

Spatial distribution of soil nutrients and ephemeral plants underneath and outside the canopy of *Porlieria chilensis* shrubs (Zygophyllaceae) in arid coastal Chile

Julio R. Gutiérrez¹, Peter L. Meserve², Luis C. Contreras¹, Hernán Vásquez¹, Fabian M. Jaksic³

¹ Departamento de Biología, Universidad de La Serena, Casilla 599, La Serena, Chile

² Department of Biological Sciences, Northern Illinois University, DeKalb, IL 60115, USA

³ Departamento de Ecología, Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

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Abstract. Soil nutrients and density and biomass of annual plants underneath and outside the canopy of *Porlieria chilensis* shrubs were measured at the end of the growing season in a protected arid coastal site in Chile. Levels of soil nitrogen, phosphorus and organic matter were significantly higher underneath than outside the canopies of shrubs. Almost 4 times as many plants occurred outside than underneath shrubs, but no significant differences in total aboveground biomass were found. Several species had higher densities and/or biomass outside rather than underneath shrubs, whereas others showed the opposite trend. Species richness was lower underneath *P. chilensis* canopy. The spatial microdistribution of ephemeral species may be explained by differential water and nutrient requirements. Comparison of the patterns observed in our protected site versus surrounding unprotected areas supports the generalization that man, by removing shrubs and trees, has changed a previous heterogeneous spatial distribution of nutrients to a more homogenous one.

Key words: Plant spatial distribution – Annual plants – Chilean desert – Soil nutrients – Fertility islands

Previous studies in North American and Australian deserts show that nutrients may become limiting to biological production during times when moisture is not limiting to plant growth (see West and Skujins 1978 for a review). Vertical and horizontal distribution of soil nutrients is strongly linked to vegetation distribution, composition, and biomass (West and Klemmenson 1978). In direct association with the scattered occurrence of vegetation in deserts, nutrients are concentrated in loci or “fertility islands” (García-Moya and McKell 1970), also called mosaics of nitrogen accumulation (Nishita and Haug

1973; Charley and West 1975) or of nitrogen availability (Tiedemann and Klemmenson 1973). These spatial patterns are largely the result of plants absorbing nutrients through their root systems and redepositing them on and in the soil as organic residues. In addition, decomposer activity is enhanced by the moderate temperature, increased infiltration and retention of soil moisture that prevail under the shade of desert shrubs (Tiedemann and Klemmenson 1973). In these fertility islands organic matter may constitute as much as 2% of the soil mass, in contrast to 0.5% or less outside the islands (Romney et al. 1978). These islands may be as fertile as typical areas of more humid ecosystems (Romney et al. 1978).

In the Mojave and Sonoran Deserts, growth of winter annuals appears to be so dependent on nutrient availability that the relatively nitrogen-rich fertility islands beneath shrubs support much larger plants with higher production efficiency than the nitrogen-poor soils in open areas (Mott and McComb 1974; Halvorson and Patten 1975; Patten 1978; Romney et al. 1978). West and Klemmenson (1978) postulated that the spatial patterns described above are likely to occur throughout the deserts of the world. However, without baseline information, it is difficult to evaluate the extent to which such a generalization, made on the basis of work conducted predominantly in North America, is applicable to floristically distinct communities such as those in Chilean deserts.

About one-third of the land area of Chile may now be classified as desert or semidesert. A significant part of the original vegetation of the Chilean arid region has been destroyed by human activities. Woody plants have been used extensively as fuel and building material for mining activities during the last two centuries (Solbrig 1984). Dry farming on foothills and overgrazing by goats and sheep have also contributed to the desertification process over a large portion of north-central Chile (Fuentes and Hajek 1978, 1979; Solbrig 1984). In 1941 a relatively pristine area was set aside as a reserve (Fray Jorge National Park), which presumably has preserved the original features of the regional plant communities.

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Correspondence to: J.R. Gutiérrez

The aim of this work is to test whether the spatial distribution of soil nutrients and ephemeral plant species in the arid ecosystem of Fray Jorge National Park fits the pattern described for North American deserts. Because our study was conducted during a relatively wet year we are confident that the species composition of local ephemerals is adequately represented.

