Light Intensities and Energy Content of Plant Communities in the Andes of South Central Chile[1]

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ABSTRACT

Areas of a mixed deciduous and evergreen forest and a pure deciduous *Nothofagus* forest near the timberline (1 000 -1 280 m altitude) in the Andes of south central Chile were studied to determine the light intensities in the understory. Additionally, the energy contents of representative forest species and of the scrub-grassland growing at full light above the timberline were determined. With the exception of the bamboo *Chusquea tenuiflora*, that grew only at high light intensities (> 40% light at full light), the most representative forest species (*D. winteri* var. *andina, E. alpina, M. disticha*) were not selective with respect to this factor. Mosses and herbs such as *Ribes* spp. and *V. reichei.* are considered as slightly sciophytic. Light intensities were poorly correlated ($r = 0.13$, $P > 0.05$) with the ash-free caloric values of leaves of all the investigated species. This correlation was highly negative ($r = 0.72$) by herbs. When the same species growing at different altitudes were compared, the higher-located ones showed greater caloric values. Energy values as a function of the genetic constitution of the plant and microclimatic and edaphic conditions are discussed.

COMPENDIO

Se investigaron las intensidades lumínicas incidentes sobre el sotobosque de bosques deciduos y siempreverdes-deciduos de *Nothofagus*, ubicados a 1 000-1 280 m de altitud en el límite vegetacional arbóreo de los Andes del Centro Sur de Chile. Adicionalmente se estudiaron los contenidos energéticos foliares de especies representativas de estas formaciones, como también de la estepa andina situada a mayor altitud. Se encontró que las especies más características del sotobosque (*D. winteri* var. *andina. E. alpina. M. disticha*), no eran selectivas con respecto al factor lumínico, exceptuándose el bambú *Chusquea tenuiflora* que se desarrolla a intensidades lumínicas altas (> 40% luz en relación a la luz a campo abierto). Musgos y herbáceas como *Ribes* spp. y *V. reichei* se comportaron como esciófitas. Las correlaciones entre los valores calóricos libres de cenizas y las intensidades lumínicas a las que crecían hierbas y arbustos, fueron positivas ($r = 0.13$) pero sin significatividad estadística ($P > 0.05$). Esta correlación fue negativa y altamente significativa para las hierbas ($r = 0.72$). No hubo significancia entre el valor calórico y la altitud a la cual se ubicaban las especies. Sin embargo, esta correlación se evidenció claramente cuando se trataba de una misma especie ubicada a diferente altura sobre el nivel del mar. Se discute la influencia del factor genético y de las condiciones microclimáticas y edáficas sobre los contenidos energéticos.

INTRODUCTION

The distribution and dominance of plants in the understory, as well as their vital functions and therefore productivity, are influenced by the amount of available light (18, 19) Light in the understory is determined by the season and the periodicity of the foliage of the dominant species Under the evergreen canopy, light conditions are relatively constant throughout the year, while in the case of deciduous trees light intensity decreases when sprouting begins (19) In the highland forests, where the understory remains under the snow most of the year, the light conditions in summer are decisive for growth and for the accumulation of energetic material (14)

The purpose of this paper is to study light intensities in the understory of pure and mixed *Nothofagus* forest in the Andes of South Central Chile and their possible relation with the foliar energy content in the most common species Additionally, the energy values of plants of the Andean scrub-grassland growing at full light were determined

Study Area

The studied forest types are located in Antillanca in the Andes mountains at latitude 40° 47'S, longitude 72° 12'W, in the Puyehue National Park, X Region of Chile Sites studied were at 1 000-1 125 m (mixed evergreen and deciduous, *Nothofagus betuloides – N. pumilio.* forest) and at 1 200-1 280 m monospecific *N. pumilio* forest) The scrub-grassland zone is located above timberline at approximately 1 140-1 300 m, depending on the degree of disturbance and previous volcanic eruptions (6, 21, 23)

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The understory of the mixed *Nothofagus* forest is frequently dominated by the 1-2 m tall bamboo *Chusquea tenuiflora* and the schrub *Drimys winteri* var *andina* The density and cover of *Chusquea* is often so high that tree regeneration is prevented or impaired (4) This bamboo is not present in the pure *N pumilio* forest, which has a longer snow cover and, therefore, a shorter growth period For optimal growth, this species needs a longer vegetative period (22) More information on the floristic composition of the understory of the *N. betuloides – N. pumilio* forest are given in Veblen *et al* (22) and Alberdi *et al.* (1). The soil-forming parent materials are primarily andesitic and basaltic tuff scoria, and secondarily, ash of sand size and smaller (16) The scrub-grassland is sparsely covered by plants and is characterized by a substrate of coarse volcanic scoria and sand-size tuff. Details on its phytosociological composition and soil characteristics are available (23), especially in Freiberg (6)

