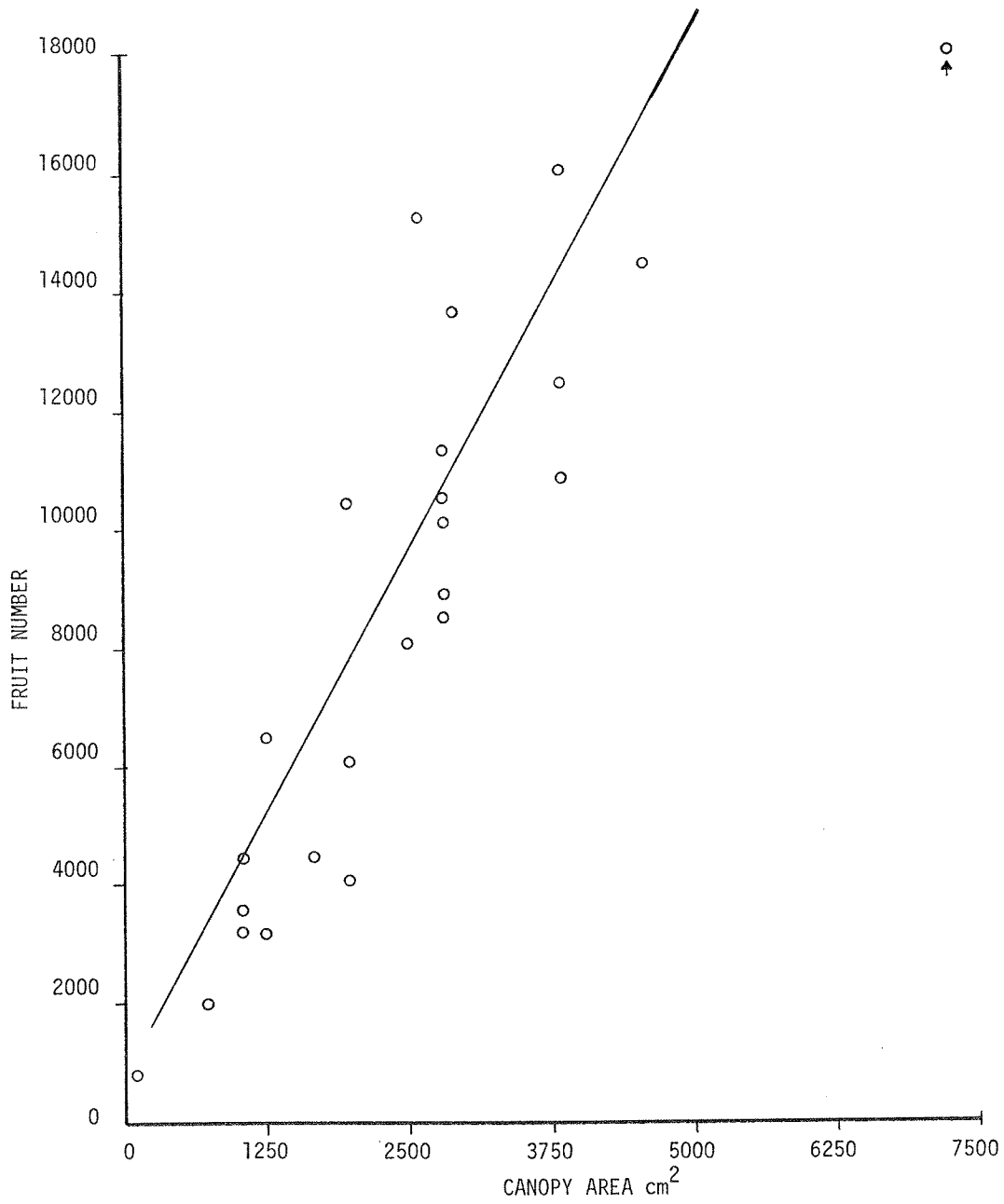


Figure 28. The relationship between fruit numbers (adjusted for non-seed parts) and canopy area in *Baileya multiradiata*. (DSCODE A3UEE14)

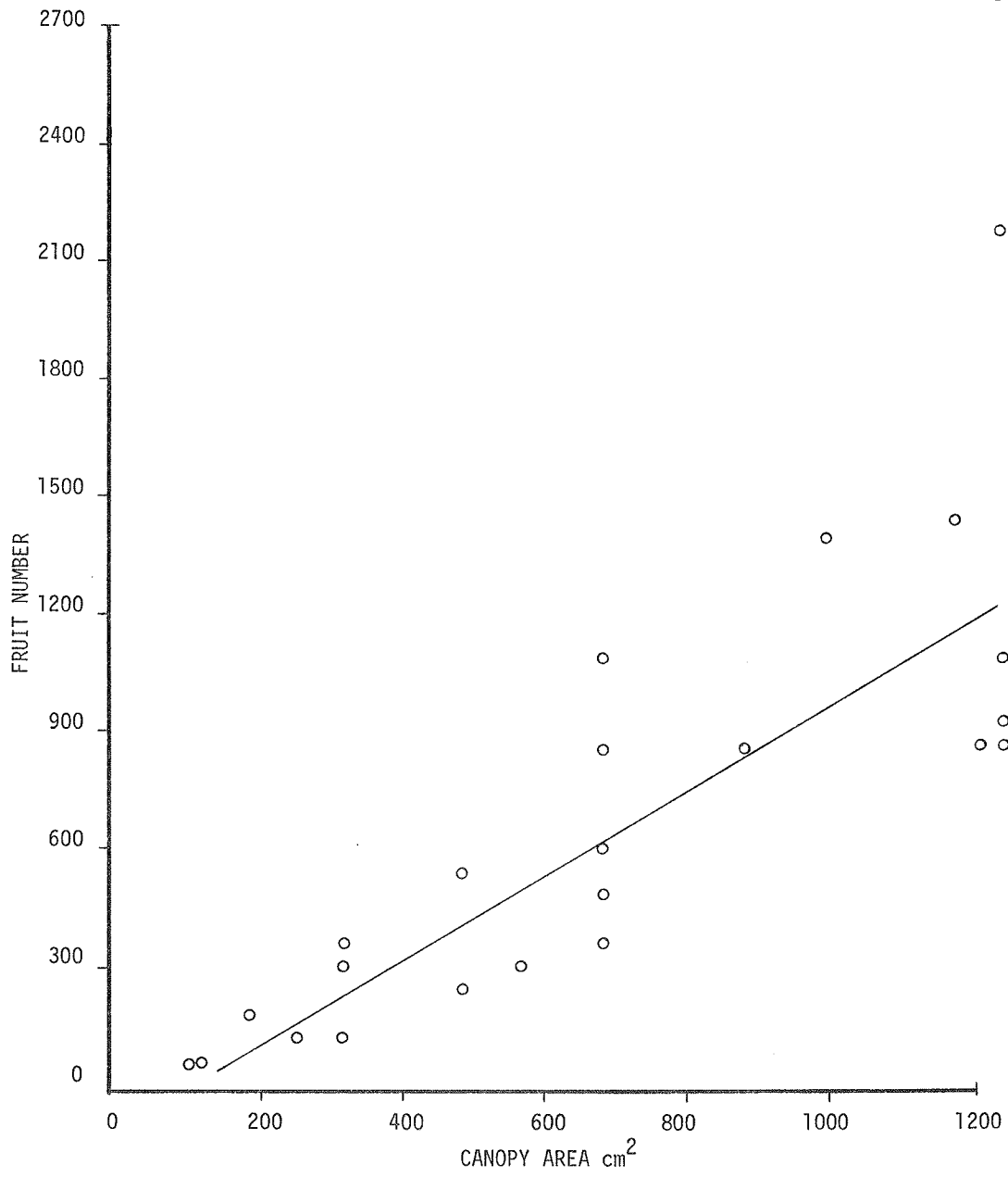


Figure 29. The relationship between fruit number (adjusted for non-seed parts) and canopy area in *Bouteloua barbata*. (DSCODE A3UEE14)

