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BÜNDCHEN, MÁRCIA; BOEGER, MARIA REGINA T.; REISSMANN, CARLOS B.;
GERONAZZO, KELLY M.

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Interspecific variation in leaf pigments and nutrients of five tree species from a subtropical forest in southern Brazil

MÁRCIA BÜNDCHEN¹, MARIA REGINA T. BOEGER², CARLOS B. REISSMANN³ and KELLY M. GERONAZZO⁴

¹Instituto Federal de Educação, Ciência e Tecnologia do Rio Grande do Sul (IFRS),
Rua Coronel Vicente, 281, Centro, 90030-040 Porto Alegre, RS, Brasil

²Programa de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas,
Universidade Federal do Paraná, Caixa Postal 19031, 81531-990 Curitiba, PR, Brasil

³Departamento de Solos e Engenharia Agrícola, Setor de Ciências Agrárias, Universidade Federal
do Paraná, Rua dos Funcionários, 1540, 80035-050 Juvevê, Curitiba, PR, Brasil

⁴Universidade Estadual do Centro Oeste, PR 103, Km 157, 84500-000 Irati, PR, Brasil

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ABSTRACT

The purpose of this study was to analyze the seasonal variation in the nutrient and pigment content of leaves from five tree species – of which three are perennial (*Cupania vernalis*, *Matayba elaeagnoides* and *Nectandra lanceolata*) and two are deciduous (*Cedrela fissilis* and *Jacaranda micrantha*) – in an ecotone between a Deciduous Seasonal Forest and a Mixed Ombrophilous Forest in the state of Santa Catarina, Brazil. Leaf samples were collected in the four seasons of the year to determine the content of macronutrients (N, K, P, Mg, Ca, S) and photosynthetic pigments (Chl_a, Chl_b, Chl_{tot}, Car_{tot}, Chl_a:Chl_b and Car_{tot}:Chl_{tot}). The principal component analysis showed that leaf pigments contributed to the formation of the first axis, which explains most of the data variance for all species, while leaf nutrient contribution showed strong interspecific variation. These results demonstrate that the studied species have different strategies for acquisition and use of mineral resources and acclimation to light, which are determinant for them to coexist in the forest environment.

Key words: chlorophyll, Araucaria forest, Deciduous Forest, macronutrients.

INTRODUCTION

Plant distribution is associated with environmental factors, and its adaptation to a particular type of environment involves optimizing the acquisition and use of resources, specifically light and nutrients. Considering that resource availability varies in the interior of forests, the capacity of

each species to use them, largely determines its competitive abilities (Grime 1977). Thus, leaf physiological traits, such as the content of nutrients and photosynthetic pigments, reflect a plant's light capture performance; the study of such characteristics provides clues to the understanding of the functional ecology of plants in different ecosystems (Poorter 2009).

Environmental conditions change throughout the day and seasons. Consequently, each habitat

Correspondence to: Márcia Bündchen
E-mail: marcia.bundchen@poa.ifrs.edu.br

presents a combination of independent environmental variables whose intensity varies during the year (Pierce et al. 2005). Climate seasonality is an important determinant of phenological events, having a direct impact on metabolic and regulating processes such as germination, sprouting, senescence, flowering, and fruiting (Taiz and Zeiger 2013). Plant response to seasonality effects has been widely studied in northern ecosystems (Chapin III 1980), Mediterranean (Valladares et al. 2000), and other strongly seasonal ecosystems, such as the Brazilian *cerrado* (Carvalho et al. 2007), where the vegetation is subjected to severe resource constraints during a period of the year and shows morphophysiological variations. The ecophysiology of plants from subtropical forests, where the transition between seasons is gradual, has not been studied in depth up until now, and general data on subtropical forests are still scarce.

