

LICHEN VEGETATIONAL GRADIENTS IN RELATION TO THE PACIFIC COAST OF BAJA CALIFORNIA: THE MARITIME INFLUENCE

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ABSTRACT

In central and south-central Baja California lichen communities change with increasing distance from the Pacific coast. Total lichen cover decreased from 15 percent on the coast to less than 0.5 percent at inland sites, and species richness decreased from 15–25 at coastal sites to three or fewer species inland. On *Fouquieria diguetii* lichen cover exceeded 60 percent at the coast and decreased to less than 1 percent inland. The presence of this rich lichen community is related to higher atmospheric moisture conditions along the coast. Two lichens absorbed water rapidly and lost water relatively slowly. In preliminary studies the coastal dominant species of this pair maintained a high rate of photosynthesis from 40 to 100 percent saturation whereas the inland dominant exhibited a narrower photosynthetic peak at 30–40 percent saturation. It is inferred that the coastal species is adapted to moister conditions.

Although the higher-plant vegetation of Baja California is relatively well known (Shreve, 1951; Shreve and Wiggins, 1964; Hastings et al., 1972; Humphrey, 1974), the lichen vegetation is rather poorly known. A study of lichens at San Quintín (Rundel et al., 1972) is the only published quantitative description of this lichen flora. From our extensive lichen collections throughout Baja California we have observed that lichen abundance and species richness decrease with increasing distance from the Pacific coast. Fruticose lichens grow luxuriantly on desert vascular plants near the coast from just south of Ensenada to the tip of the peninsula 1200 km to the south-southeast. These large lichens are apparently adapted to the maritime microclimate of the coast. One conspicuous component of this microclimate is the presence of frequent fogs, formed where cold ocean currents flow adjacent to the warm desert land. The climate becomes more continental at inland sites where fruticose lichens disappear.

In this study we have quantified the relative cover and species richness of lichens and vascular plants with distance from the coast and have initiated physiological studies to explain the observed distribution patterns.

METHODS

Vegetation. Selection of sites for sampling in Baja California was constrained by lack of accessibility in most areas. Choice of two tran-

