

Seasonality, Growth, and Net Productivity of Herbs and Shrubs of the Chilean Matorral¹

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Chile, located between 18° and 56° latitude south, has a climate which markedly varies according to geographical position (Di Castri 1968, Hajek and Di Castri 1975). Drought predominates in the north of the country and rainfall is characteristic of the central and southern regions. The natural vegetation is closely related to the different climatic patterns. The northern part of the country is desertic, while evergreens predominate in the south (Pisano 1954, Di Castri 1968, Heusser 1974, Hueck 1978). The central region, with a mediterranean climate, has a typical matorral vegetation (Di Castri 1973, Mooney and others 1974, Quintanilla 1974, Miller and others 1977, Rundel 1981).

Three physiographic regions can be distinguished in Central Chile: the Coastal Range with a highest altitude of 2200 m, the Central Valley, and the Andean Cordillera where the highest peak reaches 7000 m a.s.l. (Rundel 1981). The matorral is the dominant vegetation of the Mediterranean zone: it extends from 33° to 38° S. latitude and along an altitudinal gradient from the coast up to 2300 m a.s.l.

The study sites were Cachagua, on the coast, at 50 m a.s.l. (2-year observations); Santa Laura in the Coastal Range, at 1000 m a.s.l. (5-year observations); Quebrada Seca at 1000 m a.s.l. and Paso Marchant, at 2200 m a.s.l., both in the Andes Cordillera (5-year observations).

Evergreen sclerophyllous shrubs and trees, succulents, and drought-evading herbs predominate in Central Chile, from the coast to about 1000 m elevation (Mooney and others 1970, Mooney and others 1977, Montenegro and others 1979a). Evergreen shrubs predominate on polar-facing slopes, while drought-deciduous shrubs and succulents are mostly found on equatorial-facing slopes (Rundel 1975, Parsons 1976, Mooney and others 1977, Armesto and Martinez 1978).

¹Presented at the Symposium on Dynamics and Management of Mediterranean-type Ecosystems, June 22-26, 1981, San Diego, California.

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Abstract: The physiognomy and species composition of the matorral, as well as growth period and net productivity of shrubs, change with altitude. In shrubs, vegetative growth period is shorter at higher altitudes; leaf area indices are significantly higher at lower sites, while biomass indices increase with altitude. At the community level, productivity is lower in the montane matorral. Growth and productivity of the herbaceous understory markedly varies depending on precipitation. Most vegetative growth occurs between winter and early spring.

The midelevation matorral in the Coastal Range and the sclerophyllous scrub at the foothills of the Andes are replaced at about 1850 m by a montane evergreen scrub community (Mooney and others 1970, Rundel and Weisser 1975, Hoffmann and Hoffmann 1978, Montenegro and others 1979b). At 2300 m in the Andes the matorral gives way to a low subalpine scrub. Over 3000 m, alpine herbs and cushion plants predominate (Villagran and others 1979, Arroyo and others 1979).

Here we will analyze the phenology, dynamics of growth, net productivity, and mortality of shrubs and herbs of the Chilean matorral along an altitudinal gradient, from the coast up to 2200 m altitude in the Andean Cordillera. Our aim is to assess the fluctuations in growth and phytomass in ecosystems of semiarid area. The results of this study may help in design of optimal management practices in these ecosystems, which are being progressively affected by man's activities.

HERBACEOUS VEGETATION

Herbs are an important component of the shrub-dominated vegetation in Central Chile. Mooney and others (1977) and Keeley and Johnson (1977) found over 60 percent herb cover in the midelevation matorral zone. Native species usually grow under the canopy of shrubs, with no obvious indications of allelopathic interactions (Montenegro and others 1978), while the introduced species dominate the open areas. This is in contrast to what has been reported for the Californian chaparral, where the herb cover is poor (Mooney and others 1977), probably due to allelopathic effects (McPherson and Muller 1969, Chou and Muller 1972).

At 1000 m elevation, on the matorral zone, 75 percent of the 32 native herb species are perennials and constitute about half of the cover (Keeley and Johnson 1977). The annual cover decreases with increasing altitudes, from values of 40 percent at 1000 m elevation to 2 percent at 2000 m, in the Andes (Martínez, unpublished data). In general, on the Andes, the herb cover is found mostly under shrubs. The rocky spaces between shrubs show very low herb density.