Materials and methods

Study site

The study site is located in an interior valley (Quebrada de Las Vacas, 230 m elevation) in Fray Jorge National Park, Chile (30° 38' S, 71° 40' W), about 5 km east of the Pacific coast, on the eastern side of the coastal range, which reaches about 600 m elevation here. The park lies on the northern fringe of the Chilean mediterranean zone and on the southern edge of the Pacific Coastal Desert. The climate is semiarid mediterranean, with 90% of the 85 mm annual precipitation falling in winter months (May–September). Summer months are warm and dry but fog contributes significant additional moisture during many months (Kummerow 1966). Mean maximum temperature in the warmest month (January) is 24° C, and mean minimum temperature in the coolest month (July) is 4° C (all weather data are from the park headquarters located about 2 km east of the study site, collected and analyzed by the Oficina Meteorológica de Chile, Santiago). An important characteristic of this region is the extreme interannual variation in precipitation. In Fray Jorge, 1984, 1987 and 1991 were moderately to extremely wet years (127 mm, 168 mm, and 233 mm respectively), 1988 and 1990 were extremely dry (25 and 33 mm, respectively), and 1989 was an average year (85 mm).

The general plant community is characterized by spiny drought-deciduous and evergreen shrubs, with a herbaceous understory, and generally unvegetated sandy areas between shrubs. The specific community occupying the valley floor where the study was conducted has been termed the *Porlieria chilensis*-*Adesmia bedwellii*-*Proustia pungens* association for its most characteristic shrubs (Muñoz and Pisano 1947). The dominant species is a thorny shrub *Porlieria chilensis* (25–35% cover), followed by *Chenopodium petiolare* (9–28% cover), a suffruticose perennial distributed in the understory and margins of shrubs. Next in importance are the woody shrubs *Adesmia bedwellii* (2.6–5.7% cover) and *Proustia pungens* (2.0–9.5% cover). The flora of this region combines elements of the dry western Andean slopes with a few species from the Monte desert on the opposite side of the Andes (Sarmiento 1975).

Soil sampling

Two samples from the top 10 cm of soil (weight c. 1 kg) were taken under the canopy of each of five randomly chosen *Porlieria chilensis* shrubs. A similar number of soil samples were taken in the open 3 m away from *P. chilensis* canopy. The samples were transported to the laboratory for chemical analysis. The pH was determined in a 1 : 5 (w/v) suspension of soil in water. Organic matter was calculated from organic carbon estimated by oxidization with dichromate in presence of H₂SO₄, without application of external heat. Electrical conductivity was determined by a saturated-paste method. Available nitrogen (ammonium, nitrite and nitrate) was extracted with 2M KCl. Available phosphorus was extracted with a 0.5M NaHCO₃ solution at pH 8.5 (Olsen's method). Available potassium was extracted with 2M ammonium acetate at pH 7.0. Soil texture was determined by the Bouyoucos' densimeter method (Dewis and Freitas 1984). Student *t*-tests were used to compare chemical characteristics of soil samples collected underneath and outside shrubs.

Plant sampling

Because different plant species may respond to microhabitat conditions either by establishing more but smaller individuals or by growing fewer but larger ones, density and biomass were determined in September 1991 (at the peak of the growing season). We placed a quadrat frame of 30 × 30 cm under the canopy of each of ten randomly chosen *P. chilensis* shrubs and a similar number in the open 3 m outside *P. chilensis* canopy. All the plants inside a quadrat belonging to a given species were counted, harvested at ground level, and deposited in a paper bag. This procedure was repeated for each species. Plants were then oven-dried at 50° C for 72 h in the laboratory; the material was then weighed to the nearest milligram on a Sartorius scale. One-way ANOVAs were used to compare density and biomass of species underneath and outside shrubs. Because of large variances, data were log-transformed prior to statistical analyses.

Results

Chemical characteristics of soil samples

Electric conductivity (EC), as well as concentration of nitrogen (N), phosphorus (P), and organic matter (OM) were significantly higher underneath than outside shrubs (Table 1). There was 6 times more nitrogen, 3 times more organic matter and about double the phosphorus underneath shrubs. Soil samples, however, did not differ sig-

Table 1. Chemical characteristics of soil samples taken underneath and outside the canopy of *Porlieria chilensis* shrubs at Fray Jorge National Park, Chile; five replicates

Location		pH	EC S · m ⁻¹	N mg · Kg ⁻¹	P	K	OM g · Kg ⁻¹
Underneath	\bar{x}	6.78	0.085	41.1	35.2	320.0	2.57
	SE	0.11	0.009	6.9	1.7	31.8	0.54
Outside	\bar{x}	6.67	0.015	6.5	20.0	254.0	0.76
	SD	0.08	0.002	0.1	0.8	10.3	0.09
Student's <i>t</i>		0.80	7.67**	5.02**	7.84**	1.97	3.33*