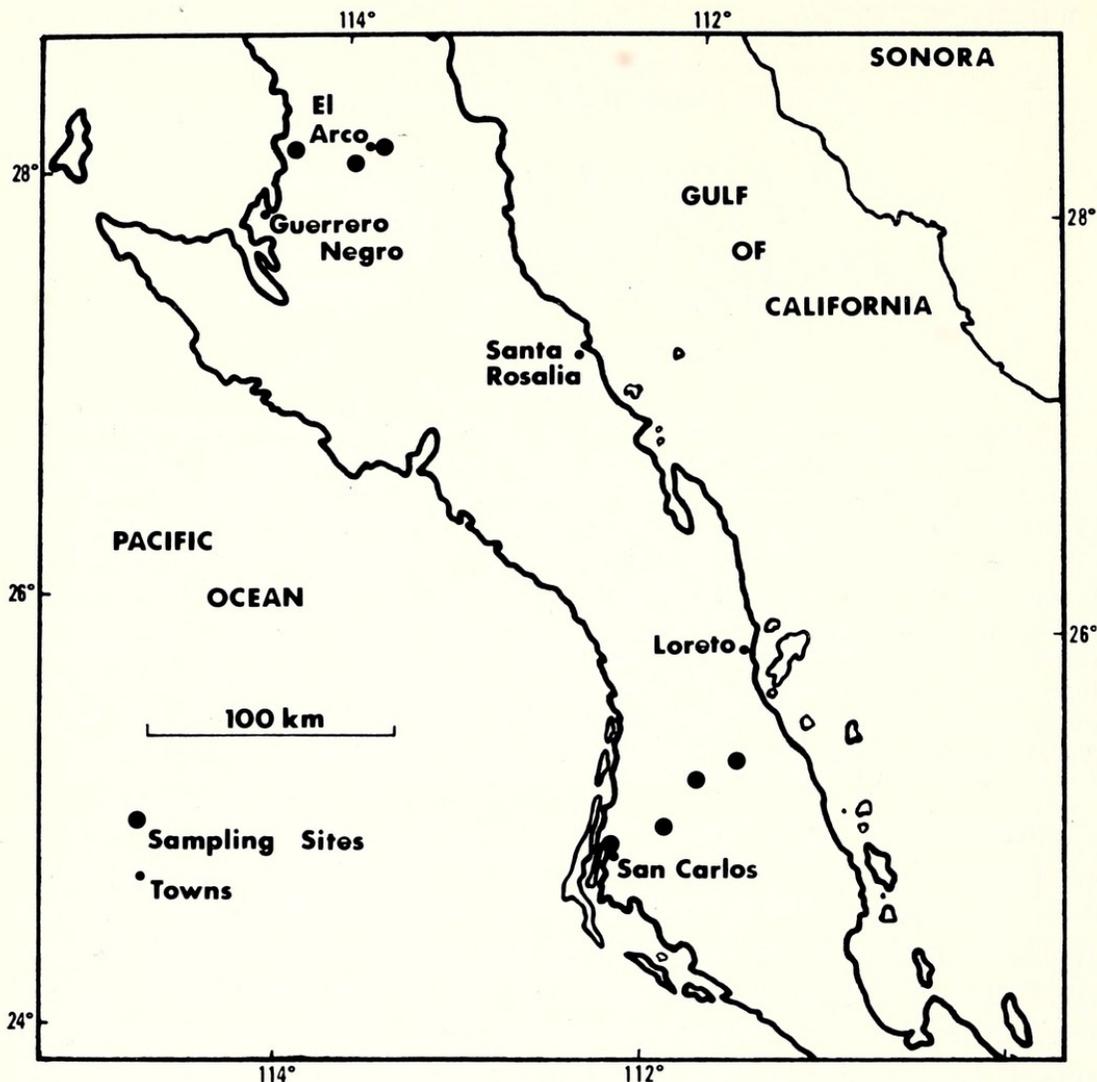


FIG. 1. Location of sampling sites in southern Baja California.

sect lines for sampling (Fig. 1) was in part dictated by the presence of roads. The San Quintín study (Rundel et al., 1972) was restricted to the north central coast, whereas our two transects include inland as well as coastal sites and are in the central and south-central portions of the peninsula. The transect from just north of Guerrero Negro to El Arco lies at approximately the midpoint of the peninsula (28°N) along the boundary of Baja California and Baja California Sur. The transect from San Carlos inland (25°N) lies approximately 300 km northwest of the southern tip of the peninsula.

These two transects have little topographic complexity. In this portion of the peninsula there is a broad coastal plain and a ridge of mountains, the Sierra de la Gigante, rising to approximately 2000 m, along the Gulf of California coast to the east. From the coastal plain to the base of the mountains the topography rises gradually as a bajada, composed of colluvial and alluvial materials eroded from the mountains.

Each transect began near sea level and rose gradually to approximately 300 m on the bajada at the terminal sites. Sampling sites were selected at 15–30 km intervals along the gradient from the coast until mountains were encountered (Fig. 1). Agricultural areas were avoided. At each site both lichens and vascular plants were sampled for cover using a m² frame. Cover was estimated to the nearest 0.1 percent (10 cm²) in 50 quadrats per site that were positioned randomly along two parallel 125 m transect lines. These were 50 m apart and ran perpendicular to the nearest road.

Because lichens may exhibit substrate specificity (Barkman, 1958), the potential effect of heterogeneity due to vascular plant variation was eliminated along the southern transect by also estimating lichen cover on *Fouquieria diguetii* (van Tiegh.) I.M. Johnston, a shrub common to all the sites. In this case cover was visually estimated to the nearest 1 percent on the *Fouquieria* shrub located closest to each quadrat.

Biomass estimates for lichen and vascular plants were also obtained at sites near the coast. Within each quadrat two 1-dm² subquadrats were nested randomly and the column of lichen and vascular plant tissue above the subquadrat was harvested. Lichens and vascular plants were separated by species, air dried in the field, oven dried (60°C for 24 hours) in the laboratory, and weighed to the nearest 0.1 g.

Physiology. Samples of a coastal dominant lichen *Roccella babingtonii* Mont. and an inland dominant lichen *Ramalina complanata* (Sw.) Ach. were also collected, air dried, and returned to the laboratory for subsequent physiological work.

Because CO₂ exchange by lichens is strongly dependent upon water content (Lange, 1954), the ability of these two species to absorb and retain water was investigated. To determine the rate of water absorption, five specimens of each species were submersed sequentially in distilled water at 23°C for periods of 0.17, 0.5, 1, 2, 5, 10, 30, and 120 minutes. At the end of each time period the lichens were removed from the water, shaken briefly to remove external water, and weighed. After the lichens were saturated (2 minutes in the case of *Roccella* and 30 minutes in the case of *Ramalina*), they were allowed to air dry under laboratory conditions of 23°C and approximately 40 percent relative humidity. The samples were reweighed after drying periods of 0.5, 1.0, 1.5, 2, 3, 4, 7, and 9 hours.