According to Table 1, tree canopy density and tree density were higher in the forest stand located at higher altitude, while d.b.h. of trees and shrub size were lower in this stand In the mixed evergreen-deciduous stands, *N. pumilio* predominates over *N. betuloides* The pure deciduous forest and the scrub-grassland have a 25% slope

The climate of Antillanca is cool and extremely humid Snow falls and remains from May until early December, or for longer periods, at altitudes over 1 300 m Gale-force winds are common The predominant wind direction is westerly, although strong easterly winds also occur (23)

MATERIALS AND METHODS

The presence and abundance of species was determited in the studied areas, and expresed in cover percentage Representative parcels (264 m^2) were subdivided in areas of 1 m^2 each and light intensities were measured in the morning and early and late afternoon with a luximeter above each species, as described by Kreeb (12) Light intensities were expressed as the percentage of the light measured in the open field (L% = relative irradiance) (20). In the scrub-grassland, light intensities were 100% Since *C tenuiflora* does not allow growth of the other species, a zone where this plant was nearly absent was selected for the studies in the mixed forest of *Nothofagus*. Measurements were made on cloudy days during the snow-free period (vegetative period), in January 1985, when the canopy is fully developed. During the same period leaves were collected, dried at 80°C, ground to a fine powder to make tablets and processed according to Runge (17) in an adiabatic calorimeter to obtain caloric values

RESULTS

Vegetation

The floristic composition of the studied areas are given in Table 2. The main floristic differences between the understory of *N betuloides – N. pumilio* stand (mixed forest) and the *N pumilio* stand are a greater number of species in the shrub and ground strata (with lower cover) beneath the deciduous stand, and the presence of *C. tenuiflora* and *Macrachaenium gracile* beneath the mixed evergreen-deciduous stands The scrub-grassland is sparsely cov-

Table 1. General characteristics of the study sites in Antillanca, Chile.

	Mixed stand *N. betuloides-N. pumilio*	Pure stand *N pumilio*	Scrub-grassland
Altitude (m.a.s.l.)	1 000 – 1 125	1 200 – 1 280	1 140 – 1 300
Slope (%)	–	25	25
Aspect	–	SW	SW
Canopy density (%)	70	90	–
Size of tree stratum (m)	14 (N p.)[a]; 10 (N b.)[a]	10	–
Size of shrub stratum (m)	1–2	0.3 – 0.7	0.25
Size of herb stratum (m)	0.25	0.25	0.15
Litter accumulation (cm)	2.0	2.0	–
No. Trees/100 m^2	17	33	–
d b h. range (cm)	25–40	9–30	–
No Seedlings/m^2:			
N pumilio	30	39	–
N betuloides	4	–	–

a N.p. and N.b. are *N pumilio* and *N. betuloides*, respectively; d.b.h. diameter at breast high ered with plants, prostrate shrubs (*Empetrum rubrum*, *Pernettya poeppiqqii* and *P. pumila*) being most abundant. The tussock grasses *Hierochloe juncifolia* and *Cortaderia pilosa* are common. The most abundant species of the rich forb layer are *Adesmia retusa*, *Azorella incisa* and *Quinchamalium chilense*.