P* < 0.05; *P* < 0.01

EC electrical conductivity; OM organic matter

Table 2. Texture of soil samples taken underneath and outside the canopy of *Porlieria chilensis* shrubs at Fray Jorge National Park, Chile. Replicates were five. Angular transformation of data was performed prior to the statistical analysis. None of the tests yielded significant differences

Location		Silt	Sand	Clay
		g · Kg ⁻¹		
Underneath	\bar{x}	8.60	83.60	8.40
	SE	1.36	2.32	1.02
Outside	\bar{x}	7.64	88.20	4.16
	SE	0.64	2.23	1.85
Student's <i>t</i>		0.49	1.44	1.94

nificantly with respect to pH or potassium (K). Soils underneath as well as outside shrubs were loamy sand. They did not differ in silt, sand or clay composition (Table 2). Hence, soils underneath and outside shrubs were texturally similar.

Species composition, density and biomass

There were large differences in species composition, density and biomass between areas underneath and outside *Porlieria chilensis* canopies (Table 3). A total of 29 species were found outside and 19 underneath shrub canopies. Of these, four (14%) and three (16%) species were introduced annuals, respectively. There were almost 4

times as many plant individuals outside than underneath shrub canopies, but no significant differences in total biomass were found. This indicates that in the areas under shrubs there were fewer plants but individuals were bigger.

Adesmia tenella, *Camissonia dentata*, *Calandrinia* sp. and *Lastarriaea chilensis* occurred only outside the canopy of *P. chilensis*. The same seemed to apply to *Cardionema ramosissimum*, *Crassula* sp., *Eryngium coquimbabanun*, *Erodium malacoides*, *Erodium* sp., *Helenium aromaticum*, *Homalocarpus* sp., *Oenothera coquimbensis*, *Plantago* sp. and *Quinchamalium chilense*, but their densities outside shrubs did not differ significantly from zero, either because of their low density and/or large variances. On the other hand, *Descurainia cumingiana*, *Galium aparine*, *Menonvillea* sp., *Microseris pygmaea*, *Parietaria debilis* and *Urtica urens* were found exclusively underneath the canopy of *Porlieria chilensis*, though only the density figure for *Parietaria debilis* reached significance. The remaining species were found both underneath and outside the canopy of *Porlieria chilensis*. *Moscharia pinnatifida*, *Schizanthus litoralis* and unidentified grasses were significantly denser in the former microhabitat, whereas *Plantago hispidula* and *Viola pusilla* were denser in the latter. Eight other species did not differ significantly in their density underneath or outside the canopy of *P. chilensis*.

In terms of biomass (Table 3), *Adesmia tenella*, *Camissonia dentata* and *Plantago hispidula* had higher values outside than underneath shrubs, whereas the biomass of *Moscharia pinnatifida* was almost two orders of

Table 3. Mean and SE (in parentheses) of density (number of plants · m⁻²) and aboveground-dry biomass (g · m⁻²) of ephemeral plant species outside (O) and underneath (U) the canopy of *Porlieria chilensis*; ten replicates

Species	Density			Biomass		
	O	U	<i>F</i>	O	U	<i>F</i>
<i>Adesmia tenella</i>	51.11 (25.11)	—	6.60*	2.54 (0.97)	—	7.49*
<i>Alstroemeria sierrae</i>	1.11 (1.11)	4.44 (4.44)	0.27	0.24 (0.24)	1.51 (1.51)	0.56
<i>Apium</i> sp.	25.56 (19.67)	10.00 (10.00)	0.80	0.68 (0.68)	0.04 (0.04)	0.84
<i>Camissonia dentata</i>	282.22 (167.56)	—	14.61**	5.43 (2.13)	—	8.57*
<i>Calandrinia</i> sp.	110.00 (65.56)	—	5.36*	7.58 (6.26)	—	2.04
<i>Cardionema ramosissimum</i>	13.33 (12.11)	—	1.61	0.02 (0.02)	—	1.00
<i>Crassula</i> sp.	14.44 (8.89)	—	3.16	0.06 (0.04)	—	2.08
<i>Cryptantha</i> sp.	40.00 (20.67)	16.67 (16.67)	1.91	1.10 (0.66)	0.36 (0.36)	1.03
<i>Descurainia cumingiana</i>	—	26.67 (16.78)	3.32	—	1.02 (0.84)	1.60
<i>Eryngium coquimbabanun</i>	162.22 (137.22)	—	2.13	0.80 (0.56)	—	2.10
<i>Erodium malacoides</i> ^a	8.89 (7.78)	—	1.71	4.72 (4.60)	—	1.13
<i>Erodium</i> sp. ^a	1.54 (1.44)	—	2.25	0.09 (0.08)	—	1.41
<i>Galium aparine</i> ^a	—	27.78 (20.22)	2.86	—	1.21 (0.93)	1.82