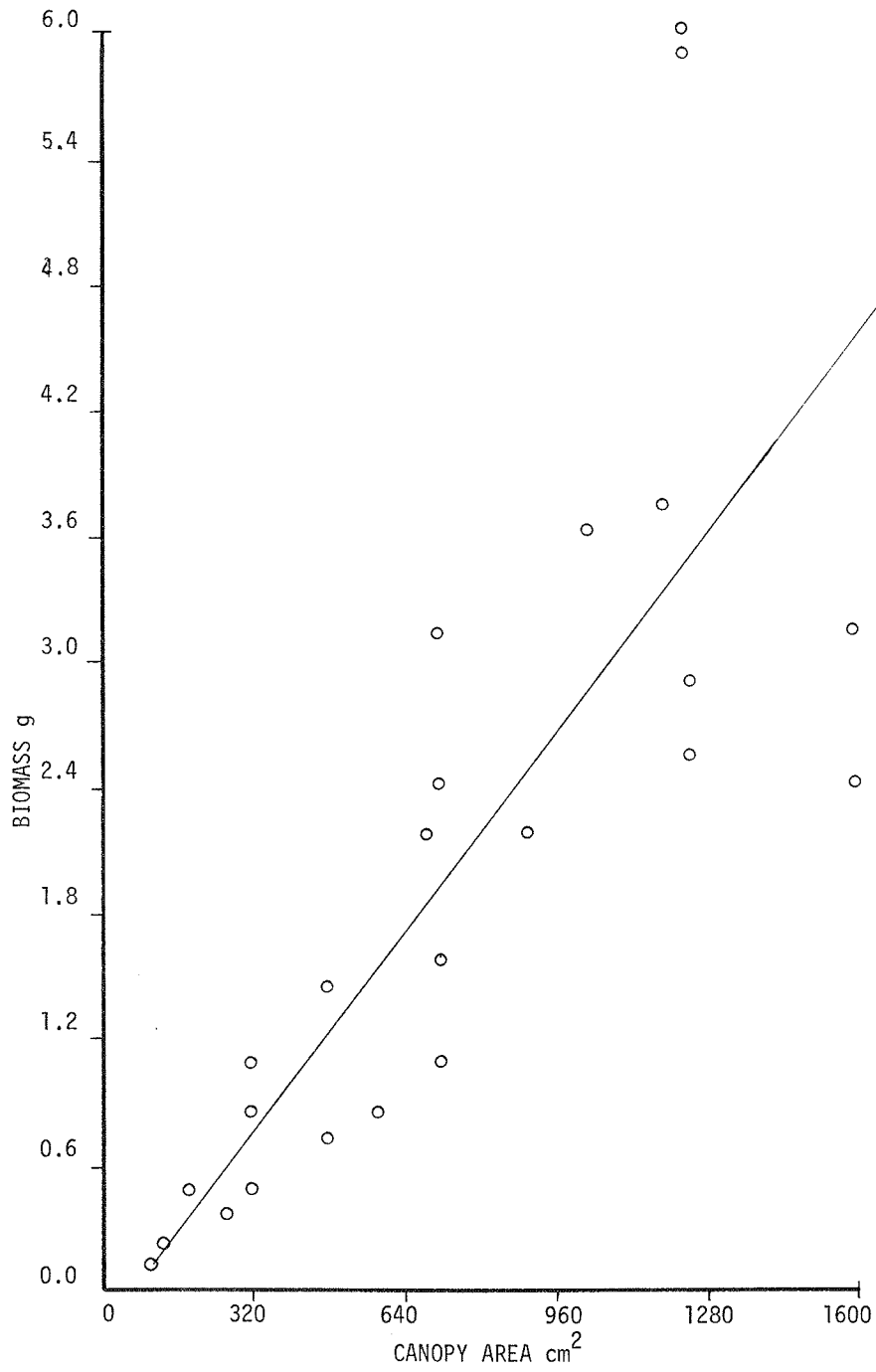


Figure 30. The relationship between above-ground biomass and canopy area in *Bouteloua barbata*. (DSCODE A3UEE14)