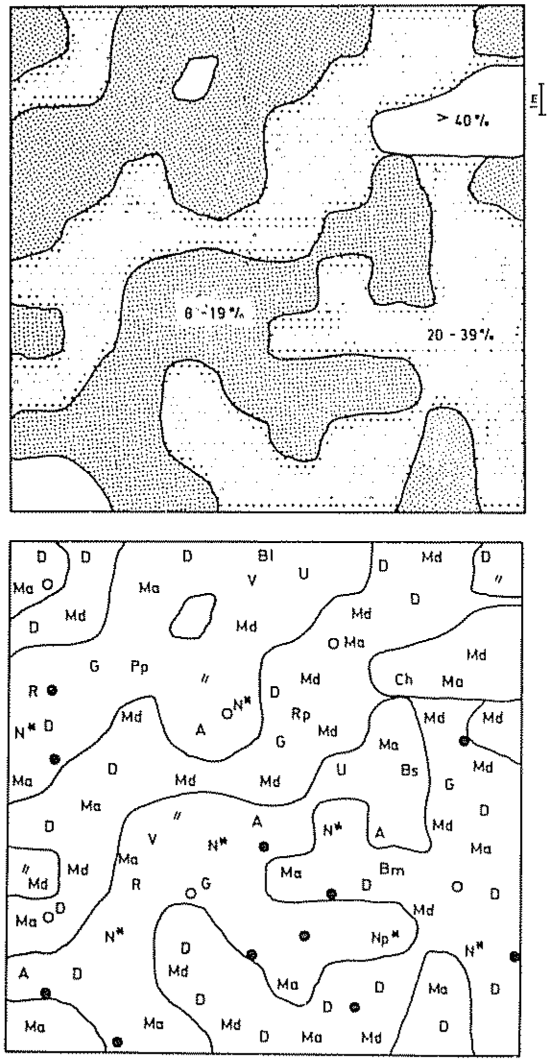

Fig. 1. Map of light intensities (above) and species distribution (below) under the canopy of the mixed evergreen and deciduous *N. betuloides – N. pumilio* forest in Antillanca. Numbers represent relative irradiance (L%). A, *Adenocaulon chilense*; Bl, *Berberis linearifolia*; Bm, *B. montana*; Bs, *Berberis serratodentata*; Ch, *Chusquea tenuiflora*; D, *Drimys winteri* var. *andina*; G, *Gunnera magellanica*; Ma, *Macrachaenium gracile*; Md, *Maytenus disticha*; N*, *Nothofagus* spp. (seedlings); •, *N. pumilio*, ○, *N. betuloides* (adult trees); Pp, *Pernettya poeppigii*; R, *Rubus geoides*; Rp, *Ribes punctatum*; U, *Unicinia phleoides*; V, *Viola reichei*; //, Mosses. Each symbol represents 1% of relative abundance (in relation to the total of number of individuals of all species of the studied area)

Relative irradiance

The understory of the mixed stand of *N. pumilio*, *N. betuloides* (Fig. 1) receives higher light intensities than the pure *N. pumilio* forest (Fig. 2). Relative irradiance values between 7-3% are not plotted in the diagram of the mixed stand, although, occasionally, isolated lower values reached this range (not shown). According to Fig. 1, *M. gracile* is the species of the mixed forest that has the greatest light amplitude (L% = > 40-8), being found in all light zones observed. *C. tenuiflora* was found only in the most illuminated areas (L% = > 40), while *Rubus qeoides*, *Uncinia phleoides*, *Berberis serrato-dentata*, *B. linearifolia*, *Adenocaulon chilense* and mosses are restricted to more shaded areas (L% = 19-8). All other species were found in zones with L% between 39-8. Shrubs such as *D. winteri* var. *andina* and *M. disticha* grow preferentially at L% between 39-20.

In the pure stand (Fig. 2), *E. alpina*, *D. winteri* var. *andina* and *G. maqellanica* are present in all the light areas established. However, when L% was higher than 20%, their numbers were lower. *O. andina*, sparsely represented in this stand, was found at L% 39-20. The remaining species, *Ribes* spp., *M. disticha*, *A. chilense* and *R. qeoides*, as well as mosses, were not present in the zone of the greatest relative irradiance. The light similarity indexes between the species in each stand are low (not shown).

In both types of stands, seedlings of *Nothofagus* (up to 10 cm high) are found in a few illuminated zones (pure stand L% = 3-19, mixed stand L% = 8-39). Plants taller than 150 cm were observed only in the forest clearings. Similar behavior has been observed by Wardle (26) in seedlings of *N. solandri* above 1 600 m in Craigieburn Range, New Zealand. *N. solandri* is very sensitive to dryness in this stage of development. Herbs were preferentially distributed in areas of lower intensities compared to shrubs in both forest types, but only in the mixed stand were differences statistically significant ($P < 0.05$).

Energy content

The highest caloric values (Table 3) were found in the forest shrub *D. winteri* var. *andina* (5 280 cal. g^{-1} dry wt.) and the dwarf shrub from the scrub-grassland *E. rubrum* (5 196 cal. g^{-1} dry wt.). The lowest caloric value (3 010 cal. g^{-1} dry wt.) was measured for the scrub-grassland herb *S. trifurcatus* growing at 1 240 m. The calculation of the energy content of the ash-free plant material gave *E. rubrum* a high value (6 038 cal. g^{-1} dry wt.). The highest reported plant caloric value (6 060 cal. g^{-1} dry wt.) is for the algae *Scenedesmus quadricauda* (11).