The growth of the herbaceous understory in all mediterranean areas along the altitudinal transect

Table 1--Dominant species along the transect on parallel 33° South latitude

Species	Family	Life - form
<i>Aster haploppapus</i>	Compositae	Summer deciduous half-shrub
<i>Flourensia thurifera</i>	Compositae	Summer deciduous shrub
<i>Baccharis concava</i>	Compositae	Evergreen sclerophyllous shrub
<i>Peumus boldus</i>	Monimiaceae	Evergreen sclerophyllous shrub
<i>Satureja gilliesii</i>	Labiatae	Summer deciduous half-shrub
<i>Talguenea quinquenervia</i>	Rhamnaceae	Thorny summer-deciduous shrub
<i>Trevoa trinervis</i>	Rhamnaceae	Thorny summer-deciduous shrub
<i>Colliguaya odorifera</i>	Euphorbiaceae	Semideciduous sclerophyllous shrub
<i>Baccharis linearis</i>	Compositae	Evergreen sclerophyllous shrub
<i>Quillaja saponaria</i>	Rosaceae	Evergreen sclerophyllous shrub
<i>Kageneckia oblonga</i>	Rosaceae	Evergreen sclerophyllous shrub
<i>Cryptocarya alba</i>	Lauraceae	Evergreen sclerophyllous shrub
<i>Lithraea caustica</i>	Anacardiaceae	Evergreen sclerophyllous shrub
<i>Porlieria chilensis</i>	Zygophyllaceae	Semideciduous sclerophyllous shrub
<i>Gochnatia fascicularis</i>	Compositae	Summer deciduous sclerophyllous shrub
<i>Valenzuela trinervis</i>	Sapindaceae	Winter deciduous shrub
<i>Colliguaya salicifolia</i>	Euphorbiaceae	Evergreen sclerophyllous shrub
<i>Escallonia myrtoidea</i>	Escalloniaceae	Evergreen malacophyllous shrub
<i>Kageneckia angustifolia</i>	Rosaceae	Evergreen sclerophyllous shrub
<i>Plantago hispidula</i>	Plantaginaceae	Native annual herb
<i>Erodium cicutarium</i>	Geraniaceae	Introduced annual herb
<i>Hypochoeris radicata</i>	Compositae	Introduced annual herb
<i>Fortunatia biflora</i>	Liliaceae	Native bulb-perennial
<i>Trisetobromus hirtus</i>	Gramineae	Native annual herb
<i>Pectocarya penicillata</i>	Boraginaceae	Native annual herb
<i>Trifolium polymorphum</i>	Papilionaceae	Native rhizome-perennial
<i>Clarkia tenella</i>	Onagraceae	Native annual herb
<i>Chaetanthera ciliata</i>	Compositae	Native annual herb
<i>Solenomelus pedunculatus</i>	Iridaceae	Native rhizome perennial
<i>Pasithea coerulea</i>	Liliaceae	Native bulb-perennial
<i>Helenium aromaticum</i>	Compositae	Native annual herb
<i>Stellaria cuspidata</i>	Caryophyllaceae	Native annual herb
<i>Loasa triloba</i>	Loasaceae	Native annual herb
<i>Madia sativa</i>	Compositae	Native annual herb
<i>Nasella chilensis</i>	Gramineae	Native rhizome-perennial
<i>Acaena pinnatifida</i>	Rosaceae	Native rhizome-perennial

is highly variable from one year to another, and seems to depend on the amount and distribution of annual precipitation (Kummerow and others 1981). In general, most of the vegetative growth in the herbaceous layer along the transect occurs between winter and early spring (fig. 1). In midsummer the annual plants and the aerial organs of the herbaceous perennials are usually dried up. Leaf area growth rate of herbaceous species is not directly correlated with altitude. The highest rates ($0.75 \text{ cm}^2/\text{day}$) are found in species located at 1000 m, in one of the midelevation areas of the Andes. This may be due to the microclimate offered by the canopies of shrubs. In the midelevation matorral of the Coastal Range, differences have been observed between vegetative fractions of exposed and protected herbs. Perennials growing among shrubs have smaller vegetative fractions than those under shrubs (Jaksić and Montenegro 1979). Exposed individuals allocate more energy to reproductive tissues than the protected ones (Hickman and Pitelka 1975). The