To measure the gross photosynthetic rate of these lichens at different water contents, a series of measurements was made using ¹⁴CO₂ incorporation following the procedure of Shimshi (1969). Pieces of each species (6–10 mg) were submerged in distilled water for 2 hours to ensure saturation, then removed and allowed to air dry. Three replicate exposures were made at approximately 10 percent moisture intervals between saturation and air dry conditions. Exposures to ¹⁴CO₂

TABLE 1. MEAN COVER (PERCENT) AND NUMBER OF SPECIES OF LICHENS AND HIGHER PLANTS ALONG TWO TRANSECTS AWAY FROM THE PACIFIC OCEAN. Data are from 50 1-m² quadrats randomly placed on two sampling lines per site. Standard deviations calculated from the means for the two sampling lines are given in parentheses. + = observed but not sampled.

Kilometers from ocean:	Lichens				El Arco Transect (28°N)				Vascular Plants			
	0	31	45		0	31	45		0	31	45	
<i>Dendrographa leucophaea</i>	4.6(2.6)	-	-						10.7(3.4)	-	-	0.5(0.5)
<i>Niebla pulchri-barbara</i>	2.6(0.9)	-	-						5.7(1.5)	3.0(3.8)	3.0(3.2)	3.0(3.2)
<i>Roccella babingtonii</i>	2.3(0.1)	-	-						3.9(2.4)	0.9(1.2)	4.0(2.2)	4.0(2.2)
<i>Niebla ceruchis</i>	4.7(3.5)	3.3(1.2)	-						-	5.4(2.4)	-	-
<i>Buellia oideale</i>	0.1(0.1)	0.7(0.7)	<0.1 -						-	4.3(1.4)	4.1(0.0)	4.1(0.0)
<i>Teloschistes chrysophthalmus</i>	-	0.2(0.2)	<0.1 -						+	1.7(1.0)	2.1(2.0)	2.1(2.0)
<i>Anaptychia erinacea</i>	-	-	0.1(0.1)						-	-	8.1(3.5)	8.1(3.5)
Other species	0.7	1.5	-						9.3	11.1	2.2	2.2
Total cover	15.0	5.7	0.2						29.6	26.4	24.0	24.0
Number of species	15	16	3						7	15	13	13

were made for approximately 22 seconds in a small plexiglass chamber at 4400 lux under fluorescent lighting at 26°C. Immediately after the exposure the samples were placed in scintillation vials on ice to reduce respiratory release of the $^{14}\text{CO}_2$. Subsequently the samples were dried at 100°C for 24 hours, weighed and then combusted in an oxygenated atmosphere following the technique of Tieszen et al. (1974). The released $^{14}\text{CO}_2$ was trapped in 5 ml of absorbing solution (3:3:5 absolute methanol:B-phenethylamine:toluene). After adding 10 ml of scintillation cocktail, emission of beta particles was counted by a Nuclear Chicago liquid scintillation counter (Tri-Carb Model 3220). After correcting for background radiation with controlled unexposed lichen samples, the data were converted to CPM/mg thallus and the data plotted in relation to the percent thallus saturation.

RESULTS

Vegetation. In contrast to the vascular plants, the lichens exhibited marked gradients in species richness and abundance along the transects (Table 1). For the Guerrero Negro transect lichen species richness per site decreased from 15 or 16 in the coastal plain sites to 3 at the inland bajada site. For the San Carlos transect species richness decreased from a high of 25 species at the coastal site to a low of 2 species at the interior sites. A parallel decline in lichen cover was found along the two transects from 15 percent cover to 1.2 percent cover and from 15.2 percent cover to 0.1 percent cover respectively for the Guerrero Negro and San Carlos transects.

Species richness for the vascular plants exhibited lower overall variability and no obvious gradients along the transects. Vascular plant cover was fairly constant within the respective transects, varying from 24 to 30 percent for the Guerrero Negro transect and from 38 to 45 percent for the San Carlos transect except for the 30 km site on the San Carlos transect. In the course of sampling, the latter site was found to be disturbed by tree and shrub cutting activity, and consequently community cover estimates for both lichens and vascular plants were low. The higher cover values on the San Carlos transect reflect the fact that to the south the desert grades into a thorn forest community where cover exceeds 100 percent.

