EFFECTS OF FERAL ANIMALS ON WOODY VEGETATION: SANTA CRUZ ISLAND, CALIFORNIA

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INTRODUCTION

Large feral herbivores have played a significant ecological role in many areas where they have either been set free or have escaped domestication. The feral pig (Sus scrofa L.), goat (Capra hircus L.), and sheep (Ovis aries L.) have been particularly destructive of native vegetation in areas where they have been uncontrolled (Yocum 1967; Bratton 1975; Coblentz 1978). Island ecosystems are especially sensitive to these generalist herbivores, partly because most island floras have evolved without mammalian herbivorous pressures; partly because islands may often have more moderate weather and climatic conditions than their mainland counterparts, thus reducing the probability of decimating catastrophes; and partly because most islands do not have natural predators that control herbivore populations (Holdgate & Wace 1971). Sheep, goats, and pigs have been implicated in the destruction or near destruction of native forest in Hawai'i (Bryan 1937, 1950; Warner 1960; Yoshinaga, in prep.). Sheep and goats have had a significant effect on the vegetation of New Zealand and adjacent islands (Wodzicki 1950, 1961; Turbott 1963; Atkinson 1964; Hercus 1964; Howard 1964; Wilson & Orwin 1964; Wraight 1964; Holdgate 1967).

This study was designed to assess some of the effects of feral herbivores, primarily the feral Merino sheep, on selected woody vegetation types on Santa Cruz Island, California. Until recently, most plant studies on Santa Cruz Island have focused on floristics, and to some extent, on the description of community types (Dunkle 1950; Minnich 1980). Recent research has shown that the presence of feral sheep has had an important effect on the distribution and abundance of most components of island vegetation. Hobbs (1978, 1980), studying the effects of feral sheep on Pinus muricata D. Don populations, concludes that species composition, foliar cover, and regeneration were all seriously affected and that under continued heavy grazing the forested area would probably be completely converted to grassland. Minnich (1980) suggests that coastal sage-scrub is the vegetation type on the island that is most seriously affected by grazing, in combination with a reduction or elimination of fire. Brumbaugh (1980), utilizing historic records dating from the mid-19th century and aerial photographs that span nearly 40 years, documents the reduction of many chaparral stands within historic times. He also discusses some of the impacts that feral ungulates have had on geomorphic processes on the island.

The object of this study was to determine if grazing intensity has had a significant impact on chaparral shrub stature. Differences in grazing intensities between portions of the island have been established for at least three decades (Stanton & Laughrin, pers. comm.) as a result of sheep management practices. Sheep management has been accomplished mostly by fencing and has been enhanced periodically by hunting operations.

Description of the Island

Santa Cruz Island is the largest of the California Channel Islands, with an area of about 250 km^2, and is located about 30 km south of the Santa Barbara Coast (Fig. 1). The long axis of the island is oriented in a generally east-west direction, spanning a distance of about 35 km; the island varies in width up to about 11 km.

The island is topographically varied, ranging from expanses of nearly level marine terraces, particularly in the western and some localized northern areas, to extremely steep scarps and deeply incised canyons. Two main ridges, separated by a linear alluvial valley, form the bulk of the island's mass. The northern range, with a ridgeline extending for several kilometers at an elevation greater than 550 m, has the most rugged overall relief on the island, with steep canyons and many slopes greater then 45°. The southern ridge rises steeply out of the Central Valley (see Fig. 3 for place name locations) to a ridgeline that averages about 390 m in elevation, the southern flank of which is dissected by a few large dendritic drainage basins. Farther east, the isthmus is an extension of the northern ridge but at a considerably lower elevation. The isthmus ridge has rolling, undulating terrain which becomes more hummocky north and south of the ridgeline and drops precipitously to the sea on both sides. The isthmus is separated from the east end of the island by a steep north-south canyon with near-vertical, highly eroded barren terrain. The eastern end of the island is formed of a small mountain mass which descends steeply to a series of marine terraces and sea bluffs.

Geologically the island is a complex of volcanic, metamorphic, and sedimentary units with a high degree of folding and faulting. The steep northern portion is formed almost entirely of Miocene andesitic and basaltic volcanics (California State, Division of Mines and Geology 1971). The Santa Cruz Island Fault, a left lateral strike-slip fault, separates the northern and southern ridges creating the Central Valley. South of the fault, much of the southern range is composed of the Santa Cruz Island Schist of pre-Cretaceous age. Volcaniclastic members of the Blanca formation are found in this area also. The southwestern portion of the island is dominated by marine formations ranging in age from Eocene to Quaternary. Most of the isthmus area is composed of shales of the Monterey formation of middle Miocene origin.

Field observations indicate that most of the surface soils are of a loamy texture, ranging from silt and clay loams to coarser sandy loams. Soils for the most part are shallow with a great amount of erosional losses due to overgrazing by the sheep and rooting by pigs.

Climate is typical of southern California coastal areas in general. Rainfall maxima occur during the winter months, with protracted rainless periods occurring throughout most of the rest of the year. Sixty-eight years of rainfall data from the Central Valley indicate an annual average, not including fog-drip, of about 50 cm (Weisman & Rentz 1977). Maritime air moderates the climate, especially in coastal areas, in comparison to many mainland sites. Fog-drip may account for an appreciable moisture input in some coastal or windward locations (Hobbs 1978). Temperature extremes are more pronounced in the Central Valley than at coastal locations and mid-day humidity is generally lower in the Central Valley than at coastal and ridge locations.

Vegetation

Major physiognomic and floristic units were mapped from color infra-red imagery flown in 1970 (Minnich 1980). Figure 2 shows a portion of the center of the island comprising the area of this study.

Grassland forms the most extensive vegetation type on the island, dominating marine terraces, much of the heavily grazed northern portion, the Central Valley, and the isthmus. The dominant species are generally *Avena barbata* Brot.; *Bromus mollis* L.; *B. rubens* L.; *Festuca* spp.; and *Hordeum* spp. *Lamarckia aurea* (L.) Moench dominates areas with heavy sheep use, particularly the northern range. Native *Stipa* spp. become locally important, especially along the southern coastal slopes.

Chaparral is found most commonly in island-like stands surrounded by grassland. More extensive stands occur on north-facing slopes adjacent to the Central Valley and the drainages into Willows Canyon, Laguna Canyon, and Coches Prietos. Island physiognomy differs from mainland chaparral in the pronounced arborescence of most shrubs. *Quercus dumosa* Nutt. is the most common species, often found in pure stands, especially in areas where sheep grazing has been common. Other species that dominate or form important elements of the chaparral composition are *Adenostoma fasciculatum* H. & A.; *Arctostaphylos insularis* Greene; *A. tomentosa* (Pursh) Lindl. ssp. *insulicola* Wells; *Ceanothus insularis* Eastw.; *Cercocarpus betuloides* Nutt. ex T. & G.; *Heteromeles arbutifolia* M. Roem.; *Prunus lyonii* (Eastw.) Sarg.; and *Rhamnus crocea* ssp. *pirifolia* (Greene) C. B. Wolf.

Coastal sage-scrub is limited to only about 6% of the island (Minnich 1980), mostly along steep southern exposures.

Depauperate riparian woodlands and shrub thickets occupy most of the valley bottoms and occur in some steep canyon bottoms. The dominant valley shrub species is *Baccharis glutinosa*

Pers., which forms many pure stands in the Central Valley and southern drainages. Some of the steeper northern canyon bottoms contain *Populus fremontii* Wats. and semi-riparian *Quercus agrifolia* Neé.

Oak woodlands are found on north-facing slopes, steep protected canyons, and a few riparian bottom locations. Populations are extremely patchy with most stands occurring in the deeply incised northern drainages and slopes of the northern ridge. *Quercus agrifolia* is the dominant species with *Q. chrysolepis* Liebm. and *Q. tomentella* Engelm. being locally abundant. Interspecific hybrids in *Quercus* often make species identification difficult (C. Remington, pers. comm.).

Lyonothamnus floribundus Gray var. *asplenifolius* (Green) is found in small compact stands throughout much of the central portion of the island. Minnich (1980) has located a minimum of 161 *Lyonothamnus* groves from aerial imagery, mostly on north or northeast facing slopes near the tops of canyons. The majority of the groves are found between the isthmus and the western pine forest. They average about 25 m in diameter and are fairly equally represented in northern, central, and southern drainages.

Closed-coned pine forest, comprised of *Pinus muricata*, occurs in three localities in areas receiving a substantial amount of summer fog. The western population, found in and adjacent to Christy Canyon, is the largest, occupying over 100 ha. Density, physiognomy, and floristics of the three forests vary considerably, probably as a result of differing sheep influences (Hobbs 1978).

Grazing History

Ellison (1937) gives a brief account of the history of Santa Cruz Island up to the time the island was purchased by E. L. Stanton.

European discovery occurred on October 13, 1542, when Cabrillo landed. Prior to this, a substantial Chumash and pre-Chumash population had occupied the island for several thousand years (Rozaire 1967). In 1839, Andrés Castillero was given title to the island by the president of Mexico. After California attained statehood in 1850, lengthy litigation culminated in a U. S. Supreme Court decision that reaffirmed the ownership by Castillero. During the court proceedings, island supervision passed to J. B. Shaw during whose tenure large-scale sheep ranching began, 1853 being the earliest recorded date for sheep on the island (Shaw 1857). The island was sold to Justinian Caire in 1869 and remained in the Caire family until 1937.

Wheeler (1876) reported that the island had almost entirely been "given up" to sheep ranching, with no less than 60,000 head on the island at the time of his survey in 1875. He reported that due to overgrazing, many of the forests had disappeared, leaving stumps and roots in their place. Wheeler wrote:

> In areas most sheep grazed only sage-brush, cactees and the erodium or storksbill were left, everything else being swept away.....Even the sage-brush was disappearing, as year after year, the sheep had eaten away its leaves and younger shoots.....Grass is gradually disappearing before the clean sweep made by the sheep herds, whilst castus, especially Opuntia is spreading more and more.

Pigs also had been introduced to the island by the mid-19th century. Wheeler (1876) reported that wild hogs were introduced by Sebastion Viscaino in 1606, but this assertion has not been substantiated. McElrath (1967) claimed that domestic pigs were turned out on the island in the 1860's and later reverted to the wild-type. Dr. C. Stanton (pers. comm.) has said that a Mr. Box raised pigs on the island in the early 1850's and speculated that the present population may be descendants of these.