lowest rates of leaf area growth are shown by species at the montane evergreen scrub ($0.08 \text{ cm}^2/\text{day}$). Near the coast, the herb cover is mainly formed by annuals, and the herbaceous species reach greater leaf area rates than these located at higher altitudes (0.32 and $0.20 \text{ cm}^2/\text{day}$ respectively). Annuals usually reach higher rates than perennials. Biomass production of herbaceous plants in the midelevation-Coastal Range matorral varied from 100 to $200 \text{ g m}^{-2}\text{yr}^{-1}$, when precipitation was from 350 to 850 mm (Montenegro and others 1978). *Trisetobromus hirtus*, with a large number of individuals per m^2 , is the most productive species in the herbaceous layer, contributing 30 percent of the total biomass. *Chaetanthera ciliata*, less dense, contributes only 2 percent of the total biomass of this stratum.

In rainy years (851 mm), both annuals and perennials show significant increase in aerial vegetative, underground vegetative, and reproductive biomass (Montenegro and others 1978). How-

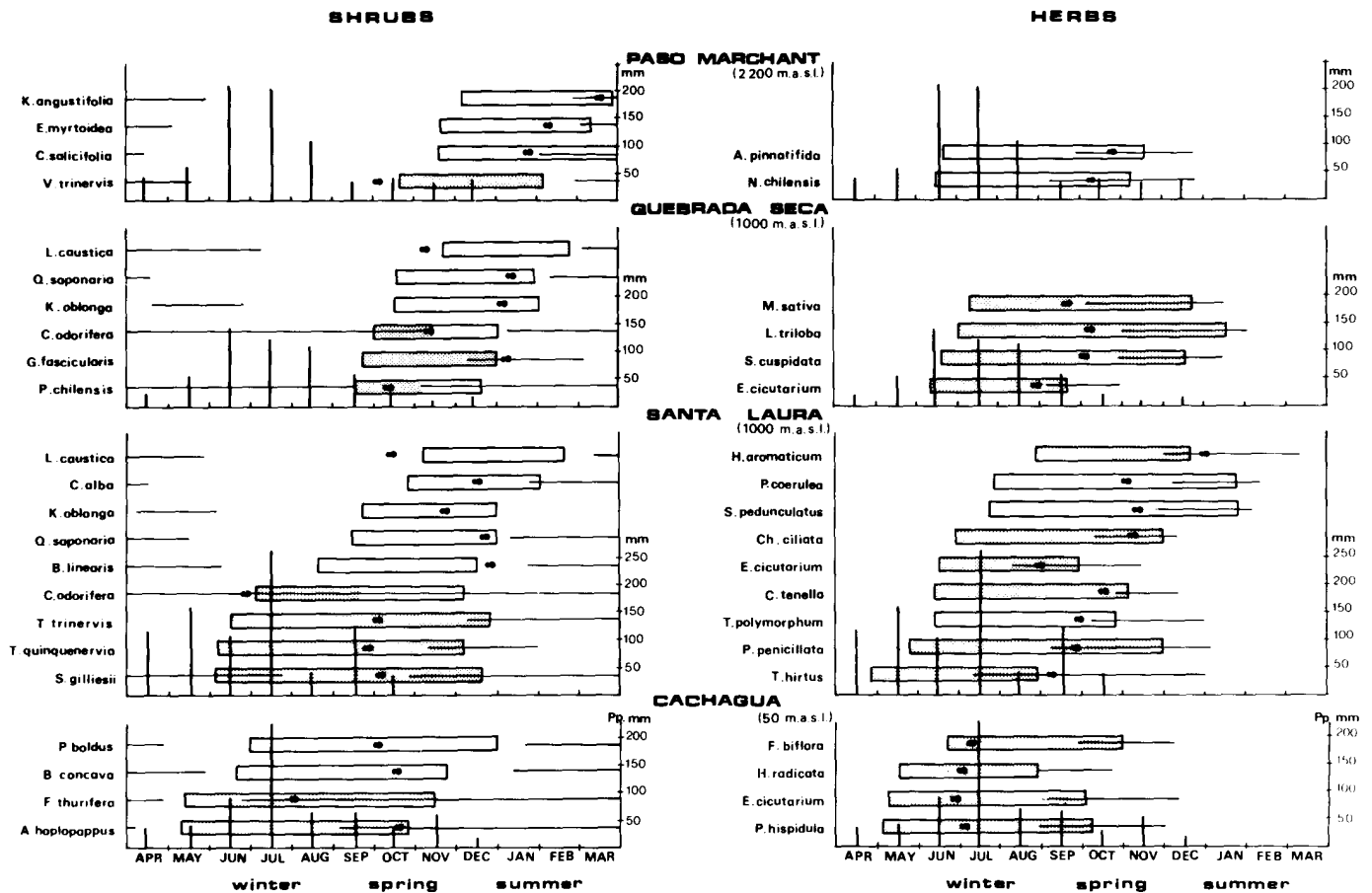


Figure 1--Phenology of shrub and herb species. Vegetative growth (□); flowering (●); leaf shedding (—). Shaded bars: deciduous shrubs

and annual herbs; white bars: evergreen shrubs and perennial herbs. Vertical lines: amount of precipitation.

ever, annuals show a significant increase in vegetative fractions in relation to reproductive fraction (Jaksić and Montenegro 1979) which is not observed in perennials. This might be ascribed to the particular biology of perennials. While annuals depend for their growth only on resources of the current year, perennials can eventually use stored carbohydrates synthesized with resources of the previous year. The effects are then likely to be observed in the next growing season.

Recent studies (Avila, unpublished data) have shown that, one year after a fire, the herb cover does not increase in number of species but increases twice in biomass. This finding would lend support to the idea that there are no allelopathic interactions between shrubs and herbs.

SHRUB VEGETATION

The vegetative growth period of shrubs is shorter at high altitudes (fig. 1). At the highest sites, growth starts about 6 months later than at the lowest. Water availability and temperature seem to influence growth initiation and