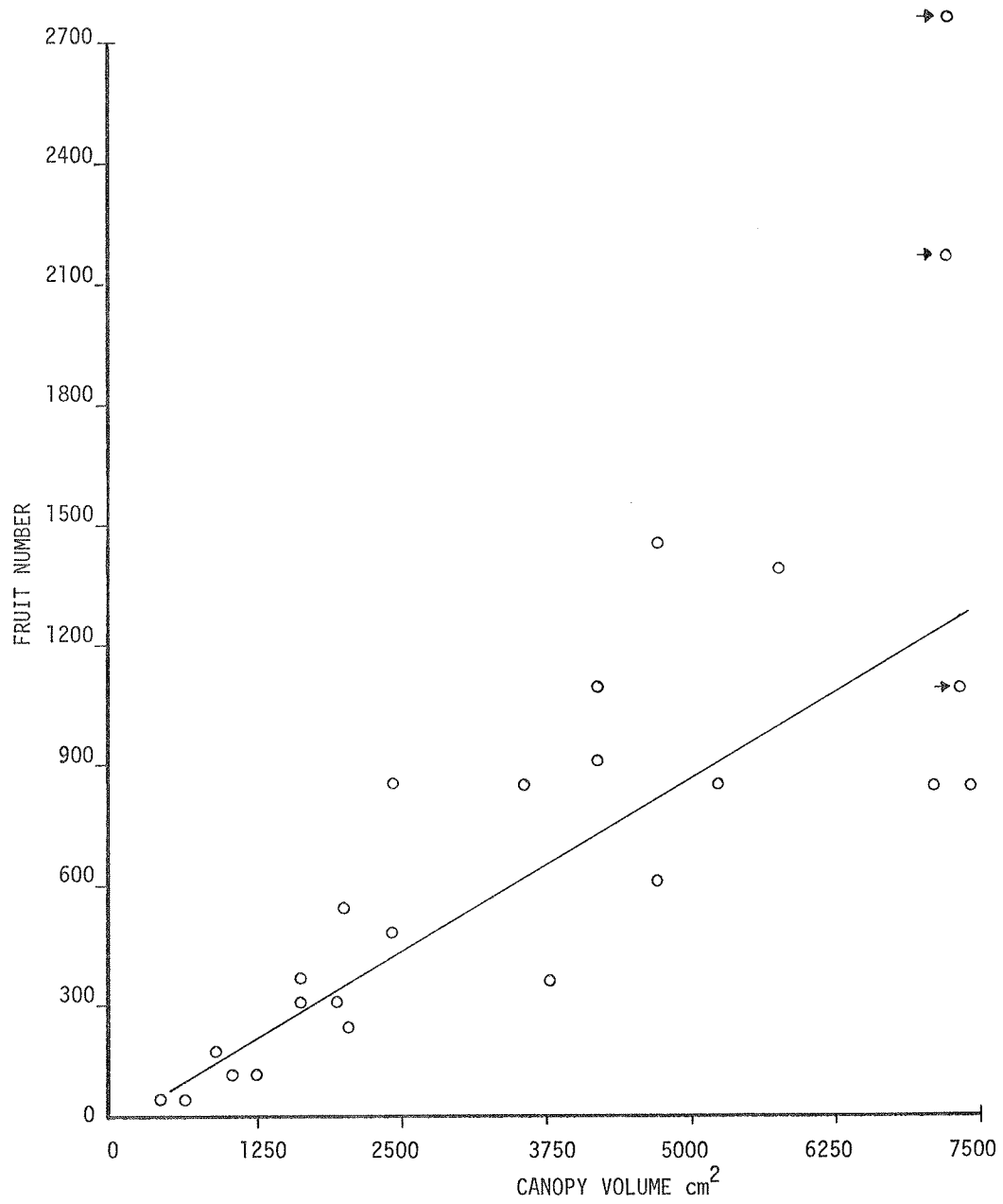


Figure 31. The relationship between number of fruits (adjusted for non-seed weight) and canopy volume in *Bouteloua barbata*. (DSCODE A3UEE14)

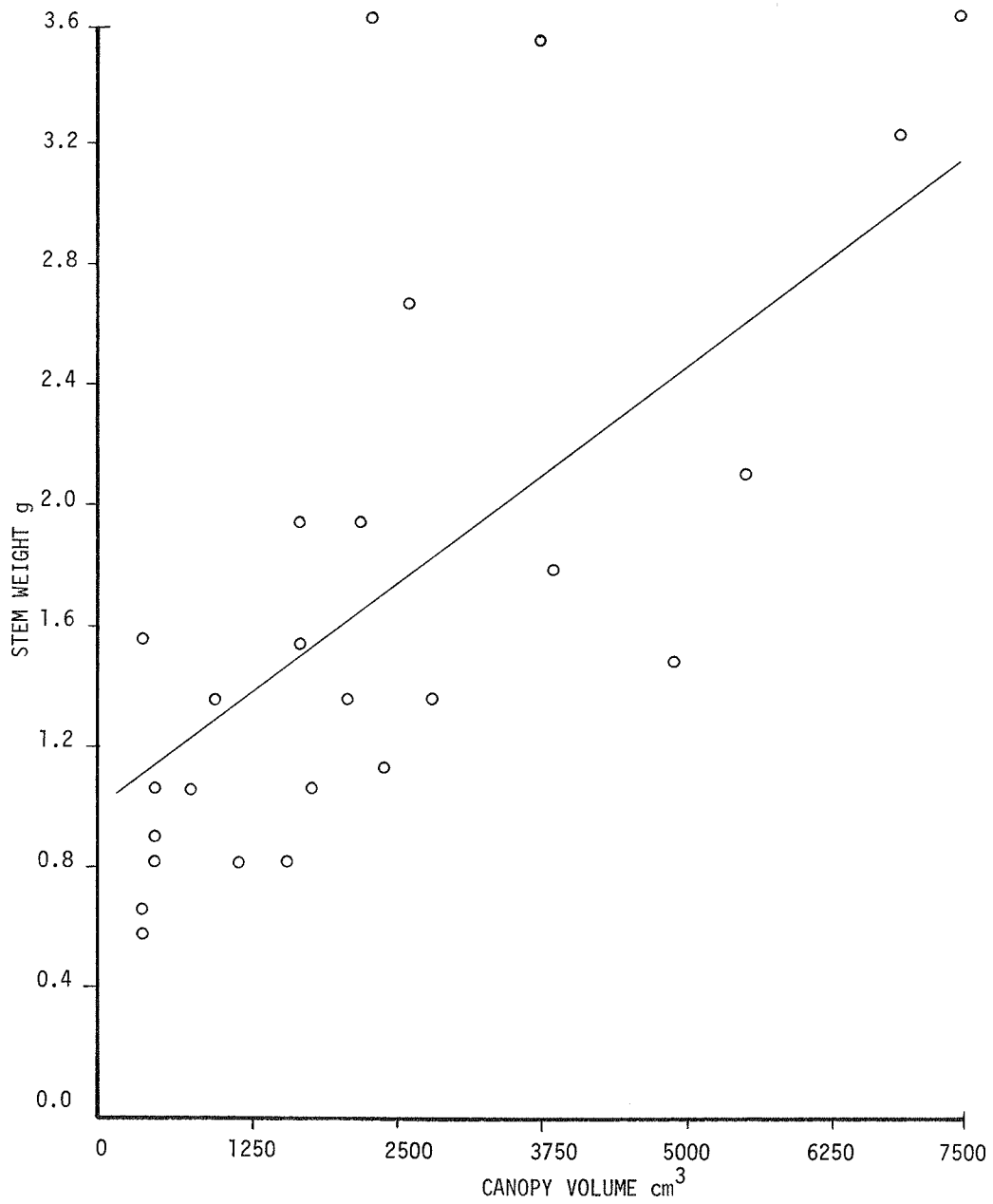


Figure 32. The relationship between stem weight and canopy volume in *Eriogonum trichopes*. (DSCODE A3UEE14)