We found marked shifts in lichen species along the transects. Several of the dominant species, including *Dendrographa leucophaea* (Tuck.) Darb., *Niebla pulchribarbara* (Rundel & Bowler) Rundel & Bowler, and *Roccella babingtonii*, and many of the less abundant species, including *Graphis* sp., *Lecanora pacifica* Tuck., *Ochrolechia pallescens* (L.) Mass., *Pertusaria* sp. and *Ramalina denticulata* Nyl., exhibited very restricted coastal distributions. Several other species exhibited somewhat broader distributions, extending from the coastal sites to one or more of the adjacent interior sites. These included the

less abundant *Buellia oidalea* (Nyl.) Tuck. and *Niebla ceruchis* (Ach.) Rundel & Bowler and the less abundant species *Caloplaca* cf. *californica* Zahlbr., *Dirinaria* sp., *Haematomma puniceum* (Sm. ex Ach.) Mass. and *Lepraria candelaris* (L.) Fr. A third group of species, including *Candelaria concolor* (Dicks.) B. Stein, *Parmelia caperata* (L.) Ach., *P. hypotropa* Nyl., *Ramalina crinita* Tuck., *R. menziesii* Tayl., *Teloschistes chrysophthalmus* (L.) Th. Fr. and *Xanthoria parietina* (L.) Th. Fr., show affinities for the midportion of the transects. Only five species, *Anaptychia erinacea* (Ach.) Trev., *Buellia oidalea*, *Physcia stellaris* (L.) Nyl., *Ramalina complanata*, and *Teloschistes chrysophthalmus* were found at the most interior sites and all of these had low cover values.

Niebla pulchribarbara was the only terricolous lichen sampled. All the other species were corticolous. Saxicolous lichens that are typical of northwestern Baja California were absent due to a scarcity of rocks.

Almost all of the lichen species were found on both transects. Exceptions included *Niebla pulchribarbara*, which apparently was at the southern end of its range at Guerrero Negro, and *Ochrolechia pallescens*, *Ramalina complanata*, and *Xanthoria parietina*, which were collected only on the southern transect. This is the first report of *Xanthoria parietina* in western North America.

Among sampling sites within a transect the vascular plants did not exhibit the marked variation in species composition found among the lichen species; however, there was considerable variation in vascular plant species between transects (Table 1). *Euphorbia* spp. were the only dominant vascular plants that exhibited a restricted coastal distribution. *Bursera microphylla* A. Gray was the only dominant restricted to the interior bajada sites. *Bursera microphylla*, *Fouquieria diguetii*, and *Machaerocereus gummosus* (Engelm.) Britt. & Rose were the only vascular plant species that were dominant on both transects. In addition, *Lycium californicum* (Nutt.) A. Gray and *Euphorbia misera* Benth. were dominant on one transect, but present in reduced abundance on the other transect. Dominant species restricted to one transect were *Acacia constricta*, *Ambrosia magdalena* (Brandege) Payne, *Atamignea emarginata* Miers, *Lycium andersonii* A. Gray, and *Prosopis juliflora* (Sw.) DC.

The patterns for less important species were similar to those for the dominant species. Only five of these species [*Jatropha cinerea* (C. G. Ortega) Muell. Arg., *Lophocereus schottii* (Engelm.) Britt. & Rose, *Pedilanthus macrocarpus* Benth., *Tillandsia recurvata* L., and *Yucca valida* Brandege] were found in common between the two transects. Two of the most conspicuous vascular plants because of their height were *Yucca valida* in the Guerrero Negro transect and *Pachycereus pringlei* (S. Wats.) Britt. & Rose in the San Carlos transect, but they contributed little to total community cover.

In general the patterns of cover and species richness of lichens on

TABLE 2. MEAN LICHEN COVER (PERCENT) AND NUMBER OF SPECIES ON *Fouquieria diguetii* ALONG A TRANSECT EAST FROM SAN CARLOS. Estimates are based on 50 shrubs per site. Standard deviations calculated from the means for the two sampling lines are given in parentheses.

Kilometers from ocean:	0	30	50	70
<i>Roccella babingtonii</i>	35.7(2.7)	4.2(0.9)	—	—
<i>Dendrographa leucophaea</i>	2.8(2.1)	0.3(0.2)	—	—
<i>Parmelia hypotropa</i>	1.6(0.1)	0.8(0.2)	—	—
<i>Niebla ceruchis</i>	11.0(3.6)	37.3(5.6)	<0.1	—
<i>Ramalina denticulata</i>	4.3(2.6)	0.3(0.1)	0.1(0.0)	—
<i>Buellia oidalea</i>	0.8(0.1)	0.6(0.1)	<0.1	—
<i>Teloschistes chrysophthalmus</i>	+ —	2.9(1.3)	+ —	—
<i>Ramalina complanata</i>	0.1(0.1)	1.1(0.1)	2.2(0.1)	0.3(0.2)
<i>Physcia stellaris</i>	—	—	1.4(0.1)	0.4(0.2)
Other species	9.0	9.1	1.0	—
Total cover	65.3	56.6	4.7	0.7
Number of species	27	27	13	2

Fouquieria diguetii (Table 2) parallel those obtained from the general community sampling. Species richness declined from 27 near the coast to 2 at the site farthest from the coast. Total lichen cover decreased from 65 percent to 0.7 percent. Lichen community dominance shifted from *Roccella babingtonii* at the coastal site to *Niebla ceruchis* at the 30 km site to *Ramalina complanata* at the interior sites. *Dendrographa leucophaea*, *Parmelia hypotropa*, and *Ramalina denticulata* all exhibited peak abundance at the coastal site. *Teloschistes chrysophthalmus* showed peak abundance at the 30 km site; *Physcia stellaris* dominated at the 50 km site.