The effects of environmental parameters, such as light quality and intensity, and nutrient availability in the soil, have been characterized mainly through testing under controlled conditions, using mostly seedlings and saplings – very few researches result from the analysis of adult trees in their habitats. As a consequence, the models and interpretations that are generated are at odds with actual responses by plants in natural environments. This study, conducted with tree species from an interface area between two forest formations in southern Brazil, was concerned with analyzing whether: *i.* trees respond to changing seasons with altered content of leaf nutrients and pigments and *ii.* there is a correlation between the content of leaf nutrients and pigments.

MATERIALS AND METHODS

The study was carried out in “Parque Natural Municipal do Rio do Peixe”, located in the municipality of Joaçaba, state of Santa Catarina, Brazil (27°10'41"S and 51°30'17"O, 770 m of

altitude), and consist of a forest fragment with 200 ha of Atlantic Forest biome (IBGE 1990) in a transition area between the Deciduous Seasonal Forest (or FED – Floresta Estacional Decidual) and the Mixed Ombrophilous Forest (or FOM – Floresta Ombrófila Mista). The area is home to species from both forest typologies, and one of the few remnants of the region's original vegetation (Raimundo 2003).

The Deciduous Seasonal Forest (FED) stretches along the Uruguay River basin, in southern Brazil (Klein 1978, Leite 2002) and, according to Ruschel et al. (2007), it is the most endangered forest ecosystem in the south of Brazil, demanding immediate efforts towards its conservation. The Mixed Ombrophilous Forest (FOM), which originally stretched across a major portion of the southern region, is currently highly fragmented. In the regions with altitude around 600 m, FOM and FED meet, forming an area of ecological tension, or ecotone, which enables the mixing of species from both forest physiognomies and bringing more diversity to these transition areas (Leite 2002).

The distribution area of FED and its interface with FOM is typically ombrophilous, with no dry periods and regular rainfall. Thermal rates determine two quite distinct periods, one centered in summer, with average temperature equal to or higher than 20 °C, and another centered in winter, with average temperature equal to or below 15 °C (Leite 2002).

The soil was determined to be “Nitossolo Bruno” following dos Santos et al. (2006), with high content of clay (> 60%), acid pH (3.9-5.0), organic matter (3.3-6%), P (2.3-4.8 mg dc⁻³), K (21->400 mg dc⁻³), exchangeable Ca (0.1-6.1 cmol dm⁻³), exchangeable Mg (0.1-2.8 cmol dm⁻³), and extractable S (8.8-25 mg dc⁻³). More details about soil classification can be found in Bündchen et al. (2013).

Within the study area, five tree species occurring in both FED and FOM were selected: *Cupania*

vernalis Cambess. (Sapindaceae), perennial, heliophytic, with pinnately compound leaves; *Matayba elaeagnoides* Radlk. (Sapindaceae), perennial, mesophytic, pinnately compound leaves; *Nectandra lanceolata* Nees & Mart. (Lauraceae), perennial, mesophytic, with simple leaves; *Cedrela fissilis* Vell. (Meliaceae), deciduous, heliophytic, with pinnately compound leaves; and *Jacaranda micrantha* Cam. (Bignoniaceae), deciduous, heliophytic, with compound leaves (Klein 1978). These species were identified by taxonomy experts from the Museu Botânico de Curitiba, state of

Paraná. All trees were 15 to 19 m high. The study was conducted in 12 months, and samples were collected every quarter in each season of the year. Climate variables for the period are in agreement with the typical averages for the period, and, for analysis purposes, fall/winter were classified as “cold period” and spring/summer were classified as “warm period” (Table I), following Leite (2002). For each species, five specimens in the canopy were marked and used for the collection of mature leaves which were fully expanded and fully exposed to sunlight.

TABLE I
Climatic parameter averages: rainfall, radiation, average temperature and classification of cold and warm period.