the intensity of phenological events. However, the correlation between phenophases and environment is not synchronous for all species (Kummerow and others 1951). Seasonal activity starts with shoot elongation and development of leaf area in most species, and with the development of flower buds in a few others. In general, deciduous and semideciduous shrubs show a winter-growth or spring-growth period, whereas evergreens grow mainly in spring or summer. In some deciduous species, the differentiation of buds which give rise to brachyblasts and flowers occurs in the previous growing period, hence only buds which originate dolichoblasts use the photosynthates of the current season (Hoffmann and Walker 1980). Leaf and branch shedding of deciduous shrubs occurs in summer. The summer deciduous *Trevoa trinervis* one *Talguenea quinquenervia* shed their brachyblasts at the onset of the drought period (Hoffmann 1972, Hoffmann and Walker 1980). This seasonal leaf and stem tissue reduction is an important factor in controlling water loss (Orshan (1964). In other summer deciduous such as *Florencia thurifera*, *Gochnatia fascicularis*, and *Satureja gilliesii*, leaves gradually dry up with increasing drought stress, but they remain on the

shrub throughout summer and fall. *Satureja gilliesii* has been described as a poikilohydric plant (Montenegro and others 1979c), since its leaves are able to withstand the drought period, under marked dehydration, but they regain turgidity and probably photosynthetic capacity as soon as soil moisture is available. *Valenzuelia trinervis*, growing on the montane matorral, is a winter deciduous.

The semideciduous *Colliguaya odorifera* and *Porlieria chilensis* retain their leaves for one season; these leaves are then gradually shed during the following growing season, as new leaves are formed. Maximum leaf ages were found in the evergreens *Cryptocarya alba* and *Lithraea caustica*, which keep their leaves for periods of 3 and 4 years respectively.

Growth patterns of the shrubs along the altitudinal transect have been studied, using the following methodology: 10 individuals of each species were monitored in each altitude site; two branches of each individual shrub were tagged at the level of the last leaf formed during the previous growth period. The length of the newly formed shoot and that of each leaf on it was measured throughout the growth season. Sileptic shoots arising from axillary buds of the current year were also measured. The area of each leaf

growing on the tagged branches was determined by a correlation factor between length and area (Montenegro and others 1979a).

