UNIVERSIDAD DE CHILE -FACULTAD DE CIENCIAS -ESCUELA DE PREGRADO

"FOLIAR TRAIT VARIATION ALONG A CLIMATIC AND EDAPHIC GRADIENT IN CHILE: CONTRASTS BETWEEN MEDITERRANEAN AND TEMPERATE FOREST"

Seminario de Título entregado a la Universidad de Chile en cumplimiento parcial de los requisitos para optar al Título de Bióloga con mención en Medio Ambiente

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Mayo, 2014

Santiago - Chile

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INFORME DE APROBACIÓN SEMINARIO DE TÍTULO

Se informa a la Escuela de Pregrado de la Facultad de Ciencias, que el Seminario de Título presentado por la candidata:

Camila Cifuentes Croquevielle

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Ha sido aprobado por la Comisión evaluadora y revisora, como requisito parcial, para optar al título profesional de Biólogo con Mención en Medio Ambiente.

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RESUMEN

Pregunta: ¿Cuáles son los patrones de variación que siguen los rasgos funcionales (LMA y contenido de N y P foliar) de la flora leñosa nativa de los bosques mediterráneos y templados de Chile?

Métodos: Seleccionamos 16 localidades en Chile, entre los 32° y 43°S, de bosques de ecosistemas mediterráneos y bosques templados, en los cuales se realizaron muestreos de hojas de flora nativa leñosa y suelos. Con las hojas se midieron tres rasgos foliares: LMA, contenido de N y de P, los cuales fueron contrastados con el contenido de N y P de los suelos de cada sitio. Con esta información se elaboró una base de datos, la cual fue complementada con datos climáticos de cada localidad. La información obtenida de los bosques chilenos fue comparada con la de una base de datos mundial de rasgos foliares (GLOPNET). Para estudiar las relaciones entre los rasgos foliares y las variables climáticas y edáficas, se realizaron regresiones bivariadas y un análisis de componentes principales (PCA).

Resultados: Se encontraron relaciones significativas entre las variables climáticas y el contenido de nutrientes del suelo con la latitud, desde un ambiente árido, con alto componente continental y limitación de N en los suelos en las localidades de clima mediterráneo del norte; hacia ambientes más húmedos y con limitación de P en los suelos en los bosques templados de las localidades del sur. Los contenidos de N y P foliares disminuyeron uniformemente de norte a sur, y se encontró que estaban significativamente relacionados tanto con las variables climáticas como con el contenido de nutrientes de los suelos a lo largo del gradiente latitudinal. Por otro lado, el LMA no mostró cambios significativos con la latitud, como tampoco con el contenido de nutrientes de los suelos o las variables climáticas. Sin embargo, se encontró menor

LMA promedio y mayor coeficiente de variación en los bosques mediterráneos de Chile, en comparación con los bosques mediterráneos de otros lugares del mundo, así como con los bosques templados de Chile. Se encontraron relaciones negativas entre el LMA y los contenidos de N y P foliares.

Conclusión: La alta dispersión encontrada en los datos de los rasgos foliares de los bosques de clima mediterráneo, sugiere que la heterogeneidad ambiental promueve la variación de rasgos. Por otro lado, la acentuada limitación de P en los suelos de los bosques templados podría estar limitando la adquisición tanto de P como de N foliar. Las diferentes tendencias encontradas en los patrones de variación de los rasgos foliares asociadas a cambios latitudinales en los factores abióticos, sugiere que las especies leñosas presentes en los bosques mediterráneos y templados de Chile poseen diferentes estrategias de utilización de recursos, debido a sus diferentes adaptaciones a stress abiótico.

ABSTRACT

Question: What trends do functional foliar traits (LMA, P and N content) of Chilean native woody species follow along a 1500-km long latitudinal gradient in rainfall and soil nutrients?

Location: Chilean mediterranean and temperate forests.

Methods: We selected 16 localities from 32° to 43°S, from mediterranean and temperate forests in Chile, where leaves of woody plants and soils were collected. We measured three foliar traits: LMA, N content and P content which were contrasted with soil N and P content from each site. A database of foliar traits of trees and shrubs was

compiled from this information and supplemented with climatic and soil data from each of the sampling localities. Data for Chilean forests were compared with a global foliar trait dataset (GLOPNET). We ran bivariate regressions and a principal component analysis (PCA) between foliar traits, climatic variables, and soil nutrient concentrations.

Results: Climatic and soil nutrient variables were significantly related to latitude, from dry, continental, and N-limited soils in the northern mediterranean-climate forest localities, to more humid, and P-limited soils in southern temperate rainforests. Foliar N and P declined uniformly from north to south and were significantly related to climatic variables, as well as with changes in soil nutrient content along the gradient. LMA did not change significantly either with latitude, soil P or N content, or climatic variables. Nonetheless, we found that Chilean mediterranean forests had lower average LMA and higher coefficients of variation than Chilean temperate forests and other mediterranean biomes worldwide. Foliar traits were negatively correlated among them (LMA versus N and P content).

Conclusions: High dispersion in foliar trait values of Chilean mediterranean-climate forests suggests the idea that environmental heterogeneity enhanced trait variation, while in temperate rain forests accentuated soil P scarcity could be limiting foliar P and N acquisition. Different trends of foliar trait variation associated with latitudinal changes in abiotic factors suggest that mediterranean and temperate rainforest woody plants have different resource use strategies due to their different adaptations to abiotic stress.

1. Introduction

Approximately 90% of a plant's dry weight originates from the products of photosynthesis that occur mainly at leaf level (Poorter, Remkes & Lambers, 1990). Accordingly, ecologists have become increasingly interested in understanding how foliar traits influence photosynthesis and how abiotic conditions influence plant physiology (Reich et al. 1997, Reich et al. 1999, Wright et al. 2004, Messier, McGill & Lechowicz, 2010). The range of foliar trait variation is generally considered to represent plant adaptations to environmental factors that affect plant growth and community composition (Westoby et al. 2002). Variations in precipitation, temperature, and soil nutrient availability are assumed to promote convergence in foliar trait values among coexisting species (Chapin et al. 1987, Reich et al.1997, Reich et al. 1999, Westoby et al. 2002). Accordingly, in a given ecosystem a range of values of different foliar traits promote efficient resource capture and use, as well as nutrient conservation strategies (Chapin et al. 1987; Lavorel & Garnier 2002, Westoby et al. 2002). For example, under conditions of low water and nutrient availability, plants tend to have thick leathery-leaves, as is the case of sclerophyllous leaves in semiarid and mediterranean-climate ecosystems (i.e., Mooney and Dunn 1970, Mooney 1977, Cody & Mooney 1978, Rundel 1981, Reich et al. 1997). Therefore, in these regions, plants tend to extend leaf lifespan and reduce nutrient concentrations in green leaves, and these foliar traits are tightly associated with efficient water conservation and nutrient use strategies (Wright & Westoby 2003, Wright et al. 2004). Therefore, the study of leaf traits has become a link between abiotic factors and species performance.