Season	Rainfall (mm)	Radiation (W/m ²)	Temperature (°C)	Period
Autumn	86.3	306.7	15.2	Cold
Winter	262.4	270.4	14.1	
Spring	193.5	382.4	20.8	Warm
Summer	207.9	376.6	22.2	

In order to determine the nutrients [Nitrogen (N), Phosphorus (P), Potassium (K), Calcium (Ca), Magnesium (Mg) and Sulfur (S)], fully expanded mature leaves were collected from each specimen in the canopy (a compound sample x five species x five specimens x four seasons), washed with deionized water, dehydrated in an oven at 60 °C and crushed. The samples were sent to the Laboratory of Fertility of Instituto Agronômico de Campinas (IAC-SP) and subjected to nitric-perchloric digestion. All element concentrations were estimated using argon plasma optical emission spectrometry (ICP OES). Nitrogen was measured using the Kjeldahl method.

Pigments were extracted using 80% acetone on fresh leaf samples (five leaves x five specimens x five species x four collections) and measured with a spectrophotometer. The content of chlorophyll *a* (Chl_a), chlorophyll *b* (Chl_b) and total chlorophyll (Chl_{tot}) was determined as described by Porra et

al. (1989), and total carotenoids (Car_{tot}) followed Lichtenthaler and Wellburn (1985). Based on these data, the chlorophyll *a*:chlorophyll *b* ratio (Chl_a:Chl_b) and the total carotenoids:total chlorophyll ratio (Car_{tot}:Chl_{tot}) were calculated.

The experimental design was entirely randomized with a factor (season), of which the other variables (pigments and nutrients) were considered to be dependent. Thus, the five species were analyzed individually.

Principal component analyses (PCAs) were performed in order to describe the data by identifying the most representative variables and the ones that presented a higher correlation coefficient. Based on this correlation structure, shown by the PCA axes, we tried to identify the variables that could explain a higher percentage of data than the individual measures on the field. In this context, we decided to evaluate the score of the most representative PCA axes by applying one-

way ANOVA. Variance homogeneity was verified previously by applying Bartlett's test at 5% (Zar 1999). The Kruskal-Wallis test (nonparametric) was used when the premise of using ANOVA (homogeneity of variances) could not be met. To test gaussianity, we used the Kolmogorov-Smirnov test. The latent root criterion (Kaiser) was applied to determine the minimum number of axes to be considered. In this case, only eigenvalues greater than one were considered relevant (Johnson and Wichern 1998) and variable correlation was verified by using Spearman's correlation test. In all analyses, the results were considered significant at $p < 0.05$. All statistical analyses were performed using Statistica software (Statistica, version 7.0 Statsoft Inc., USA).

RESULTS

Most foliar nutrient concentrations showed pronounced interspecific variation. Among species, Mg presented the highest variation, while N presented the lowest variation. Nitrogen and P from the leaves of *J. micrantha*, K from *N. lanceolata*, Ca from *C. fissilis*, Mg from *M. elaeagnoides* and S from *C. vernalis* showed the highest variation among seasons. For pigments, total chlorophyll presented highest variation and chlorophyll_b the lowest. Among seasons, Chl_a showed the highest variation from *M. elaeagnoides* leaves, Chl_b and total chlorophyll showed the highest variation from *J. micrantha*, carotenoids showed the higher variation from *N. lanceolata*. Compared to deciduous trees, perennial species presented a higher variation, among seasons, for P, K, Mg, S, chlorophyll_a, total chlorophyll and carotenoids.

Principal component analysis (PCA) showed that the evaluated leaf parameters (photosynthetic pigments and nutrients) contribute differently to axis formation in the species on the FED/FOM interface. In general terms, pigments contributed to the first axes, explaining most of the data variance. Nutrients, on the other hand, correlated with the

other axes, explaining a smaller percentage of information.