In 1937 E. L. Stanton purchased most of the island, while the remaining approximately 10% at the east end was transferred to the Gherini family. Cattle ranching has been of major importance on the Stanton portion of the island while sheep ranching has dominated the Gherini land. In the early 1950's the Stantons began a major fencing program and divided the island into large pasture units (Fig. 3). Attempts were made to restrict sheep to the northern range west of Cañon del Puerto. Hobbs (1978) has given a more complete description of fencing and sheep removal. Sheep can still be found in the more rugged portions of the south side of the island, but are not as numerous as in the northern section. Sheep are even more uncommon in the central section, although following periods of intense rainfall, many of the fences wash out allowing sheep access into areas not normally occupied by them.

The total sheep population was estimated at between 10,000 and 20,000 in 1977 (Laughrin, pers. comm.). The population may have increased substantially in the following two years, perhaps by as much as two to three times, because of unusually high rainfall favoring herbaceous growth. Observations in the field between late 1977 and early 1979 indicated that lambing occurred at least twice and possibly three times per year during these inordinately wet years.

Observations of feral pigs are usually difficult due to their evasive behavior and primarily nocturnal habits, and accurate estimates of their population size have not been made. Feral pigs are distributed widely throughout the island, with fences apparently having little or no effect on their overall range or movements.

FIELD METHODS

Shrub Study Sites

Study sites were chosen using methods incorporating field observation, topographic maps, and aerial photography. Extensive and intensive observations were made on foot in different parts of the island to plan methods of sampling and to choose study sites. A major study zone (Fig. 2) was chosen that forms a large belt running across the middle of the island from north to south, coast to coast between Cañada Larga on the west and the Stanton Ranch on the east. This study zone occupies about 3500 ha and covers three substrate types (volcanic basalts, schists, and volcaniclastics), contrasting grazing regimes, and includes most types of shrub vegetation on the island.

Within the study zone 9 study areas were chosen based upon field observation and aerial infra-red and black-and-white imagery. The infra-red imagery was flown in July 1970 and the black-and-white photographs in 1929, 1952, and 1964. Infra-red imagery is in the possession of the Geography Department, University of California, Los Angeles, and the black-and-white photographs are in the possession of the University of California Field Station located on Santa Cruz Island. Three study sites were located in the lightly grazed portion, three in the moderately grazed portion, and three in the heavily grazed portion of the study zone. Grazing intensity was determined by the location of fences and a knowledge of how many sheep were usually present, based on personal communication with island personnel and on field observations.

The heavily grazed part of the island is the area north of the fenceline that follows the southern base of the northern range (Fig. 3), extending between Cañada Puerto and the western end of the island. The moderately grazed area includes most of the island south of the southern range ridgetop, including the Sierra Blanca Range, Willows Canyon, Laguna Canyon, and the southern flanks of the isthmus ridge. The lightly grazed area, for the purposes of this study, is principally that portion of the island between the heavily and moderately grazed portions; that is, the area between the fenceline at the base of the northern range and the fenceline along the crest of the southern range, between Cañada Puerto and the ocean at Christy Ranch, including the Central Valley and the north-facing slopes of the southern range.

Grazing intensity is defined, for the purposes of this study, on the basis of the relative numbers of sheep expected in a given area over a fairly long period of time; pigs are found throughout the island and apparently their distribution is not affected significantly by fences; cattle are grazed primarily in the lowland areas dominated by the grassland. Sheep, in large numbers, have purposely been allowed to graze the northern range between Cañada Puerto and West Point and have purposely been fenced out of the Central Valley and adjacent southern slopes, creating what is here called heavily and lightly grazed regimes. While sheep are hunted out of the southern portion of the island on a continuous basis, they are not removed as completely as they are in the central portion, partly due to difficulty of access along the southern slopes. Hence, the southern portion of the island periodically retains a fair sized sheep population and is moderately grazed in comparison to the central part. The terms "moderately, lightly, or heavily grazed" are only relevant when grazing pressure is considered over several months to a few years. This is because there have been periods of several months, especially following heavy rains and associated fence damage, when sheep have had easy access to most parts of the island. During these times the numbers of sheep may increase substantially in the "lightly" and "moderately" grazed regimes.

The present grazing regimes can be considered to have originated in the early 1950's with the establishment of the fencing program by E. L. Stanton. The condition of vegetation stature before this time is difficult to assess, although differences in coverage can be analyzed from the aerial photographs. Therefore, shrub size between the three regimes are attributed either to differences in grazing intensity since fence establishment or to differences in environmental factors between the different regimes.

Each study area was at least 0.25 km^2 and had more than about 50% shrub cover as determined by the aerial photographs, except for one more sparsely covered site in the heavily grazed portion. No study areas were located on slopes steeper than about 45°. The study areas were circumscribed on a U. S. Geological Survey (USGS) 7-1/2 minute topographic sheet (USGS 1943) with a square grid measuring 0.5 km on a side. These 0.25 km^2 sites were divided into 25-0.01 km^2 (1 ha) potential sampling sites in a grid pattern, and three sites in each study area were marked on the USGS topographic sheet and then located as accurately in the field as possible (Fig. 2).

After locating the sample sites in the field, a 50-meter baseline tape was set out across the slope within the sites such that perpendicular transects could be located upslope or downslope of the baseline. Two randomly chosen 4-meter wide belt transects were laid out for each sampling site and all woody shrub and tree species rooted inside of the transects were recorded. Field sampling was done from October 1978 through April 1979.

Measurements

Vegetation parameters recorded include frequency of species occurrence, based on individuals rooted within 1 m X 4 m contiguous quadrats along the belt transects. Physical attributes of the shrubs and trees were recorded. Transect length was vegetation dependent and variable in that the transect continued until 10 woody plants were recorded, and terminated where the canopy of the 10th plant ended. Woody plant seedlings located in each of the belt transects were censused and recorded to species as accurately as possible.

Structural measurements include stem diameter at 50 cm above the ground; canopy dimensions (upslope, across slope, and canopy depth); the quality and quantity of basal sprouts; plant height; and height to the canopy bottom.

Because the sampling was carried out over a 10-month period from fall to spring, some of the variables measured, particularly basal sprouts and seedling abundance may have been influenced as much or more by season of sampling as by grazing intensity. A greater number of samples were taken in the fall in all three grazing regimes, with 62% of the sampling completed in both moderately and lightly grazed areas in the fall and 90% of the sampling completed in the fall in the heavily grazed regime. The remainder of all samples were taken in the spring (March-April). This is an obvious sampling bias, particularly as regards the heavily grazed regime, that will need to be considered when analyzing the results.

The low number of sample sites visited in the heavily grazed area in the spring probably had the greatest effect on the numbers of woody plant seedlings encountered. Sheep would have removed nearly all seedlings by the fall of 1978 that may have existed in the heavily grazed area, and with only a minimal census in the heavily grazed regime in the spring of 1979, contrasts in the data may be misleading. Data on the number and quality of basal sprouts in the heavily grazed area may have suffered a similar bias.

A final factor to be considered is the geologic substrate upon which the plants in each regime are found. All three regimes are located on different substrates, which may affect any or all of the variables sampled. All of the heavily grazed sites are located on Miocene volcanics, primarily basalts. All of the lightly grazed sites are on pre-Cretaceous metamorphic schists. Moderately grazed sites are found on Mesozoic granitic rocks and pre-Cretaceous schists. Differences in geology will be considered in the final analysis.

RESULTS

Shrub Study Sites

The sites ranged in elevation from 137 m to 412 m and were located from 1.5 km to 4.5 km from the coast, on slopes varying from 0° to 45° (mean slope angle was 30°). A breakdown of sampling sites by aspect and the number of meters transectd in each of the grazing regimes is given in Table 1. About 2/3 of the sampling sites, including all those in the moderately grazed category, were on north-facing slopes, a bias that has to be taken into account in interpreting the results.

Species Distribution and Composition

Species frequency for the three regimes is given in Table 2. The most striking differences between the three regimes are seen in the distributions of *Adenostoma fasciculatum*, the two *Arctostaphylos* species, *Cercocarpus betuloides*, and *Quercus dumosa*. *Quercus dumosa*, by far the most common shrub species found on Santa Cruz Island, was the dominant shrub in both the heavily and lightly grazed areas, but was relatively less common in the moderately grazed southern portion of the island. *Adenostoma fasciculatum* was more evenly represented in the three regimes, but was the commonest shrub encountered in the moderately grazed southern portion. *Cercocarpus betuloides* was found more often in the heavily grazed northern range than in the other two regimes. The endemic *Arctostaphylos insularis*, which does not form a basal burl, was found about equally in the lightly and moderately grazed regimes but was not commonly encountered in the heavily grazed portion, while the sympatric *A. tomentosa* ssp. *insulicola* was relatively more numerous in the moderate and heavily grazed portions but uncommon in the lightly grazed sites.

Differences in species composition between the three regimes undoubtedly arise from a number of causes including such site differences as the effects of mineral substrate, prevailing winds, distance to coast, slope, aspect, feral animal impacts, and the pre-disturbance composition. There is no intention here to implicate grazing animals as the prime factor in the present vegetation array.

An over-riding factor influencing the post disturbance composition is species composition prior to feral animal release. It is unlikely that all of the species encountered were distributed evenly throughout the different areas of this study prior to grazing. For this reason any shrub vegetation remaining after disturbance will be a reflection, in part, of the earlier vegetation patterning.

The fact that each of the three grazing regimes is dominated by a different geologic substrate needs serious attention. The substrate and overlying soil affect such factors as soil erodibility, compaction, and moisture holding capacity. These factors, in turn, would influence species composition in grazed areas both as a result of their affect on original vegetation and as a result of their affect on the tolerance of species to grazing pressure. Without being able to compare ungrazed areas on all three substrates, it is difficult to assess which shrub species would prefer which substrate type and, therefore, what the overall affect on species patterning would be.

I believe that all of the above factors acting separately or together, plus other ecological factors such as tolerance to prevailing winds, aspect (although the majority of sites face north), exposure to salt air and so forth, are largely responsible for the species composition as presented in Table 2. However, the preponderance of *Quercus dumosa* and *Cercocarpus betuloides* in the heavily grazed regime is probably largely a function of feral animal pressure, as is the virtual absence of *Ceanothus* species under heavy grazing pressure. While the reduction of *Arctostaphylos insularis* under heavy grazing may be partially attributed to feral animals, grazing certainly does not explain the high incidence of *A. tomentosa* ssp. *insulicola* in the moderately grazed southern portion of the island. The endemic *A. insularis*, which does not form a basal burl, was found about equally in the lightly and moderately grazed regimes but was scarce in the heavily grazed portion, while the sympatric burl-forming *A. tomentosa* ssp. *insulicola* was more numerous in the moderately and heavily grazed portions.