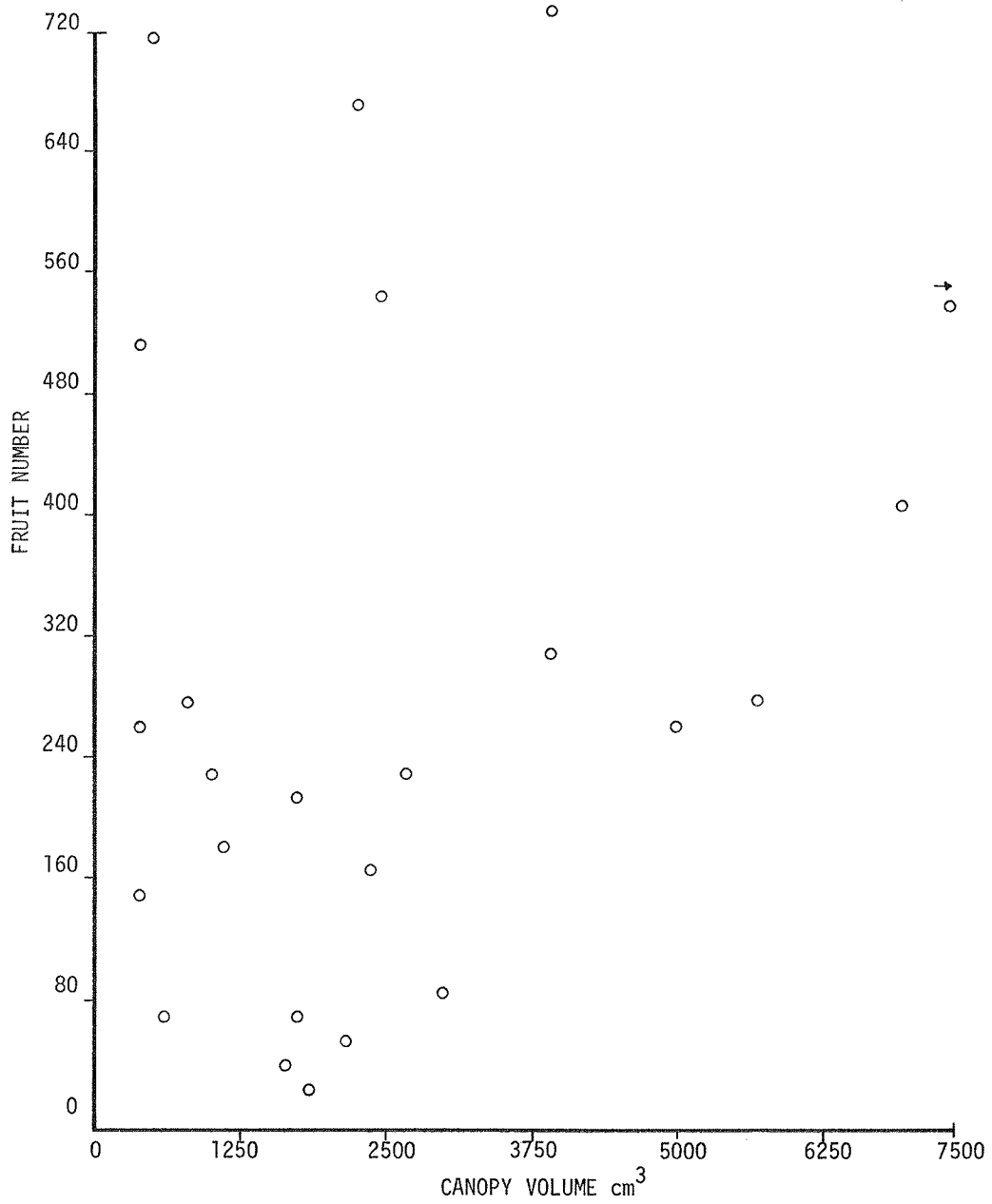


Figure 33. The relationship between fruit number and canopy volume in *Eriogonum trichopes*. (DSCODE A3UEE14)

Forager population estimates (A3UEE15) and total colony size

There was a seasonal trend in numbers of foragers in the foraging population, with peak numbers in July and August, months with the greatest seed production (Table 6). In *P. rugosus*, forager population size increased from approximately 350/colony in June to greater than 1,000 in July. The July and August estimates of forager populations of *P. californicus* and *N. cockerelli* also exceeded 1,000. *P. desertorum* colonies had forager population estimates less than 300.

Table 6. Estimated forager population numbers based on mark-recapture data *

MARCH - JUNE							
Pogrug			Novcoc				
3333			250				
630			429				
<u>1982</u>			$\bar{x} = 340$				
JUNE							
Pogrug		Novcoc		Pogdes		Pogcal	
217		606					
218		400		260		337	
824		549		184		613	
479		557		277		$\bar{x} 475$	
$\bar{x} 434$		$\bar{x} 236$		$\bar{x} 240.3$			
SD 287		$\bar{x} 469$					
		SD 156					
JULY							
Pogrug		Novcoc		Pogdes		Pogcal	
1,044		1,391		557		2,535	
1,464		1,863		1,464		2,849	
6,063		2,208		1,103		82,102	
$\bar{x} 2,857$		$\bar{x} 1,820$		3,091		14,309	
				3,826		$\bar{x} 25,448$	
				$\bar{x} 2,008$			
				SD 1,387			
AUGUST							
Pogrug		Novcoc		Pogdes		Pogcal	
1,519		585		284		1,011	
548		762				2,881	
756		1,342				$\bar{x} 1,946$	
734		1,650					
496		1,884					
479		$\bar{x} 1,245$					
818		SD 559					
$\bar{x} 764$							
SD 359							

* Estimate by Lincoln-Peterson Index. Pogrug = *P. rugosus*, Novcoc = *N. cockerelli*, Pogdes = *P. desertorum*, Pogcal = *P. californicus*, Pogbar = *P. barbatus*.

**Indicated data from Portal, Arizona

Total population estimates were obtained for three colonies of harvester ants which were completely excavated (see Descriptive notes section for details). The following population estimates were obtained:

- 30 Sept. '72 - *Pogonomyrmex rugosus* #62; workers-1595, larvae-150
- 15 Sept. '72 *Pogonomyrmex rugosus* #18; workers-2195, larvae-180
- 10 Oct. '72 *Pogonomyrmex californicus* #35; workers-1932, larvae-0

Colony distribution (A3UEE12)

The data on density estimates and nearest neighbor analysis are summarized in Table 7. *N. cockerelli* exhibited a clumped distribution ($P < .05$, Grieg-Smith, 1964) and *P. desertorum* had a highly significantly clumped distribution ($P < .001$, Grieg-Smith, 1964). The distribution of *P. rugosus* colonies was found to be random. *P. californicus* had extremely low densities (4-6 colonies/hectare) in comparison to the other species and as a consequence no formal analysis of the distribution of this species was attempted.

Table 7. Nearest-neighbor analysis for harvester ant species in the study area*

Species	PD^2	ND^2	PD^2/ND^2	Colonies/hectare
<i>Novomessor cockerelli</i>	28333	20813	1.36	18.2
<i>Pogonomyrmex desertorum</i>	4075	1473	2.76	137.9
<i>Pogonomyrmex rugosus</i>	16422	13255	1.24	21.3

*P = point, D = distance, N = neighbor

Descriptive notes (A3UEE16)

The following is summarized from the notes of Tim Cox who was responsible for most of the excavation of the *Pogonomyrmex rugosus* colonies (Figs. 34 and 35).

Excavation of colony #18 was begun 24 August 1972. Most digging was done from dawn to approximately 1100 hrs. The flow of ants from the chambers was very constant in the first meter of excavation but became very sporadic below that depth. Below 1 m, the ants were extremely reluctant to leave the passage unless air was forced in on them or unless actually dug up. On the second morning many ants could be found outside the colony galleries at the new ground level, but they did not seem to attempt to forage as they did not leave the immediate vicinity of the new entrance by more than 0.3 cm.

Ants recovered in the top meter of digging were of uniform size and courage, the apparent primary foragers of the colony. After this depth, however, many unpigmented workers were captured and as the excavation continued, more and more larger, dark ants were taken. These ants were not only of an extremely large size (1/4 larger) but were very courageous and seemed to possess a better sense of direction as to danger. Many young, unpigmented workers were taken from this depth on. Their numbers increased with the depth and their size was the average "forager" size.

Excavation had proceeded to approximately 1.7 m by 26 August. The following morning a heavy rain (11mm) had fallen the previous night and had filled approximately 0.3 m of the hole. It appears that at the end of excavation the previous day we had been within 0.45 m of the queen's chambers and that the rain had forced the ants to make an emergency chamber or convert an already existing chamber into a temporary queen's chamber overnight, since a new entrance and mound of earth was found approximately 1.5 m from the original main entrance.

Upon excavation, the queen was taken at approximately 1 m depth primarily with young "white" workers, and some of the very large workers.

Larvae were found in two chambers approximately 0.6 m down and were found again only at the maximum depth of the excavation (1.7 m).

The colony 62 excavation incurred the same ant flow consistency, location and approximate number of larvae, approximate depth of excavation, and general characteristics of ant behavior. The only real difference was that the queen was taken at the maximum depth excavated and was found with many larvae and young ants in a prehibernation condition as excavation was in the early fall.