In *N. lanceolata* (Fig. 1a), the first four axes explain 89.4% of the variance, and 40.7% of data variance can be attributed to the first axis. In *M. elaeagnoides* (Fig. 1b), 81.3% of the variance was determined by the first three axes, while the first axis was responsible for 38% of data variance. In *C. vernalis* (Fig. 1c), 89.7% of data variance was explained by four axes, 36.7% of which can be attributed to the first axis. In *J. micrantha* (Fig. 1d), four axes determine 90.1% of the information, of which 36.8% are explained by the first axis.

In these four species, variables Chl_a, Chl_b, Chl_{tot} and Chl_{tot}:Car_{tot} are strongly correlated with the first axis. The Chl_a:Chl_b ratio positively correlated with the first axis in the perennial species and *C. fissilis*. On the other hand, the correlation of nutrients with the first axis was lower and showed a strong specific characteristic (Table II).

In *C. fissilis* (Fig. 1e), 84% of the variance can be explained by the first three axes (first axis = 55.8%). In this species, most variables – except N, Car_{tot} and Chl_{tot}:Car_{tot} – showed a strong contribution to the first axis, unlike the other species in which the contribution of pigments and nutrients with greater weight was distributed among the functions that represent different axes (Table II).

The correlation coefficients that correspond to the second axis (Table II) were positive for K, P and S in *N. lanceolata*, K and P in *M. elaeagnoides* and N, K and P in *C. vernalis*. Among the deciduous species, *J. micrantha* showed N and P negatively correlated with the second axis, and in *C. fissilis* only N was negatively correlated with the second axis (Table II).

The ANOVA carried out with the scores, showed that seasonal differences are reflected in the participation of pigments and nutrients in axis formation for each species studied (Table III). As previous studies had shown, *N. lanceolata*, *M. elaeagnoides*, *C. vernalis* and *J. micrantha* present