Species composition is presented here more as background for assessing the structural variables presented later than to establish an overall species pattern for the three regimes.

The number of seedlings encountered in the transects of each of the grazing regimes is listed in Table 3. Species identification of chaparral seedlings is difficult and these data should be interpreted with caution. However, the overall difference in total seedling number is obvious. The limited number of sites transected in the heavily grazed regime in the spring, when newly germinated seedlings would be most prevalent, undoubtedly had an influence on the seedling census presented here. Even considering this bias, however, I believe that the seedling population in the heavily grazed area is substantially less than in the other areas, regardless of season.

Quercus dumosa, which forms the dominant adult shrub in most of the study sites (Table 2), is also the dominant seedling in the area studied (Table 3). Fairly large numbers of *Heteromeles arbutifolia*, *Ceanothus insularis*, and *Rhamnus crocea* ssp. *pirifolia* seedlings are found in areas of reduced sheep grazing, although these shrubs are not well-represented in the adult populations.

Shrub Structure

The results of structural analysis of the shrub stands in the three different areas indicated a general increase in stature (Figs. 4 & 6; Table 4) as the grazing intensity increased, plus ~~an increase in the number of smaller shrubs in the more lightly~~ grazed areas. Mean values of stem diameter, canopy area, height to canopy bottom, shrub height, and canopy depth were all similar when contrasting the lightly and moderately grazed regimes, while values were substantially greater in all cases in the heavily grazed regime. This increase in shrub size is probably a result, either directly or indirectly, of the increased grazing intensity. Height to canopy bottom, partly a function of browsing of the lower foliage, was greater on average by nearly 0.4 m in the heavily grazed portion than in either of the other two areas.

While there was a slight increase in the number of trunks per shrub in the more heavily grazed areas (Table 4), this variable was not substantially affected by grazing; all areas had a preponderance of single stemmed shrubs (Fig. 5).

One of the most striking differences observed between the three grazing regimes was the quantity and quality of basal sprouts (Fig. 7). Due mainly to the high proportion of non-sprouting species, all regimes had many individuals without sprouts. However, the proportion of individuals without sprouts in the heavily grazed regime was inordinately high. This is partly a result of the season of sampling (few samples taken from the heavily grazed area in the spring). However, I observed a quick removal of basal sprouts by sheep throughout the heavily grazed area in the spring and I believe this area would show a significant decrease in sprouts in any season. There was a much higher proportion of individuals with dense, high quality sprouts in the lightly grazed regime than in either of the other two areas.

Individual Species Analysis

Because species composition varied significantly between the three grazing regimes, an analysis of the two most abundant species common to all three regimes was undertaken. An analysis of the same variables was made for *Quercus dumosa* and *Adenostoma fasciculatum* as for the previous analysis of all shrubs. In order to help reduce variation caused by unmeasured environmental factors such as moisture availability or insolation, this analysis was restricted to shrubs growing on north-facing slopes (315° - 045°).

Quercus dumosa

As with the entire shrub complex, the mean values for most *Quercus dumosa* variables indicate a general increase in size with increased grazing pressure (Figs. 8-11; Table 5). The same cautions in interpretation of the data as for the combined analysis must be considered. Other factors than sheep grazing may be significant in the study areas.

Quercus dumosa tends to be a larger than average shrub among the chaparral plants studied here. In most other variables, *Q. dumosa* shows similar trends to the entire shrub array. The most obvious exception is in basal sprouting behavior.

Quercus dumosa has a higher percentage of healthy basal sprouts (Fig. 11) in all three grazing regimes when compared to all shrubs combined. This undoubtedly is due partly to the number of non-sprouting species in the overall assessment. It is also likely that *Q. dumosa* sprouts are not as palatable as other chaparral species. The preponderance of very healthy *Q. dumosa* sprouts in the moderately grazed regime may be related to the relative openness of the vegetation in this area in combination with a reduction in sheep. Light penetration below the canopy may stimulate sprouting. As explained previously, the time of sampling may also have affected the results of the sprouting analysis, particularly in the heavily grazed area which was not sampled heavily in the spring.

Adenostoma fasciculatum

Adenostoma fasciculatum also showed a trend towards increasing size as grazing pressure increased (Figs. 12-15; Table 6). A comparison of Tables 4 and 6 shows that Adenostoma is generally a smaller than average chaparral shrub, except in depth of canopy. Nearly the same magnitude of change occurred in the structural variables for Adenostoma as for Quercus suggesting that although the two species differ in average size, from a structural perspective they both appear to have responded similarly to grazing pressure.

One of the most significant differences in Adenostoma between the three regimes is the quantity and quality of basal sprouts (Fig. 15). Comparing the data for Quercus with that of Adenostoma suggests that Adenostoma is much more palatable and, therefore, more vulnerable from a direct grazing standpoint, than is Quercus. The differences in season of sampling would not account for these differences in sprouting behavior between the two species.

DISCUSSION AND CONCLUSIONS

Vegetation response resulting both directly and indirectly from the herbivore presence is suggested by the data. Average shrub size, as measured by trunk diameter, canopy area, and height, shows a definite trend toward increase with an increase in grazing pressure. In the heavily grazed areas shrubs tend to have a noticeable browse line, with a greater average distance between the canopy bottom and the ground than in lightly grazed areas. One apparent response to this herbivorous pruning is an increase in plant height. Surprisingly, though, plant height increase seems to be more than compensating for browsing, as indicated by a greater average canopy depth (distance between bottom and top of canopy) in the heavily grazed area. The general increase in stature with an increase in grazing intensity appears to corroborate, in part, the hypothesis that grazing is a major factor contributing to island shrub "gigantism" (Minnich 1980).

An increase in the number of smaller diameter shrubs under reduced grazing intensity, plus the presence of shrub seedlings which were absent from the heavily grazed area, suggests that some recruitment of chaparral shrubs is occurring, although it is not immediately evident that recruitment is keeping pace with mortality. If age class is in fact correlated with size class, a younger aged population has become established in areas where sheep have been reduced in number over the past two to three decades. Field reconnaissance indicates that following winter rains Cercocarpus betuloides seedlings were very common along the lower south slope of the heavily grazed northern range adjacent to the Central Valley. The seedlings did not become established, however, either because of the effects of grazing on the soil profile or because they are being eaten by the sheep.

Burl-sprouting species appear to respond rapidly to reduction or removal of sheep, as suggested by the difference in sprouting behavior between the three grazing regimes and vigorous basal sprouting within exclosures. Heteromeles arbutifolia, Quercus dumosa, and Cercocarpus betuloides all began to sprout vigorously from the base following sheep exclusion. Quercus dumosa has a relatively large number of sprouts in all three grazing regimes. Even young sprouts may be less palatable than other shrub species because of the spiny, leathery leaves and tannin compounds. Similar low palatability has been suggested for Q. wislizenii A. DC. (Bissell & Weir 1957).

Decline in vigor leading toward senescence also appears to be correlated with an increase in grazing pressure. The data and field observations suggest that different species have different degrees of tolerance to grazing. Species with large root burls appeared to tolerate grazing pressures somewhat better than those without any burl or with relatively small ones. In many parts of the heavily grazed northern range the most common species remaining were Cercocarpus betuloides, Heteromeles arbutifolia, Quercus dumosa, and Rhamnus crocea ssp. pirifolia, all of which have substantial root structures. Arctostaphylos tomentosa ssp. insulicola, a basal sprouting species, was much more prevalent in the heavily grazed regime than was A. insularis, a non-sprouting form, although both were sympatric where grazing was not as intense. Adenostoma fasciculatum, Ceanothus arboreus Greene, and C. insularis do not appear to fare as well under severe grazing intensity. For Ceanothus this may be due to the relatively short life-span of most individuals, together with a lack of root burls. Adenostoma appears to have a smaller root structure than the other sprouting species, which may be a disadvantage under heavy grazing pressure.

Recent soil loss in some areas of the heavily grazed northern section appears to be as great as 0.2 to 0.3 m, as evidenced by exposed root burls. There has undoubtedly been a tremendous loss of available plant nutrients in the heavily grazed portion; no leaf litter was found in most sites in the northern range. Soil loss together with nutrient loss may also tend to favor those species with large, well-established root structures. Nutrient deficiency, exposed roots resulting from root trampling, increased wind-shear stress resulting from the opening of the canopy, and increased insect attack all appear to be contributing to the general decline in species health in the heavily grazed portions of the island. Brumbaugh (1980) has demonstrated, by comparing 1929 and 1970 aerial photographs, that many existing shrub stands have decreased in areal extent. Those individuals remaining are probably either the healthiest members of the former population or are located in the most favorable sites.

Substrate differences may also have accounted for some of the variation in structure. It is unlikely, however, that the trends suggested by the data would be strictly correlated with substrate. Studies in areas where substrate changes within a given grazing intensity would help to clarify this.

Predictions of vegetation recovery following sheep or pig removal are as yet tenuous. It seems likely that within a short period after feral animal removal a fairly continuous grass-herb cover will occupy many areas that are now bare throughout most of the year. Coastal sage-scrub species might become established, as witnessed in localized areas that have been removed from grazing. Areas within chaparral stands will probably witness an increase in younger aged shrubs concurrent with a continued senescence of the older shrubs. An increase in plant biomass and litter accumulation will undoubtedly increase the frequency and extent of fire in the grassland and chaparral communities, perhaps leading to a more mainland-type physiognomy. However, it is unlikely that by simply eliminating feral animals from Santa Cruz Island, succession will restore a prehistoric assemblage of communities, as has been recently asserted (Minnich 1980). Massive soil and nutrient losses, drastic reductions in the extent of many species and communities, and the presence of European introductions will undoubtedly lead to a different configuration of the community types and species composition than previously existed. The reestablishment of some members of the pre-sheep communities to their former levels may take decades, if in fact, they ever occur.

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TABLE 1. Distribution of chaparral sampling sites by aspect and grazing intensity, Santa Cruz Island, California.

Aspect	No. Sites	Grazing Intensity (meters transected) Light	Moderate	Heavy	Total
N	16	223	340	121	684
E	5	35	0	183	218
S	3	148	0	142	290
W	3	0	78	53	131
TOTAL TRANSECT LENGTH (in m)		406	418	499	1323
AREA SAMPLED (in 4 m wide belt in m^2)		1624	1672	1996	5292

TABLE 2. Frequency of chaparral shrubs in 1 m X 4 m contiguous quadrats for three different grazing regimes (light, moderate, heavy), Santa Cruz Island, California.