Pogonomyrmex barbatus: On 5 November 1972, we went to the Aguirre Springs area 35 km ENE of Las Cruces, Dona Ana Co., New Mexico to collect *Pogonomyrmex barbatus* for laboratory studies. At 1100 hr there was some foraging activity. The soil surface temperature was estimated to be between 20-30 C. The foragers were bringing fruits of

2.3.3.2.-52

Bouteloua gracilis and *Bouteloua curtipendula* to the nest. One nest was excavated to the depth of 0.45 m (Fig. 36). Storage galleries were filled with fruits of *Bouteloua curtipendula*. Over 800 workers and larvae were removed from the galleries.

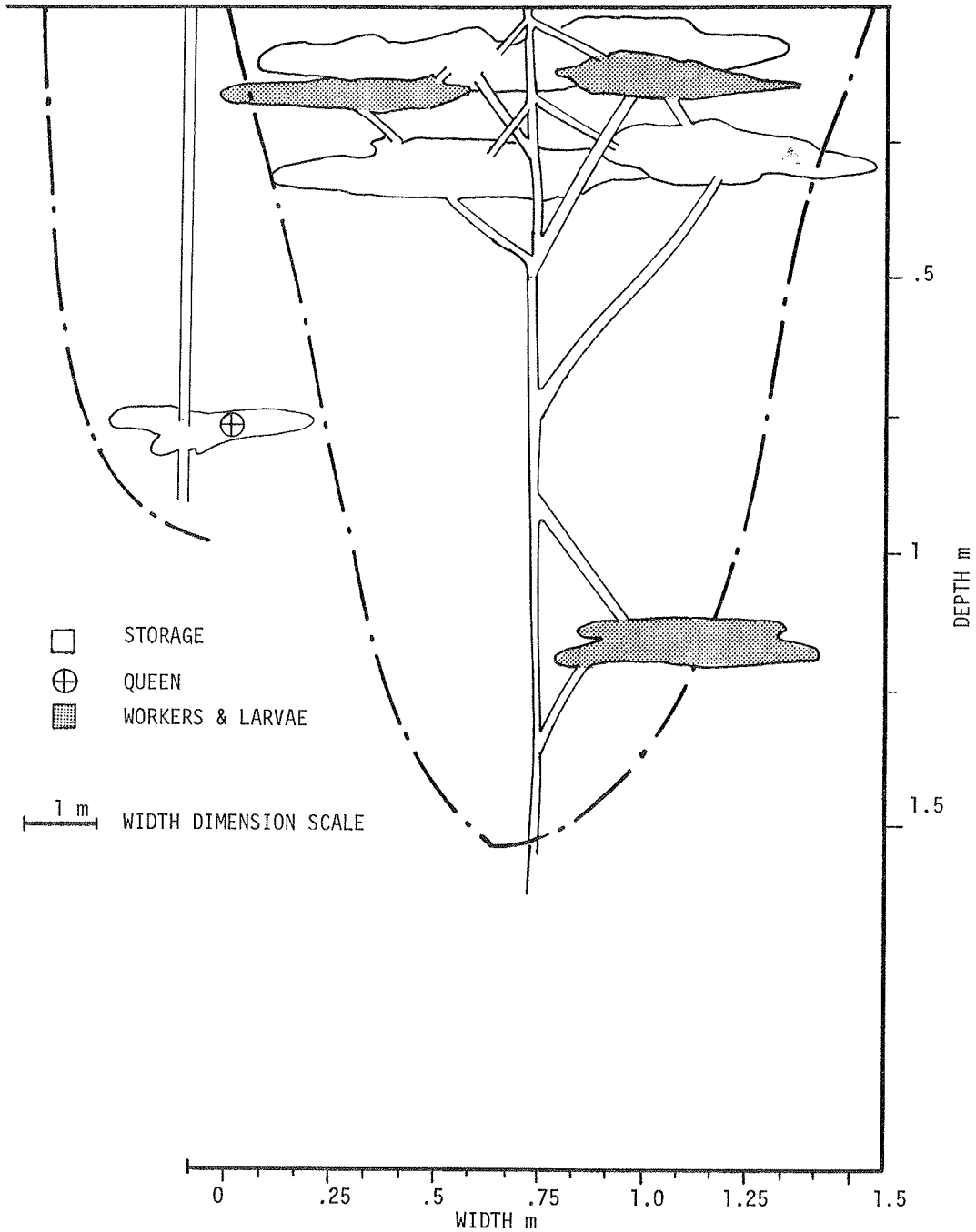


Figure 34. Relationships of storage and nest chambers of *Pogonomyrmex rugosus* colony 18, excavated in August, 1972. The depth and one width dimension are shown on the x and y axis, the second width dimension may be obtained by use of the width dimension scale.