Maximum lichen biomass values of approximately 120 g/m² (Table 3) were obtained at the coastal sites where the lichen to vascular plant biomass ratio was approximately 1:3. At interior sites this ratio was lower, reflecting the decreased proportion of lichens in the community.

TABLE 3. MEAN ABOVE-GROUND BIOMASS (g/m²) OF LICHENS AND VASCULAR PLANTS. Sites are specified by distance from the Pacific Ocean. Means are based on 50 1-dm² quadrats from two sampling lines. Standard deviations are given in parentheses. Values at 50 and 70 km sites on the San Carlos transect were not obtained because of the scarcity of lichens.

Location	Lichens	Vascular Plants	L/VP ratio
El Arco transect			
0 km	121.2(14.7)	343.6(40.3)	.352
31 km	19.5(8.3)	105.3(59.5)	.185
45 km	1.6(1.6)	230.1(62.4)	.007
San Carlos transect			
0 km	112.3(67.2)	303.4(62.4)	.370
30 km	18.9(5.2)	185.8(107.3)	.096

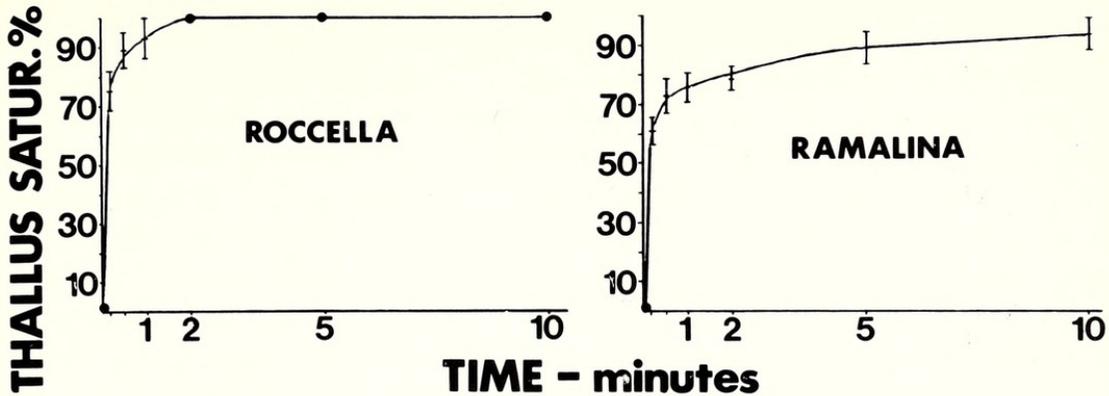


FIG. 2. Water absorption by *Roccella babingtonii* and *Ramalina complanata* as a function of submersion time in distilled water at 23°C. Intervals of ± 1 S.D. are constructed about the means.

Physiology. The uptake of water by the two species tested was extremely rapid (Fig. 2). Within 10 seconds thalli were more than 60 percent saturated. Complete saturation of *Roccella babingtonii* occurred after submersion for 2 minutes whereas *Ramalina complanata* took up to 30 minutes to become saturated. Loss of water occurred similarly for both species: approximately 50 percent in the first 1.5 hours, 80 percent in 3 hours, and 96 percent in 9 hours (Fig. 3).

Relative photosynthesis as a function of thallus saturation (Fig. 4) yielded very different curves for the two species. In both species photosynthesis was zero when the thallus was dry; appreciable photosynthesis occurred when thallus saturation was 20 percent of maximum. In *Ramalina complanata* maximum photosynthesis occurred in the 30–