Leaf mass per unit area (LMA), the ratio between leaf dry mass and leaf area is considered a key trait for defining plant carbon acquisition strategies (Lambers &

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Poorter 1992), and an important indicator of plant environmental constraints (Chapin et al. 1987, Reich et al. 1997, Grime 2001, Lavorel & Garnier 2002, Westoby et al. 2002, Wright et al. 2004, Poorter et al. 2009). LMA is best understood as an index of the leaf-level cost of light interception (Poorter et al. 2009), where high LMA values mean high biomass investment on supporting structures, such as lignin and cellulose in leaf tissues (e. g., sclerophyllous leaves); whereas low LMA values represent high investments on photosynthetic tissues and carbon fixing compounds (Lavorel & Garnier, 2002; Wright et al. 2004). Accordingly, plant species with low LMA tend to dominate more productive habitats (Reich et al. 2003, Poortet et al. 2009), whereas species with high LMA are expected to prevail in habitats with limited productivity (Wright & Westoby 2003, Poorter et al. 2009). These inferences come from the fact that leaf traits associated with plants response capacity, such as maximum photosynthetic rates, are negatively correlated with LMA across more than 2,500 plant species from a broad range of environmental conditions (Reich et al. 1997, Wright et al. 2004), therefore, low LMA leaves are those with high carbon acquisition capacities. Higher leaf area per unit mass (i.e. low LMA) enhances light capture (Reich et al. 1997, Wright et al. 2004), reduces gas diffusion resistance and promotes nutrient allocation to chlorophyll and RUBISCO (Niinemets & Sack 2006). Hence, plant with thin leaves or low LMA tend to thrive in highly productive environments. Conversely, plants with high LMA or thick leaves are associated with long leaved leaves that promote nutrient use efficiency at the cost of carbon gain and dominate in low resourced environments (Reich et al. 1997, Westoby et al. 2002, Wright et al. 2004).

Although leaf N and P concentrations tend to decrease with mean annual temperature (MAT) and latitude across biomes worldwide, Reich and Oleksyn (2004)

found that the relationship between MAT and foliar Nitrogen (N) for 1,280 species from 452 sites was extremely weak ($r^2 = -0.05$), whereas the relationship between MAT and foliar Phosphorus (P) was rather strong ($r^2 = -0.34$). The explanation for these contrasting patterns between MAT and foliar nutrient concentrations is that foliar N and P tend to increase with latitude because old-highly leached soils from the warm and rainy tropics are nutrient starved, whereas young soils from temperate less rainy regions are nutrient rich (Reich and Oleksyn 2004). A different study tested the relationship between foliar N for 74 plant species from different ecosystems such as forests, deserts, and shrubs, all in the Tibetan Plateau in China, and found weak effects of MAT not only on foliar N but also in LMA (He et al. 2006). The authors explain these results adducing that the MAT values were on the cool range (i.e. -9.7 to 6.8 °C) and concluded that even in a cold, extreme, high-altitude environment such as that of the Tibetan Plateau the modulation of leaf traits by climate was weak (He et al. 2006). Therefore, leaf trait correlations documented globally, independent of growth form, biome or climate (Reich et al., 1997; Wright et al., 2004), suggest that global-scale variations in leaf functional traits (Reich et al. 1997; Sterner & Elser 2002; McGroddy et al. 2004; Reich & Oleksyn 2004; Wright et al. 2004; Kerkhoff et al. 2005) could be the result of variation in soil nutrient status. However, few studies have evaluated simultaneously the effects of climatic variables and soil nutrient availability on leaf trait variation (i.a Ordoñez et al. 2005).

Soil nitrogen (N) and phosphorus (P) content, as well as temperature, rainfall and light intensity, are the main environmental factors that influence patterns of LMA and leaf nutrient concentrations (Reich et al. 1997, Ordoñez et al. 2009, Poorter et al. 2009). Even though foliar N and P contents are not directly influenced by plant's

carbon economy, foliar N:P ratio (ratio of N to P concentration) is a good indicator of soil N or P limitation (Koerseklman et al. 1996), which in turn lead to changes in foliar traits (Güsewell 2004). Mason et al. (2012) demonstrated that declining soil nutrient availability drives changes in plant trait syndromes, from resource-acquisition strategies towards resource-retention strategies. Considering that different environments impose contrasting selective pressures on plants, it can be expected that environmental variability should drive traits such as LMA and leaf nutrient content to divergent values. According to global comparisons, LMA varies more than 100-fold among 3800 species (Poorter et al. 2009), while leaf N and P concentrations vary around nine times among 1280 species (Reich & Oleksyn 2004). Such variability can be attributed to differences among plant functional groups. For instance, evergreen tree species have the highest LMA values and the lowest foliar N content (Reich & Oleksyn 2004), while herbs and pioneer tree species have the lowest LMA values and the greatest foliar N content (Reich et al. 1997). At the same time, leaf trait variation has been related to contrasting environmental conditions, exemplified by differences between tropical forests, with lower LMA and higher N content, compared to desert species, which have the highest LMA values and generally low foliar nutrient contents (Reich et al. 1997, Poorter et al. 2009).

In this study, we took advantage of the contrasting distribution of mediterranean and temperate forests in Chile, which differ in precipitation and dry-season length across more than 20 degrees of latitude (Armesto et al.1996). Furthermore, mediterranean and temperate forests are found in different parent materials such as those from Chilean Coastal Range, to deep tephra in the northern Los Lagos region and a mixture of basalts, andesites and granites in the southern Los Lagos. Similarly,

soils in northern Mediterranean Chile are older than soils in southern Chile, where temperate rainforests dominate. Therefore, these broad vegetation gradients make Chilean forest ecosystems a suitable model to analyse interspecific foliar trait variation within different ecosystems and soil types across the latitudinal gradient. This study of foliar trait variation across different Chilean forest ecosystems seeks to understand how differences in climate and soil nutrient availability influence differences in LMA as well as foliar N and P. To address this question we investigated the relationships between LMA and foliar-and-soil N and P across forest ecosystems in a latitudinal climate gradient, for a complete sample of the woody flora of native forests between 32° and 43°S. Specifically, we asked whether the latitudinal climate gradient was associated with a latitudinal gradient in soil N and P contents, and how these variables in turn modulate woody species' foliar traits. We tested the following hypotheses:

i) Leaves from Chilean mediterranean forests should have higher LMA than those from the southern temperate localities, because of longer summer drought and increased seasonal variation in rainfall, compared to temperate rainforests in the south.

ii) Foliar nutrient contents should follow a parallel trend to soil nutrient concentrations across the latitudinal gradient. Because of the lower productivity of mediterranean forests, soil and foliar N should increase from north to south, where higher productivity should be related to longer wet season and higher soil N content. On the other hand, we expect soil and foliar P content to decrease from north to south because of nutrient leaching due to high rainfall regime in the south (Ruthsatz & Villagrán 1991).

iii) LMA of forest trees and foliar nutrient content should show contrasting trends in mediterranean and temperate forest localities. The mediterranean woody flora,

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subjected to a longer dry season and higher rainfall variability among years, should have a "slow return" resource strategy, characterized by higher LMA and lower foliar nutrient content. In contrast, temperate rainforest species subjected to higher rainfall and a longer wet season, should have a "faster return" resource strategy, with lower LMA and higher foliar nutrient content.