The flushing pattern of most of the study species follows the classical sigmoid curve. However, the leaf area curves of *Kageneckia oblonga* and *K. angustifolia* exhibit two periods of more intensive growth (Montenegro and others 1979b, Montenegro and Aljaro 1979). The time of bud burst for species in the coastal scrub and for some species in the midelevation matorral in the Coastal Range depends mainly on water availability (fig. 1). Bud burst seemed to be markedly affected by temperature at higher altitudes, since most shrubs began shoot growth within a relatively short timespan. Bud break occurred in a period of 22 days in species located at 1000 m, and 27 days at 2000 m. however, leaf area growth rate is not significantly different in comparisons between localities (table 2). Species on the Coastal Range site show a larger leaf area per shoot and longer individual shoots (Montenegro and others 1979a, Kummerow and others 1981), but require a longer growth period than species located on the Andean Cordillera sites.

A comparison of current leaf area indices between individuals of the same species growing at different sites shows values significantly higher

Table 2--Net Productivity of leaf area for dominant species in mid elevation (A), foothill (B), and montane (C), matorral zones.

SITE	ALTITUDE	SPECIES	Total leaf area/shoot (cm ²)	Rate of leaf area growth (m ² day)	Growth period (days)	Leaf-area ¹ Index m ² m ⁻² yr ⁻¹	
COASTAL RANGE	SANTA LAURA 1000m	A	<i>C. odorifera</i>	35.3 ± 21.1	0.23	150	0.72
		<i>L. caustica</i>	100.9 ± 98.0	1.02	99	0.33	
		<i>K. oblonga</i>	87.2 ± 42.0	0.74	117	2.04	
		<i>Q. saponaria</i>	40.7 ± 24.0	0.46	88	1.30	
		<i>T. quinquenervia</i>	16.9 ± 2.8	0.10	171	1.14	
		<i>T. trinervis</i>	22.4 ± 4.6	0.14	156	2.34	
		<i>S. gilliesii</i>	20.0 ± 2.3	0.12	168	1.07	
		<i>C. alba</i>	110.4 ± 43.7	1.14	97	3.43	
		<i>E. pulverulenta</i>	211.2 ± 54.7	1.90	120	2.14	
ANDEAN CORDILLERA	QUEBRADA SECA 1000 m	B	<i>G. fascicularis</i>	17.16 ± 6.36	0.23	73	0.49
		<i>K. oblonga</i>	126.04 ± 28.66	1.05	119	0.66	
		<i>Q. saponaria</i>	22.33 ± 3.41	0.40	55	0.41	
		<i>L. caustica</i>	4.17 ± 0.73	0.06	71	0.02	
		<i>C. odorifera</i>	15.18 ± 3.39	0.19	76	0.39	
		<i>P. chilensis</i>	3.36 ± 0.63	0.06	61	0.05	
		<i>T. quinquenervia</i>	10.4 ± 1.9	0.18	56	0.74	
PASO MARCHANT 2200 m	C	<i>K. angustifolia</i>	12.02 ± 5.66	0.12	98	0.60	
	<i>V. trinervis</i>	7.21 ± 3.93	0.06	106	0.14		
	<i>C. salicifolia</i>	27.76 ± 15.03	0.31	87	1.80		

¹ Values correspond to the area occupied by the indicated species and not to the community as a whole.

for species of the Coastal Range. Besides having a larger amount of leaf area per shoot, they have more branches that initiate growth.

The current biomass index, calculated by the area occupied by the shrubs (table 3) shows significantly higher values for species located at higher altitudes. However, at the community level, the absolute cover decreases with altitude from almost 60 percent at the midelevation matorral (Mooney and others 1977, Armesto and Martínez 1978) to 20 percent at the montane matorral (Martínez, unpublished data).

Lithraea caustica has the lowest biomass index (table 3) and is one of the shrubs which suffers more damage from phytophagous insects (Montenegro and others 1980a, Fuentes and others 1981); but its net productivity increases at the community level due to its high percent (11.1) of relative cover. Instead, *Kageneckia oblonga*, with a high biomass index, only reaches 3.6 percent of relative cover (Mooney and others 1967). *Lithraea caustica* shows morphological and physiological adaptations which allow it to live throughout the aridity gradient from equator-facing slopes to pole-facing slopes (Mooney and Kummerow 1971, Kummerow and others 1977, Montenegro and others 1980b, Montenegro and others 1980c). *Kageneckia oblonga* is found only on mesic sites.