Species	% of Quadrats Light	Moderate	Heavy
Quercus dumosa	13	7	7
Adenostoma fasciculatum	9	10	3
Arctostaphylos insularis	3	3	*
Cercocarpus betuloides	2	1	4
Ceanothus insularis	2	*	1
Heteromeles arbutifolia	2	1	*
Rhus ovata	1	1	0
Quercus spp.	1	0	0
Ceanothus arboreus	*	0	0
Arctostaphylos tomentosa ssp. *insulicola*	*	7	1
Prunus lyonii	*	1	1
Baccharis pilularis	*	1	0
Baccharis plummerae	*	*	0
Rhamnus crocea ssp. *pirifolia*	0	1	*
Dendromecon rigida	0	*	0
TOTAL	34	33	17

* Less than 1%

TABLE 3. Number of seedlings found in belt transects in each grazing regime, Santa Cruz Island, California.

Species	Grazing Intensity Light	Moderate	Heavy
Quercus dumosa	47	16	1
Cercocarpus betuloides	39	24	0
Heteromeles arbutifolia	21	24	0
Rhamnus crocea ssp. *pirifolia*	14	14	0
Ceanothus insularis	13	1	0
Prunus lyonii	8	4	0
Quercus agrifolia	4	0	0
Adenostoma fasciculatum	3	0	0
Comarostaphylos diversifolia	2	0	0
Rhus ovata	1	0	0
Rhus integrifolia	1	0	0
Arctostaphylos spp.	0	1	0
TOTAL	153	84	1
AREA (in m^2)	1920	1380	3188
DENSITY (plants/ha)	796	442	3

TABLE 4. Analysis of shrub variables in each grazing regime, Santa Cruz Island, California.

Variable	Grazing Intensity	Number of Plants Sampled	Mean± (S.E.)	95% Conf. Inter.
Diameter at 50 cm (in cm)	Light	170	10.5(0.43)	9.7-11.4
	Moderate	154	10.1(0.49)	9.1-11.1
	Heavy	184	12.4(0.43)	11.5-13.2
# Trunks/ Shrub	Light	169	1.5(0.11)	1.3- 1.7
	Moderate	152	1.4(0.08)	1.2- 1.5
	Heavy	183	1.6(0.09)	1.4- 1.7
Canopy Area (in m^2)	Light	169	22.7(1.90)	19.0-26.4
	Moderate	153	18.2(2.00)	14.2-22.2
	Heavy	184	40.9(3.80)	33.4-48.5
Height to Canopy Bottom (in m)	Light	169	1.0(0.08)	0.8- 1.2
	Moderate	150	1.0(0.06)	0.9- 1.3
	Heavy	183	1.4(0.07)	1.3- 1.5
Shrub Height (in m)	Light	170	2.9(0.10)	2.7- 3.1
	Moderate	154	2.7(0.10)	2.5- 2.9
	Heavy	183	3.2(0.08)	3.0- 3.3
Canopy Depth (in m)	Light	169	1.6(0.07)	1.5- 1.8
	Moderate	153	1.5(0.06)	1.3- 1.6
	Heavy	184	1.8(0.08)	1.6- 1.9
Quality and Quantity of Basal Sprouts	Light	168	2.8(0.15)	2.5- 3.1
	Moderate	151	2.3(0.15)	2.0- 2.6
	Heavy	183	1.5(0.13)	1.3- 1.8

TABLE 5. Analysis of Quercus dumosa variables in each grazing regime, north facing slopes, Santa Cruz Island, California.

Variable	Grazing Intensity	Number of Plants Sampled	Mean± (S.E.)	95% Conf. Inter.
Diameter at 50 cm (in cm)	Light	38	11.3(0.70)	9.9-12.7
	Moderate	14	11.4(0.78)	9.7-13.1
	Heavy	41	13.4(0.99)	11.3-15.4
# Trunks/ Shrub	Light	37	1.2(0.07)	1.0- 1.3
	Moderate	14	1.2(0.15)	0.9- 1.5
	Heavy	41	1.6(0.21)	1.2- 2.1
Canopy Area (in m^2)	Light	37	24.1(4.19)	15.6-32.6
	Moderate	14	27.2(6.25)	13.7-40.7
	Heavy	41	57.8(12.07)	33.4-82.2
Height to Canopy Bottom (in m)	Light	37	1.2(0.23)	0.8- 1.7
	Moderate	14	0.8(0.21)	0.3- 1.2
	Heavy	41	1.5(0.18)	1.1- 1.9
Shrub Height (in m)	Light	38	3.4(0.30)	2.7- 4.0
	Moderate	14	3.2(0.31)	2.5- 3.9
	Heavy	41	3.3(0.20)	2.9- 3.7
Canopy Depth (in m)	Light	37	1.2(0.15)	0.9- 1.5
	Moderate	14	1.8(0.35)	1.0- 2.6
	Heavy	41	1.8(0.19)	1.4- 2.1
Quality and Quantity of Basal Sprouts	Light	37	3.2(0.28)	2.6- 3.8
	Moderate	14	4.0(0.31)	3.3- 4.7
	Heavy	41	3.1(0.24)	2.6- 3.6

TABLE 6. Analysis of Adenostoma fasciculatum variables in each grazing regime, north facing slopes, Santa Cruz Island, California.

Variable	Grazing Intensity	Number of Plants Sampled	Mean± (S.E.)	95% Conf. Inter.
Diameter at 50 cm (in cm)	Light	41	8.7(0.5)	7.7- 9.7
	Moderate	50	8.6(0.3)	7.9- 9.2
	Heavy	26	10.3(0.6)	9.0-11.7
# Trunks/ Shrub	Light	41	1.1(0.1)	1.0- 1.3
	Moderate	50	1.4(0.1)	1.2- 1.7
	Heavy	26	1.5(0.2)	1.2- 1.9
Canopy Area (in m^2)	Light	41	11.6(1.3)	9.0-14.2
	Moderate	50	16.7(2.6)	11.5-21.8
	Heavy	26	20.1(4.4)	11.1-29.8
Height to Canopy Bottom (in m)	Light	41	0.9(0.1)	0.7- 1.2
	Moderate	50	1.2(0.1)	1.0- 1.3
	Heavy	26	1.5(0.1)	1.3- 1.7
Shrub Height (in m)	Light	41	2.4(0.1)	2.3- 2.7
	Moderate	50	2.7(0.1)	2.4- 2.9
	Heavy	26	3.2(0.2)	2.8- 3.6
Canopy Depth (in m)	Light	41	1.5(0.1)	1.2- 1.7
	Moderate	50	1.5(0.1)	1.3- 1.7
	Heavy	26	1.7(0.2)	1.4- 2.1
Quality and Quantity of Basal Sprouts	Light	41	3.0(0.3)	2.5- 3.6
	Moderate	50	1.9(0.2)	1.6- 2.2
	Heavy	26	0.9(0.2)	0.4- 1.4

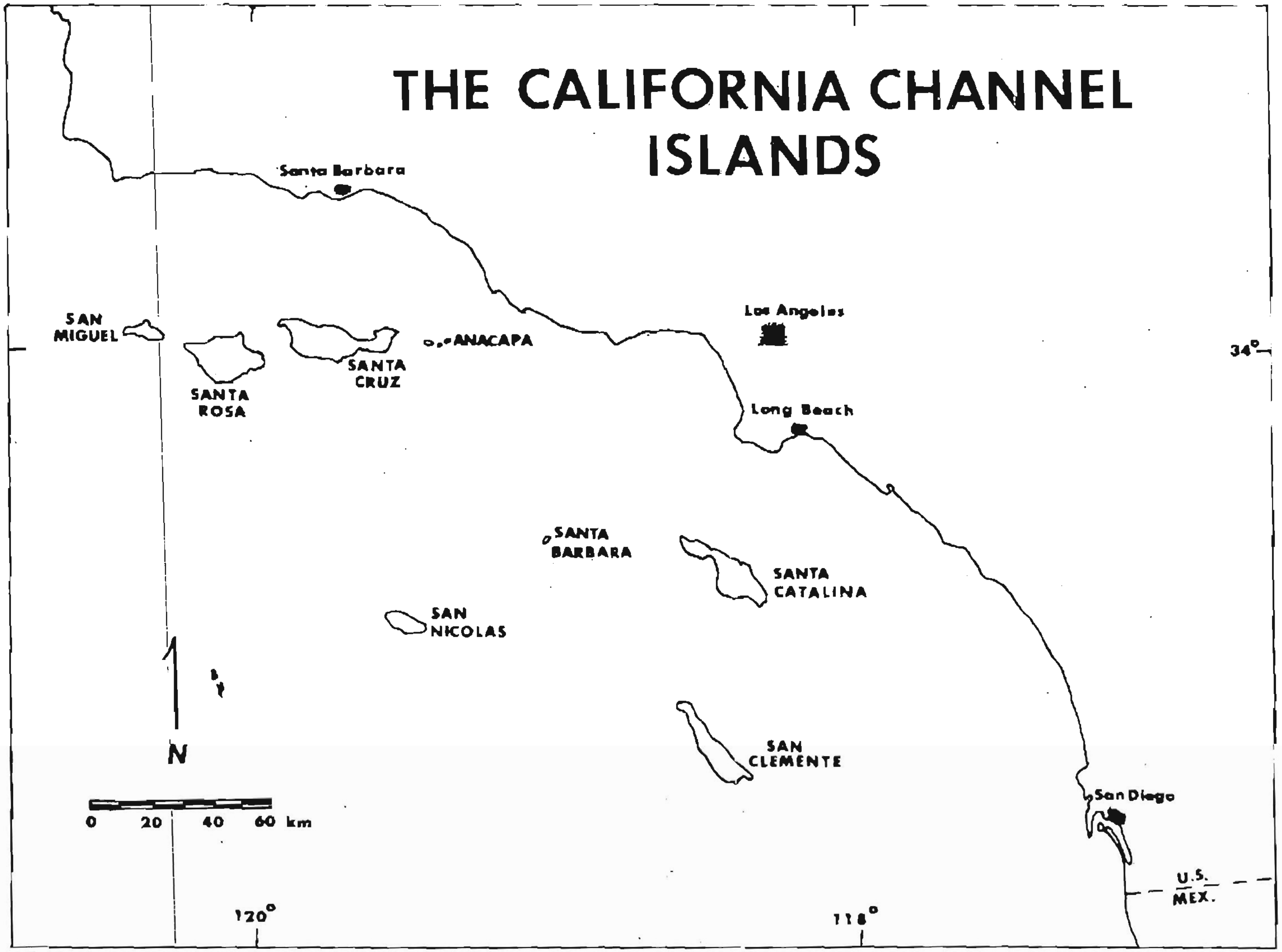


FIG. 1 Adapted from Hobbs, 1978

Fig. 2 Distribution of Vegetation Types within the Major Study Zone, Santa Cruz Island, California