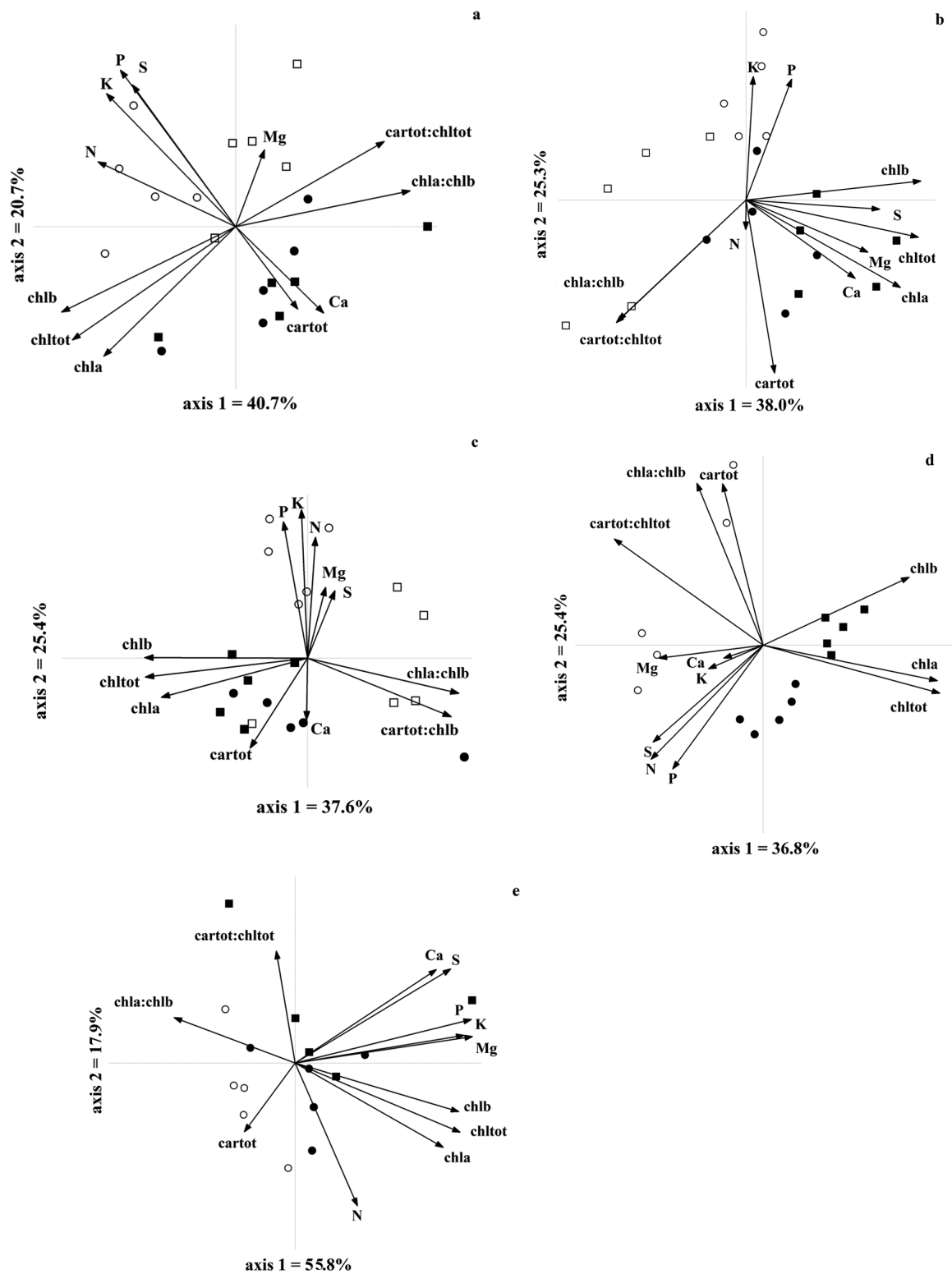


Figure 1 - PCA ordination diagram of variables (photosynthetic pigments and nutrients). Legend: Warm period (Black Squares = Summer. Black Circles = Spring). Cold period (Open Circles = Winter. Open Squares = Autumn). **(a)** *Nectandra lanceolata*; **(b)** *Matayba elaeagnoides*; **(c)** *Cupania vernalis*; **(d)** *Jacaranda micrantha*; **(e)** *Cedrela fissilis*.

TABLE II

Principal component analyses (PCAs). Legend: NEC: *Nectandra lanceolata*; MAT: *Matayba elaeagnoides*; CUP: *Cupania vernalis*; JAC: *Jacaranda micrantha*; CED: *Cedrela fissilis*; Chl_a: Chlorophyll a; Chl_b: chlorophyll b; Chl_{tot}: total chlorophyll; Car_a: total carotenoid. Chl_a:Chl_b: Chlorophyll a: chlorophyll b ratio; Car_{tot}:Chl_{tot}: total carotenoid: total chlorophyll ratio; Axis %: percentage of data variation explained by axis and Cum %: cumulative percentage of data variation. Chlorophyll and carotenoid values are in mol.mg⁻¹. Bold numbers represent the variables that have higher correlations with the axis.