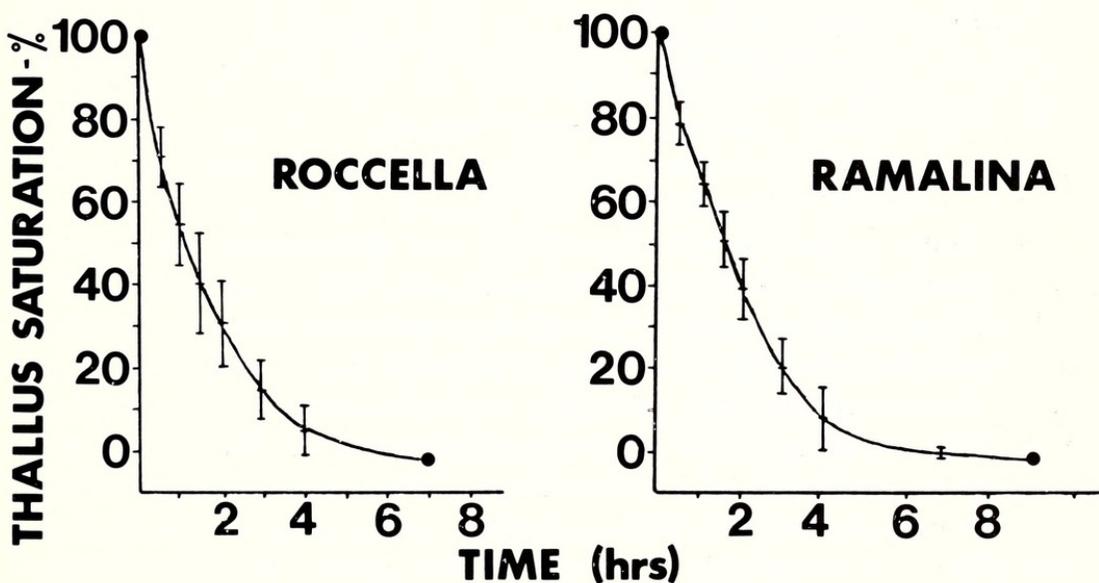


FIG. 3. Water loss as a function of time by *Roccella babingtonii* and *Ramalina complanata* under laboratory conditions of 23°C, 40 percent relative humidity, and 1000 lux. Intervals of ± 1 S.D. are constructed about the means.

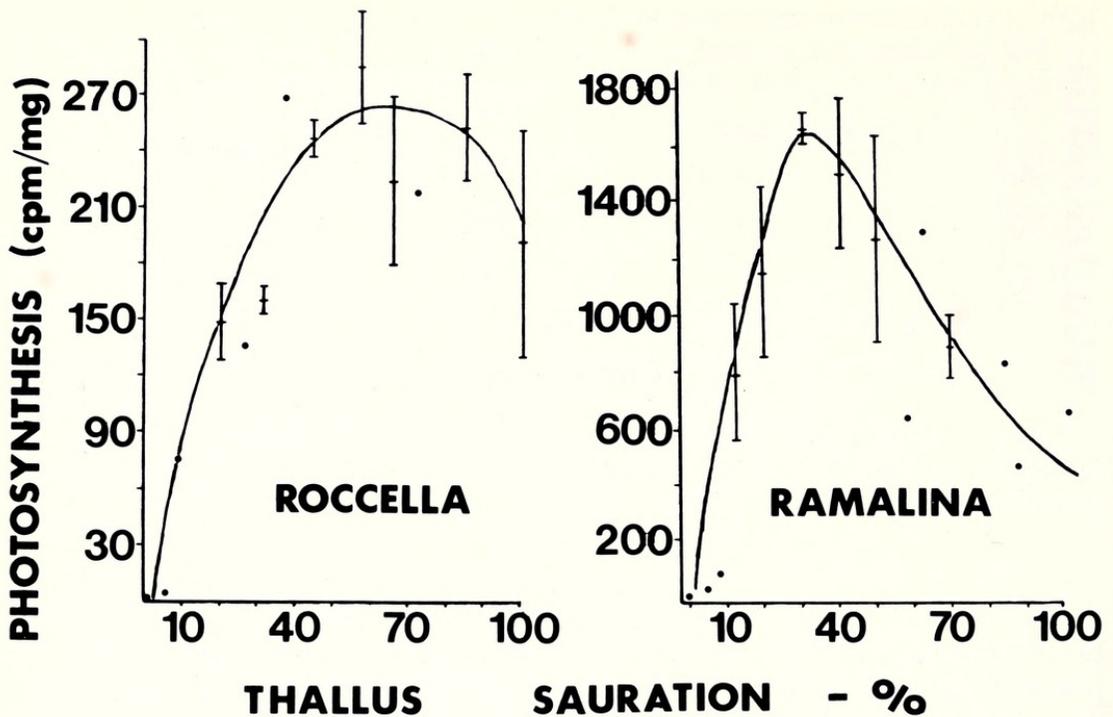


FIG. 4. Rate of photosynthesis by *Roccella babingtonii* and *Ramalina complanata* as a function of percent saturation as measured by $^{14}\text{CO}_2$ incorporation at 26°C and 4400 lux. Intervals of ± 1 S.D. are constructed about the means.