Table 2. List of species and cover of a mixed evergreen and deciduous *Nothofagus betuloides* – *Nothofagus pumilio* forest, a pure *N. pumilio* forest and a scrub-grassland stand in Antillanca/Chile. + % cover 5%; r % cover 1 %.

Mixed forest	Cover %	Pure forest	Cover %	Scrub-grassland	Cover %
Trees		Trees		Shrubs	
Nothofagus pumilio (P. et E.) Krasser	80	*Nothofagus pumilio* P. et E.) Krasser	90	*Empetrum rubrum* Vahl ex Willd	30
Nothofagus betuloides (Mirb.) Blume	5			*Pernettya pumila* (L. f.) Hooker	10
				Pernettya poeppigii (DC.) Klotzsch	5
Shrub and tree seedlings	80	Shrubs and tree seedlings	70	Herbs	
Drimys winteri Forst var. *andina* Reiche	60	*Drimys winteri* Forst var. *andina* Reiche		*Hierochloe juncifolia* (Hackel) Parodi	30
Maytenus disticha (Hook f) Urban	20	*Maytenus disticha* (Hook.f.) Urban	30	*Adesmia retusa* Gris.	10
Chusquea tenuiflora Phil	5	*Ribes punctatum* R. et P.	5	*Azorella incisa* (Griseb.) Wedd.	10
Berberis linearifolia Phil.	+	*Berberis montana* Gay	r	*Cortaderia pilosa* (D'Urv.) Hack	10
Berberis serrato – dentata Lechler	+	*Nothofagus pumilio* (P. et E.) Krasser	+	*Quinchamalium chilense* Mol.	5
Ovidia andina (Poepp. et Endl.) Meissn.	+	*Ovidia andina* (Poepp. et Endl.) Meissn.	r	*Acaena microcephala* Schlecht.	+
Ribes punctatum R. et P	+	*Pernettya pumila* (L. f.) Hooker	r	*Perezia pedicularidifolia* Less.	+
Berberis montana Gay	+	*Ribes cucullatum* H. et A.	+	*Sisyrinchium arenarium* Poepp.	+
Pernettya poeppigii (DC.) Klotzsch	+	*Baccharis* sp.	+	*Euphrasia flavicans* Phil.	+
Nothofagus pumilio (P. et E.) Krasser	+	*Escallonia alpina* var. *alpina* Sleumer	+	*Senecio chionophyllus* Phil.	+
				Chloraea gaudichaudii Brongn.	r
				Senecio triodon Phil.	+
Herbs		Herbs		*Silene andicola* Gill. ex Hook. et Arn	+
				Acaena pinnatifida R. et Pav.	+
Gunnera magellanica Lam.	80	*Adenocaulon chilense* Less.	50	*Baccharis magellanica* (Lam.) Pers	+
Viola reichei Skottsb.	70	*Viola reichei* Skottsb.	+		
Uncinia phleoides (Cav.) Pers.	5	*Rubus geoides* Sm.	+		
Hierochloe juncifolia (Hackel) Parodi	+	*Gunnera magellanica* Lam	+	Mosses	
Adenocaulon chilense Less.	+	*Perezia pedicularidifolia* Less.	+		
Macrachaenium gracile Hook. f	+	*Acaena ovalifolia* R. et P.	+	*Racomitrium willii* (C.Müll.) Kindb.	50
Rubus geoides Sm.	+	*Codonorchis lessonii* (D'Urv.) Lindl	r		
Codonorchis lessonii (D'Urv.) Lindl.	r	*Hierochloe juncifolia* (Hackel) Parodi.	r		
Lagenophora hirsuta Less	r	*Lagenophora hariotii* Franchet	r		
		Senecio triodon Phil.	r		
		Chloraea gaudichaudii Brongn.	r		
Ferns		Ferns			
Licopodium magellanicum (Beauv.) Swartz	+	*Blechnum* sp.	r		
		Hymenophyllum spp	+		
		Licopodium magellanicum (Beauv.) Swartz	+		
Mosses		Mosses			
Musci spp.	40	*Dicranoloma billardierii* (Schw.) Par.	5		
		Musci spp.	+		

Table 3. Energy and ash content of leaves of species of the *Nothofagus* forest and the scrub-grassland in Antillanca, Chile in relation their average of relative irradiance. Species are presented in order of decreasing ash free caloric values. Material was collected on January, 1984. Plant nomenclature according to Muñoz (1980).