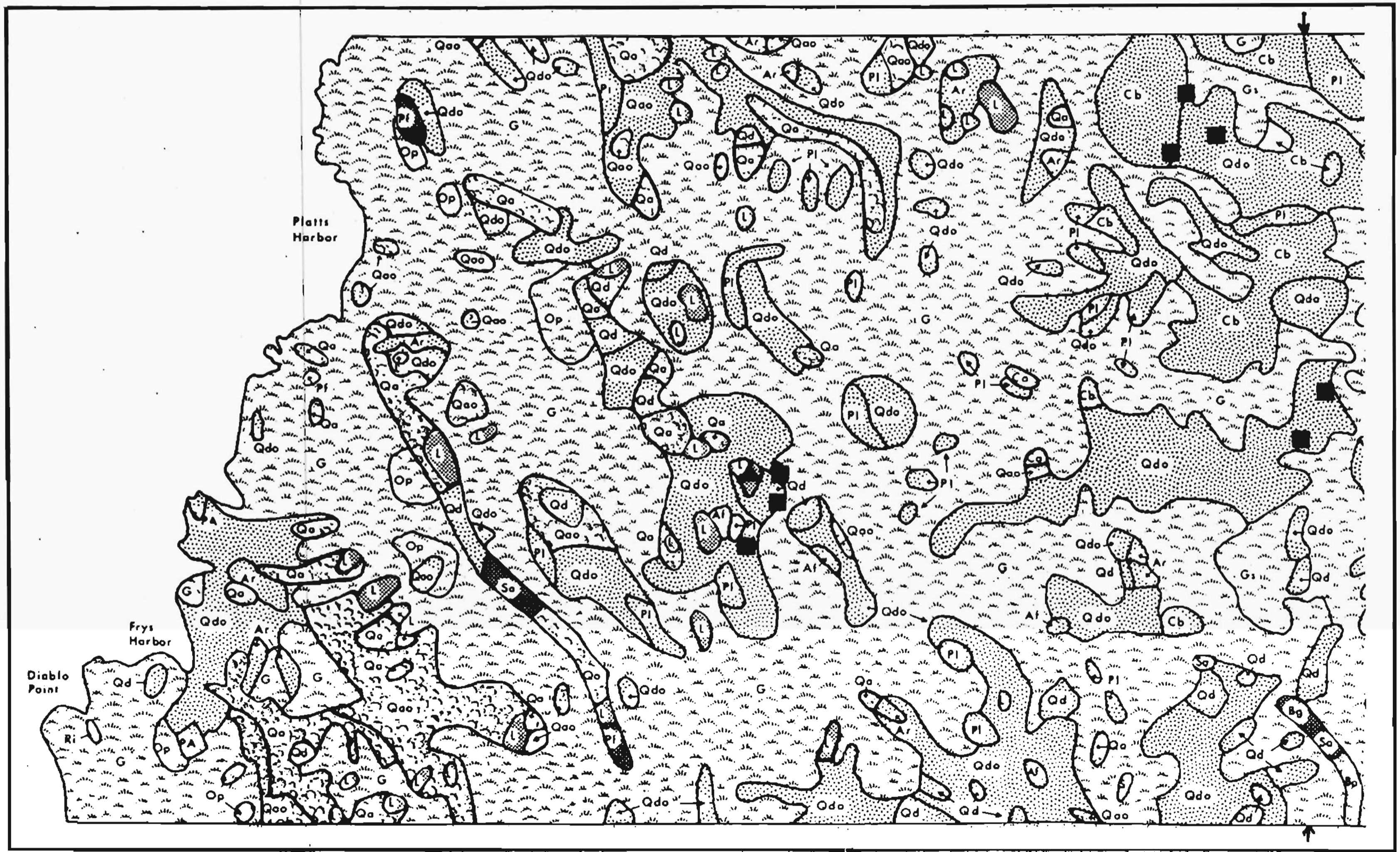
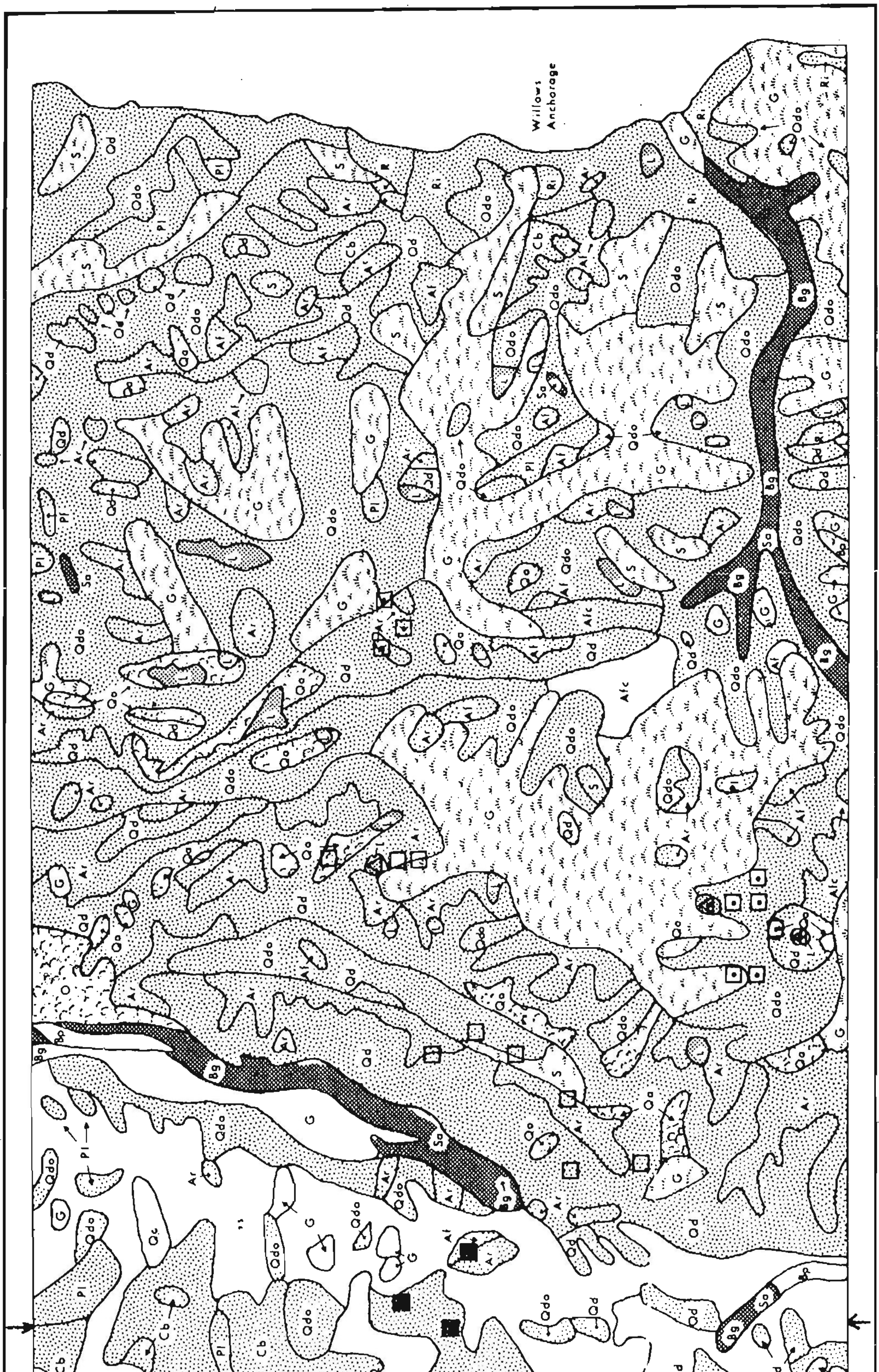


Fig. 2 Continued



Key to Fig. 2

Grassland	
Bp	Baccharis pilularis
G	Grassland
Gs	Grassland with scattered mixed shrubs
S	Coastal Sage scrub
Op	Opuntia littoralis

Chaparral	
Qd	Quercus dumosa
Oda	Open Quercus dumosa
Cb	Cercocarpus betuloides
Af	Adenostoma fasciculatum
Afc	Closed Adenostoma fasciculatum
Pl	Prunus lyonii
Ar	Arctostaphylos spp
PA	Prunus and Arctostaphylos mix
Ri	Rhus integrifolia

Woodland	
Ha	Heteromeles arbutifolia
Ca	Ceanothus arboreus
Oa	Quercus agrifolia
Oao	Open Quercus agrifolia
O	Ornamentals