Table 3. (continued)

Species	Density			Biomass		
	O	U	F	O	U	F
<i>Gamochaeta</i> sp.	2.22 (1.44)	1.11 (1.11)	0.36	0.02 (0.01)	0.01 (0.01)	1.67
Graminae	2.22 (1.44)	70.00 (32.67)	7.72*	0.01 (0.01)	1.73 (0.94)	3.68
<i>Helenium aromaticum</i>	6.67 (6.67)	–	1.00	0.19 (0.19)	–	1.00
<i>Homalocarpus</i> sp.	2.22 (2.22)	–	1.00	0.02 (0.02)	–	1.00
<i>Lastarriaea chilensis</i>	154.44 (128.77)	–	7.08*	1.81 (1.47)	–	1.86
<i>Leucocoryne purpurea</i>	32.22 (18.00)	1.11 (1.11)	2.89	0.50 (0.29)	0.04 (0.04)	2.43
<i>Linaria texana</i> ^a	63.33 (39.00)	–	5.17*	0.63 (0.50)	–	1.67
<i>Menonvillea</i> sp.	–	4.44 (4.44)	1.00	–	0.14 (0.14)	1.00
<i>Microseris pygmaea</i>	–	16.67 (13.33)	2.02	–	0.28 (0.24)	1.40
<i>Moscharia pinnatifida</i>	20.00 (15.44)	482.22 (147.56)	57.47**	0.91 (0.58)	93.63 (14.87)	175.76**
<i>Oenothera coquimbensis</i>	12.22 (0.78)	–	2.11	9.14 (0.70)	–	1.32
<i>Oxalis</i> sp.	60.00 (32.56)	52.22 (10.33)	0.77	1.76 (1.54)	0.80 (0.28)	0.18
<i>Parietaria debilis</i>	–	88.89 (44.44)	8.56**	–	1.36 (0.72)	4.04
<i>Plantago hispidula</i>	2572.22 (1029.44)	144.22 (69.11)	15.69**	57.27 (12.26)	4.03 (1.94)	27.09**
<i>Plantago</i> sp.	1.11 (1.11)	–	1.00	0.04 (0.04)	–	1.00
<i>Quinchamalium chilense</i>	2.22 (2.22)	–	1.00	0.28 (0.28)	–	1.00
<i>Rodophiala phycelloides</i>	2.22 (1.44)	1.11 (1.11)	0.36	4.61 (4.01)	5.28 (5.28)	0.04
<i>Schismus arabicus</i> ^a	28.89 (19.00)	2.22 (2.22)	2.62	0.16 (0.10)	0.01 (0.01)	2.18
<i>Schizanthus litoralis</i>	6.67 (3.44)	62.22 (24.66)	7.03*	0.89 (0.76)	5.39 (2.52)	4.03
Unknown	6.67 (5.56)	–	1.81	0.42 (0.41)	–	1.04
<i>Urtica urens</i> ^a	–	50.00 (50.00)	1.00	–	1.44 (1.44)	1.00
<i>Viola pusilla</i>	181.11 (78.11)	3.33 (1.70)	11.64**	2.01 (1.12)	0.03 (0.01)	3.70
Native plants	3674.44 (1078.89)	983.33 (183.89)	8.06*	89.97 (11.02)	115.63 (15.02)	1.27
Exotic plants	103.33 (59.00)	80.00 (57.56)	0.53	5.59 (4.74)	2.66 (1.84)	0.13
Total	3867.78 (1052.89)	1063.33 (194.11)	10.05**	95.57 (13.32)	118.29 (15.28)	0.98

* $P < 0.05$; ** $P < 0.01$ ^a Exotic

magnitude higher underneath than outside the canopy of *Porlieria chilensis*. *Plantago hispidula*, the most abundant annual species outside shrubs, has been described as a weedy native or ruderal species by Walkowiak and Simonetti (1981).

Most exotic plants had larger densities and biomasses outside than underneath shrubs (Table 3), but the dif-

ferences were not significant. Of the six exotic species found, four (*Erodium malacoides*, *Erodium* sp., *Linaria texana* and *Schismus arabicus*) had larger densities and biomasses outside than underneath shrubs, and the two remaining (*Galium aparine* and *Urtica urens*) showed the opposite trend. However, only *L. texana* showed significant differences.