2. Methods

2.1 Site selection

To assess the variation in LMA, as well as in soil and leaf -N and -P contents along the latitudinal gradient from mediterranean and temperate forests in Chile, we compiled a dataset based on literature records and field sampling. We selected vegetation types to represent different plant communities and ecosystems along the latitudinal range within 32°S to 43°S. Our main criterion was to include localities from mediterranean climate in the north, which supports sclerophyllous forests and woodlands (Fig. 1), to temperate forests in the south, which include Valdivian and North Patagonian rainforests (Fig. 2) (Arroyo et al. 1993, Villagrán et al. 1995), passing through transitional semideciduous forests (35°-38° S) (Fig. 3). In these different ecosystems we chose at least three mircrosites with well-preserved native forest (*n*=33).
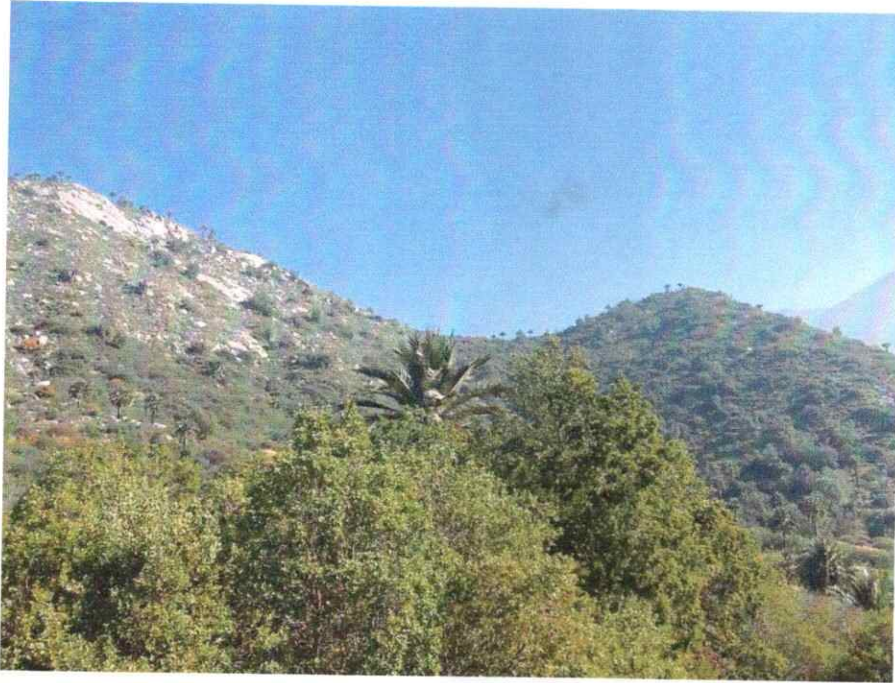
Figure 1. Mediterranean-climate forest ecosystem located in La Campana National Park, central Chile.

Figure 2. Temperate forest ecosystem located in Senda Darwin biological station, at Chiloé island.
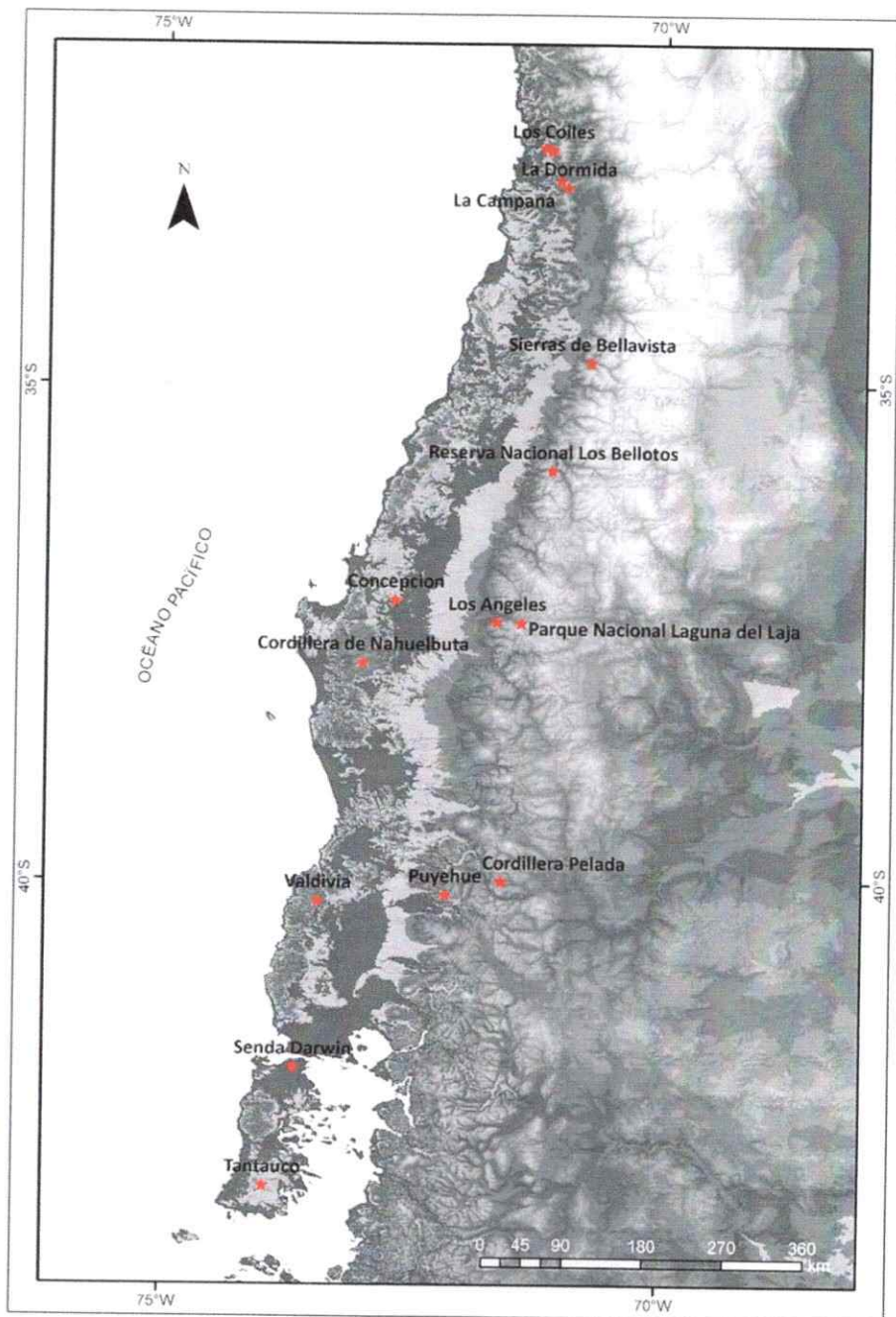
Figure 3. Study area in south-central Chilean mediterranian and temperate forest ecosystems, between 32°S to 43°S. Sites are marked with red dots.

2.2 Data collection

At each site, three circular plots (radius = 3 m) with at least three adult trees were set for soil and foliar samples of adult individuals of all species present. Leaf samples for LMA and foliar nutrient concentrations were obtained from one sun-exposed branch per individual tree by collecting 20 fully expanded leaves, uniform in colour, and not older than one year. For LMA calculation, leaves were digitalized and imported to Sigma Scan software (SPSS, Inc., Chicago, IL) to determinate leaf area; then, leaves were oven-dried for at least 72 h at 65°C until constant weight. Finally, LMA was calculated as the ratio between leaf dry mass and leaf area (gm^{-2}). Dried leaves were ground and used for chemical analyses. Foliar N was determined by flash combustion in a Carlo Erba NA 2500 Elemental Analyser, and foliar P was extracted in a concentrated sulphuric acid–water–peroxide solution in a Digesdahl Digestion machine and determined colorimetrically with molybdenum-blue (Steubing & Fangmeier 1992).

For soil nutrient content, we collected three soil samples from the same microsites where leaf samples were collected. We took the upper 10 cm of mineral soil and these are the data largely reported here. Soils were oven-dried for 72 h at 65°C and total N and P were calculated following the same procedures as those for foliar analyses. Additionally, N:P ratios were calculated for soil and leaf samples with the aim of inferring N or P limitation (Koerseklman et al. 1996, Güsewell 2004) as eventual constraints on foliar traits.