Riparian	
Bg	Baccharis glutinosa
Sa	Salix spp
Pf	Populus fremontii

L	Lyonothamnus floribundus

Grazing Regimes

	Light	Moderate	Heavy
Shrub Study Sites:	□	⊡	■
Lyonothamnus Study Sites:	△	◬	▲

E

N S

W

0 ¼ ½ ¾ 1 KM

Original data compiled by Richard Minnich

LOCATION OF FENCES AND EXCLOSURES

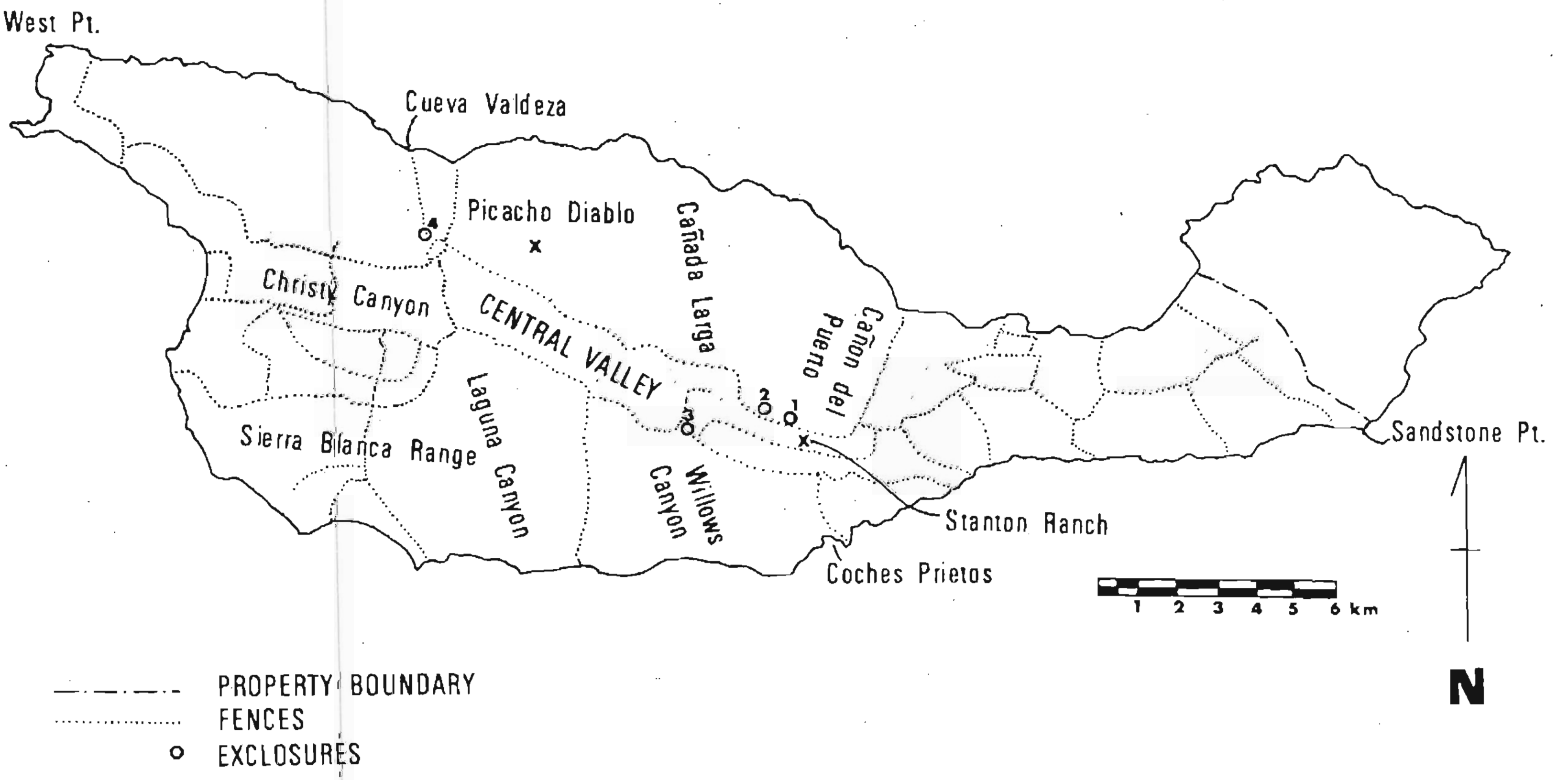


FIGURE 3

SOURCE: Dr. Carey Stanton

FIGURE 4. Percentage distribution of trunk diameter classes for chaparral shrubs in three different grazing regimes, Santa Cruz Island, California.

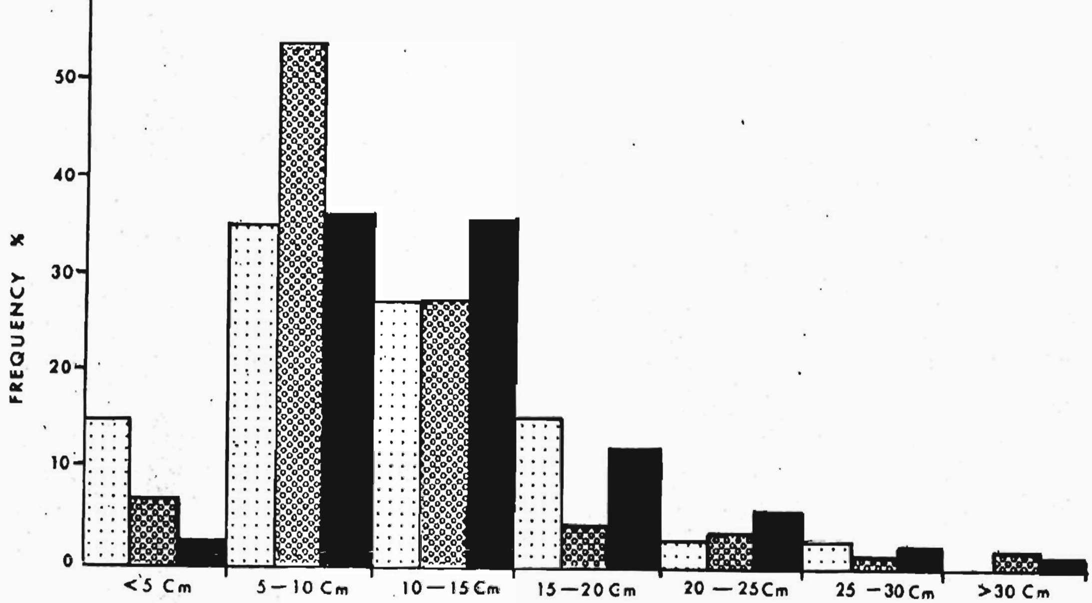
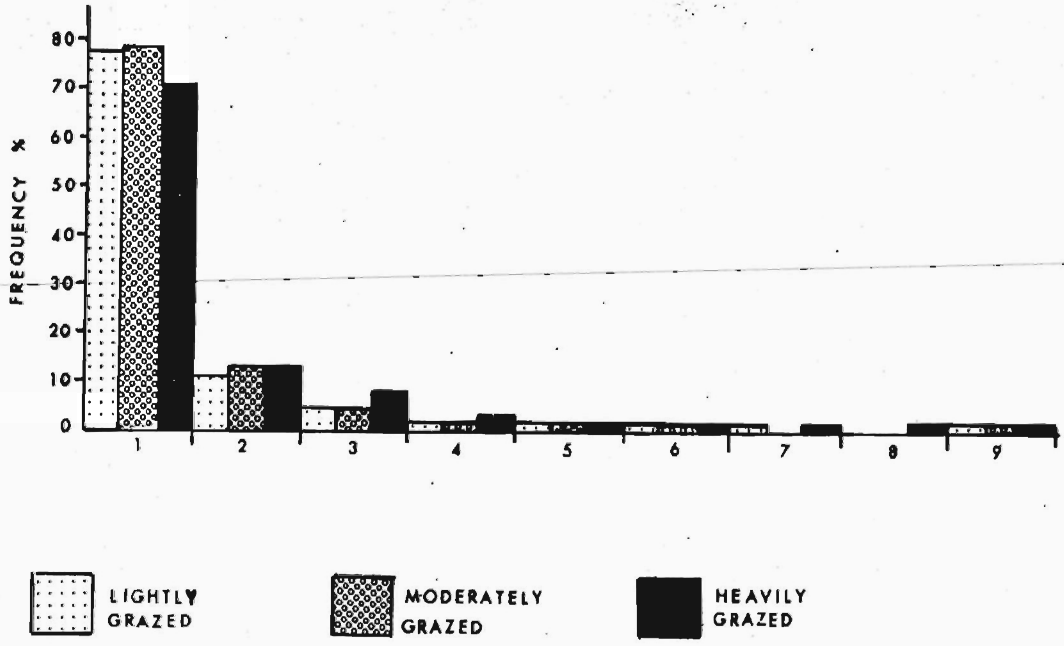


FIGURE 5. Percentage distribution of the number of trunks per chaparral shrub in three different grazing regimes, Santa Cruz Island, California.



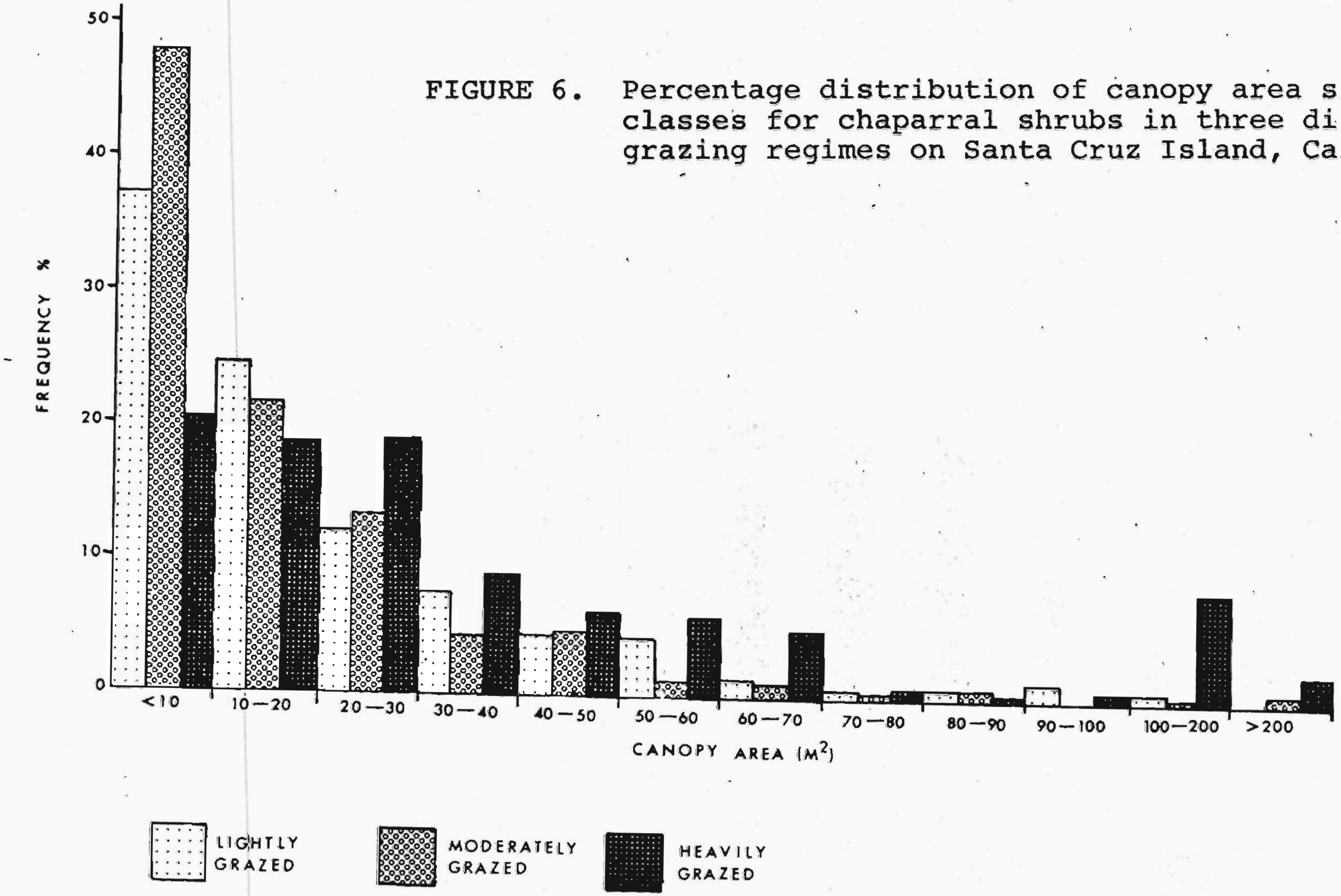


FIGURE 6. Percentage distribution of canopy area size classes for chaparral shrubs in three different grazing regimes on Santa Cruz Island, California.