40 percent saturation range and declined to values less than 50 percent of maximum when 90–100 percent saturated. Linear regression showed that this decline was highly significant ($p < 0.01$). In contrast, the rate of photosynthesis of *Roccella babingtonii* was almost maximal for all measurements between 40–100 percent saturation. There is a slight drop in mean photosynthetic rate for *Roccella* above 40 percent saturation, but this was not significant ($p \approx 0.20$) when tested by linear regression.

DISCUSSION

The Pacific coastal lichen communities of Baja California together with a smaller zone along the southern coast of Sonora and northern Sinaloa form a unique component of the Sonoran Desert lichen flora. The abundance of the large fruticose species in the genera *Dendrographa*, *Niebla*, *Ramalina*, *Roccella*, and *Teloschistes* is one of the most conspicuous aspects of the coastal community. These genera are absent from eastern Baja California and from almost all mainland areas of the Sonoran Desert. In contrast, interior desert regions are dominated by crustose lichen species in the genera *Acarospora*, *Caloplaca*, *Dermatocarpon*, *Lecanora*, *Peltula*, and the foliose species in the genus *Parmelia* subg. *Xanthoparmelia* (Nash, 1975; Nash et al., 1977). The absence of the latter group of species from the Baja Cali-

fornia transects was due to lack of available substrates. Almost all of the interior Sonoran Desert lichens are saxicolous and terricolous. Rocks were absent from most of our sampling sites and the sandy soils of the coastal plain are probably so unstable that terricolous lichens cannot become established. In the northern Pacific coast of Baja California, where rock outcrops and firmer soils do exist, saxicolous and terricolous lichens can be found in abundance. Many of these species are restricted to the coastal habitat.

A second aspect of the southern coastal Baja California lichen communities is the preponderance of corticolous species. All but one of the lichens sampled (*Niebla pulchribarbara*) grew epiphytically on shrubs or small trees. In contrast, corticolous lichens are almost completely absent from the mainland Sonoran Desert areas, where the few species are restricted to more humid locations along permanent sources of water (Nash, 1975; Nash et al., 1977). Furthermore, lichen abundance is much greater in coastal Baja California than at interior Sonoran Desert sites. Estimates of lichen cover (0.03–8.1 percent) and biomass (0.02–38.3 g/m²) at US IBP Desert Biome sites (Nash et al., 1977) are far lower than those found near the coast of Baja California.

The ecology of the large fruticose lichens found at the coastal sites is not fully understood. Many of the species are known to range from the tip of Baja California north into southern California (Hale, 1969). In addition, we have found a small area in southern Sonora where several of the species also occur. One common denominator for all locations is the presence of a maritime influence that results in higher atmospheric moisture conditions. Because of the desert environment of Baja California, high atmospheric moisture conditions are not continually present. We hypothesize that one important variable may be the periodicity of dry and moist conditions. For example, Ahmadjian and Heikkilä (1970) have demonstrated that alternating dry and wet conditions are necessary for the maintenance of symbiosis in *Endocarpon pusillum*. Furthermore, these species do not occur in northern California where fog is more continually present. A better understanding of the distribution patterns will require study of more variables, including temperature.

On a world-wide basis the coastal Baja California lichen community is not unique. Galun (1963) reported the occurrence of different *Ramalina*, *Teloschistes*, and *Xanthoria* species in the Negev Desert where dew, apparently from moist air from the Mediterranean Sea, allows these large lichens to survive in otherwise arid conditions. Other fog-induced lichen communities are known from the Namib Desert of South Africa (Walter, 1937; Vogel, 1955) and the Atacama Desert of South America (Follman, 1967; Thomson and Iltis, 1968). The common denominator for all of these communities is apparently high atmospheric moisture as dew or fog.

At this time it is difficult to quantify appropriate moisture param-

eters that may account for the presence of the lichen dominated coastal community of Baja California. It is clear from the literature and from data presented here that, to be active physiologically, lichens must imbibe water. However, the pattern of increased lichen abundance and species richness near the coast does not reflect greater precipitation on the coast. In fact, the precipitation patterns reported by Hastings and Humphrey (1969) are opposite to expectations of greater precipitation correlated with greater lichen community development. Thus, for the northern transect (28°N), a coastal site at Vizcaíno receives 8 cm and the inland site at El Arco receives 14 cm per year. Likewise, farther south (26°N) the coastal site of La Poza Grande receives 6 cm and the inland site at Comondu receives 14 cm per year.