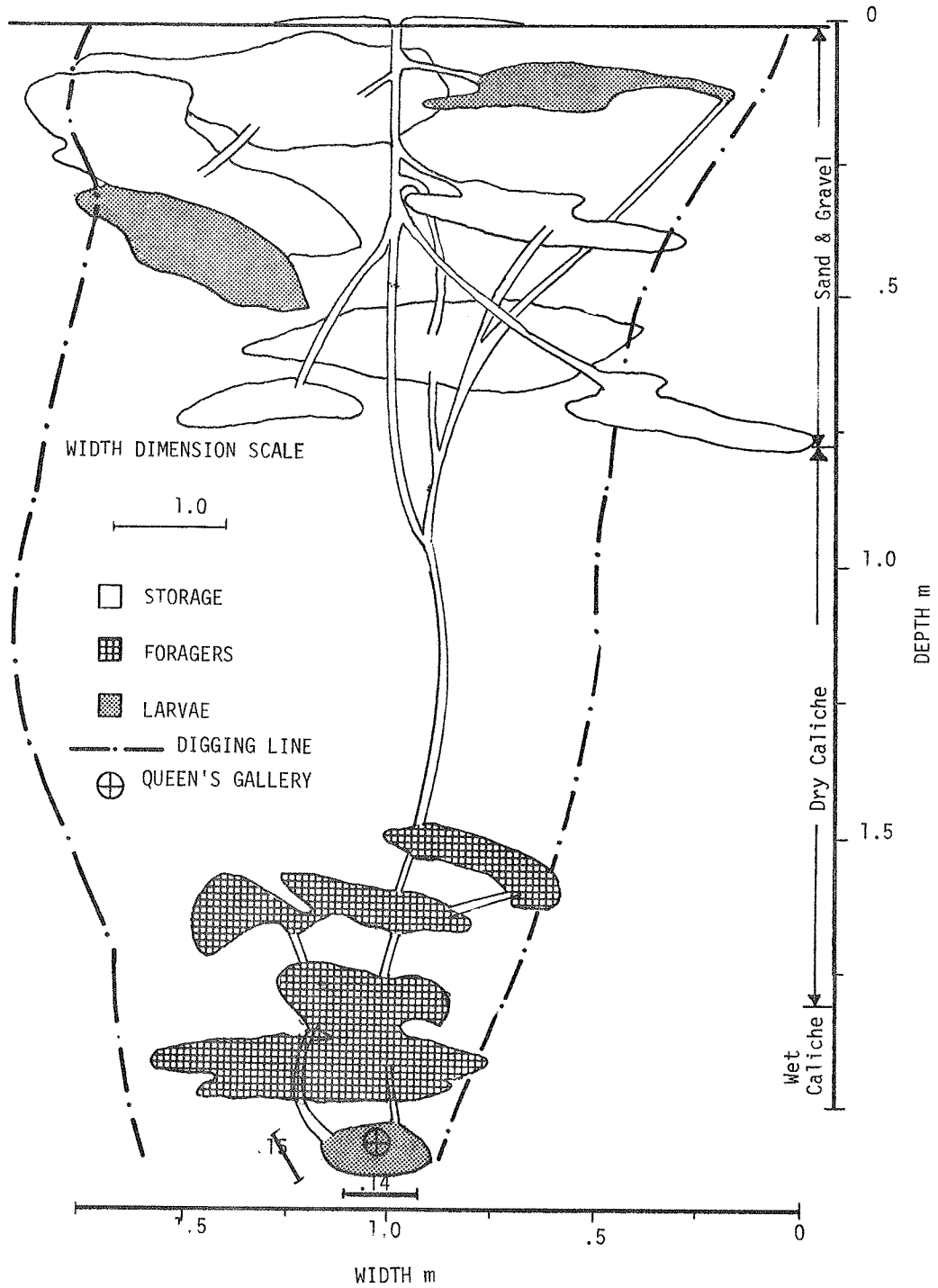


Figure 35. Relationship of storage and nest chambers of *Pogonomyrmex rugosus* colony 62, excavated in August, 1972. Method of presentation the same as in Figure 34.

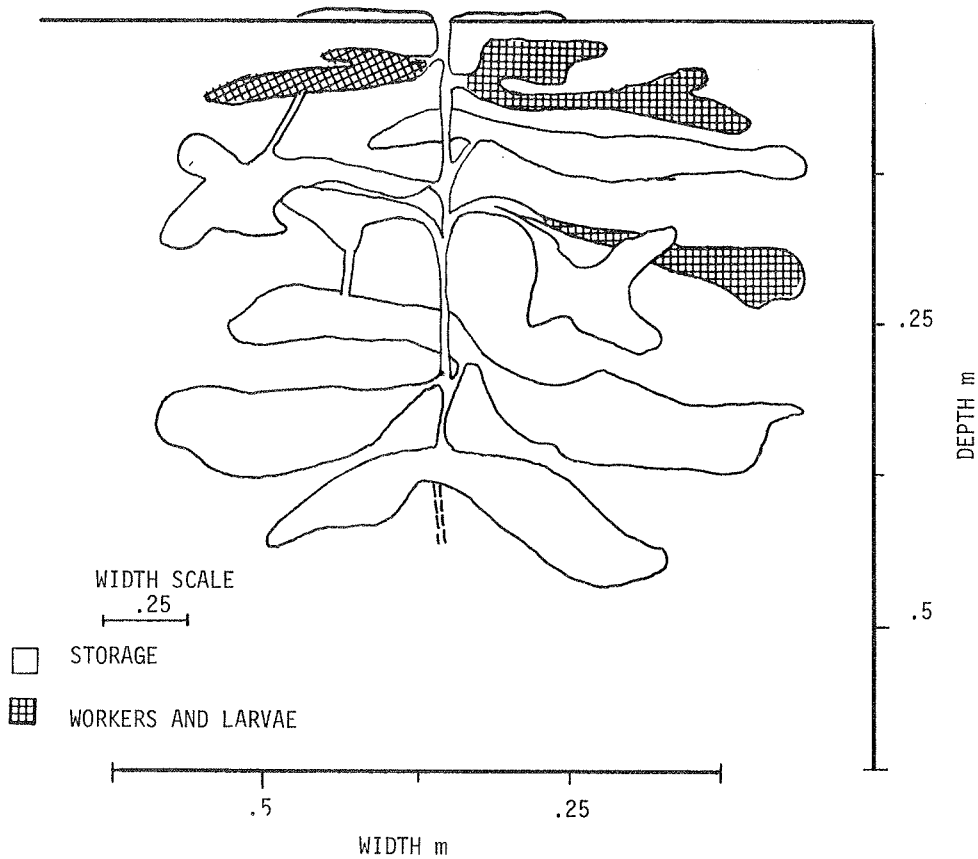


Figure 36. The relationship of nest chambers in a partially excavated colony of *Pogonomyrmex barbatus*.

A general survey of the area lower on the alluvial fan showed that *P. barbatus* was the only large harvester ant in the scrub oak-grass community. In drier sites at lower elevations in the grass-mesquite association, *P. rugosus* replaced *P. barbatus*, with *P. barbatus* extending into areas dominated by *P. rugosus* on the edges of larger watercourses. This suggests that *P. barbatus* requires moister habitats than *P. rugosus*.

Foraging and nest structure of *Pogonomyrmex barbatus*. (A3UEE03 and A3UEE16): The mesquite-acacia community near Portal, Arizona, supports dense populations of *Pogonomyrmex barbatus* (28 colonies/hectare). In July we spent several days in this area obtaining data on this species, primarily for comparison with *P. rugosus*. Unlike

P. rugosus, *P. barbatus* did not forage at night. Some data was obtained on foraging activity as affected by soil surface temperature and saturation deficit. The data in Table 9 show that foraging activity in this species is highest at soil surface temperatures between 25-40 C and at saturation deficits $<30 \text{ g/m}^3$. While making these observations at soil surface temperatures between 55-56 C, and a saturation deficit of 37 g/m^3 , I was able to stimulate emergence of foragers from *P. barbatus* colonies by casting a shadow on the mound. Foragers that departed the mound made a short excursion (less than 2 m) in the sun, then quickly sought shade. If trapped in the open, these ants would climb into the vegetation or remain in the shadow of a stick or rock, making but brief forays toward the nest then retreating quickly to the lower temperature environment. The soil surface temperature where my shadow was cast dropped quickly to 47 C, which was apparently low enough to result in egress of some foragers from the colony.

A 6 m circle was cleared around a *Pogonomyrmex barbatus* nest and some foraging behavior experiments were conducted with colored seeds. In experiments 1 and 2, seed distribution per unit area was uniform and in experiments 3 and 4, the 4 m line was saturated with dyed grain. The foraging behavior of *P. barbatus* was similar to that of *P. rugosus*. Intensity of foraging exhibited a log decay with distance from the nest and even forage distribution, but increased in response to greater forage concentration (Table 8).

Table 8. The effect of distance and forage concentration of foraging activity of *Pogonomyrmex barbatus**

Experiment Number	Distance to colony in meters		
	3m	4m	6m
Number to the nest/minute			
Pogbar #1 Exp. 1	4.2	1.2	.4
2	2.4	.8	1.2
3	3.4	2.9	.7
4	6.1	7.6	.6

	3m	5m	6m
Pogbar #2 Exp. 1			
2	1.4		
3	1.6		
4	6.1	.4	.2
	5.2	4.6	.4

*See text for details.

While these are scant data on which to base speculation, it is tempting to hypothesize that foraging response is the same to distance and forage concentration in all harvester ant species.

Table 9. The relationship of foraging activity and soil surface temperature and saturation deficit in *Pogonomyrma barbatum**

Soil Surface Temperature	Saturation Deficit							
	0-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40
16-20	29.5							
21-25								
26-30					188			
31-35					297	14.5		
36-40				214				
41-45							24.1	
46-50								
51-55							3.25	0
56-60							0	

*Table values are number to nest/minute.

