Factors Affecting Leaf Size of Chaparral Shrubs on the California Islands

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INTRODUCTION

Correlations between leaf size and environmental factors have been well documented (Gates 1968, Vogel 1970, Parkhurst and Loucks 1972, Givnish and Vermeij 1976, Grier and Running 1977, Smith and Nobel 1977, Smith 1978, Werger and Ellenbroek 1978), and interest in this subject dates to studies by Theophrastus in the 4th century B.C. (Hort 1916). In recent years, the concept of water-use efficiency has become the focus of considerable experimental research on the interrelationships between leaf characteristics and the environment (Ehrler 1969, Meinzer and Rundel 1973, Schultze *et al.* 1975, Ehleringer *et al.* 1976). Results from these studies suggest that there is an optimum balance between the photosynthetic gain by a leaf and the concomitant water loss from transpiration and evaporation. This loss is strongly coupled with environmental variables such as air temperature, relative humidity, solar radiation, and convective and conductive forces. Biotic variables include leaf temperature and leaf resistance to transpirational losses, both of which are a direct function of leaf dimension.

In general, plants native to arid habitats are characterized by small, thick leaves with small cells, thick cuticles, and well-developed mechanical tissues. In contrast, plants native to mesic areas bear large, thin leaves with large cells, thin cuticles, and poorly-developed mechanical tissues (Shields 1951, Kummerow 1973). However, the leaf characteristics of a single species may vary in response to seasonal patterns and exposure to intense solar radiation (Bjorkman and Holmgren 1963, Kummerow 1973, Smith and Nobel 1977).

I have observed distinct leaf size differences in chaparral shrubs common to the Santa Ynez Mountains on the mainland of Santa Barbara County and to the California Islands, where leaf size correlations with environmental parameters are not obvious. Although many shrub species are common to the two areas, the physiognomy of island and mainland stands of chaparral is drastically different. Chaparral on the mainland consists of dense, impenetrable stands of sclerophyllous shrubs with very little understory (Cooper 1922, Hanes 1977, Mooney *et al.* 1977). Light, nutrients, and moisture availability may be extremely limited in mature chaparral vegetation, and, coupled with fire, these factors play a major role in controlling the development of seedlings, herbs, and understory shrubs (McPherson and Muller 1967, Hanes 1977, Schlesinger and Gill in press). In addition, the build-up of allelopathic toxins may interfere with seedling establishment in older stands (Muller 1966, Muller *et al.* 1968). In contrast, insular chaparral vegetation often forms an open woodland of large-leaved, arborescent shrubs intermingling with grassland and coastal sage scrub on south-facing slopes, and a more dense aggregation of oaks and mesic chaparral associates on north-facing slopes (Philbrick and Haller 1977, Bjorndalen 1978).

The observed variation of shrub density in the chaparral of the Santa Ynez Mountains and Santa Cruz Island has been documented elsewhere (Hochberg 1980). Mainland sites are dominated by an essentially complete overstory of large shrubs (83.9 to 99.1 per cent cover),

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with small shrubs and a few herbs scattered in pockets or among rocky outcrops in the chaparral. Island sites, on the other hand, are covered by an open shrubland in which large shrubs are aspect dominant and form 40.9 to 47.0 per cent cover. Small shrubs, herbs, and grasses grow around and under the large shrubs and actually represent the majority of cover.

There are several factors which may contribute to the openness of island chaparral. Unlike chaparral on the mainland, fire does not presently play a major role in the vegetation dynamics of the California Islands. As a result, altered nutrient-cycling patterns, potential accumulation of allelopathic toxins, and the dependence of many chaparral shrubs on fire for seed germination may result in decreased shrub density. It is not presently known what effects these variables have on island plants. Furthermore, the higher incidence of intensive grazing by feral animals on the islands may interfere with seedling establishment and longevity. Hobbs (1978) contrasts the relative openness and the difference in age structure of the grazed northern pine forests on Santa Cruz Island with the dense tangle of trees and chaparral underbrush of the fence-protected western and eastern pine forests.

In this paper, environmental factors are briefly summarized and differences in leaf dimensions between island and mainland habitats are documented. A preliminary attempt is made to isolate those factors which make the largest contributions to the uniqueness of island chaparral shrubs and their environment.

METHODS

Meteorological data.—In order to examine the role of climatic factors on island and mainland chaparral, coastal and interior collecting and climate monitoring sites were established in the Santa Ynez Mountains and on Santa Cruz Island in January of 1977, as described in Hochberg (1980). All sites are typical chaparral habitats on southerly slope exposures at elevations between 225 and 400 m.

The mainland coastal study area consists of two sites on a ridge above Maria Ygnacio Creek. The mainland interior site is located above Kelly Creek in Los Laureles Canyon. The island coastal site occupies a ridge above Albert Anchorage. The island interior site is located on the slopes above Islay Canyon.

Meteorological data from the mainland coastal monitoring stations have been supplied by Dr. W. H. Schlesinger and are also reported in Schlesinger and Gill (in press) and Schlesinger and Hasey (1980). A total of five meteorological stations has been established in a transect from 350 m to 1,050 m (Schlesinger and Hasey 1980); pertinent data from the sites at 350 m and 560 m are reported here. Meteorological data from the mainland interior site are on file at the Los Prietos Ranger Station.

Meteorological stations were established at the island sites to record precipitation, wind speed, temperature, relative humidity, and solar radiation. Precipitation was measured using a Tru-Chek wedge-shaped rain gauge. Both a Taylor maximum-minimum thermometer and a Weather Measure hygrothermograph, model H311, were utilized for temperature data. Relative humidity was recorded on weekly hygrothermograph charts and checked periodically with a wet and dry bulb sling psychrometer. Average wind speed was determined with a Belfort Instrument Company anemometer. A Weather Measure solar radiometer (model R401) was added to the island interior site in June 1978. In addition, vapor pressure deficits were calculated according to methods described in Hochberg (1980). Insufficient data were available for determinations of vapor pressure deficits at the island coastal site or minimum vapor pressure deficit levels at the mainland interior site.

