Relationship between Animal Activity and Bare Areas Associated with California Sagebrush in Annual Grassland

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Highlight: *Thickets of California sagebrush support large populations of small mammals which eliminate grassland vegetation from the vicinity of the shrubs. The effect of the shrubs is density dependent, with greatest effect at more than 50% canopy coverage and virtually no effect at 25% cover and less. The amount of grassland exclusion diminishes rapidly with distance from the shrub stands, but extends beyond the well-defined border zone as rabbit trails. Although scattered shrubs do not exclude grassland vegetation, they apparently protect the grass under their canopies from grazing by cattle. The extent of the bare areas fluctuates greatly over periods of years. The areas denuded by small mammals are populated by diminutive species which do not live in the unbroken grassland, and show a greater species diversity than unbroken grassland.*

California sagebrush (*Artemisia californica*) is a common shrub invader of grasslands in coastal southern and central California. It is a dominant shrub species of the California coastal sage scrub, or soft chaparral, and is often associated with sage (*Salvia* spp.) and coyote brush (*Baccharis pilularis*). Stands of coastal sage scrub, when in contact with grassland, produce a pattern of grassland exclusion, leaving bare areas under and fringing the shrub stands. No such grassland exclusion is seen with scattered or single shrubs of California sagebrush.

Various mechanisms have been proposed to account for the bareness associated with the thickets of shrubs, including allelopathy (or poisoning by volatile toxins) by Muller (1966), trampling and grazing by cattle (Wells, 1964), and grazing and seed predation by small mammals (Wells, 1964; Bartholomew, 1970). Of the three proposed causes of bareness associated with the coastal sage scrub, cattle can be dismissed, since the bare areas are equally pronounced in areas where cattle have been excluded for years. Allelopathy was shown to be important for certain forbs, but not to be important for the major grasses of the annual grassland (Halligan, 1973). Competition for moisture was hypothesized as a cause of the bareness associated with big sagebrush (Robertson, 1947; Frischknecht, 1963), although it was only of minor importance in the case of California sagebrush (Halligan, 1973).

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In this paper I intend to briefly describe the herb pattern associated with California sagebrush, and to present its major cause.

Materials and Methods

Four study sites were used. The major site was located at the La Purisima State Historical Park, near Lompoc, Calif. Another major site was located immediately west of the intersection of San Marcos Pass Road and San Antonio Creek Road in Santa Barbara, Calif. Two additional sampling sites were located about a mile from each of the major sites. The one near the La Purisima site was the only site located in grassland grazed by cattle, and will be referred to as the Lompoc site. The one near the San Marcos site will be called the Santa Barbara site.

All sites were located in a semiarid Mediterranean climate, with a moist cool growing season, generally extending from November to April, and a warm dry dormant season extending from May through October. The La Purisima site averages about 14 inches (36 cm) of precipitation per year while the San Marcos averages about 22 inches (56 cm) (Personal communication: Santa Barbara County Flood Control and Water Conservation District). However, the San Marcos site is warmer and has a higher estimated annual rate of evapotranspiration (Elford et al., 1965). The La Purisima site is located on a sandy loam soil, while the San Marcos site is located on a clay soil (Halligan, 1972).

Four permanent transects were placed at La Purisima. These consisted of 1- cm × 10-cm quadrats extending from within the shrub zone, across the border zone, and into the grassland. They were sampled biweekly in 1969-70, and twice yearly through 1972. Two other transects were placed at San Marcos. Densities of each species were monitored, along with evidences of grazing (clipped leaves), heights of some species, and condition (e. g. wilting). These transects were supplemented with over 100 5-cm × 5-cm quadrats in the three zones.

To determine the relationship between shrub density, and development of bare areas, 16 quadrats, measuring 20 ft (6 m) by 20 ft (6 m) were sampled in an area of variable shrub densities, at the Santa Barbara site. In each quadrat three quantities were determined: 1) the area occupied by shrub canopies, 2) the amount of bare area under the shrub canopies, and 3) the amount of bare area not under the shrub canopies. By definition, a bare area is essentially devoid of vegetation, as compared to surrounding grassland. These include animal trails, dirt mounds, and areas without much herb growth. The demarkation between bare areas and grassland was sharp, with little intermediate vegetation. From these measurements, the percentage cover by the shrub canopies is calculated, along

Fig. 1. *A stand of California sagebrush in annual grassland showing the bare-looking border zone between the shrubs and grassland. Fence in middle background is the fence exclosure.*

with the percentage bare area under and between the shrubs.