Climatic information for each site was obtained from meteorological stations located closer to each sampling site (Luebert & Pliscoff 2006). We include the following variables: mean annual temperature (MAT), mean annual rainfall (MAR), continental

index (Ic), potential evapotranspiration (EP). Additionally we calculated the "de Martonne effective precipitation index" (Ip), defined as the ratio between MAR and MAT+10. We consider to use Ip as it is a proxy of the degree of climate aridity (Oliver & Fairbridge 1987) and it has been previously used for Chilean ecosystems (Grau & Veblen 2000). Similarly we considered that the use of climatic variables together with the Ip index would provide more integrated information of the . For example, seasonality in Mediterranean Chilea should be stronger than in temperate Chile, and the sole consideration of MAT or MAP may not account for this difference. Furthermore, moving from coastal to Andean ecosystems could give rise to the influence of continentally in climatic patterns and the Ic index could disentangle this spatial variation.

Finally, in order to compare the range of variation of leaf traits within our study sites relative to those leaf traits from large-scale studies, we used the dataset Glopnet (Wright et al. 2004). From this dataset we took LMA, as well as foliar N and P concentrations from this study. We only used data corresponding to woody species, and these included 35 countries and 127 localities from forest and woodland ecosystems. In the Glopnet dataset latitude was not included, therefore, we obtained missing latitudes from Global Gazetteer web site (www.calle.com/world/index.html).

2.3 Data analyses

Based on these data sets we compared linear regressions of LMA versus latitude for Chilean forests and worldwide forest and woodland biomes. Additionally, we compared Chilean biomes and their analogous mediterranean and temperate forests worldwide, and we ran Pearson's correlation analyses between average LMA, and its variation coefficient for both biomes.

To explore the relationships between foliar traits, climatic variables, and soil nutrient contents in the Chilean latitudinal gradient we ran linear regressions and bivariate analyses. Data were normalized using log_{10}-transformation when the normality assumption was violated. In addition, we used principal component analysis (PCA) with the aim of reducing multivariate traits variation and summarizing trait information on two orthogonal axes (PCA1 and PCA2). Differences in foliar traits between Chilean mediterranean and temperate forests were assessed with ANOSIM, where the R test statistic ranges from 0 to 1. Values near 0 indicate no difference between mediterranean and temperate forests, whereas values closer to 1 mean strong dissimilarity between woody species in these ecosystems (Rees et al., 2004). Additionally, we ran linear regressions between the first PCA axis (PCA1) and the climatic and soil variables (nutrient contents) with the aim of exploring their influence on leaf trait variability. All the statistical analyses were done in R (R Development Core Team, 2005).

3. Results

3.1 Climatic differences along the latitudinal gradient

The data set for Chilean native forest species included the following variables: LMA, foliar N and P contents for 250 samples of 51 woody species distributed across 16 localities; 10 localities from mediterranean forests and six from temperate rain forests (Table 1). Within the Coastal Range we sampled seven localities, six from which were to the north and one to the south of the transition between temperate-evergreen rainforest and sclerophyllous semi-deciduous forest. Other six were made in the Andes

range, four in the southern forest transition and two in the northern (Arroyo et al. 1993). All climatic variables obtained for the localities studied were significantly correlated with latitude (P < 0.001), with lower rainfall, shorter growing season, higher mean annual temperature higher potential evapotranspiration and continental index in the northern localities, and the opposite trends southwards (Table 2). Therefore, we used increasing latitude as a proxy for declining aridity and increasing growing season length for the analysis of foliar trait variation.

Table 1. Chilean tree species from mediterranean and temperate forest ecosystems present in t

Species	Cuesta El Melon	Quillota	P. N. La Campana	Cuesta La Dormida	Sierras de Bellavista	Res Nac Los
Adenopeltis serrata	X	X				
Aextoxicon punctatum						
Amomyrtus luma						
Amomyrtus meli						
Araucaria araucana						
Aristotelia chilensis		X				
Austrocedrus chilensis						
Azara celastrina	X					
Azara petiolaris					X	
Azara serrata		X				
Beilschmiedia miersii		X				
Caldcluvia paniculata						
Colliguaja sp	X		X			
Cryptocarya alba	X	X	X	X		
Dasyphyllum diacanthoides						
Desfontainia spinosa						
Drimys winteri					X	
Embothrium coccineum						
Eucryphia cordifolia						
Gevuina avellana						
Laureliopsis philippiana						
Lithraea caustica	X	X	X			
Lomatia dentata						
Lomatia hirsuta						
Luma apiculata						
Luma chequen	X		X			
Myrceugenia parvifolia						
Myrceugenia planipes						
Nothofagus antarctica						
Nothofagus betuloides						
Nothofagus dombeyi						
Nothofagus glauca						
Nothofagus nitida						
Nothofagus obliqua					X	
Ovidia pillo-pillo						
Persea lingue		X				
Peumus boldus	X	X	X			
Podocarpus nubigena						
Podocarpus saligna						
Porlieria chilensis		X				
Quillaja saponaria		X	X			
Raukaua laetevirens						
Saxegothaea conspicua						
Schinus latifolius	X	X				

…an	Concepción	Los Ángeles	P. N. Laguna del Laja	Cordillera de Nahuelbuta	Cordillera Pelada	Puyehue	Valdivia	Senda Darwin
						X	X	
							X	X
								X
				X				
						X		
X								
								X
	X							
						X		
				X				
	X			X		X	X	X
						X	X	X
	X					X	X	X
						X		
						X	X	X
		X						
X			X	X				
	X			X		X		
				X				
						X	X	X
							X	
	X		X	X		X		
		X					X	X
		X		X				
							X	
X		X		X				
					X	X		X
X	X				X			
								X
				X		X		X

Table 2. Climatic variables for localities studied in south-central Chile: mean annual temperature[1] (MAT, °C), mean annual precipitations (MAP, $mm \cdot year^{-1}$), evapotranspiration index (EP), continentality index (Ic, °C), de Martonne specific precipitation index (Ip), number of woody species collected at each site (N), foliar N (%), foliar P (%), soil N (%), soil P (%), LMA ($g \cdot m^{-2}$) and the data source