In order to assess the frequency and extent of fog cover at the four study areas, a series of satellite images was reviewed. Landsat satellite images, such as those shown in Figures 8 and 9, are available at the Department of Geography, University of California, Santa Barbara for selected dates between 1972 and the present. The satellite orbits over the Santa Barbara area every 14 days at 9:30 to 10:00 a.m. and records existing cloud cover using a multispectral optical scanner. All four study areas on both the mainland and island are clearly visible in these images; however, it is not possible to distinguish the two sites within the mainland coastal study area. Tallies of clear, partly overcast, and overcast "days" (at 9:30 a.m.) have been made from examination of these images.

Soils.—Three soil samples were collected at each study site for soil textural analysis utilizing methods described by Bouyoncos (1936). This process was repeated twice during the study. The approximate proportion of organic matter in the soil was established by ashing three 2-g samples of dry soil in a muffle furnace for four hours at 500°C. This procedure was also repeated twice during the study.

Leaf size.—For this investigation, three taxonomically unrelated chaparral shrub species were chosen in order to quantify the general trend of differential leaf size. Each species has an island and a mainland subspecies. The three pairs of subspecies being studied are: *Ceanothus megacarpus* Nutt. subsp. *megacarpus* from the mainland (Fig. 1), and *Ceanothus megacarpus* Nutt. subsp. *insularis* (Eastw.) Raven from the California Islands (Fig. 2); *Prunus ilicifolia* (Nutt.) Walp subsp. *ilicifolia* from the mainland (Fig. 3), and *Prunus ilicifolia* (Nutt.) Walp subsp. *lyonii* Raven from the California Islands (Fig. 4); and *Dendromecon rigida* Benth. subsp. *rigida* from the mainland (Fig. 5), and *Dendromecon rigida* Nutt. subsp. *harfordii* (Kell.) Raven from the Northern Channel Islands (Fig. 6). All of these have been classified as separate species at one time or another based on numerous morphological distinctions. In addition, all three pairs of subspecies have maintained their differences in common garden environments at both the Santa Barbara Botanic Garden and the University of California at Santa Barbara.

Thirty plants of each species were sampled, when present, in each of the four study areas. Sixty leaves were removed per shrub from low, medium, and high branches in each cardinal compass direction. Care was taken to sample only mature leaves and leaves not damaged by insect predation. The sample leaves were placed in a bag and mixed together; a subsample of 30 leaves was then randomly drawn from each bag. Petioles were clipped off each leaf, and leaf profiles were recorded on contact photographic proof paper. Leaf length and width were measured directly from the photographic images within 0.1 cm, and leaf area was determined using a polar planimeter with an accuracy of 99 per cent for leaves greater than 10 cm^2 and 95 per cent for leaves smaller than 10 cm^2. The leaves were also weighed so that correlations between leaf area and leaf weight could be made for use in dimension analysis studies.

In addition to the shrub samples taken at the four major study sites, 10 shrubs of each species were sampled at several other subjectively selected localities (including Santa Rosa Island) in order to show the range of variation in leaf size in both island and mainland populations. Student's *t*-tests were used to determine the significance levels of all leaf dimensions.

Dimension analysis.—Dimension analysis studies were undertaken during November-December 1977 and January 1978 for comparative measurements of total leaf area for each of the species pairs (Schlesinger and Gill 1978). Fifteen branches were collected from different individuals of each pair of subspecies on both the island and the mainland (seven from *Prunus* due to branch size and the corresponding impact on the island chaparral habitat). Branch diameters of all stems originating at or below 15 cm above the ground were also measured. Dead wood was removed and woody and foliar components were separated, dried, and weighed. Total leaf area per plant was determined by use of the formula:

$$\text{total leaf area} = \frac{\text{mean leaf area of 30 leaves}}{\text{mean leaf weight of 30 leaves}} \times \text{total leaf weight.}$$

FIGURE 1. *Bigpod Ceanothus*, Ceanothus megacarpus *Nutt. subsp.* megacarpus.

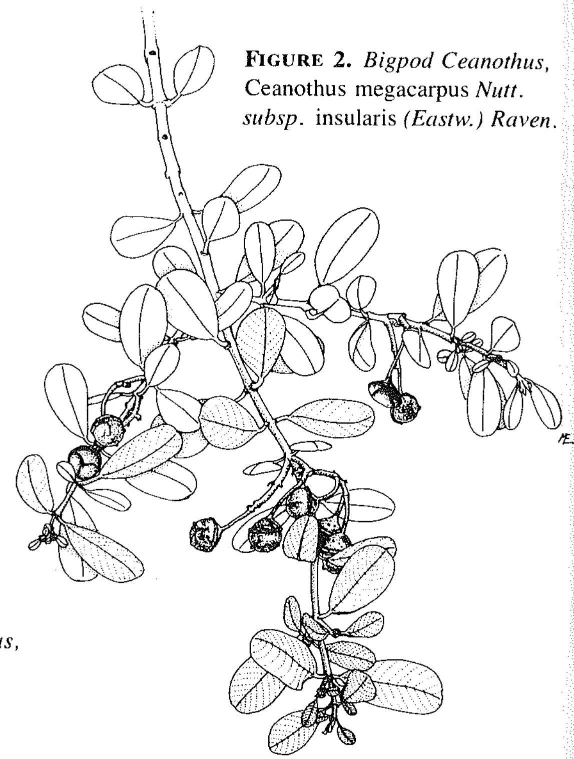

FIGURE 2. *Bigpod Ceanothus*, Ceanothus megacarpus *Nutt. subsp.* insularis *(Eastw.) Raven*.