	Collecting locality (m.a.s.l)	Energy content ($cal.g^{-1}$) ash-free	with ash	Ash content (%)	Relative irradiance (L%)
FOREST					
a) Trees					
Nothofagus dombeyi (Fagaceae)	1 000	5 309	5 167	2.7	–
Nothofagus betuloides (Fagaceae)	1 040	5 216	5 102	2.2	–
Nothofagus pumilio (Fagaceae)	1 040	5 071	4 839	4 6	–
b) Shrubs					
Drymys winteri var *andina* (Winteraceae)	1 280	5 451	5 280	3 1	13 3
Pernettya poeppigii (Ericaceae)	1 080	5 450	5 210	4.4	34.8
Pernettya poeppigii (Ericaceae)	1 000	5 378	5 088	5.4	14.6
Drimys winteri var. *andina* (Winteraceae)	1 000	5 374	5 199	3.2	26.1
Berberis linearifolia (Berberidaceae)	1 000	5 345	5 129	4 0	15 8
Maytenus disticha (Celastraceae)	1 080	5 192	4 925	5.1	38.4
Maytenus disticha (Celastraceae)	1 000	5 157	4 891	5.1	35 6
Ribes punctatum (Saxifragaceae)	1 000	5 116	4 665	8.8	26 4
Escallonia alpina (Escalloniaceae)	1 280	5 144	4 877	4 6	14 5
Berberis montana (Berberidaceae)	1 280	5 066	4 918	2.4	27 6
Embothrium coccineum (Proteaceae)	1 040	5 040	4 891	2.9	35 0
Ovidia andina (Thymelaceae)	1 000	4 991	4 710	5 6	36 6
Ribes punctatum (Saxifragaceae)	1 280	4 920	4 537	7 8	18.4
Chusquea tenuiflora (Poaceae)	1 000	4 883	4 246	13.1	48 0
Berberis serrato-dentata	1 000	4 684	4 526	3.4	15 8
c) Herbs					
Rubus geoides (Rosaceae)	1 080	5 121	4 061	20 7	12.2
Rubus geoides (Rosaceae)	1 280	5 103	4 898	4.0	13 0
Adenocaulon chilense (Asteraceae)	1 280	5 090	4 511	11.4	12.2
Adenocaulon chilense (Asteraceae)	1 000	4 997	4 258	9.4	10 3
Macrachaenium gracile (Asteraceae)	1 000	4 980	4 311	13 4	19 3
Uncinia phleoides (Cyperaceae)	1 280	4 907	4 502	8 3	17 5
Viola reichei (Violaceae)	1 125	4 793	4 003	16 5	13 5
Macrachaenium gracile (Asteraceae)	1 125	4 730	4 162	12 0	19 3
Gunnera magellanica	1 125	4 693	4 426	5 7	32.3

Continuation Table 3.

SCRUB GRASSLAND					
a) Dwarf shrubs					
Empetrum rubrum (Empetraceae)	1 140	6 038	5 196	14 0	100.0
Baccharis magellanica (Asteraceae)	1 350	5 668	5 337	5 8	100.0
Baccharis magellanica (Asteraceae)	1 140	5 624	5 118	3 8	100.0
Pernettya poeppigii (Ericaceae)	1 140	5 508	5 122	7 0	100.0
Pernettya pumila (Ericaceae)	1 140	5 460	5 079	7 0	100.0
Pernettya pumila (Ericaceae)	1 080	5 314	5 071	4 0	100.0
b) Herbs					
Perezia pedicularidifolia (Asteraceae)	1 350	5 355	4 721	11 9	100.0
Senecio Chinophilum (Asteraceae)	1 350	5 242	4 341	17 2	100.0
Chloraea gaudichaudii (Orchidaceae)	1 300	5 131	4 775	6 6	100.0
Lucilia frigida (Asteraceae)	1 380	5 102	3 879	24 0	100.0
Silene andicola (Caryophyllaceae)	1 300	5 084	4 125	18 9	100.0
Adesmia retusa (Fabaceae)	1 190	5 054	4 037	20.9	100.0
Acaena pinnatifida (Rosaceae)	1 240	4 915	3 758	23 6	100.0
Quinchamalium chilense (Santalaceae)	1 350	4 813	4 428	8 0	100.0
Azorella incisa (Apiaceae)	1 240	4 656	3 820	17.7	100.0
Senecio trifurcatus (Asteraceae)	1 240	4 623	3 010	10.0	100.0
Senecio trifurcatus (Asteraceae)	1 140	4 459	3 876	13.9	100.0

The fully sun-exposed herbs of the scrub-grassland produced the highest ash content (Table 3). That agrees well with behavior of sun-exposed leaves (17).