| Locality	Site	Latitude °S	MAT	MAR	EP	Ic	Ip	N	Foliar N	Foliar P	Soil N	Soil P	LMA	Data
Cuesta El Melon	1	32.61	14.3	435	704	8.3	17.90	5	1.36	0.14	0.30	0.02	127.77	Cifuentes et al.
Cuesta El Melon	2	32.61	14.3	435	704	8.3	17.90	6	1.59	0.11	0.28	0.03	85.19	Cifuentes et al.
Quillota	1	32.63	14.3	435	704	8.3	17.90	11	2.37	0.14	0.53	0.10	107.04	Cifuentes et al.
Quillota	2	32.63	14.3	435	704	8.3	17.90	4	1.59	0.14	0.34	0.06	102.51	Cifuentes et al.
Quillota	3	32.66	14.3	435	704	8.3	17.90	3	1.91	0.10	0.34	0.09	174.69	Cifuentes et al.
Paqrque Nacional La Campana	1	32.93	14.9	363	739	13.0	14.58	3	1.24	0.10	0.17	0.04	173.43	Cifuentes et al.
Paqrque Nacional La Campana	2	32.93	14.9	363	739	13.0	14.58	3	1.22	0.14	0.42	0.05	121.09	Cifuentes et al.
Paqrque Nacional La Campana	3	32.93	14.9	363	739	13.0	14.58	2	1.78	0.10	0.20	0.02	196.56	Cifuentes et al.
Paqrque Nacional La Campana'	4	32.98	14.9	363	739	13.0	14.58	3	1.16	0.14	0.85	0.07	146.18	Cifuentes et al.
Cuesta La Dormida	1	33.01	14.9	363	739	13.0	14.58	2	1.10	0.12	0.37	0.06	188.27	Cifuentes et al.
Sierras de Bellavista	1	34.77	14.5	629	728	13.3	25.67	4	2.03	0.13	0.43	0.04	56.08	Gaxiola et al.
Reserva Nacional Los Bellotos	1	35.87	13.3	1640	687	11.5	70.39	6	2.24	0.23	0.63	0.11	62.94	Gaxiola et al.
Chillan	1	37.00	9.5	2211	593	12.0	113.38	4					148.30	GLOPNET
Concepcion	1	37.17	13.1	1294	673	8.9	56.02	6					145.19	GLOPNET
Los Angeles	1	37.39	12.3	1530	661	10.1	68.61	8	1.57	0.16	0.44	0.06	78.22	Gaxiola et al.
Parque Nacional Laguna del Laja	1	37.40	6.8	2012	514	12.9	119.76	2		0.09	0.27	0.04	116.84	Gaxiola et al.
Cordillera de Nahuelbuta	3	37.77	13.3	1055	690	11.4	45.28	4	1.13	0.11	0.50	0.08	81.74	Gaxiola et al.
Cordillera de Nahuelbuta	4	37.78	13.3	1055	690	11.4	45.28	4	2.32	0.21	0.93	0.10	91.44	Gaxiola et al.
Cordillera de Nahuelbuta	1	37.83	13.3	1055	690	11.4	45.28	7	1.29	0.12	0.59	0.07	99.32	Gaxiola et al.
Cordillera de Nahuelbuta	2	37.83	13.3	1055	690	11.4	45.28	3	0.92	0.08	0.20	0.03	88.83	Gaxiola et al.
Cordillera Pelada	1	40.00	11.6	1267	640	9.3	58.66	3	0.97		1.07		171.53	GLOPNET
Puyehue	1	40.14	13.9	1641	699	9.5	68.66	13	1.05				126.02	GLOPNET
Valdivia	1	40.20	10.8	2035	623	8.2	97.84	11	0.51		1.24		134.75	GLOPNET
Estación Biológica Senda Darwin	1	41.88	10.5	2148	612	5.9	104.78	7	1.36	0.05	0.77	0.12	92.04	Cifuentes et al.
Estación Biológica Senda Darwin	2	41.88	10.5	2148	612	5.9	104.78	5	1.04	0.04	1.52	0.04	114.69	Cifuentes et al.
Estación Biológica Senda Darwin	3	41.88	10.5	2148	612	5.9	104.78	5	0.91	0.05	1.70	0.03	95.54	Cifuentes et al.
Estación Biológica Senda Darwin	4	41.88	10.5	2148	612	5.9	104.78	4	1.24	0.06	1.74	0.05	77.74	Cifuentes et al.
Estación Biológica Senda Darwin	5	41.88	10.5	2148	612	5.9	104.78	7	0.91	0.05	1.66	0.05	102.03	Cifuentes et al.
Parque Tantauco	1	43.04	9.7	1279	595	5.4	64.92	6	1.22	0.05	1.23	0.04	101.12	Cifuentes et al.
Parque Tantauco	2	43.05	9.7	1279	595	5.4	64.92	5	1.09	0.03	1.91	0.03	85.10	Cifuentes et al.
Parque Tantauco	3	43.08	9.7	1279	595	5.4	64.92	8	1.30	0.04	1.03	0.02	133.02	Cifuentes et al.
Parque Tantauco	4	43.09	9.7	1279	595	5.4	64.92	9	0.99	0.04	0.86	0.03	108.81	Cifuentes et al.
Parque Tantauco	5	43.10	9.7	1279	595	5.4	64.92	5	1.02	0.07	1.14	0.05	124.89	Cifuentes et al.

3.2 Large-scale comparisons

LMA did not show a significant trend along the latitudinal gradient for Chilean forest species. Although LMA was negatively related to latitude in world forests data (P <0.001), this relationship was not significant for Chilean woody species (P > 0.1; Fig. 2, a). When comparing Chilean temperate and mediterranean forests and their analogous worldwide, we found that Chilean mediterranean woody species had in average lower LMA than woody species for other world's mediterranean climates (P < 0.001); while Chilean temperate species showed no difference from other global temperate forests (Fig. 4, b). Even though we expected larger variation in the LMAs of woody species from mediterranean environments in the global dataset, because information were derived from several continental regions, the coefficient of variation for LMA did not differ between Chilean and World's mediterranean data sets (41.69% and 43.52%, respectively). In contrast, variation in LMA among Chilean temperate forest species was significantly lower than for the World's LMA data set (26.28% and 60.31%, respectively, P<0.001; Fig. 4, b).
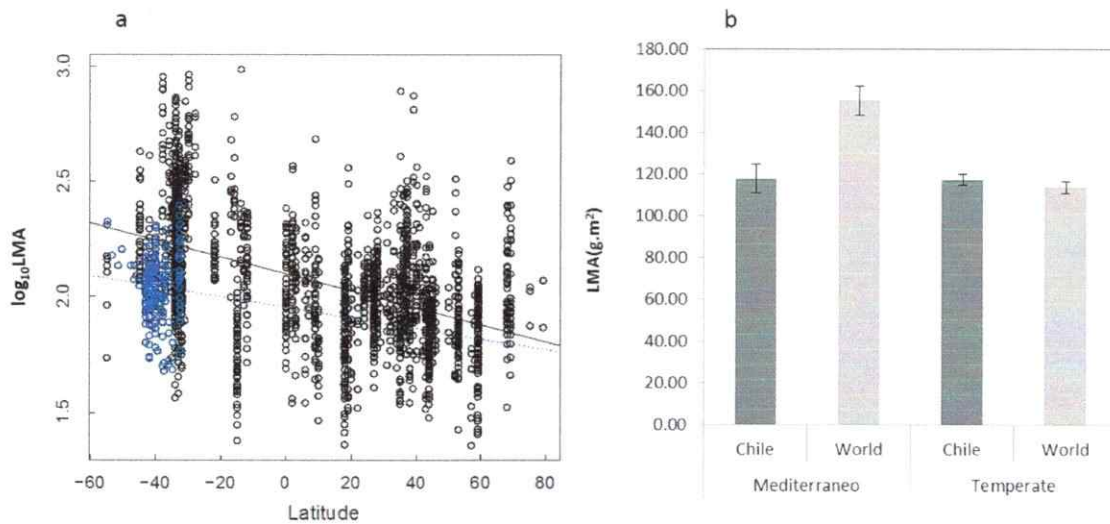
Figure 4. a) Relationship between latitude and LMA (g·m^{-2}) of woody species from worldwide (black circles) and Chilean forest species (blue circles). Tendency lines are solid for significant relationships (P<0.001) and dashed for non-significant relationships (P>0.05). b) Bar plot comparing mean LMA of woody species within Chilean forests versus World's mediterranean and temperate forests.