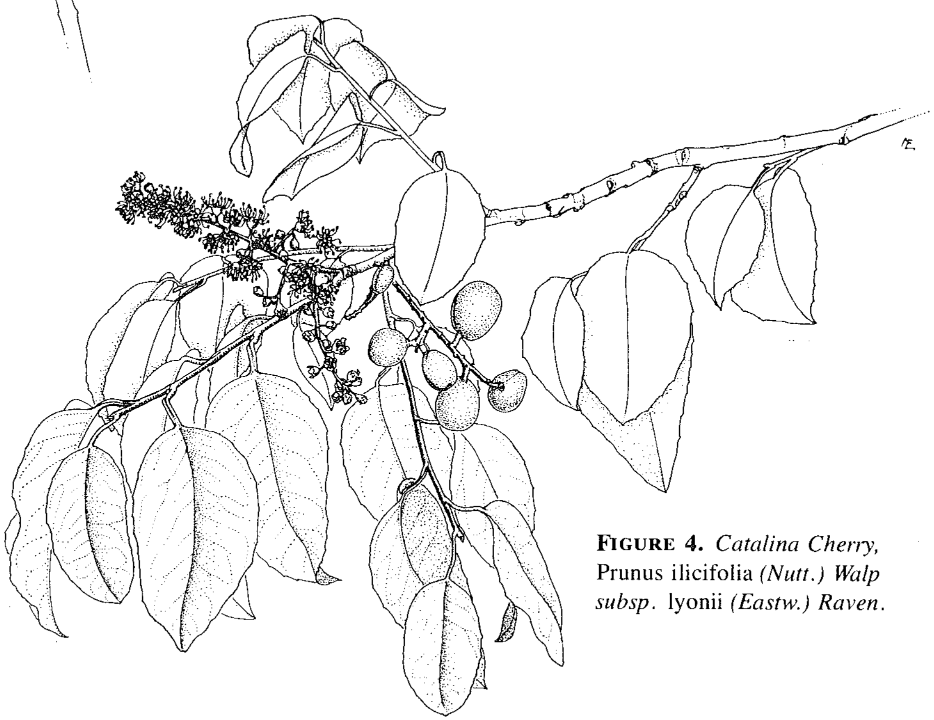

FIGURE 4. *Catalina Cherry*, Prunus ilicifolia *(Nutt.) Walp subsp.* lyonii *(Eastw.) Raven*.

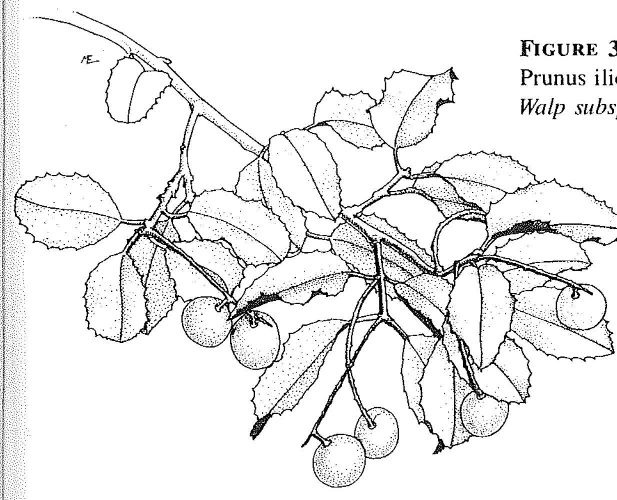

FIGURE 3. *Hollyleaf Cherry*, Prunus ilicifolia *(Nutt.) Walp subsp.* ilicifolia.

FIGURE 5. *Bush Poppy*, Dendromecon rigida *Benth. subsp.* rigida.

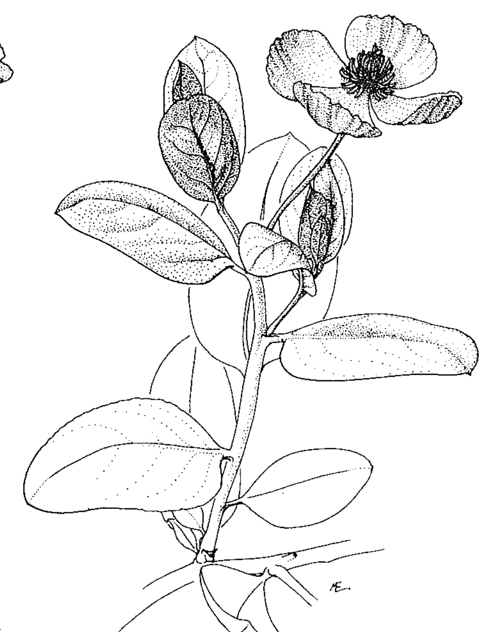

FIGURE 6. *Island Bush Poppy*, Dendromecon rigida *Benth. subsp.* harfordii *(Kell.) Raven*.

TABLE 1. Summary of climatic data for coastal and interior sites on Santa Cruz Island and in the Santa Ynez Mountains (1978 data for all sites except the island coastal site, where only 1977 data are available).

	Santa Cruz Island		Mainland		
	Coastal	Interior	Coastal		Interior
Elevation (m)	229	225	350	560	306
Precipitation (mm)					
1977-1978	1113	1115	1352†		1006
10-year average	509*	509*	495†		521
Temperature (°C)					
Mean annual	19.3	19.0	18.6	18.9	17.3
Mean January minimum	19.0	11.3	11.4	9.4	7.5
Mean July maximum	31.2*	27.2	30.4	32.5	33.5
Extremes	2.0 - 42.2	2.1 - 43.3	3.0 - 44.0	0.0 - 42.5	−7.8 - 41.0
Relative humidity (%)					
Mean annual	N.A.	68.9	67.4	62.6	N.A.
Mean July minimum	40.3*	48.1	40.7	34.8	31.8
Wind velocity (kph)					
Mean annual	5.3	2.3	1.4		10.6

N.A. = not available.

*Sufficient data not available; determined by linear regression.

†Data from Santa Barbara Botanic Garden.

Leaf anatomy.—In May 1978, six one-year-old leaves were collected from each subspecies for anatomical studies. Prepared slides of leaf cross-sections were made and the following parameters were measured: upper and lower surface cuticle thickness, upper and lower surface epidermal cell thickness, and leaf thickness at the immediate periphery of the central midvein. Epidermal peels were made during June 1979 for stomatal counts. Five leaves per subspecies, with six peels per leaf, were mounted on slides, and stomata were counted within a standard area. Because *Ceanothus megacarpus* stomata occur in crypts, the stomatal frequency was not determined. Also in June 1979, 15 leaves from each subspecies were randomly collected, weighed, and subsequently oven-dried and reweighed to calculate leaf water content. The significance of all measurements was tested using Student's t-tests.