FIGURE 7. Percentage distribution of basal sprouting behavior for chaparral shrubs in three different grazing regimes, Santa Cruz Island, California.

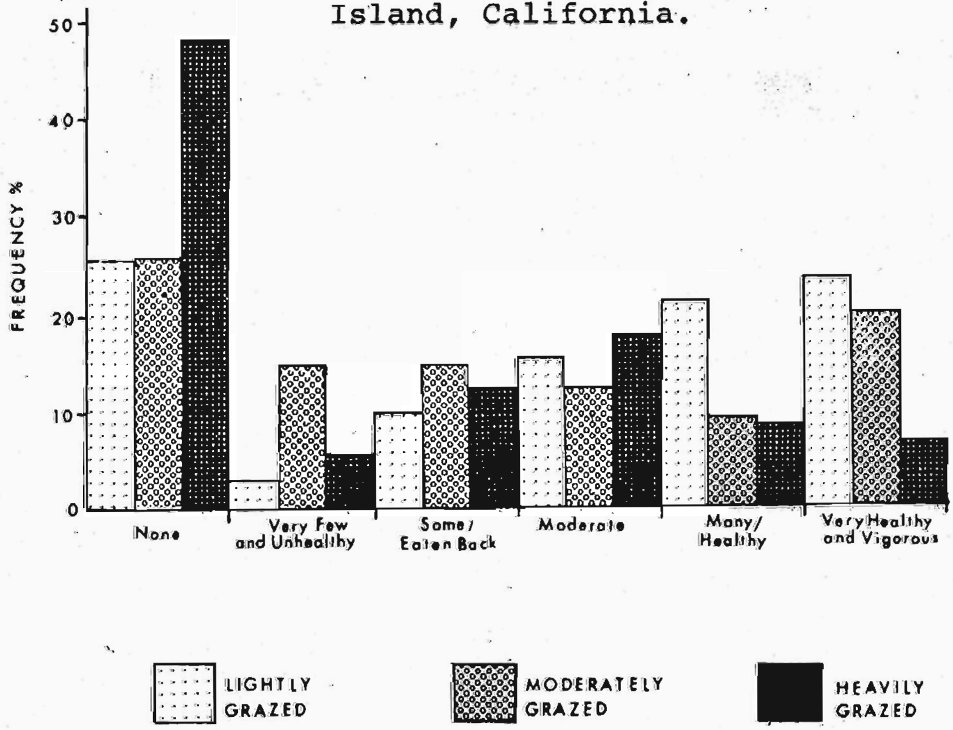


FIGURE 8. Percentage distribution of trunk diameter classes for _Quercus dumosa_ in three different grazing regimes, Santa Cruz Island, California.

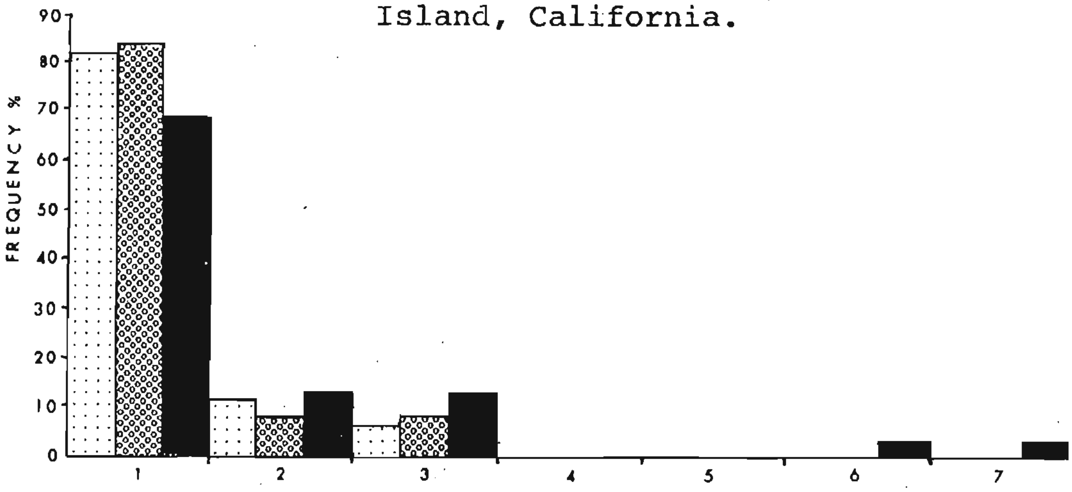


FIGURE 9. Percentage distribution of the number of trunks per _Quercus dumosa_ shrub in three different grazing regimes, Santa Cruz Island, California.

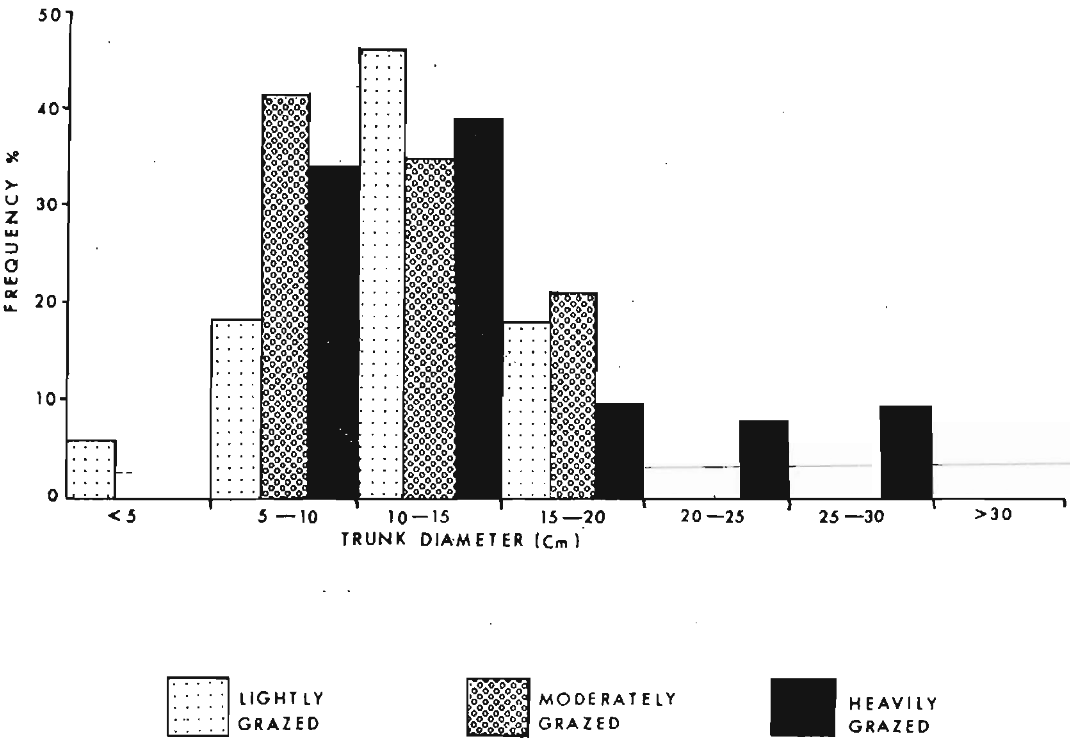


FIGURE 10. Percentage distribution of canopy area size classes for Quercus dumosa in three different grazing regimes, Santa Cruz Island, California.

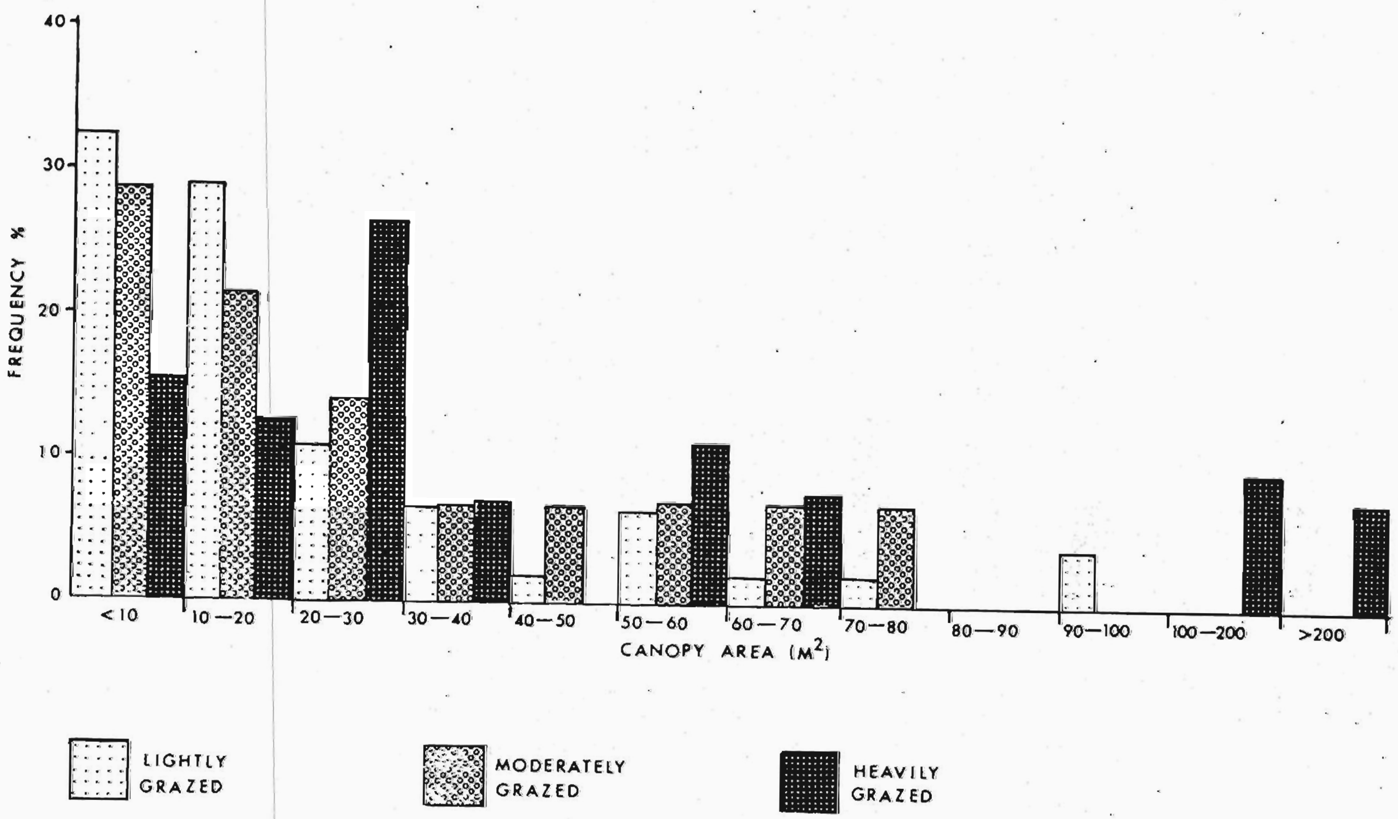


FIGURE 11. Percentage distribution of basal sprouting behavior for *Quercus dumosa* in three different grazing regimes on Santa Cruz Island, California.