Although precipitation is lower on the coast, atmospheric moisture is undoubtedly higher on the coast because of the maritime influence and this factor probably accounts for the lichen abundance. Lange (1969; Lange et al., 1970a, 1970b) has shown that the fruticose desert lichen *Ramalina maciformis* (Del.) Bory is capable of maintaining a positive photosynthetic balance in the Negev Desert where dew is the major water source. Even on nights when dew does not occur, sufficient water may be imbibed under high relative humidity conditions to allow brief periods of photosynthetic activity immediately after sunrise.

Unfortunately, in Baja California we cannot cite data on the frequency of occurrence of fog or dew. However, we have experienced both phenomena personally while traveling the Pacific Coast of Baja California and it is reasonable to infer from our general climatic knowledge that both must occur frequently. The prevailing northwest winds that occur along the entire Pacific coast of Baja California (Humphrey, 1974) bring relatively cool, moist air onto the coastal regions because they flow across the relatively cold California Current prior to reaching the peninsula (Mosiño Alemán and Garcia, 1974). Presence of this maritime air over land is inferred from the fact that temperature means are lower by 2–3°C at coastal sites compared with corresponding locations inland. In relation to our northern transect (28°N), Hastings and Humphrey (1969) reported that the mean annual temperature at coastal Vizcaíno is 18.8°C whereas the inland site at El Arco has a mean annual temperature of 20.6°C. Likewise, to the south (26°N) the coastal site of La Poza Grande has a mean annual temperature of 20.0°C whereas Comondu, the corresponding location inland, has a mean of 22.8°C. With radiative cooling, which occurs during the night, moist air will reach the condensation point and dew or ground fog will form. Such ground fogs are typical of southern California's maritime province (Bailey, 1966) at least as far south as Vizcaíno (Humphrey, 1974). Furthermore, the presence of fog will reduce solar radiation at ground level and thus result in lower temperatures. The extent of maritime influence inland from the coast is

not known exactly but it is germane that the width of the maritime climatic zone delimited by Bailey (1966) in southern California is approximately as broad as the zone of lichen abundance along the coast of Baja California.

The saturation curves (Fig. 2) demonstrate the capacity of two Baja Californian lichens to absorb water rapidly, a phenomenon characteristic of many lichens (Ahmadjian, 1967). The submersion technique is not directly analogous to the response of a lichen to fog or dew, but we have observed that lichens sprayed with a water mist also imbibe water rapidly. Rapid water imbibition would be advantageous to lichens in environments where fog and dew are important water sources. Sufficient imbibition of water to activate photosynthesis and respiration should occur in Baja Californian lichens that are exposed to light fogs. In our personal experience we have repeatedly observed lichens at San Carlos to be fully saturated at dawn, with water dripping from the thalli. In contrast to water absorption, water loss from these lichens occurs more slowly (Fig. 3). The rate of water loss will, of course, vary with ambient conditions, being relatively slow on cool, overcast days and relatively rapid on warm, clear days. But whenever these lichens are partially moistened during daylight hours, a positive photosynthetic pulse is predicted, based on Lange's work cited earlier. These papers and unpublished data of the senior author show that for several desert lichens, respiration rates are independent of thallus saturation above 20 percent. Although we have no data on respiration of *Roccella* or *Ramalina*, the shapes of their net photosynthetic curves should be similar to the gross photosynthetic curves derived here.

We assume that in the absence of nonmarine water sources the intensity of foggy conditions should be reduced inland. If this assumption is correct, the photosynthetic curves (Fig. 4) may reflect adaptations that are functionally important in the ecological segregation of the species along the lichen gradient (*Roccella* coastal and *Ramalina* inland). Photosynthesis of *Ramalina* is markedly reduced at 100 percent saturation compared with photosynthesis at 30–40 percent saturation but photosynthesis of *Roccella* is essentially unchanged as 100 percent saturation is reached. *Ramalina* occurs in an environment where saturation probably occurs less frequently. Even in the same environment, *Ramalina* would reach saturation less frequently because the water absorption rate is slower (Fig. 2). If the observed differences in rates of relative gross photosynthesis between *Ramalina* and *Roccella* (Fig. 4) represent true population differences (variable densities of algal cells among lichen samples lead to widely disparate photosynthetic values), then *Ramalina* will be able to fix an equal amount of photosynthate in a shorter time period and should be expected to survive better in the drier portion of the transect where it is found.

The observed photosynthetic differences (Fig. 4) probably also re-

flect anatomical differences. *Ramalina* has a relatively thick cortex whereas *Roccella* has a relatively thin one. Saturation of the extracellular air spaces in the *Ramalina* combined with its thick cortex would impede CO₂ exchange more effectively.

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