RESULTS AND DISCUSSION

Meteorological data.—Results from the environmental monitoring stations are summarized in Table 1. Precipitation totals from all sites are comparable and none of the data is significantly different at $P < 0.05$. Mean wind velocity is affected primarily by local topography and is not consistently high or low on either the island or mainland. Mean annual temperatures differ by only 1 to 2°C at the various sites; the mean annual temperature at the mainland interior site appears lower than that of the other sites because of significantly lower temperature minima during the winter months (Hochberg 1980). Mean annual relative humidity figures are also insignificantly different. However, during the months of July through October, substantial

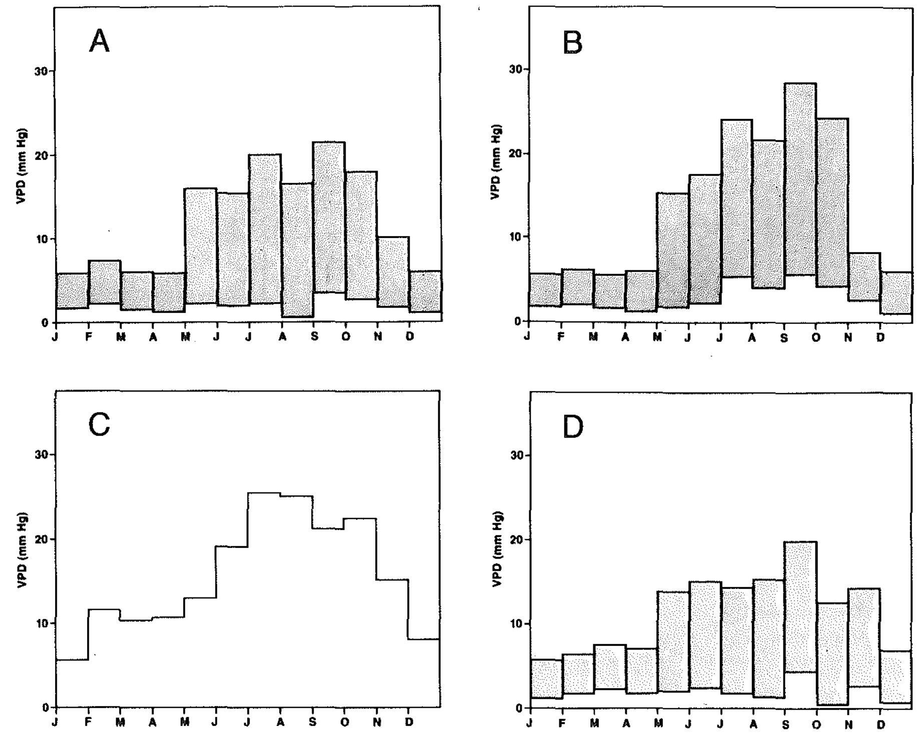

FIGURE 7. *Range in vapor pressure deficits in mm Hg on the mainland and island.* **a:** *lower mainland coastal site.* **b:** *upper mainland coastal site.* **c:** *mainland interior site (maximum values available only).* **d:** *island interior site.*

differences in relative humidity (Table 1) and vapor pressure deficits exist between the various sites (Fig. 7).

The highest vapor pressure deficit values are recorded during July through October at the mainland sites. At the upper mainland coastal site and the mainland interior site, the maximum vapor pressure deficit for July through October varies from 21.7 to 28.0 mm Hg. During the same time period, the maximum vapor pressure deficit at the lower mainland coastal site and the island interior site fluctuates from 11.8 to 20.7 mm Hg. Although averages of the vapor pressure deficits during the entire 12-month period at each site are not statistically significant at $P < 0.05$, maximum vapor pressure deficit values from the July through October period are significantly higher at the upper mainland coastal site and the mainland interior site than at either the lower mainland coastal site or the island interior site (Mann-Whitney test: $P < 0.01$). Dr. W. H. Schlesinger (pers. comm.) has observed that the lower coastal mainland site is frequently within the fog inversion layer, while the upper mainland coastal site often remains above the fog zone or at least clears off earlier in the day.

The relative frequency of clear, partly overcast, and overcast days at the various sites is shown in Table 2. In addition to yearly totals, the data have been subdivided into two additional categories to distinguish overcast days during winter storms from summer overcast due to fog.

TABLE 2. Summary of cloud cover in Landsat satellite imagery for the period 1972-1978.

	Clear		Partly overcast		Overcast		
	no. days	%	no. days	%	no. days	%	
Mainland							
Coastal:							
Total	78	66.1	8	6.8	32	27.1	n = 118
June-October	34	65.4	5	9.6	13	25.1	n = 52
November-May	44	66.7	3	4.5	19	28.8	n = 66
Interior:							
Total	92	78.0	7	5.9	19	16.1	n = 118
June-October	44	84.6	3	5.8	5	9.6	n = 52
November-May	48	73.7	4	6.1	14	21.2	n = 66
Santa Cruz Island							
Coastal:							
Total	68	57.6	18	15.3	32	27.1	n = 118
June-October	25	48.1	9	17.3	18	34.6	n = 52
November-May	43	65.2	9	13.6	14	21.2	n = 66
Interior:							
Total	80	67.8	12	10.2	26	22.0	n = 118
June-October	37	71.2	4	7.7	11	21.2	n = 52
November-May	43	65.2	8	12.1	15	22.7	n = 66

During the months of November through May, the cloud cover at the two island sites is virtually identical, whereas the mainland interior site averages slightly more clear days and fewer overcast days than the mainland coastal site. During June through October, the mainland interior site again experiences the greatest proportion of clear days. The island interior site records more clear days and fewer overcast days than the island coastal site and approximately the same number of clear and overcast days as the mainland coastal site. In fact, during June through October there is at least some cloud or fog cover at the island coastal site 52 per cent of the time; this figure drops to 35 per cent at the mainland coastal site, 29 per cent at the island interior site, and 15 per cent at the mainland interior site. However, it is also important to point out that the proportion of overcast days at all sites is artificially high since the Landsat images are taken in the morning before the fog has dissipated at most sites. Figures 8 and 9 illustrate fairly typical summer fog patterns, with dense fog in the Santa Barbara Channel and the coastal lowlands, but clear skies in the interior and at higher elevations near the coast.