	NEC			MAT			CUP			JAC			CED		
	A1	A2	A3	A4	A1	A2	A3	A4	A1	A2	A3	A4	A1	A2	E3
Eigenvalues	4.88	3.23	1.57	1.04	4.56	3.04	2.16	2.12	3.05	2.12	1.07	4.41	3.05	2.15	1.23
N	-0.68	0.32	-0.55	0.12	0.00	-0.15	-0.52	0.05	0.74	-0.21	0.46	0.58	-0.61	0.07	0.06
K	-0.64	0.66	0.05	0.26	-0.04	0.65	-0.59	-0.03	0.90	0.22	-0.10	0.23	-0.21	-0.89	0.14
P	-0.57	0.77	-0.10	0.06	-0.25	0.64	-0.39	-0.14	0.83	0.38	-0.30	0.50	-0.63	0.06	0.13
Ca	0.44	-0.43	-0.39	0.49	-0.58	-0.41	-0.63	0.00	-0.38	0.77	-0.07	0.23	-0.02	0.77	0.32
Mg	0.14	0.38	-0.22	-0.82	-0.64	-0.27	-0.49	0.11	0.43	0.29	0.75	0.57	-0.02	0.54	0.20
S	-0.51	0.70	-0.41	0.08	-0.71	-0.05	-0.55	0.17	0.40	0.81	-0.24	0.61	-0.47	0.28	0.13
Chl_a	-0.65	-0.64	-0.29	-0.09	-0.81	-0.47	0.30	-0.89	-0.23	0.30	0.13	-0.90	-0.17	0.23	0.16
Chl_b	-0.86	-0.42	0.22	-0.05	-0.92	0.09	0.37	-0.99	0.01	-0.07	-0.04	-0.77	0.36	0.20	-0.36
Chl_{tot}	-0.81	-0.56	-0.02	-0.07	-0.90	-0.20	0.35	-0.98	-0.11	0.10	0.04	-0.92	-0.25	0.20	-0.15
Chl_a:Chl_b	0.86	0.18	-0.30	0.02	0.68	-0.63	-0.19	0.92	-0.22	0.22	0.03	0.35	0.86	0.02	0.56
Car_{tot}	0.31	-0.41	-0.80	-0.11	-0.15	-0.91	-0.03	-0.35	-0.54	0.58	0.32	0.21	0.86	0.06	0.59
Car_{tot}:Chl_{tot}	0.74	0.42	0.10	0.10	0.67	-0.66	-0.26	0.87	-0.35	0.23	0.11	0.77	0.56	0.00	-0.43
Axis %	40.7	27	13.1	8.7	38	25.3	18	37.6	25.4	17.7	9	36.8	25.4	15.8	10.3
Cum %	40.7	67.6	80.7	89.4	38	63.3	81.3	37.6	63.1	80.7	89.7	36.8	62.2	78	84

significance related to the scores of the first axis, which is formed primarily by photosynthetic pigments in these species. The three perennial species also showed significant variance for the scores of the second axis, which had K and P

contribution. In *C. fissilis*, there were no seasonal differences between the scores of the first two axes, which correspond to 74% of data variance; the scores of the third axis, however, showed variation during the study period.

TABLE III
One-way ANOVA (season) made with the scores of the PCA axes that had eigenvalues > 1 (Kaiser criterion). Legend: SS: sum of squares; DF: degrees of freedom; QM: mean square; F: F values and P: significance.

	SQ	GL	QM	F	P
<i>Nectandra lanceolata</i>					
Axis 1	10.14	3	3.37	5.48	0.009
Axis 2	12.01	3	4.00	8.03	0.002
Axis 3	3.90	3	1.30	1.29	0.31
Axis 4	1.04	3	0.34	0.29	0.83
<i>Matayba elaeagnoides</i>					
Axis 1	15.81	3	5.27	20.16	<0.001
Axis 2	11.04	3	3.68	6.58	0.004
Axis 3	4.58	3	1.53	1.58	0.23
<i>Cupania vernalis</i>					
Axis 1	8.39	3	2.80	3.85	0.029
Axis 2	14.59	3	4.86	14.37	<0.001
Axis 3	0.72	3	0.24	0.20	0.89
Axis 4	5.67	3	1.89	2.11	0.14
<i>Jacaranda micrantha</i>					
Axis 1	12.40	2	6.20	28.58	<0.001
Axis 2		Kruskal-Wallis t=9.5; p=0.008			
Axis 3	0.07	2	0.03	0.03	0.97
Axis 4		Kruskal-Wallis t=6.7; p=0.03			
<i>Cedrela fissilis</i>					
Axis 1	4.61	3	2.30	2.66	0.11
Axis 2	5.33	3	2.67	3.31	0.07
Axis 3	6.24	3	3.12	4.28	0.04