DISCUSSION

Novomessor cockerelli exhibited the greatest difference in foraging pattern in the species investigated. In *N. cockerelli* maximum foraging activity was in the early evening, coincident with the activity of insects. While *N. cockerelli* will take seeds or fruits, arthropods and arthropod parts apparently are the preferred forage. Sufficient night samples of foraged materials were not obtained to compare with day samples for determination of significant differences in materials foraged at night in either *N. cockerelli* or *P. rugosus*. These data would be necessary to evaluate the significance of nocturnal activity in these species. It is possible that *P. rugosus* switches preference to arthropods when foraging at night. Nocturnalism is advantageous to an insect scavenger or predator in the desert, since there is a marked rise in insect activity after dark.

The forager activity patterns in the three species of *Pogonomyrma* exhibit differences in the temporal components of the niches of these species. While there is coincidence in maximum foraging activity in the three species at 45 C, the foraging rate in *P. rugosus* dropped sharply at higher temperatures, while the rates of *P. desertorum* and *P. californicus* remained fairly high. The greater insensitivity of these species to high saturation deficits and temperatures greater than 45 C allow them to forage for the items preferred by *P. rugosus* with reduced competition. Although there is considerable overlap in food preference and time of foraging in the three species, their foraging behavior differs. *P. desertorum* and *P. californicus* frequently forage in the forbs,

cutting fruits from the plants and dropping to the ground with their booty. The heavier *P. rugosus* workers were observed foraging in the dense canopy of *Tridens pulchellus* but not on the sparsely branched forbs. *P. desertorum* and *P. californicus* appear to have greater niche overlap than either of these species with *P. rugosus*. However, in the intensive study area the density of *P. californicus* was considerably lower than *P. desertorum*. Aspects of competition and niche overlap in these species is the subject of the MS thesis of Helen Hart (R.A. on this study).

The large differences in soil temperatures at initiation of foraging in the spring and cessation of foraging in the fall were unexpected. We had assumed that soil temperatures at 40-50 cm would represent the thermal barrier for movement to the surface where mid-day soil surface temperatures are sufficiently high for foraging even in mid-winter. We had also assumed that the soil temperature barrier to movement would be the same for initiation and cessation of foraging. The first assumption need not be rejected but the second requires modification. If seasonal acclimation occurred, the minimum temperature for activity could be lowered, allowing an extended foraging period in the fall. This would be particularly adaptive in the Chihuahuan Desert, where late summer annuals are the most reliable source of forage, and fruit ripening of many species occurs in late September and October. We are currently investigating maximum and minimum activity temperatures (ACTmax and ACTmin) in the laboratory and will investigate the effects of acclimation on ACTmax and ACTmin.

The data clearly demonstrate that both saturation deficit (or some other measure of air water content) and temperature are parameters which must be considered in order to predict foraging activity in harvester ants. However, Eddy (1970) reported that relative humidity had no influence on activity in *P. occidentalis*. Other factors affecting activity probably act more as "on-off" switches than rate regulators. Light intensity appears to affect the behavior of some species. *P. californicus* and *P. desertorum* cease foraging at dusk, even when soil surface temperatures and saturation deficits are favorable for foraging. Eddy determined that *P. occidentalis* ceased activity at light intensities <300 ft. candles and above 7000 ft. candles. Box (1960) reported that *P. barbatus* in south Texas foraged mostly at night. In eastern Arizona, we found that *P. barbatus* ceased foraging at dusk although temperature and moisture conditions were favorable for foraging. This suggests the possibility of geographical differences in the behavior patterns of the same species.

Lavigne et al. (1971) analyzed factors affecting foraging in *P. occidentalis* and found that there were two peaks in activity as measured foragers egress from the colony. Bursts of egress activity were noted in our studies but the return rate of foragers did not result in bursts as such. Since we were interested in predicting the number of fruits brought to the colony per unit time, we felt the return rate to be a more meaningful number.

The technique of using dyed grain for studying foraging intensity and colony interactions was used by Willard and Crowell (1965) in studies of *Pogonomyrmex owyheei*. Their experiments showed that in *P. owyheei* complete overlapping of foraging occurred where mound density was high. They reported variation in foraging intensity as a function of distance and with direction from the nest. An evaluation of their data is complicated by small sample sizes and the extended periods of single observations.

The log decay of foraging effort as a function of distance from the colony indicates a random search pattern. However, when the concentration of forage resource was increased, the foraging effort was increased at that distance. Some foraging occurred at a distance greater than the highly concentrated forage. This indicates that some foragers probably act as scouts and always forage at great distances from the colony. Factors in addition to food concentration and distance may affect the foraging intensity of ants, 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*. In our studies we found that foraging intensity decreased markedly after we had conducted our dyed seed experiments for several days in succession. When colonies 18 and 62 were excavated, the storage chambers were found filled with dyed grain. In *Pogonomyrmex* we hypothesize that foraging intensity may decrease when storage chambers are filled and/or all workers and larvae are satiated. This aspect of foraging behavior must be quantified before an accurate model of foraging in harvester ants can be constructed.

The variation in success rate of returning foragers is difficult to interpret since success rate was found to be independent of soil temperature, saturation deficit, and hour of the day. Further experiments examining success rate as a function of forage resource distribution may provide the answer to this question. However, this may also be an intrinsic part of the foraging behavior of *P. rugosus* and *N. cockerelli*. *P. californicus* and *P. desertorum* foragers return to the colony at a lower rate than *P. rugosus* and *N. cockerelli*, but few, if any, unsuccessful foragers were observed in the former two. We might hypothesize that foragers of *P. rugosus* and *N. cockerelli* search for a fixed period and return to the nest if unsuccessful and that *P. californicus* and *P. desertorum* search until successful. Experiments designed to test this hypothesis will be conducted in 1973.

There appears to be little if any direct aggressive interaction between workers of different colonies of the same species or of different species. The degree of overlap of foraging territories and the shapes of foraging territories cannot be explained by interaction between colonies. If foraging of colonies were random and unaffected by the foraging activities of adjacent colonies, foraging territories would be circular or nearly so. However, this is not the situation in *P. rugosus* and *N. cockerelli*.

Distortion of the foraging territory appears not to be the result of interaction between colonies. The foraging territory of colony 50 did not change after colony 18, which had a foraging area overlapping with 50, had been completely excavated. The constancy and distorted shapes of foraging territories require explanation but no reasonable hypothesis can be offered.

Forage preferences of *Pogonomyrmex* were not a simple function of seed availability. There appeared to be a correlation between phenology and relative abundance of seeds and their importance as forage items. *Eriogonum trichopes* and *E. abertianum* var. *abertianum*, which set fruit in early June and continued to flower and fruit throughout July and August, were the most important. In July, when *Chenopodium* matured, the fruits of this species increased in importance. These relationships suggest that forage preference may be a function of the forage item previously brought in. Thus both phenology, abundance and rate of maturation of fruits appear to be considerations in forage selection in *Pogonomyrmex*. Selectivity of forage items in *Veromessor pergandei* was reported by Tevis (1958), who pointed out that this species did not gather the most abundant seeds.