Soils.—Soil textures and organic matter at the four study areas are shown in Table 3. The proportion of clay in the soil is similar at the two island sites and at the mainland coastal site but is somewhat lower at the mainland interior site. The ratio of sand to silt is noticeably different between the island and mainland sites, however. This ratio is always less than one on the island (coastal = 0.71:1; interior = 0.44:1), whereas on the mainland it varies from 3.5:1 (coastal) to 5.7:1 (interior). These results are not too surprising since the mainland interior site is located on the Coldwater Sandstone Formation and the mainland coastal site is located on the Sespe Formation, a sedimentary deposit containing high proportions of sand (Dibblee 1966). The island sites, on the other hand, are both situated on Santa Cruz Island Schist, a volcanic formation containing lower proportions of sand and correspondingly higher proportions of silt (Weaver 1969). The percolation of water out of the root zone of plants down to lower levels is

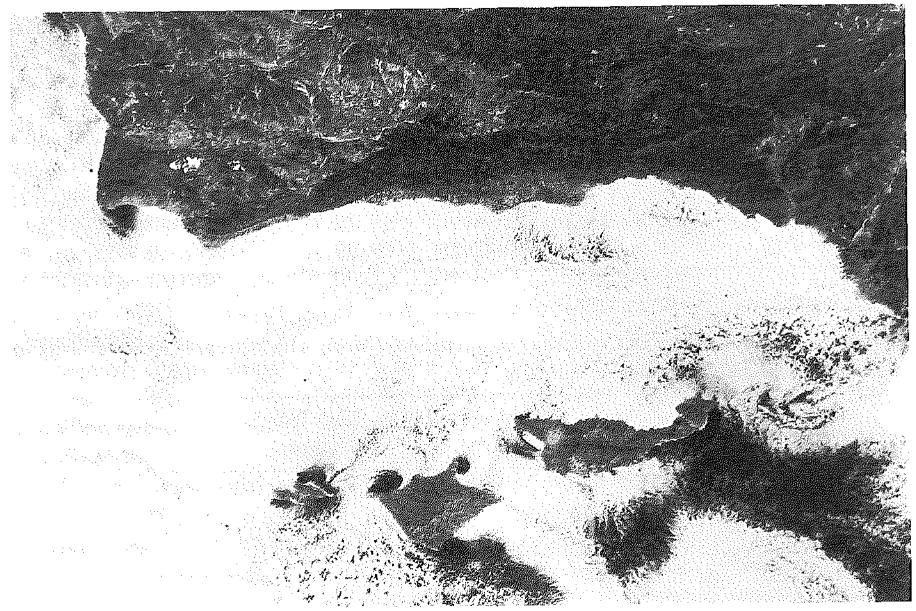

FIGURE 8. *Distribution of fog on 1 August 1974 along the Santa Barbara coast and Northern Channel Islands.*

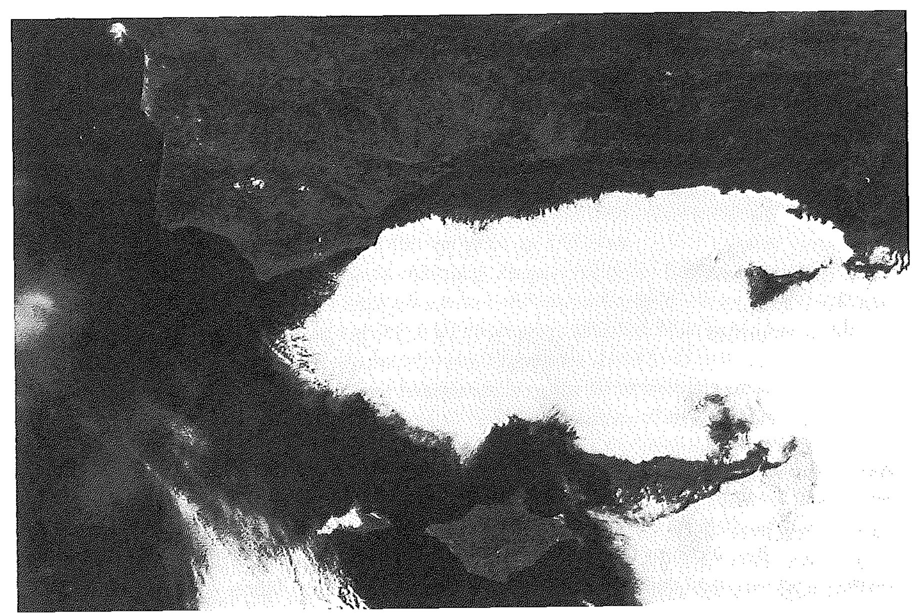

FIGURE 9. *Heavy fog on 13 September 1976 along the Santa Barbara coast and around Santa Cruz Island.*

TABLE 3. Characteristics of island and mainland soils (percentage composition).

	Clay	Silt	Sand	Organic matter
Mainland				
Coastal	23.0	17.0	60.0	4.3
Interior	13.0	13.0	74.0	10.3
Island				
Coastal	21.2	46.1	32.7	7.5
Interior	22.0	54.3	23.7	5.4

TABLE 4. Leaf dimensions of *Ceanothus megacarpus*. (Mean with standard error; numbers in parentheses indicate the range in leaf size.)

	Leaf area (cm^2)	Leaf length (cm)	Leaf width (cm)
Santa Ynez Mountains			
Coastal sites:			
Primary coastal site	1.55 ± 0.08	1.58 ± 0.05	1.05 ± 0.03
(*n* = 30)	(0.5 - 3.0)	(0.7 - 2.4)	(0.6 - 1.4)
Rattlesnake Canyon	2.10 ± 0.18	1.98 ± 0.10	1.10 ± 0.05
(*n* = 10)	(0.7 - 3.1)	(0.7 - 2.6)	(0.6 - 1.5)
San Roque Canyon	1.50 ± 0.15	1.61 ± 0.09	1.03 ± 0.04
(*n* = 10)	(0.6 - 3.0)	(0.6 - 2.2)	(0.5 - 1.5)
Santa Cruz Island			
Coastal sites:			
Primary coastal site	4.50 ± 0.12	2.73 ± 0.06	1.79 ± 0.03
(*n* = 30)	(2.5 - 6.6)	(2.1 - 4.1)	(1.2 - 2.4)
Laguna Canyon	3.53 ± 0.16	2.79 ± 0.10	1.65 ± 0.04
(*n* = 10)	(1.8 - 3.5)	(1.8 - 4.6)	(1.2 - 2.0)
Interior sites:			
Primary interior site	3.88 ± 0.13	2.85 ± 0.06	1.76 ± 0.04
(*n* = 30)	(1.6 - 7.0)	(1.9 - 4.3)	(1.2 - 2.9)
Central Valley	3.59 ± 0.22	2.62 ± 0.07	1.54 ± 0.05
(*n* = 10)	(1.9 - 6.0)	(2.0 - 3.8)	(1.2 - 2.1)
Santa Rosa Island			
Black Mountain	3.01 ± 0.15	2.78 ± 0.07	1.68 ± 0.05
(*n* = 10)	(1.8 - 3.5)	(1.5 - 5.2)	(1.2 - 2.1)

accelerated in sandy soils. Hence, the water-holding capacity of the island soils should be higher due to the more favorable sand-to-silt ratios there. In general, island soils are deeper as well (R. Brumbaugh, pers. comm.). Results from the organic matter analysis are inconclusive.