DISCUSSION

In general, the studied species showed high interspecific variation in foliar macronutrient concentration, indicating selective absorption from a common pool in the soil. Chlorophyll and carotenoid concentrations also varied significantly among species and seasons. The correlation between leaf pigments and Chl_a , Chl_b and Chl_{tot} with the first

axis, which explains most of the data variance, suggests that these parameters change throughout the year for all species. These results allow us to infer that seasonal and climatic variations have an impact on chlorophyll content, although such relation is not similar for all the studied species. Photosynthetic pigments are indicators of the level of plant acclimation to the environment, and for many species there is a consistent relationship

between pigment content and light (Minotta and Pinzaui 1996). In general, chlorophyll content decreases with increased irradiance, because when there is greater availability of photosynthetic active radiation, photosystems can operate at satisfactory levels for metabolism with less chlorophyll. On the other hand, low irradiance causes chlorophyll content and accessory pigments to increase so as to absorb more light energy and transfer it to reaction centers (Taiz and Zeiger 2013, Zhang et al. 2009). Skillman et al. (1996) observed that leaf chlorophyll content was considerably higher in summer for herbaceous species of deciduous forests. These results, seemingly disparate, may be attributed to metabolic differences between herbaceous and woody plants, as well as to less light availability in the herbaceous layer of deciduous forests in the northern summer, when trees are covered with leaves that prevent light from reaching the interior of the forest.

The balance between chlorophyll and carotenoids is related to plant adaptation to different light conditions, which, in this study, was reflected in the $Car_{tot}:Chl_{tot}$ ratio. In turn, the $Car_{tot}:Chl_{tot}$ ratio correlated with the first axis in all species except *C. fissilis*, in which it was correlated with the second axis. According to Rosevear et al. (2001), plants present significant interspecific variation in carotenoid concentration. In addition, as different units are increasingly used to express concentration, different study results should be interpreted with caution. For instance, sun leaves presented higher Car_{tot} than shade leaves when the calculation was based on leaf area; however, the contrary was shown based on dry leaf weight (Valladares et al. 2000).

PCA results showed that the nutritional needs of species on the FED/FOM interface differ, showing strong interspecific variation of nutrient contribution to axis formation, which is interpreted as a reflection of different strategies for acquisition, use and conservation of nutrients by forest species.

Interspecific variation in leaf nutrient content has been reported in other studies and interpreted as one of the factors that influences distribution and abundance of forest species, according to their distinct nutritional requirements (Herrera and Finegan 1997, Masunaga et al. 1998).

The leaf nutrient content of the analyzed species in this study was usually similar to or higher than that found in other forest studies (Vitousek and Sanford Jr 1986, Herrera and Finegan 1997, Boeger et al. 2005, Wu et al. 2007). These data suggest that all studied species have the ability to acquire vital elements from the soil, regardless of their phenological pattern (deciduous or perennial). In deciduous species occurring in strongly seasonal environments, leaf senescence generally involves moving nutrients from the leaves to other parts of the plant (Buchanan-Wollaston 1997). However, plants from mesic environments may respond to the changing seasons by dropping their leaves without undergoing drastic physiological alterations, as the main environmental factor that induces leaf senescence is photoperiod change (Fracheboud et al. 2009, Keskitalo et al. 2005).

Previous studies have shown that plants grown in fertile soils or in the later stages of succession have high nutrient concentration in their green and photosynthetic active leaves, and reduced efficiency of nutrient retranslocation from their senescent leaves (Kobe et al. 2005, Martínez-Sánchez 2005, Yan et al. 2006). It should be noted that the nutritional status of leaves doesn't always correlate with that of the soil, demonstrating that plants with very distinct strategies for acquisition and use of nutrients may coexist.