3.3 Foliar nutrient content traits and soil nutrients in Chile

We related soil nutrient contents in Chilean localities with foliar nutrient contents and with the variation of LMA. Soil N and soil P showed contrasting trends along the latitudinal gradient; soil N concentration increased (P < 0.001) with latitude (from north to south), while soil P concentration decreased with latitude (P < 0.01; Fig. 5, a, b). Contrary to expectations, foliar N and P both declined southwards (Fig. 5, c, d) and hence did not follow soil trends for N. Comparisons between soil and leaf nutrients showed a positive correlation between soil and foliar P (r = 0.42, P < 0.001), but a negative correlation between soil and foliar N contents (r= -0.4, P < 0.001).
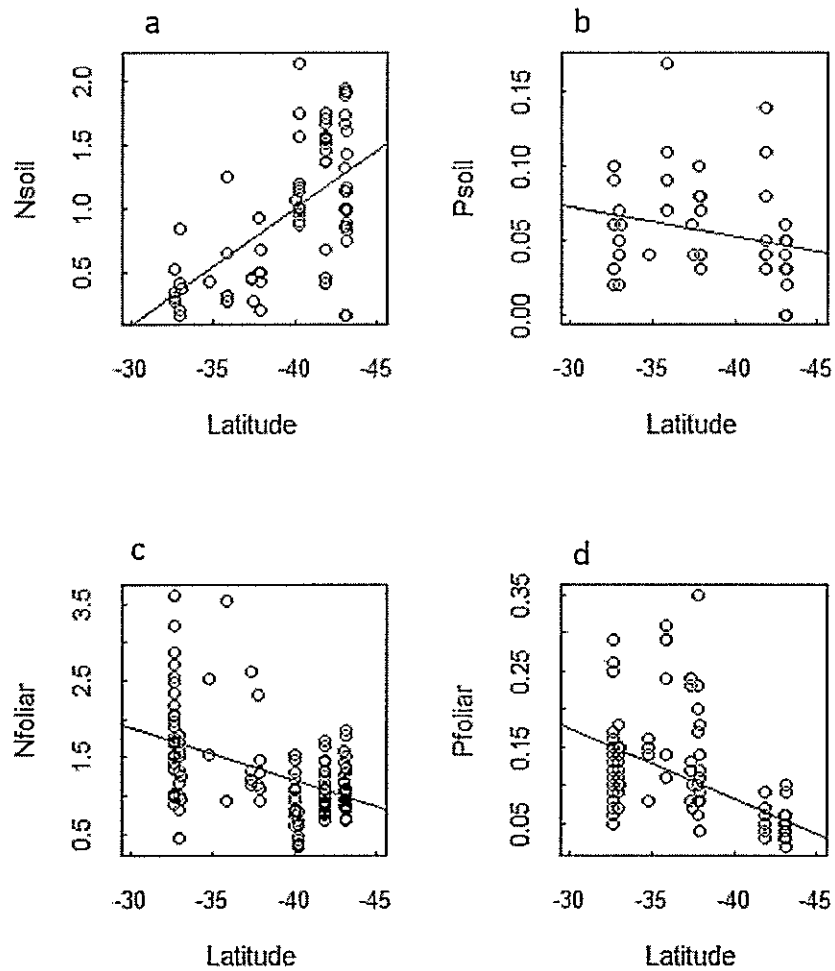
Figure 5. Latitudinal variation in soil nutrient contents for Chilean localities (% dry weight) (a,b) and foliar nutrient content for Chilean species (%) (c,d). Solid lines indicate significant regression coefficients ($P<0.001$).

The average foliar N:P ratio of woody species from temperate forests was 25.6 (± 1.2), suggesting strong P limitation at higher latitudes in the rainforest environments (Koerseklman et al. 1996, Güsewell 2004). Conversely, mediterranean woody species had an average N:P ratio of 13.7 (± 0.9), suggesting in turn nitrogen limitation

(Güsewell 2004, Pekin et al. 2012). Foliar and soil N:P ratios were positively related (Fig. 6), and when a hypothetical slope of 1 was traced, all except 5 species from temperate rain forests were below the hypothetical line, suggesting that foliar P content in the foliage of woody species was higher than expected from soil P content.
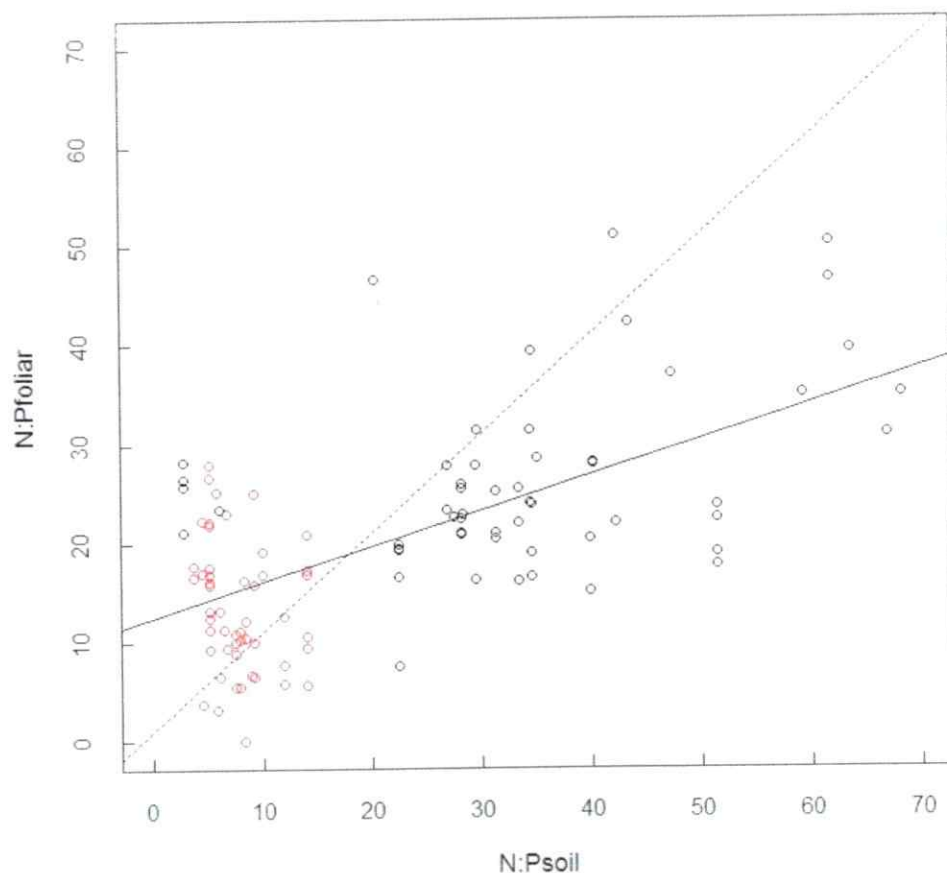
Figure 6. Soil and foliar NP ratio relationship for Chilean forest species and localities from which they were collected. Red circles are species from mediterranean forests (32-37°S) and black circles are species from temperate forests (38-40°S) and. Solid line is the data regression ($P<0.001$) and the dashed line is the hypothetical 1:1 soil-foliar NP ratio.

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Corroborating global patterns, negative relations were found between foliar nutrient contents and LMA, as well as between foliar NP ratio and LMA (Fig. 7). Furthermore, such as with LMA, the coefficient of variation in foliar NP ratio was significantly lower for species from Chilean temperate rain forests than for species from mediterranean forests (36% and 48%, respectively, $P < 0.05$).
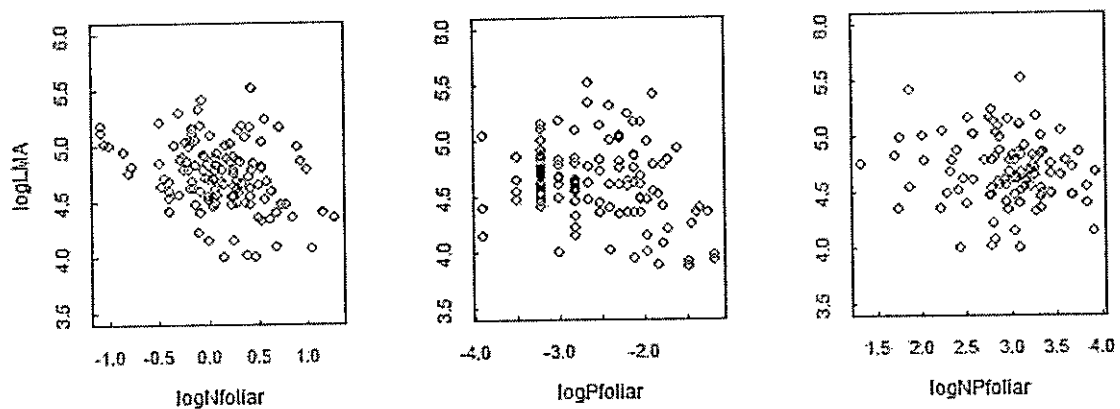
Figure 7. Correlations between foliar nutrient contents and LMA (g·m^{-2}) for the woody species studied in forests of south-central Chile (foliar N and P contents and LMA are $\log_{10}$-scaled). a) Foliar N content ($r = -0.32$, $P < 0.001$), b) foliar P content ($r = -0.25$, $P < 0.01$) and c) NP ratio ($r = -0.2$, $P = 0.05$),