Leaf size.—Results from the leaf size study reveal significant differences ($P < 0.0001$) between the three island and mainland pairs of chaparral shrubs (Tables 4 to 6). Leaves from island plants are at least one and one-half to three times larger than leaves from mainland plants.

Comparative data for *Ceanothus megacarpus* (Table 4) indicate an average leaf area of 3.8 cm^2 from Santa Cruz Island sites and 1.8 cm^2 from mainland sites. The variation in leaf size

TABLE 5. Leaf dimensions of *Prunus ilicifolia*. (Mean with standard error; numbers in parentheses indicate the range in leaf size.)

	Leaf area (cm^2)	Leaf length (cm)	Leaf width (cm)
Santa Ynez Mountains			
Coastal sites:			
Primary coastal site	9.49 ± 0.27	4.12 ± 0.17	2.69 ± 0.06
(*n* = 30)	(3.6 - 18.1)	(1.8 - 5.4)	(1.5 - 4.3)
Mission Canyon	9.05 ± 0.40	3.38 ± 0.18	2.48 ± 0.06
(*n* = 10)	(3.8 - 17.2)	(2.1 - 8.0)	(1.6 - 3.7)
Interior site:			
Primary interior site	9.32 ± 0.34	3.60 ± 0.16	2.62 ± 0.03
(*n* = 30)	(4.1 - 15.6)	(2.1 - 5.4)	(1.6 - 3.4)
Santa Cruz Island			
Coastal site:			
Primary coastal site	25.36 ± 0.80	7.04 ± 0.20	4.31 ± 0.09
(*n* = 30)	(8.7 - 62.3)	(4.3 - 12.3)	(1.8 - 7.5)
Interior sites:			
Primary interior site	22.07 ± 0.71	5.98 ± 0.22	3.48 ± 0.11
(*n* = 30)	(10.1 - 48.3)	(4.5 - 10.6)	(1.8 - 6.2)
Central Valley	23.56 ± 1.37	6.32 ± 0.42	3.56 ± 0.17
(*n* = 10)	(9.2 - 53.4)	(4.8 - 13.3)	(2.0 - 8.1)
Santa Rosa Island			
Cherry Canyon	22.51 ± 1.43	6.43 ± 0.39	3.50 ± 0.19
(*n* = 10)	(8.7 - 56.1)	(4.2 - 15.0)	(1.8 - 8.1)

between plants at coastal and interior island sites is not significant. Mainland leaf sizes averaging 1.3 cm^2 were obtained by Gill (unpubl. data) in the Santa Ynez Mountains. The leaf sizes of Santa Rosa Island *Ceanothus megacarpus* are also significantly larger than any of the mainland populations, albeit somewhat smaller than Santa Cruz Island *Ceanothus*. The ratio of leaf length to width remains between 1.63:1 and 1.65:1 at all sites, indicating that the leaf shape retains similar proportions in spite of the variance in leaf area.

Leaf size comparisons of island and mainland *Prunus ilicifolia* follow a pattern similar to those of *Ceanothus megacarpus* (Table 5). Leaves of *Prunus ilicifolia* subsp. *ilicifolia* from the mainland have an average area of 9.2 cm^2 at the three sites sampled; Harrison *et al*. (1971) report a mean leaf area of 9.3 cm^2 in the Santa Monica Mountains. Leaves of *Prunus ilicifolia* subsp. *lyonii* from Santa Cruz and Santa Rosa Islands are larger with an average area of 24.1 cm^2. As before, there are no significant differences in leaf size between plants at coastal and interior sites. The leaf length-to-width ratio is somewhat larger in the island populations (1.71:1 to 1.84:1) than in mainland populations (1.42:1), reflecting the more narrowly ovate, pointed leaves representative of *Prunus ilicifolia* subsp. *lyonii*.

As in the other two subspecies pairs, the island populations of *Dendromecon rigida* have significantly larger leaves than the mainland population (Table 6). The island plants have a mean leaf area of 18.5 cm^2 for all sites, in contrast to 3.9 cm^2 for the one site sampled on the mainland. Furthermore, there are no significant differences between the leaf dimensions of *Dendromecon* at the insular coastal or interior sites. The leaf length-to-width ratio is smaller on the islands (Santa Cruz Island = 2.1:1; Santa Rosa Island = 1.86:1) than the length-to-width

Table 6. Leaf dimensions of *Dendromecon rigida*. (Mean with standard error; numbers in parentheses indicate the range in leaf size.)

	Leaf area (cm^2)	Leaf length (cm)	Leaf width (cm)
Santa Ynez Mountains			
Coastal sites:			
Primary coastal site	3.94 ± 0.47	4.51 ± 0.10	1.51 ± 0.10
(n = 30)	(1.6 - 9.9)	(1.5 - 10.2)	(0.8 - 3.2)
Santa Cruz Island			
Coastal sites:			
Primary coastal site	18.26 ± 0.78	6.89 ± 0.16	3.41 ± 0.11
(n = 30)	(6.3 - 52.3)	(3.5 - 10.6)	(1.8 - 5.1)
Laguna Canyon	17.34 ± 1.58	6.36 ± 0.31	3.15 ± 0.15
(n = 10)	(10.1 - 60.3)	(4.0 - 12.6)	(1.9 - 6.0)
Coches Prietos	21.90 ± 1.80	7.27 ± 0.21	3.58 ± 0.21
(n = 10)	(9.4 - 56.3)	(4.1 - 11.5)	(2.0 - 5.1)
Interior sites:			
Primary interior site	15.49 ± 1.01	5.71 ± 0.18	3.06 ± 0.11
(n = 30)	(5.0 - 55.1)	(3.8 - 11.7)	(1.8 - 6.2)
Central Valley	14.92 ± 1.64	7.01 ± 0.21	3.01 ± 0.18
(n = 10)	(4.9 - 40.2)	(3.6 - 10.2)	(1.8 - 3.9)
Santa Rosa Island			
Black Mountain	17.58	6.08	3.27
(n = 1)	(6.5 - 25.0)	(4.2 - 6.8)	(2.0 - 4.5)

ratio of 2.99:1 recorded from mainland plants. Thus, island leaves of *Dendromecon rigida* are proportionately wider as well as larger than mainland leaves (Figs. 5 and 6).