Nitrogen content was high in the leaves of all species and presented little variation among seasons, which might be interpreted as a reflection of high soil nutrient availability, as argued by Wright et al. (2001), who observed a positive correlation between fertile soils and leaf N. However, N didn't contribute to the formation of the first PCA

axis in four out of five species, nor did it show correlation with leaf pigments (except Chl_a in *C. fissilis*). Because N is an element associated with photosynthetic apparatus components, particularly chlorophyll and proteins, this fraction of leaf N tends to be relatively constant for all species. Positive correlations between leaf N and chlorophyll have been described, but these relations may vary quite significantly among species, depending on soil availability, efficient use of nitrogen, position of leaf in the canopy and N allocation to different leaf components (Evans 1989, Kull and Niinemets 1998, Hikosaka 2004). The contribution of the other elements in axis formation showed a strong specific characteristic, reflecting once again that, in natural environments, coexisting species may use different metabolic strategies of resource acquisition and use.

In the subtropical forest of southern Brazil, the events most likely to cause temperature and water stress are circumstantial, occurring occasionally throughout the colder and warmer season, respectively (Leite and Klein 1990). Therefore, trees in these forests are not subjected to continuous stress – such as occurs in higher regions, where freezing temperatures are frequent throughout winter; or in dry seasonal forests, which experience a severe period of water stress to which plants respond by altering their metabolic processes. It could therefore be inferred that the variations observed in the plants on the FED/FOM interface are less evident than those of strongly seasonal environments and result in two distinct climate periods, as shown by the PCA graphic representation.

In summary, our results show that there is interspecific variation in the content of leaf photosynthetic pigments and nutrients in tree species occurring on the FED/FOM interface of the subtropical forest in southern Brazil, and this variation is more conspicuous for photosynthetic pigments than leaf nutrients. Of the twelve variables evaluated, photosynthetic pigments, Chl_a , Chl_b and

Chl_{tot} were particularly important in all species, correlating with the first PCA axis, which explains most of the data and shows that the synchronized changes are not as pronounced as those described in strongly seasonal ecosystems. Leaf pigments are indicators of tree acclimation to seasonal changes.

On the other hand, the contribution of the other variables to axis formation was species-specific that, in terms of leaf nutrients, can be partially attributed to their availability in the soil. This available soil nutrients does not impose limitations to nutrient acquisition and contributes for leaf nutrient concentration to be high and relatively constant throughout the year.

Different strategies for acquisition and use of resources are fundamental for these species to coexist in the forest environment. Our results are important for understanding the nutritional dynamics of subtropical forest ecosystems, considering the different requirements between species, and thereby generate information that will help define strategies for conservation and management of representative fragments of this vegetation.

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RESUMO

O objetivo deste estudo foi analisar a variação sazonal no conteúdo foliar de nutrientes e pigmentos em cinco espécies de árvores, sendo três perenes (*Cupania vernalis*, *Matayba elaeagnoides* e *Nectandra lanceolata*)

e duas decíduas (*Cedrela fissilis* e *Jacaranda micrantha*) – em um ecótono entre a Floresta Estacional Decidual e a Floresta Ombrófila Mista em Santa Catarina, Brasil. As amostras de folhas foram coletadas nas quatro estações do ano para determinar o conteúdo de macronutrientes (N, K, P, Mg, Ca, S) e pigmentos fotossintéticos (Chl_a , Chl_b , Chl_{tot} , Car_{tot} , $\text{Chl}_a:\text{Chl}_b$ e $\text{Car}_{\text{tot}}:\text{Chl}_{\text{tot}}$). A análise de componentes principais revelou que os pigmentos foliares contribuíram na formação do primeiro eixo, o que explica a maior parte da variação dos dados, para todas as espécies, enquanto a contribuição dos nutrientes mostrou forte variação interespecífica. Estes resultados indicam que as espécies estudadas apresentam diferentes estratégias para aquisição e uso dos recursos minerais e aclimatação à luminosidade, as quais são fundamentais para sua coexistência no ambiente florestal.

Palavras-chave: clorofila, floresta com Araucária, Floresta Decidual, macronutrientes.

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