Five transects 30 ft (9 m) long and 1 ft (30 cm) wide were used to sample the grassland-shrubland contact, at the Santa Barbara site. These transects were intended to determine the extent of the bare areas fringing a large shrub stand, and to measure the bareness beyond the border zone. The transects were broken into 1-ft (30 cm)-square quadrats in which the proportion of bare area to grassland vegetation was noted. Again, the sharp distinction between bare areas and grassland facilitated this measurement. The width of the border zone in each transect was also recorded.

A fence exclosure at the La Purisima site was constructed of ½ inch (1.27 cm) mesh hardware cloth placed 6 inches (15 cm) into the ground and extending 18 inches (45 cm) into the air. This exclosure (Fig. 1) measured 50 ft by 60 ft (16 X 20 m) and enclosed substantial areas of all three vegetation zones. Brush rabbits (*Sylvilagus*) were completely excluded, while mice (*Peromyscus* and *Reithrodontomys*) required constant trapping to maintain a low population. Birds were not excluded. The vegetation inside the exclosure was sampled on two permanent transects extending across all three zones, and that outside was sampled with two other transects.

Box exclosures were constructed of 3/8 inch (0.9 cm) mesh hardware cloth measuring 2 ft (60 cm) square and 9 inches (23 cm) high, to exclude all mammals and birds. Control box exclosures were raised 5 inches (13 cm) above the ground to allow free access to small animals (Fig. 2). One set of box exclosures was placed in the shrub zone at San Marcos and one set in the border zone; two sets were placed in the shrub zone at La Purisima, one of the sets within the fence exclosure. The San Marcos box exclosures were sown in June with 100 ripgut brome spikelets, 100 wild oat caryopses, and 100 foxtail chess spikelets. La Purisima box exclosures were sown with 400 ripgut brome caryopses. All seeds were collected from the respective study sites in May.

Emergent seedlings were counted in each box exclosure in November, after the first rains of the wet season; and the grass shoots were weighed (oven dry) in April, at the time of flowering. Samples of dominant specimens of the grasses from adjacent grassland were also weighed for comparison.

The only work done in an area grazed by cattle was sampling at the Lompoc site to ascertain the effect of cattle on the vegetation pattern associated with California sagebrush. Sampling was conducted in an area of scattered sagebrush in February. Fifteen shrubs were sampled for heights of grasses and evidence of grazing (clipped leaves) along with grassland controls. Sixteen other shrubs were sampled for grass density and numbers of tillers, using 5- cm X 5-cm quadrats sampled in pairs, one under a shrub and the other in the grassland 4 ft away from the shrub sample. Only robust species of grasses were considered, viz. brome, chess and wild oats, but not fescue.

Table 1. Percent composition[1] of the three herb zones at the La Purisima site.

Species[2]	Grass-land	Border zone	Shrub zone
Grassland species			
Ripgut brome (*Bromus rigidus*)	62	1	1
Tarweed (*Madia sativa*)	11	1	0
Soft chess (*Bromus mollis*)	3	0	0
Border zone species			
Chorizanthe coriacea	*[3]	28	0
Camissonia angustifolia	*	6	0
Camissonia hirtella	*	2	0
Cryptantha leiocarpa	*	2	0
Navarretia atractyloides	0	1	0
Shrub zone species			
Calif. sagebrush seedlings (*Artemisia californica*)	0	7	18
Pigmy weed (*Tillaea erecta*)	0	5	33
Chickweed (*Stellaria media*)	*	1	15
Pterostegia drymarioides	*	1	9
Widespread and occasional species			
Foxtail fescue (*Festuca megalura*)	21	27	12
Miners lettuce (*Montia perfoliata*)	*	15	7
Horseweed (*Conyza canadensis*)	*	1	1
Toadflax (*Linaria canadensis*)	*	0	1
Coyote brush seedlings (*Baccharis pilularis*)	0	1	*
Nemophila pedunculata	0	1	0

[1] Percent composition is based on density.