The data in this study support the contention of Tevis (1958) that, while the foraging activity of harvester ants has a small effect on the total seed production of annuals, their activity can be significant by affecting the seed reserves of preferred plant species (e.g., *Eriogonum trichopes*). Willard and Crowell (1965) provided a list of plant species foraged by *P. owyheeii*, ranked as to relative abundance in storage chambers excavated, but provided no data on abundance or seed production of plants in the area. Eddy (1970) found that *P. occidentalis* foragers brought in seeds of almost every species of plant in the area and that there was a high correlation between the rank of cover of a plant species and the number of seeds of that species foraged. Additional studies of foraging habits of species of harvester ants in relation to seed production may confirm this hypothesis.

The foraging strategy of *N. cockerelli* appears to be more like that reported for *V. pergandei* (Went et al., 1972), which brings almost anything back to the nest: sticks, leaves, good and bad fruits, dead insects or parts, and fecal material. Foragers of *N. cockerelli* carried a similar spectrum of materials to the colony. Examination of these materials revealed that a preponderance of the foraged items was invaded by fungal hyphae. Even the whole fruits of *Eriogonum* spp. were predominantly infected with hyphae. Examination of the materials excavated from the upper meter of a *N. cockerelli* nest by Crawford and Wooten in their millipede study (1973), revealed numerous large balls of organic material and hyphae in the upper chambers. In addition, there appears to be increased fungal invasion of the soil surrounding chambers of this species. As a consequence of these observations, we suggest that *N. cockerelli* may be culturing fungi as a food source.

2.3.3.2.-60

All of the harvester ant species studied foraged on termites when these were available, and also brought in insect carrion. This is probably important to the health of such colonies by providing a protein source for peak reproduction and growth. With further study we may be able to assess the role of harvester ants as termite predators.

In the species of annuals sampled to obtain predictive equations for plant parts as a function of some easily-measured length dimension, good correlations were obtained for most species except for fruit numbers in *E. trichopes* and *E. abertianum*. These species of *Eriogonum* exhibited nearly continuous growth pattern and fruit production during about 90 days of the growing season. Consequently, when these plants were sampled at a supposed peak in fruit maturity, many of the fruits had been lost even as the plants were growing. This problem can be overcome by placing seed fall traps around the bases of a number of these plants at the beginning of the growing season to obtain data on rate and sum of fruit production, which can be regressed on canopy volume or area. In the other species of annuals, fruit maturation on any one plant was fairly synchronous. Therefore, the relationship of fruit numbers to a canopy dimension could be predicted with fair reliability.

The technique of allometric analysis of annuals and perennial forbs to provide equations for predicting biomass of plant parts appears to have some general applicability, especially where fairly frequent periodic sampling without removal is desirable. Coupling these equations with a plotless technique (point-quarter) for estimating density provides a method for rapid estimation of biomass production, seed production, etc., in an area regardless of the density of annuals. In exceedingly dry years, such as 1971 at the Jornada, the sparsity of annuals makes quadrat sampling an unreliable method for estimating production of annuals, but this is not a criticism of the plotless method.

Forager population and colony size estimates (A3UEE15). The peak forager population sizes recorded in July may in fact reflect the magnitude of total colony size. Two colonies of *P. rugosus* and a *P. californicus* colony excavated in August and September had total populations of approximately 2000 individuals. Mobilizing essentially the entire adult population for foraging at times of peak fruit production and favorable climatic conditions would be an important feature of the social behavior of desert seed-foraging insects. The behavior would insure maximum storage of food items at peak availability. Since ants are limited to selection of seeds or fruits on the soil surface or on plants, wind or water can reduce the available food base very rapidly. We noted virtual disappearance of fruit caches around the base of *Eriogonum* plants following heavy rains. These fruits apparently are transported by surface flow and buried in places where plant materials obstruct sheet flow. These observations suggest that

harvester ants must maximally exploit these resources before they are dispersed or made unavailable by climatic events. We have two sets of soil surface samples obtained prior to and following a sheet flow event. These samples are currently being processed to determine changes in seed availability.

Brian (1971) criticized nest excavation as a means of getting at colony size, stating that with regard to large diffuse colonies, it is easy to be persuaded that the whole colony has been discovered. We are certain that our excavation of the two *P. rugosus* colonies recovered all but an insignificant number of the colony members. Since we were unsuccessful in obtaining the queen in the *P. californicus* excavation, we are not as confident of that colony size estimate.

Brian (1971) also provided a critique of mark-recapture methods. He pointed out that ants and termites remove paint. However, if such studies are conducted over a 24-48 hr period, sufficient paint marks remain to identify recaptures. Consequently we feel that our estimates of forager population size are fairly reliable.

Laboratory experiments in 1971 indicated that rhodamine- (a fluorescent vital stain) dyed food might provide reliable estimates for whole colony populations. In 1972, we attempted to apply this technique to field populations. Metal cone barriers were built to place around colonies to starve them prior to providing rhodamine-dyed seeds. Problems encountered in retaining the colony within the barriers caused this approach to be abandoned in order to obtain other kinds of data.

To the casual observer there appears to be a degree of regularity in the distribution of harvester ant colonies. Our analysis showed a clumped distribution in *Novomessor* and *P. desertorum* and a random distribution in *P. rugosus*. The high degree of clumping in *P. desertorum* may indicate multiple entrances to the same colony. We did not place sufficient emphasis on mark-recapture and excavation in this species to provide an answer to this question. The factors resulting in a clumped distribution in these species require further analysis.

EXPECTATIONS

1. The colony density of harvester ants of the genus *Pheidole* appears to be fairly high in numerous areas in the hot deserts. We shall apply the techniques devised for studies of the larger harvester ants to evaluate the effects of climatic factors on foraging, forager population numbers and foraging preferences.

2. Dr. George Ettershank has continued to experiment with rhodamine-tagging techniques. With his assistance, we will continue field assessment of this technique for estimating population size.

3. We recognize the need for more data on the foraging habits of *N. cockerelli* and *P. rugosus* at night. These studies will be scheduled at regular intervals in 1973.

4. In order to test the generalizations of foraging habits and predictability of preferred species of forage we will study the food habits-plant production relationships in several different plant communities.

5. We will attempt to fill in gaps in our understanding of the foraging behavior of *P. barbatus* and attempt to obtain some data on the enigmatic *P. apache*.

6. The relative success of our 1972 mark-recapture program suggests that continued efforts with that technique plus removal studies may provide reliable estimates of population size.

7. We will continue our studies of oxygen consumption, water loss and temperature relationships to the harvester ant species in our laboratory colonies.

ACKNOWLEDGEMENTS

Special recognition is due George Ettershank, co-author of the 1971 report, who has continued to make significant contributions to this work by his suggestions and continuous input of ideas. James Zimmerman directed the work on this project while I was on sabbatical leave in the spring. Linda Whitford assisted with data summarization. Paul Whitson, John Ludwig and Richard Spellenberg provided valuable ideas for studying annual plants and identified plants and seeds. The diligent efforts of my field assistants are gratefully acknowledged. Their sweat and muscle provided the bulk of the data: Helen Hart, Rebecca Delson, Barry O'Laughlin, Tim Cox, Ken Rall, Fred Dax, Hank Becker, and Beverly Stock. Special thanks are due to my son Brett for providing the simple and very workable idea of clearing circles around ant colonies to study foraging behavior.

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