3.4 Climate and soils as controls of leaf trait variability

Foliar nutrient content and LMA showed different patterns of change in relation to the abiotic factors analysed in this study. We found significant relationships for all bivariate regressions among foliar NP ratios, climatic variables, and soil nutrient contents. Temperature (MAT), EP and Ic were all negatively associated with foliar NP ratio of Chilean woody species; while the latter foliar trait was positively related to

rainfall (MAP), Ip and soil N. In turn, all bivariate regressions including LMA, climatic variables and soil nutrient contents, were non-significant (Table 3). The lack of regression was unforeseen because previous studies have often reported climatic influences on LMA (Wright et al. 2004, Wright et al. 2005, Poorter et al. 2009, etc.).

Table 3. Regressions between the foliar traits LMA ($g \cdot m^{-2}$), foliar NP ratios, and climatic variables, MAT (°C), MAP ($mm \cdot year^{-1}$), EP ($mm \cdot d^{-1}$), Ic (°C), Ip, Nsoil (%), Psoil (%) and soil NP ratio. Coefficients (Est.), r^2 and F-values are given for each regression. Significance levels are given as: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; · , $P < 0.1$; N.S, $P > 0.1$.

	LMA	Foliar N:P
MAT	Est.= 0.59, R^2= -0.002 $F_{1,242}$ =0.44 N.S	Est.=-2.75 , R^2= 0.35 $F_{1,110}$=59.19 ***
MAP	Est.=-0.004 , R^2= 0.0006 $F_{1,242}$ =1.135 N.S	Est.=0.01, R^2= 0.11 $F_{1,110}$=15.23 ***
EP	Est.=0.062, R^2= 0.003 $F_{1,208}$ = 1.65 N.S	Est.=-0.11, R^2= 0.35 $F_{1,110}$=61.67 ***
Ic	Est.=2.0, R^2= 0.013 $F_{1,208}$ =3.74 N.S	Est.=-2.16, R^2= 0.35 $F_{1,110}$=61.78 ***
Ip	Est.=-0.07, R^2= 0.0003 $F_{1,242}$ = 1.07 N.S	Est.=0.12, R^2= 0.14 $F_{1,110}$=19.63 ***
Nsoil	Est.=-8.86, R^2= 0.01 $F_{1,141}$ =2.57 N.S	Est.=8.76, R^2= 0.22 $F_{1,105}$=30.21 ***
Psoil	Est.=-184.3, R^2= 0.02 $F_{1,49}$ = 1.259 N.S	Est.=-57.26, R^2= 0.02 $F_{1,105}$=3.5 ·
N:Psoil	Est.=-1.228, R^2= 0.006 $F_{1,129}$ = 3.382 ·	Est.=0.36, R^2= 0.37 $F_{1,105}$=63.68 ***

The main PCA axis (PCA1) that explained 98% of the total foliar trait variance among woody species, showed that mediterranean and temperate forests of Chile differed significantly with regard to foliar traits (R = 0.047, $P < 0.0001$; Fig. 8). To assess the strength of the correlation of woody species' PCA scores with abiotic

factors, we correlated the values for this axis with each climatic variable (MAT, MAP, EP, Ic and Ip) and soil nutrient content (soil-N, soil-P). We found that the axis scores correlated positively to MAT (r=0.31, *P*=0.003), EP (r=0.35, *P*=0.0008) and Ic (r=0.46, *P*<0.001); and negatively to MAP (r=-0.35, *P*=0.0006), Ip (r=-0.35, *P*=0.0007), Nsoil (r=-0.29, *P*=0.006) and Psoil (r=-0.06, *P*=0.59).
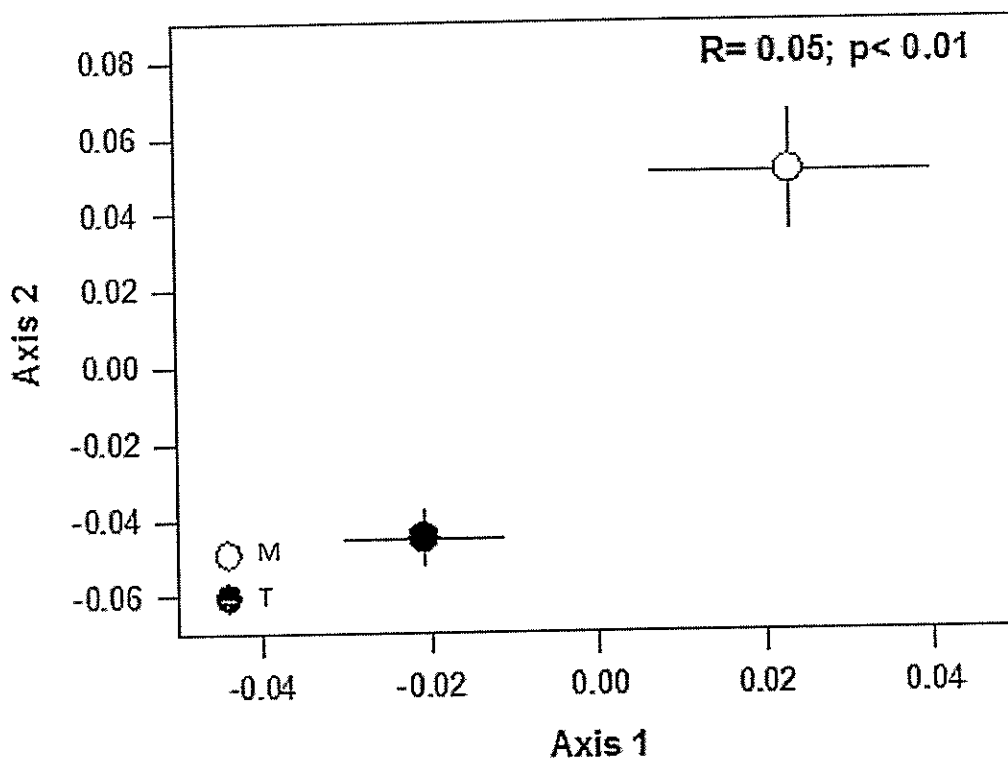
Figure 8. Principal component analysis based on three functional traits data: LMA, foliar-N content and foliar-P content from mediterranean and temperate Chilean woody species. White dot (M) is the central value of foliar traits data from mediterranean forest woody species. Black dot (T) is the central value of the foliar traits of temperate forest woody species. Data is significantly different between mediterranean and temperate forests (R = 0.047, P = 0.0001).

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4. Discussion

Patterns of change in climatic variables and soil nutrients from northern to southern localities in mediterranean and temperate forests of Chile, conform a pronounced latitudinal gradient, from semiarid climate with a short growing season and soil nitrogen scarcity in northern sites, to wet-temperate climate with a longer growing season and soil phosphorus limitation in southern sites (Fig. 7). Thereby, we used comparisons among forests along this latitudinal gradient, as a methodological approach to assess the influence of abiotic factors on community foliar traits.