Although a large biomass is allocated to the reproductive fraction (fig. 2), recent studies (O. Balboa, pers. commun.) have proven that production of seeds can greatly vary from one year to another, and that seed viability is rather low.

These findings suggest that the regeneration of the system as a whole depends to a great extent on vegetative reproduction.

The data on growth rate and net productivity suggest that the montane matorral could be the most vulnerable community along the gradient. Recent studies (Aljaro and Montenegro, unpublished data) have shown that, due to frequent defoliation and browsing by goats, the productivity of some of the species of these communities has decreased significantly. In management practices, the timing and intensity of grazing might well be adjusted to vegetative or reproductive periods.

Acknowledgments: The authors are grateful to Professors H. A. Mooney, P. C. Miller, J. Kummerow, and J. Martinez for valuable discussions on this research. Supported by grants DEB 7713944 from National Science Foundation, DIUC 302/77; 43/80; 73/81 and 71/81 from the Catholic University of Chile and by grant UNEP/UNESCO 1105-77-01. The technical assistance of Mr. Luis Gonzalez is greatly appreciated.

Table 3--Net Biomass productivity for dominant species in the mid elevation (A), foothill (B), and montane (C) matorral zones.

SITE	ALTITUDE	SPECIES	Gram Dry weight of Average Shoots			Biomass index g m ⁻² yr ⁻¹	Shrub cover ¹ Relative percent	
			Leaves	Stems	Reproductive Structures			
COASTAL RANGE	SANTA LAURA 1000 m	A	<i>C. odorifera</i>	0.41 ± 0.18	0.09 ± 0.03	0.57 ± 0.48	114	7.10
		<i>L. caustica</i>	1.25 ± 1.23	0.32 ± 0.39	0.42 ± 0.43	65.4	11.10	
		<i>K. oblonga</i>	1.83 ± 0.38	0.48 ± 0.33	0.17 ± 0.08	580.9	3.66	
		<i>Q. saponaria</i>	0.46 ± 0.33	0.06 ± 0.05	0.41 ± 0.18	298.7	0.54	
		<i>T. quinquenervia</i>	0.22 ± 0.03	0.28 ± 0.06	0.21 ± 0.02	480.6	0.10	
		<i>T. trinervis</i>	0.13 ± 0.16	0.17 ± 0.27	0.03 ± 0.02	345.6	8.47	
		<i>S. gilliesii</i>	0.28 ± 0.12	0.35 ± 0.29	0.30 ± 0.06	268.1	13.27	
		<i>C. alba</i>	1.07 ± 0.61	0.18 ± 0.12	0.11 ± 0.01	422.8	28.32	
ANDEAN CORDILLERA	QUEBRADA SECA 1000 m	B	<i>G. fascicularis</i>	0.37 ± 0.22	0.52 ± 0.14	0.43 ± 0.22	384.9	27.13
		<i>K. oblonga</i>	1.08 ± 0.53	0.21 ± 0.11	0.19 ± 0.04	78.7	13.87	
		<i>Q. saponaria</i>	0.42 ± 0.31	0.08 ± 0.04	0.35 ± 0.16	161.5	3.33	
		<i>L. caustica</i>	0.46 ± 0.10	0.06 ± 0.05	0.34 ± 0.12	43.5	10.87	
		<i>C. odorifera</i>	0.32 ± 0.13	0.04 ± 0.03	0.38 ± 0.19	193.7	11.50	
		<i>P. chilensis</i>	0.16 ± 0.07	0.13 ± 0.05	0.10 ± 0.02	67.9	5.47	
		<i>T. quinquenervia</i>	0.11 ± 0.02	0.17 ± 0.04	0.18 ± 0.03	331.6	13.43	
		PASO MARCHABT 22000 m	C	<i>K. angustifolia</i>	0.58 ± 0.19	0.24 ± 0.09	0.04 ± 0.06	438.1
<i>V. trinervis</i>	0.16 ± 0.08		0.06 ± 0.02	0.09 ± 0.04	67.9	17.27		
<i>C. salicifolia</i>	0.46 ± 0.29		0.04 ± 0.02	0.22 ± 0.03	481.4	22.90		