Because the initial island and mainland samples of *Dendromecon rigida* had been taken at different times of the year and because of the unexpectedly small leaf size of the mainland population, a new mainland sample was taken from five shrubs in May 1979. The mean leaf area of the new sample is 8.3 cm^2 (s.e. ±0.77), the mean leaf length is 7.99 cm (±0.38), and the mean leaf width is 1.99 cm (±0.07). However, these dimensions are still significantly smaller than those from island material. The larger leaf area in 1979 undoubtedly is a reflection of the timing of the sampling period. The initial sample was taken in fall 1977 following two years of drought, and the later sample was taken in spring following two years of substantial precipitation. These results suggest that prevailing climatic conditions have a major effect on the mean leaf size of this chaparral species and may affect the other species in a similar manner. Since island and mainland samples of *Prunus* and *Ceanothus* were taken at the same time of year, however, an examination of seasonal changes in leaf area for these species will be deferred until future studies. Seasonality in leaf characteristics has been documented by several authors for other xerophytic shrubs (Orshan 1964, Cunningham and Strain 1969, Smith and Nobel 1977).

Dimension analysis.—One interesting question raised early in this study was how the total leaf surface area per plant, or per branch, compared between island and mainland populations, and, more importantly, if differences in this total leaf area were a function of area per leaf or of the number of leaves per plant. The total photosynthetic surface area could be identical in both

Table 7. Total shrub size for species pairs from Santa Cruz Island and the Santa Ynez Mountains.

	Dendromecon rigida		*Ceanothus megacarpus*		*Prunus ilicifolia*	
	Island	Mainland	Island	Mainland	Island	Mainland
Mean number of branches/shrub at 15 cm above ground	16.2	3.5	7.4	1.3	6.0	21.6
Range in measured branch diameters (cm)	0.5 - 15.0	0.5 - 4.0	0.5 - 10.2	0.5 - 3.5	0.5 - 30.0	0.1 - 6.8
Total leaf area/shrub (cm^2)	127,574	2,331			728,347	206,193
Open canopy:			57,983	3,685		
Closed canopy:				1,660		
Total leaf number/shrub	8,236	792			28,720	22,064
Open canopy:			14,937	2,378		
Closed canopy:				1,071		

habitats, maintained by fewer larger leaves on the islands and numerous small leaves on the mainland. As a consequence, a dimension analysis study was initiated to establish comparative measurements of total leaf area per shrub for each of the species pairs.

Table 7 summarizes the total branch number, leaf area, and leaf number per shrub calculated for *Dendromecon*, *Ceanothus*, and *Prunus*. The island subspecies of both *Ceanothus* and *Dendromecon* have more branches originating at or below 15 cm above the ground when compared with the mainland subspecies. The arborescent island *Prunus*, on the other hand, generally has only a single main trunk with a few slender sprouts at the base, whereas the mainland *Prunus* is shrubbier with many basal branches. Each of the island subspecies has a much greater total leaf area per shrub, which, in *Ceanothus* and *Dendromecon*, can be attributed both to increased area per leaf and to the greater number of branches. The mainland *Ceanothus* is the only plant which shows significant changes in total leaf area depending on whether branches have been collected in an open site, such as a fuel break, or in a closed canopy of dense chaparral. However, shrubs of mature *Dendromecon* and *Prunus* were most frequently encountered at the open margins of dense stands.

Table 8 compares branches of the same diameter in the three subspecies pairs. The data for *Dendromecon* clearly indicate that for a given branch of the same diameter, leaf number remains constant while leaf size increases on the island. The results for *Ceanothus* are more difficult to interpret, however; island *Ceanothus* tends to grow in open habitats while the mainland type does not. Thus, results comparing island *Ceanothus* from an open habitat and mainland *Ceanothus* from a dense canopy are similar to *Dendromecon*, with striking similarities in leaf numbers but increased surface area per leaf in insular environments. For the *Ceanothus* growing in the two open habitats, however, total leaf area per branch is relatively constant for island and mainland forms, while leaf number roughly doubles for the mainland type. Hence, for equivalent branch diameters, mainland *Ceanothus* growing in open environments has approximately twice as many leaves and the same total leaf surface area as the island form, while mainland *Ceanothus* growing in a closed canopy has the same number of leaves and half the total leaf surface area when compared to the island form.

TABLE 8. Leaf area comparisons for branches of the same diameter between species pairs.

	Dendromecon rigida		*Ceanothus megacarpus*		*Prunus ilicifolia*	
	Island	Mainland	Island	Mainland	Island	Mainland
Branch diameter = 2.0						
Leaf area (cm²)	2,084	460	2,059		9,369	7,440
Open canopy:				1,826		
Closed canopy:				723		
Leaf number	145	156	530		387	800
Open canopy:				1,178		
Closed canopy:				467		
Branch diameter = 3.0						
Leaf area (cm²)	7,710	1,383	4,647		17,700	14,008
Open canopy:				4,650		
Closed canopy:				2,135		
Leaf number	498	470	1,197		731	1,506
Open canopy:				3,000		
Closed canopy:				1,380		

Unlike either of the other two species, the mainland *Prunus* has many more major stems than the island *Prunus*, elevating the total leaf area appreciably. In addition, the mainland *Prunus* has about double the leaf number per branch, bringing the total leaf area per branch closer to the island form, much like the *Ceanothus megacarpus* in the open canopy.

Hence, in all three pairs of subspecies the island plants have both larger leaves and total shrub leaf area. Island *Prunus* has fewer branches per shrub and fewer leaves per branch when compared with mainland *Prunus*. In addition to its larger leaves, however, it reaches much greater proportions and has more leaves per plant than the mainland form. Island *Ceanothus* and *Dendromecon*, on the other hand, have both larger leaves and more branches and leaves per shrub than their mainland counterparts.