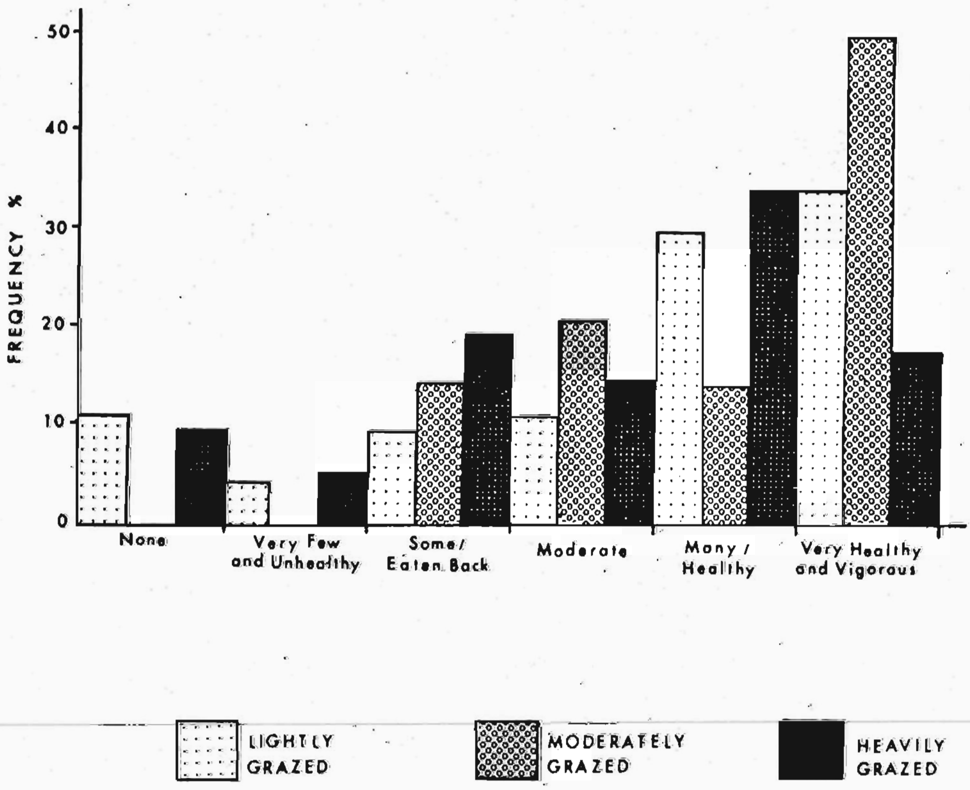


FIGURE 12. Percentage distribution of trunk diameter classes for Adenostoma fasciculatum in three different grazing regimes, Santa Cruz Island, California.

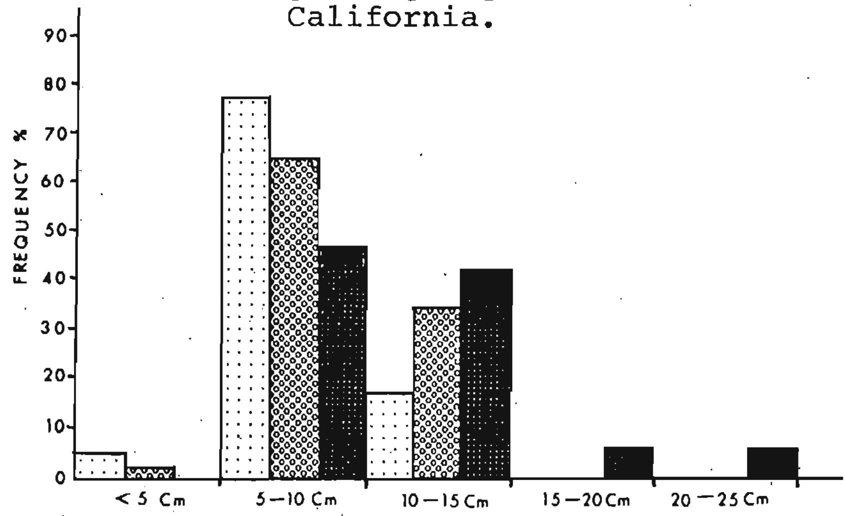


FIGURE 13. Percentage distribution of the number of trunks per Adenostoma fasciculatum shrub in three different grazing regimes Santa Cruz Island, California.

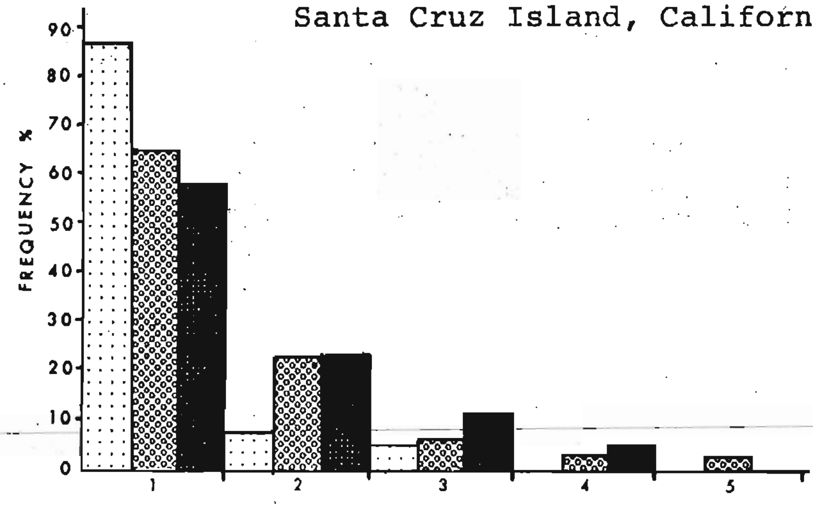


FIGURE 14. Percentage distribution of canopy area size classes for _Adenostoma fasciculatum_ in three different grazing regimes, Santa Cruz Island, California.

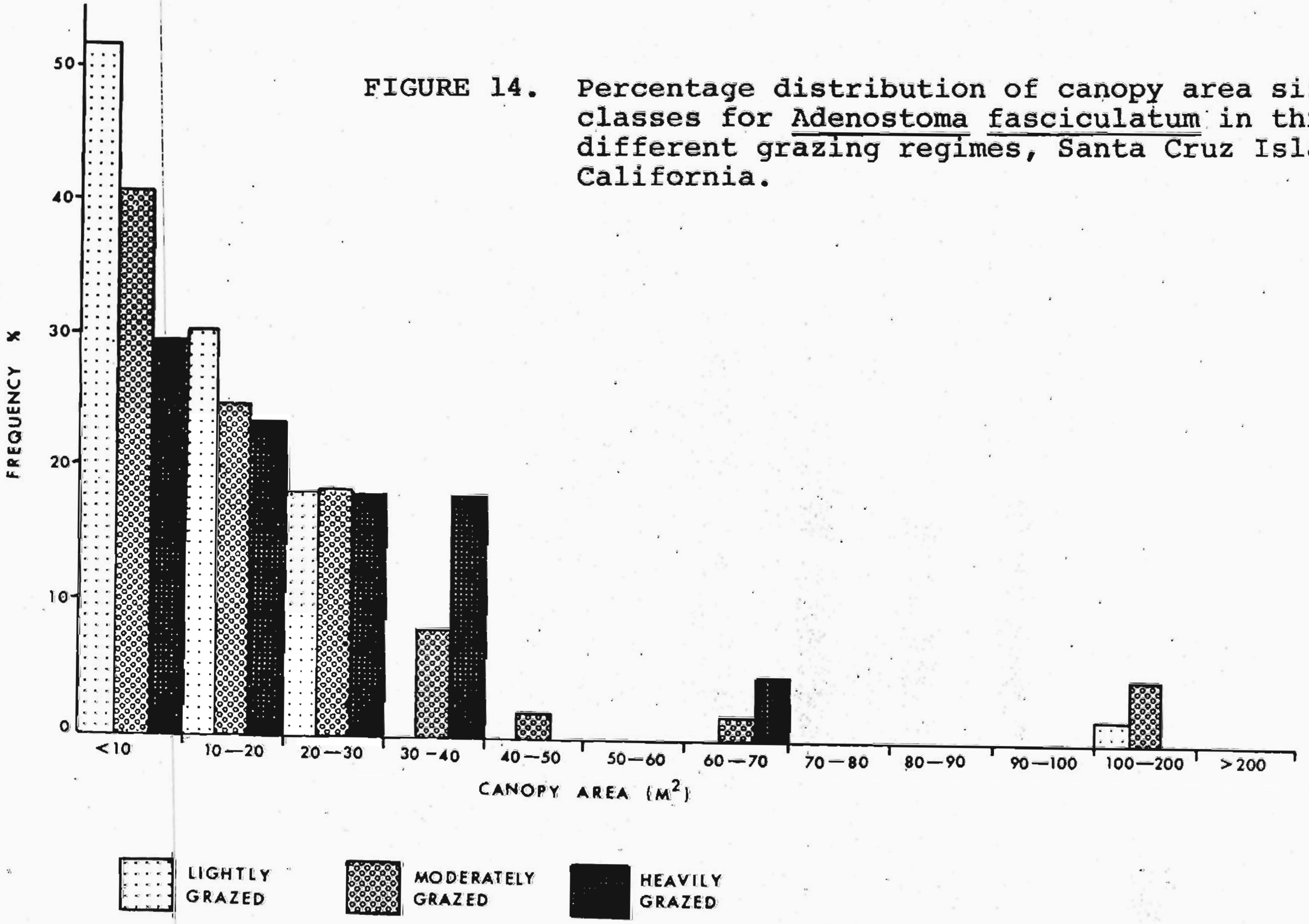


FIGURE 15. Percentage distribution of basal sprouting behavior for *Adenostoma fasciculatum* in three different grazing regimes, Santa Cruz Island, California.