[2] Only species constituting more than 1% of the population of at least one vegetation zone at La Purisima are in this table. Species abundant at other study sites include: grassland—wild oats (*Avena fatua*), *Hypochoeris glabra*, foxtail chess (*Bromus rubens*), and filaree (*Erodium cicutarium, E. moschatum*); border and shrub zones—scarlet pimpernel (*Anagallis arvensis*); and shrub zone—figwort (*Scrophularia californica*).

[3] Asterisk denotes less than 1%. Most of the asterisked species in the grassland were found in rabbit trails.

Results

The vegetation associated with California sagebrush is arranged into three distinct zones, both in terms of species composition and in terms of physiognomy (Fig. 1). The species present in each zone differs radically from the other two zones (Table 1). The larger species predominate in the grassland at La Purisima, averaging 29.8 cm in height in April. The shrub and border zones support much smaller species, with average heights of 2.9 cm in the border zone and 2.1 cm in the shrub zone. The cover by live leaves in January is 32.3% in the grassland, 0.9% in the border zone, and 1.5% in the shrub zone. The density in the border zone is 64% of the grassland density; that of the shrub zone is 49% of the grassland density (Halligan, 1973). The herbs of the shrub and border zone are small, lower, less dense, and of different species than those of the grassland. The species diversity of the grassland based on percentage composition is 0.56, while that of both the shrub and border zones is 0.82.

In stands of shrubs with less than 30% canopy coverage, less than 5% of the areas both under the shrubs and in the grassland is bare (Fig. 3). Where there is between 30% and 50% canopy coverage, bare areas both under the shrubs and between the shrubs rise rapidly. In stands of over 50% canopy coverage by shrubs, more than 75% of the area under the shrub canopies is bare, and between 25% and 70% of the area between the canopies is bare. Apparently, 30% cover is the

Fig. 2. *The shrub zone exclosures outside the fence exclosure at La Purisima. Upper left: open box exclosure before growing season. Upper right: closed box exclosure before growing season. Lower left: open box exclosure at end of growing season. Lower right: closed box exclosure at end of growing season. Exclosures were removed to facilitate viewing.*

critical density at which the shrubs begin to exert a controlling influence on the grassland. The grassland vegetation is more severely affected beneath the shrubs than between them.

The bareness associated with dense stands decreases with distance from the edge of the stands (Fig. 4). The bareness extends beyond the well-defined border zone in the form of rabbit trails, which either radiate from the shrub stands or parallel the edges of the stands, often connecting adjacent stands or areas of the same stand. The trails decrease rapidly in number and influence with distance from the stands, as reflected in the distribution of bare area in Figure 4. The width of border zone around larger thickets varies in width from 0 m to over 3 m. Eleven measurements of border zone width taken during the first year each site was studied gave an average of 0.8 m, ranging from 0 m to 1.4 m.

Although the vegetation inside the fence exclosure originally was similar to the vegetation outside, within the first growing season it had become noticably and measureably lusher (Table 2). Ripgut brome outside the exclosure was severely grazed by small mammals, accounting for its low height and lack of reproduction. I observed that individual grasses were sporadically truncated almost to the ground, usually accompanied by deposition of rabbit fecal pellets, strongly suggesting grazing. The inflorescences were almost invariably clipped before anthesis. Foxtail fescue was less severely grazed, and a moderate percentage were able to reproduce with horizontal inflorescences. Small mammals apparently selectively graze the coarser grasses more intensively than the fine-leaved fescue.

The border zone changed considerably in width over the period of this study. During the 1969-70 growing season, the border zone within the fence exclosure remained stable or became slightly narrower, while outside the exclosure it increased considerably in width (Table 3). By the first part of the 1970-71 growing season, the grassland had encroached considerably into the border zone within the fence exclosure.

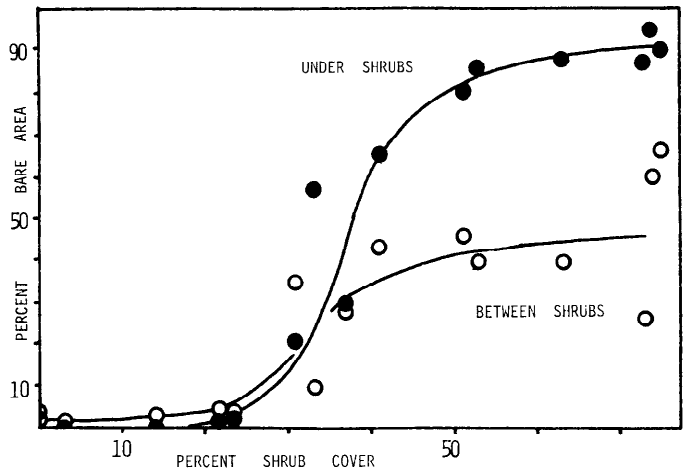

Fig. 3. *Relationship between shrub canopy coverage and percentage bare area under and between shrubs.*