Leaf anatomy.—A comparison of five anatomical leaf characteristics known to be correlated with moisture availability (Stocker 1960, Kummerow 1973) shows several differences between island and mainland leaves (Table 9). Cuticle thickness measurements do not appear to follow any pattern. Island leaves of *Ceanothus megacarpus* have significantly thicker cuticles on the upper leaf surface than mainland leaves, but mainland leaves of *Prunus ilicifolia* have significantly thicker cuticles on the upper leaf surface than island leaves; no statistical differences were indicated for cuticle thicknesses of leaves from *Dendromecon rigida*. Furthermore, the cuticle thicknesses reported from *Prunus* and *Dendromecon* are somewhat misleading since the leaf surfaces of both species are covered with additional layers of wax not included in this measurement.

Both smaller leaves and decreased cell size are often associated with plants from xeric habitats. Coupled with a reduction in cell size is an increase in the number of stomata per unit area (Stocker 1960). The epidermal cell widths in island leaves of both *Ceanothus* and *Prunus* are statistically greater than their mainland counterparts, and island *Prunus* has lower stomatal

TABLE 9. Comparisons of five xeromorphic characters between species pairs (* = differences statistically significant at $P < 0.05$).

	Ceanothus megacarpus		*Prunus ilicifolia*		*Dendromecon rigida*	
	Mainland	Island	Mainland	Island	Mainland	Island
Leaf thickness (mm)	0.39	0.37	0.28	0.28	0.32	0.38
Cuticle thickness (μ)						
Upper leaf	6.9	8.1*	2.9	2.3*	1.8	2.0
Lower leaf	3.4	3.2	1.4	1.5	1.5	1.5
Epidermal cell width (μ)						
Upper	17.8	30.7*	20.0	24.6*	27.7	29.5
Lower	8.8	10.9*	15.5	15.4	24.1	26.0
Stomatal frequency (no. per mm²)			452	321*	191	178
Per cent water content	48.0	46.0	51.7	54.1*	30.7	34.7*

frequencies than mainland *Prunus* as well. Per cent water content is significantly greater in island leaves of *Dendromecon* and *Prunus*. The range of expression of xeromorphy in island and mainland leaves needs to be examined more thoroughly in order to elucidate seasonal and long-term trends. In a similar study, Krause and Kummerow (1977) report few differences in the xeromorphic structure of leaves collected from species common to north- and south-facing slopes.

CONCLUSION

Measurements of leaf length, width, and area for the chaparral shrubs *Ceanothus megacarpus*, *Dendromecon rigida*, and *Prunus ilicifolia* show that populations on the Northern Channel Islands have significantly larger leaves than the mainland populations. In addition, the total leaf area per plant is consistently greater for the island subspecies.

An examination of island and mainland climates at or above 225 m indicates a number of similarities. Variables such as precipitation, mean annual temperatures, and yearly temperature extremes are essentially the same at all sites, and wind velocity averages reveal no sharp distinctions between the island and mainland, although these differences do exist on occasion. In spite of these similarities, humidity and vapor pressure deficit figures and, to a lesser degree, cloud cover show that the islands may be significantly moister. In addition, the presence of deep soils with enhanced water-holding capacities may provide island chaparral with more available moisture year-round, and, in particular, decreased moisture stress during the warm months.

Energy budget analysis of the effects of environmental factors on leaf dimensions indicate that lower stomatal resistances are required by the large-leaved island plants than by mainland plants in order to maintain leaf temperatures at biological optima (Hochberg 1980). Reduced evapo-transpiration rates, greater soil moisture retention, and decreased competition from other woody shrubs may all contribute towards enhanced water availability in island chaparral habitats. In addition, the larger leaves on island plants may reflect an adaptation to even more mesic conditions during the late Pleistocene (Axelrod 1967).

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Zonation of Coastal Plant Species and their Correlation with Salt Levels in the Soil

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INTRODUCTION

This study was an investigation of the processes leading to the establishment of a coastal vegetation pattern, and the factors which maintain or change a vegetation pattern over time. The simplest explanation for a zoned or banded distribution of species is the presence of an environmental gradient coupled with differential tolerance of the species to environmental factors in the gradient. An example is the banding of species at a right angle to onshore winds in exposed coastal regions. Onshore winds carry high levels of salt aerosol, and the strongest wind occurs closest to the ocean. This results in the deposition of high levels of salt aerosol and, consequently, leads to higher salt levels in the soil closest to the ocean. As the wind moves inland it carries less aerosol and the soil is less saline. Along this gradient the more salt-tolerant plant species would be expected in the regions close to the coast and less salt-tolerant forms would be expected in the interior soils.

Support for this hypothesis has been given in some preliminary work by Barbour *et al.* (1973), who found a strong association between species distributions and soil salinities. Lugo and Snedaker (1974) tested the hypothesis that soil salinities were responsible for zonation in mangrove regions and found that differential salt tolerance could not account for the zonation of species in mangroves. The present study was designed to test the hypothesis that differential salt tolerance can account for species distribution along a salt gradient on coastal headlands. To do this, I describe the zoned pattern along coastal headlands, examine the correlation of the distribution pattern with soil salinities, test salinity tolerances of the species involved in the pattern, and test these correlations with field manipulations.

DESCRIPTION OF THE STUDY SITE

The study was conducted on Fraser Point, the extreme western (and windward) end of Santa Cruz Island, 35 km off the coast of Santa Barbara, California. The study site was on the coastal headland 20 m above sea level, bounded on three sides by cliffs. The substrate is rocky with a shallow layer of soil varying in texture from clay to sand. Vegetation is a low-lying assemblage of annuals and perennials that appears to be sorted into bands paralleling the edge of the sea bluff.

The zonation of vegetation was quantified using two continuous line transects running from the seaward cliff (west) to the interior (east). Species were recorded at 10-cm intervals for 240 m (Fig. 1). A marked zonation is apparent for the three annual species. *Mesembryanthemum crystallinum* L. is found along the seaward edge of the headland. *Hordeum leporinum* Link. is found in the central portion of the headland, and *Lasthenia chrysostoma* (F. and M.) Greene is found in the most interior portion. The perennial species do not show as striking a zonation pattern. *Frankenia grandiflora* Cham. and Schlecht. is associated with the *Mesembryanthemum* and *Hordeum* zones. *Atriplex semibaccata* R. Br. is found in greatest abundance in the *Hordeum* zone. *Atriplex californica* Moq. in DC. and *Salicornia subterminalis* Parish. are

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