The average caloric values for the analyzed species and growth forms (Table 4) registered high energy contents for the woody species and lower energy contents for herbs. This same relationship was found in the Alpine tundra (2), Mediterranean region (9) and Valdivian rain forest (18). For all the forest species (trees, herbs and shrubs) tested here, the average was 4 716 cal g^{-1} dry wt and for the scrub-grassland species (dwarf shrubs and herbs) 4 335 cal g^{-1} dry wt. Considering the caloric values of the ash-free dry material, the grassland species demonstrated a slightly higher energy (5 179 cal g^{-1} dry wt.) than the forest species (5 082 cal g^{-1} dry wt). This last value was higher than that corresponding to a Valdivian rain forest (4 668 cal. g^{-1} dry wt.) in South Central Chile (18). The correlations between the caloric values without ash and the average light intensities (Table 3) at which the herbs and shrubs grew were positive ($r = 0.13$), but not statistically significant ($P = > 0.05$). However, when similar life forms were compared, the correlation was negative ($r = 0.72$ and $r = 0.28$ for herbs and shrubs respectively). The correlations between caloric values and altitude ($r = 0.16$ for herbs and shrubs, $r = 0.28$ for shrubs and $r = 0.36$ for herbs) were statistically not significant ($P = > 0.05$). The relation between these two parameters is more evident for the same species growing at different altitudes (*D. winteri* var *andina*, *P. poeppiqii*, *P. pumila*, *M. disticha*, *B. maqellanica* and *S. trifurcatus* (see (Table 3)

DISCUSSION

Ellenberg (5) studied the ecological behavior of Central European vascular plants and established nine categories according to the relative irradiance at which they grew best According to this scheme, the scrub-grassland species were authentic heliophytes Of the forest species, *C tenuiflora* was the most light-dependent *D. winteri* var *andina*, *E alpina*, *M gracile* and *G. maqellanica* were not especially selective with respect to light They are present in areas between 39 to 5% relative irradiance, but grew preferentially in areas above 10% and were also found in the margins of the forest and in the Andean scrub, in areas much exposed to light (not represented in light diagrams) The other species (*Ribes* spp., *V reichei* and mosses) could be considered as slightly sciophytic

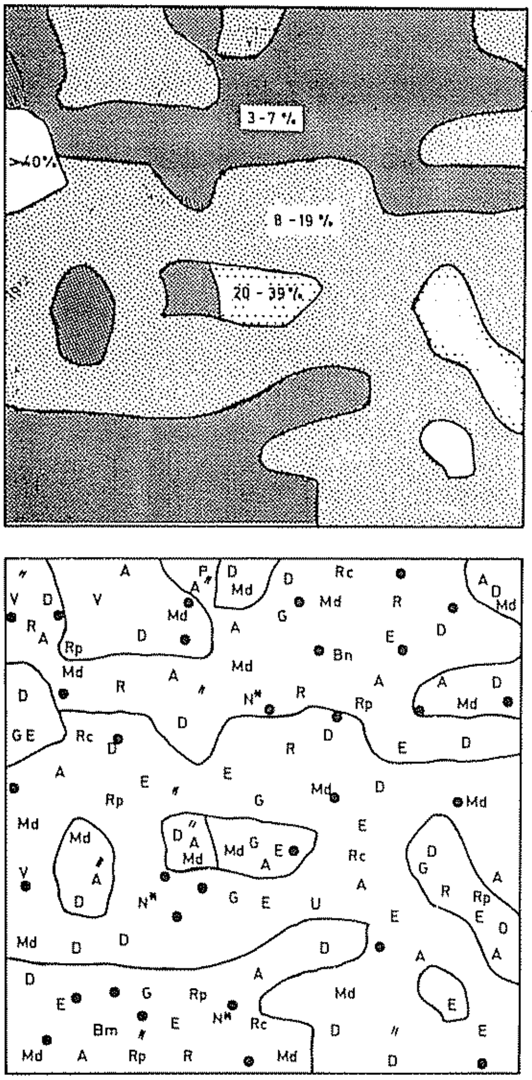

Fig. 2. Map of light (above) and species distribution under the canopy of the monospecific deciduous *N Pumilio* forest in Antillanca. Numbers represent relative irradiance (L%). E, *Escallonia alpina*; N*, *N pumilio* (seedlings); P, *Perezia pedicularifolia*. Rc, *Ribes cucullatum* Others symbols as in Fig 1