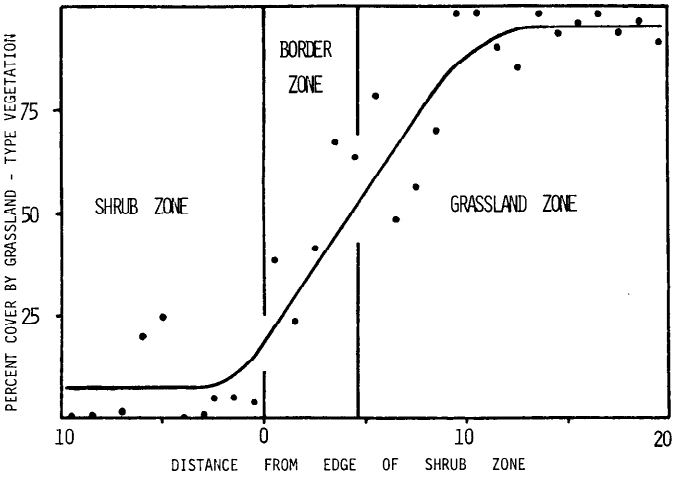

Fig. 4. *Percentage cover by grassland vegetation across the contact between shrub and grassland communities. Distance is in feet.*

Outside the exclosure the grassland withdrew, leaving the border zone wider. I observed that the grassland was decimated in episodes, leaving irregular islands of untouched grassland interspersed with areas of grasses clipped close to the ground. Among the clipped grasses were an abundance of rabbit fecal pellets (Fig. 5). Inside the exclosure the grassland did not encroach much into the border zone within a given growing season, except by vegetative proliferation of existing plants. However, over the dry season, seeds of grassland species were disseminated into the border zone. These remained on the ground within the fence exclosure, but disappeared outside the fence exclosure. The following growing season, the seeds germinated and formed the basis for the advance of the grassland into the border zone.

The emergence of grass seedlings in the open box exclosures (Table 4) was low for the large-seeded grasses (wild oats and ripgut), but was relatively high for the smaller-seeded foxtail chess. None of these three species emerged in the vicinity of the box exclosures due to natural recruitment, but foxtail fescue, a grass with tiny seeds, emerged both within and around the box exclosures from naturally dispersed seed. I observed that most wild oat and ripgut brome seeds disappeared from the open exclosures over the dry season, but I observed little disappearance of foxtail chess seeds. Seed predation by small animals is suggested by an earlier experiment where the disappearance over the dry season of wild oat seeds buried in the shrub zone was accompanied by considerable disturbance of the soil. Emergence of ripgut brome in the box exclosures at La Purisima paralleled that at San Marcos, except that the seeds did not disappear under the open box exclosure within the fence exclosure, but instead were cracked open, perhaps by insects or birds.

The dry weights of the shoots of the grasses in the closed exclosures (Table 5) suggest that in the absence of grazing, conditions are favorable for the growth of grasses in the shrub zone, but less so in the border zone. The open exclosures contained no live grasses of the three species sown the previous June, but did contain dead, truncated stumps of the sown grasses (Fig. 2). However, there were numerous live individuals of foxtail fescue, a small, thin-leaved grass which grew naturally throughout the shrub and border zones.

Grasses under scattered shrubs in grassland grazed by cattle were four times taller than those in the adjacent grassland

Table 2. Survival (%) to fruiting and average maximum height (cm) of ripgut brome and foxtail fescue where protected from grazing (inside exclosure) and open to grazing.[1]

Species and location	Survival	Height
Ripgut brome		
Inside exclosure	40	17.5
Outside exclosure	0	2.5
Foxtail fescue		
Inside exclosure	48	8.9
Outside exclosure	17	3.5

[1] All individuals measured were in the border zone.