Discussion

Went (1942) documented the micro-distribution of annual plants in scrub communities of the Sonoran and Mojave Deserts and concluded that while some herbs were strongly associated with specific shrubs, others were not. This association appeared to be related to the organic matter accumulated under shrubs, which provided a nutrient-rich microhabitat for annuals. Patten (1978) documented a greater productivity of some annuals under the canopy of *Cercidium microphyllum*, as compared to open spaces in the Sonoran Desert, and Parker et al. (1982) found higher density and biomass for many annuals associated with higher levels of nitrogen measured under the canopies of *Larrea tridentata* in the Chihuahuan Desert.

In contrast, our results show that plant density was higher in the open than underneath the canopy of *P. chilensis*, but biomass was about the same, i.e. lower numbers but bigger plants under the shrubs. This density difference is determined chiefly by the weedy native *Plantago hispidula*. Density of this species is up to one order of magnitude higher in disturbed than in undisturbed coastal sand-dune communities (Walkowiak and Simonetti 1981). Species richness was lower under shrub canopies. Higher nutrient availability under shrubs was demonstrated by chemical soil analysis, and this factor apparently increased the yield of some annual species (e.g. *M. pinnatifida*) but it would also have reduced species richness. This inverse relationship between production and species richness, known as the paradox of enrichment (Rosenzweig 1987), may result because the dominant species are often better able to capitalize on increased nutrient availability and thus can increase their biomass or density at the expense of other species (Pyke and Archer 1991). For instance, Inouye et al. (1987) found that species richness declined with increased total nitrogen in old fields in Minnesota. However, when there is greater heterogeneity in resource abundance, species that would be competitors in more homogeneous environments may coexist through small-scale spatial segregation (Tilman 1980, 1982). Data on soil nutrients underneath and outside the canopy of *P. chilensis* suggest that annual plants living relatively close to each other may be exposed to significantly different rates of nutrient supply. An alternative but not exclusive explanation for the absence of some species under shrubs is that they are shade-intolerant. This could be true for *Calandrinia* sp., because this species is more abundant in equatorial-facing slopes and has sun-tracking flowers (JRG, personal observation), but not for the mesophytic mediterranean *Plantago*. However, further research is needed to test these hypotheses.

In our study site, the dominant species under shrubs were seldom found in dry years (Gutiérrez et al. in press) and were completely absent from areas without woody shrubs (Gutiérrez 1992). Although *Porlieria chilensis* is one of the most abundant shrub species in undisturbed sites it is nowadays considered an endangered species (Benoit 1989) due to the intense exploitation that it has borne. Human-related disturbances such as vegetation

clearing, burning and overgrazing have all contributed to the process of desertification in Chile. Clearing of large areas probably increased the erosion and dispersal of nutrients stored under shrubs, thus affecting the survival of the ephemeral plants that were restricted to these nutrient-rich microsites. The same disturbance, on the other hand, may have provided favorable sites to those species now abundant in the inter-shrub spaces, mainly exotics. In an old field of the Chilean coastal desert, 40 km north of Fray Jorge, Gutiérrez (1992) found that 40% (6 of 15) of ephemeral plants were exotics. Similar results were reported by Armesto and Vidiella (1993) for the same site.

Human disturbance appears to have differently affected the plant communities in the Chilean coastal desert and in North American deserts. In North America overgrazing appears to be the main factor changing the previously grass-dominated communities to shrub-dominated communities (Schlesinger et al. 1990). Hence, desertification in North America has altered a previous, relatively uniform distribution of water and nitrogen by increasing their spatial and temporal heterogeneity, thus leading to changes in community composition and biogeochemical processes (Schlesinger et al. 1990). Similarly, we propose that man, by removing shrubs and trees previously present in the Chilean coastal desert may have changed a formerly heterogeneous spatial distribution of nutrients and water to the more homogeneous one observed today (Gutiérrez et al. 1992). The clearing of large areas also reduces the soil moisture-holding capacity and increases its evaporation rate (Keeley and Johnson 1977; Jaksic and Montenegro 1979), thus allowing the invasion of introduced annual species and prompting the reduction of native ephemeral species associated with shrubs and trees. As a consequence, restoration of disturbed lands in the Chilean coastal desert should consider not only soil fertilization schemes but also revegetation with native shrubs and trees, in order to reconstruct the formerly heterogeneous pattern of fertility islands.

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