4.1 LMA along the latitudinal gradient

There was no significant relationship between LMA and latitude in the Chilean forests data set, in contrast to the trend observed in the global data set (Fig. 4, a). We expected LMA to decrease from north to south along the Chilean latitudinal gradient, from high LMA in mediterranean–climate forests, to low LMA in high productivity temperate rain forests. Mean LMA of Chilean mediterranean and temperate woody species did not differ significantly; however, Chilean mediterranean woody species had a significantly lower LMA than species from other mediterranean ecosystems of the world (Fig. 4, b). This was completely unexpected because within the worldwide leaf traits spectrum, mediterranean woody species tend to have higher LMAs compared to other forest ecosystems (Dominguez et al. 2012). Interestingly, when we examined the coefficients of variation (CV) of LMA in these data sets, we found that Chilean mediterranean woody species had higher CVs than species from other mediterranean ecosystems worldwide (i.e., Spanish mediterranean: 26%, Australian mediterranean: 19%). All the mediterranean datasets (n = 727) in the global database put together had

the same coefficient of variation as the woody species in Chilean mediterranean forests ($n = 91$). Such remarkable foliar trait divergence in Chilean mediterranean forests could be a consequence of enhanced niche partitioning, where woody species with dissimilar LMAs are more likely to coexist in one ecosystem depending on their divergent resource acquisition strategies in heterogeneous environments (Dwyer et al. 2013). Furthermore, because of their topographical complexity and the influence of the transition zones with two contrastingly different vegetation types (i.e. the semiarid scrub to the north and the mixed deciduous-evergreen temperate forest to the south), Chilean mediterranean ecosystems correspond to a highly heterogeneous vegetation mosaic (Armesto et al. 2007), recognized as one of the world's biodiversity hotspots (Médail & Quézel, 1999, Myers et al. 2000). Therefore, we suggest that the high floristic diversity and pronounced vegetation heterogeneity proper of Chilean mediterranean ecosystems may enhance variability of functional foliar traits to a degree that surpasses other analogous world ecosystems.

4.2 Co-variation of foliar traits and abiotic variables

For the Chilean mediterranean woody flora, foliar N-to-P ratio was as low as values reported by Güsewell (2004) for extremely nutrient-poor Australian mediterranean ecosystems (13.7 and 13.6, respectively), reflecting strong N limitation. On the other hand, foliar N:P ratios for woody plants from Chilean temperate rain forests were considerably higher than for the temperate forest flora of New Zaeland (25.6 vs. 16.0, respectively), which are indicative of strong P limitation in Chile (Richardson et al. 2004, Koerseklman et al. 1996, Güsewell 2004). Within Chile, low foliar N:P ratios were found in nearly all temperate forest sites, regardless of soil N:P

ratios (Fig. 6), which suggests that temperate woody species could be resorbing P and thus achieving higher foliar P than expected from soil availability (Vitousek 1984, Reed et al. 2012).

Although soil P variation across sites explained foliar P decline over the 20 degrees of latitude, soil N did not. We hypothesize that low soil P concentration observed in southern temperate rainforests could be limiting protein construction and thus reducing foliar N content (Niklas et al. 2005, Reed et al. 2012). We have shown that Chilean temperate forests had the lowest CV for LMA and foliar NP ratios. In this context, we hypothesize that low soil P in Chilean temperate rainforests could be imposing a constraint on LMA dispersion in Chilean temperate rain forests in a similar way Mason et al. (2012) demonstrated that plant traits tend to converge at low soil P concentration, thus indicating that low soil fertility limits resource-use strategies for coexistence.

Negative correlations between LMA and foliar N and P (Fig. 7) support the idea of an integrated spectrum of leaf trait variation within Chilean forests (Wright et al. 2004). Although LMA values were unrelated to abiotic variables along the Chilean latitudinal gradient, leaf P and N contents decreased from mediterranean forests to temperate rainforests in the south (Table 3). We expected to find low nutrient contents and high LMA values in mediterranean forests, as these are typical characteristics of plants inhabiting semiarid, short-growing season, and low soil nutrient sites. However, we found that woody plants from mediterranean forests had the highest nutrient content (Fig. 5, c, d) and on average, the same LMA than plants from temperate forests (Fig. 4, b). High foliar N content could be the by-product of efficient water conservation strategy in response to the extended dry season of northern sites, thus reflecting a resource

conservation strategy (Field et al. 1983, Lajtha & Whitford 1989, DeLucia & Schlesinger 1991, Wright & Westoby 2002). In turn, high variability in LMA as in foliar NP ratio may indicate that environmental heterogeneity is forcing plants to display different resource use strategies. These findings suggest that as a consequence of environmental heterogeneity, the Chilean mediterranean woody plants are subjected to multiple drivers that may diversify resource use strategies.

Finally, the Chilean temperate flora had more predictable LMA values on the basis of the worldwide temperate biome data set, not as foliar nutrient content. Considering that leaf and soil nutrient contents are correlated in this data set (Fig. 6), we argue that soil P availability may be affecting foliar traits in the following manner; (i) at low soil P availability, woody species with high re-translocation capacity can achieve higher foliar P than expected from soil availabilities (Seaman et al. 2014), and hence foliar P values could be decoupled from soil. (ii) Low soil P availability could affect foliar N because P limitation hampers protein construction, resulting in low foliar N contents. iii) Nutrient limitation could therefore be imposing constrains on trait variation and thus reducing the spectrum of possible resource use strategies (Lambers et al. 2008, Mason et al. 2012) in Chilean temperate rain forests.

Our findings thus far support the idea that, even conserving the general trade-offs of the foliar traits spectrum, contrasting abiotic controls may influence trait variation in opposite directions. PCA1 was positively correlated to MAT, EP and Ic, which means that high temperatures, climate seasonality (as explained by different growing season length) as well as high potential evapotranspiration are all related to foliar trait dispersion. This would explain why foliar traits in the Chilean mediterranean woody flora had higher variation coefficients. On the other hand, PCA1 was negatively related

to MAP, Ip and soil N, all of which are indicative of greater resource availability, less abiotic constraints on productivity, and longer growing seasons. Thus, when constraints on productivity are lower, LMA varies less, i.e., values are more tightly distributed. However, soil P was not significantly related to this PCA axis, which could mean that P limitation could be constraining functional trait variation in Chilean forests, as demonstrated by Mason et al. (2012). We conclude that in more heterogeneous habitats, multiple resource acquisition strategies are needed (Cornwell and Ackerly 2009), resulting in increased foliar traits variation.

5. Conclusions

Here we reported a local view of climatic and soil influences on functional foliar trait variation in Chilean forest species. Our analysis indicated that Chilean forests could represent a special case of the worldwide leaf economic spectrum (Wright et al. 2004). Of the traits analyzed here, LMA had the lowest variation across a broad latitudinal gradient of vegetation, soils and climatic variables, probably reflecting two contrasting resource use strategies, one characteristic of mediterranean woody flora and the other associated with temperate forest species. These two different strategies are expressed in the coefficients of variation observed among traits, rather than in different mean values, thus displaying the diversity of foliar traits combinations that can be achieved under contrasting environmental conditions. Still, further research is needed in order to understand how soil nutrient content influences foliar traits, as well as the central mechanisms of how C and nutrient plant economies are linked (Güsewell 2004). We argue that integrating influences of climate and soil properties on plant functional traits

may be central to modeling possible effects of global change scenarios on species distribution and performance.

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