Table 3. Comparison of the changes in the width (m) of the border zone along four transects, two inside the fence exclosure and two outside the fence exclosure.

Location of transect	Nov. 1969	Apr. 1970	Nov. 1970
Inside exclosure	0.4	0.3	0.1
	0.9	0.9	0.5
Outside exclosure	0.6	1.0	1.8
	0.9	1.3	–

Table 4. Emergence (% of control) of sown grasses inside open box exclosures as a percentage of the emergence in corresponding closed box exclosures.

Species	Shrub zone	Border zone
San Marcos site		
Ripgut grass	6.7	5.7
Wild oats	0.0	5.0
Foxtail chess	53.1	75.7
La Purisima site		
Ripgut		
Outside fence exclosure	0.0	–
Inside fence exclosure	6.0	–

Table 5. Dry weights of shoots of sown grasses inside box exclosures, as a percentage of dry weight of corresponding species in the grassland.

	Shrub zone		Border zone	
Species	Closed	Open	Closed	Open
Ripgut grass	316	0	104	0
Wild oats	65	0	58	0
Foxtail chess	174	0	37	0

Fig. 5. *An area of grassland regression and consequent border zone expansion. Left third is the old border zone. Middle third (wider at the base and narrower at the top) is the area of border zone expansion. Right third is the grassland.*

Fig. 6. *Scattered shrubs in grassland ungrazed by cattle, showing the growth of grasses under the shrubs, except for small mammal trails.*

(Table 6). The percentages of clipped grasses suggest that the grasses in the grassland were much more heavily grazed than those under the shrubs. Evidence of clipping underestimates the amount of grazing since clipped leaves are difficult to identify as such soon after grazing. The density of robust grasses (brome, chess, and wild oats, but not foxtail fescue) was about twice as high under the shrubs as in the adjacent grassland. The grasses in the grassland had about three times the tillers (other than the main stem) of the grasses under the shrubs, indicating a more horizontal growth pattern in the grassland.

Discussion and Conclusions

The hypothesis that small mammals contribute to the bareness associated with California sagebrush is supported by the box exclosure experiments, by the fence exclosure experiment, and by the observation of clipped stumps of grasses in areas of grassland regression.

Seed size appears to be an important factor influencing seed predation, with larger seeds being taken more readily than smaller seeds. In general, the dominant species of the grassland have large seeds, while those of the shrub zone have small seeds. Grazing by small mammals tends to be directed at the coarser grasses, as seen in the relative performance of foxtail fescue and the larger grasses in the fence and box exclosure experiments. Other species of the shrub and border zones avoid grazing through their small size, as in most shrub zone species; through their spininess, as in *Navarretia* and *Chorizanthe*; or perhaps through their unpalatability, as in *Croton* and *Satureja*.

Table 6. Comparison of grasses[1] under scattered shrubs with grasses in surrounding grassland in February at the Lompoc site, an area grazed by cattle.

Measurement	Under shrub	In adjacent grassland
Height (cm)	26.1	6.5
Chess and wild oats/25 cm² (no.)	5.6	2.9
Secondary tillers/plant (no.)	0.31	1.07
Samples grazed (%)	26.6	73.3

[1] Grasses include brome, chess and wild oats but not foxtail fescue.

The width of the border zone varies with time. At La Purisima the border zone expanded from about 1 m wide in 1970 to between 2 and 4 m wide in 1973. At San Marcos, the border zone over the same period of time was not observed to change appreciably. Muller (1971) noted the reverse effect in mixed stands of California sagebrush and sage (*Salvia leucophylla*). Between 1964 and 1968 the border zone which originally was about 2 meters wide was invaded completely by grassland.

The formation of bare areas is characteristic of large stands of contiguous or clustered shrubs. Scattered shrubs in grassland generally do not have associated bare areas (Fig. 3 and 6). The effect of the shrubs is density dependent. When the shrubs are scattered, grassland vegetation is not inhibited under the shrubs; and in grassland grazed by cattle, the grasses under the shrubs are taller and denser than in the grassland. Apparently, the grasses under the shrubs are protected from cattle grazing by the branches of the shrubs.

An important aspect of grazing is the opportunity given to small herbs to grow in areas denuded of grassland. A large proportion of the species found at the two study sites grow only in denuded areas and are dependent upon grazing for their bare habitat.

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