Steubing *et al.* (18), studying the understory of a Valdivian rain forest of South Central Chile, characterized *Chusquea quila* as an heliophyte The same behavior is observed in other species of this genus. They grow rapidly in forest gaps attaining heights over 7 m Their vigorous growth supresses the other understory components and plays an increasing role in forest regeneration (22), being an important element of the secondary scrub (10)

The positive influence of light over the energy contents of plants was described by Long (14). This is not shown in the present study Contrarily, this correlation was highly negative in herbs When the caloric values of the same species growing under different light intensities are compared, the relation is found to be direct Thus, with *P. poeppiqii*, decreasing energy differences were not very evident. Only in the case of shrubs did the higher caloric values of the scrub-grassland represent an adaptative response to the environmental stress of this habitat (6)

Table 5 shows the energy contents in an altitudinal gradient of various communities from the Valdivian region, varying from vascular hydrophytes at sea level to plants of the Andean heights Consistent with the

Table 4. **Average caloric values and ash content of leaves of various growth forms present in the forest stands and scrub-grassland in Antillanca, Chile.**

	Caloric values (cal. g^{-1} D.W.) ash-free	Caloric values (cal. g^{-1} D.W.) with ash	ash content %
Forest			
Trees	5 199	5 036	3.2
Shrubs	5 146	4 873	5.3
Herbs	4 935	4 348	11.3
Average all species	5 082	4 716	7.0
Scrub-grassland			
Dwarf shrubs	5 602	5 154	6.9
Herbs	4 949	4 070	15.7
Average all species	5 179	4 335	12.6

Differences between caloric values of herbs and shrubs significant at level $p < 0.01$.

Table 5. Average energy values (ash free) of leaves of dominant vegetation in differents communities of the Region de Los Lagos (Chile).

Community	Altitude (m)a.s.l.	n	Caloric value ($cal.g^{-1}$)	Ref.
Vascular hydrophytes	9	18	4 093	Steubing *et al.* (1980)
Swamp forest of Myrtaceae	120	13	4 175	a
Valdivian rainforest	200	30	4 668	Steubing *et al.* (18)
Andean *Nothofagus* forest (evergreen-deciduous and deciduous)	1 000–1 280	27	5 082	b
Scrub grassland	1 140–1 350	17	5 179	b

a Our unpublished values
b Data from present study

values were obtained when grown in the shade (under forest canopy) with respect to growth in scrub-grassland (full light). On the other hand. *C. tenuiflora,* a heliophyte, has a lower caloric value than *D. winteri* var. *andina* that grew in relatively darker areas. These observations are also suported by the data of Steubing *et al.* (18) for other species. Thus, caloric values are also a function of the genetic constitution of the plant (8).

Differences in caloric values exist between vegetation growing in different ecological communities, as a function not only of genetic factors, but also of environmental condition (7, 8). We had expected that the average of the energy values of all the plants of the scrub-grassland (with more unfavourable microclimatic conditions) would be greater than those of the forest, with more favourable conditions, but the less favourable thermal and nutritional conditions of the Andes mountains (1), the energy contents found here were higher than those found in the lowlands. Similar results have been found in other continents by Brzoska (3) and Tschager *et al.* (20). However, Verduin (25) has not found evidence that the higher energy content observed in highly stressed environments has any adaptative or survival value.

Lipid accumulation increases the energy content in alpine plants (13, 20). It seems that plants under environmental stress are likely to divert photosynthates to more highly reduced products, such as fats, oils and resins (25). Low temperatures in alpine environments and low nitrogen availability on low humus soils may further enhance lipid biosynthesis (20). Since it is not known which chemical compounds are involved in determining the energy contents of Andean plants, it would be of interest to determine lipid, protein and carbohydrate composition, as well as presence of stress metabolites.

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