¹ Shrub cover data for Santa Laura after Mooney and others 1977 and for the Andean Cordillera sites

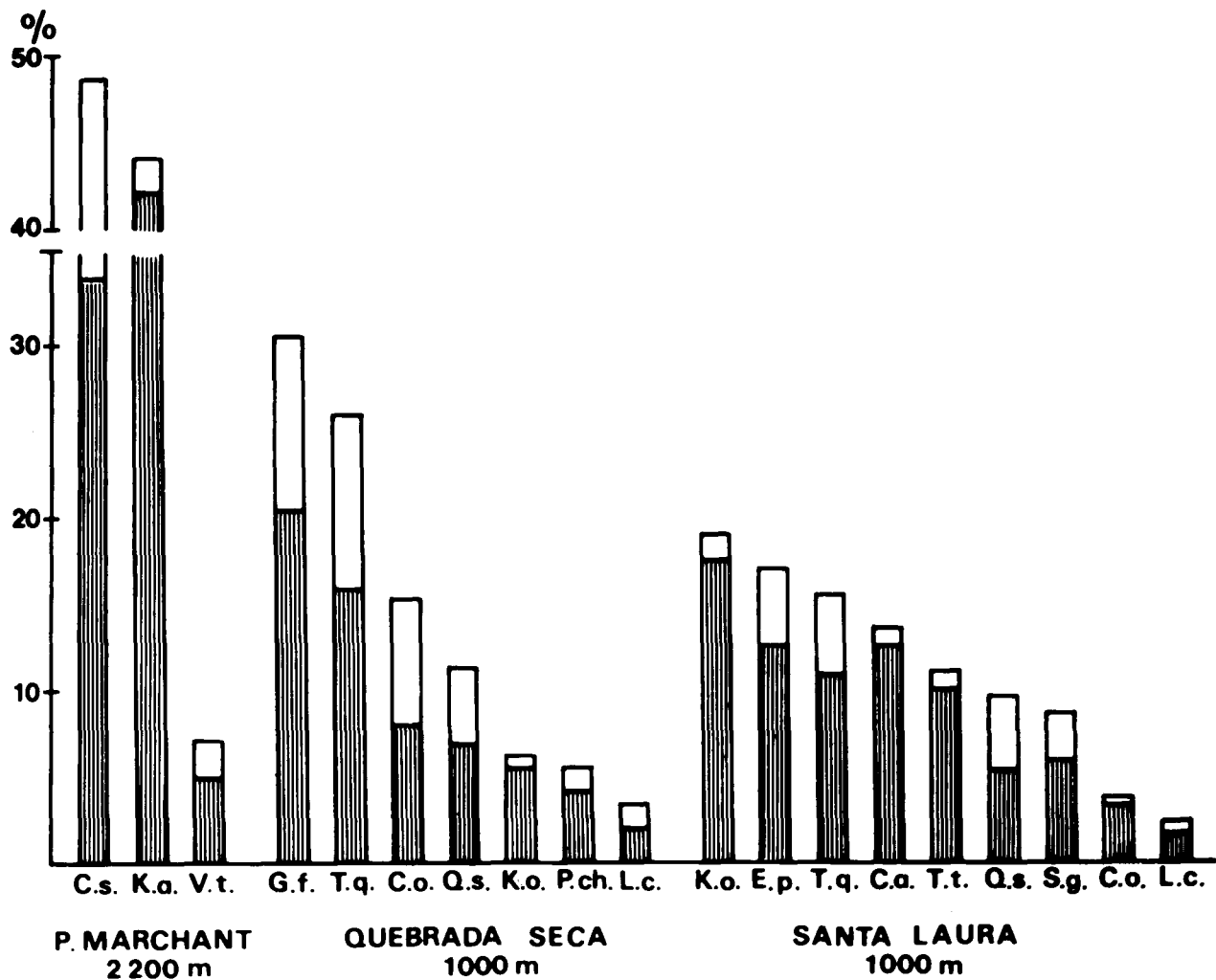


Figure 2--Relative percent of current biomass for shrubs in every study site. Shaded bars: vegetative fractions; white bars: reproductive fraction.

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