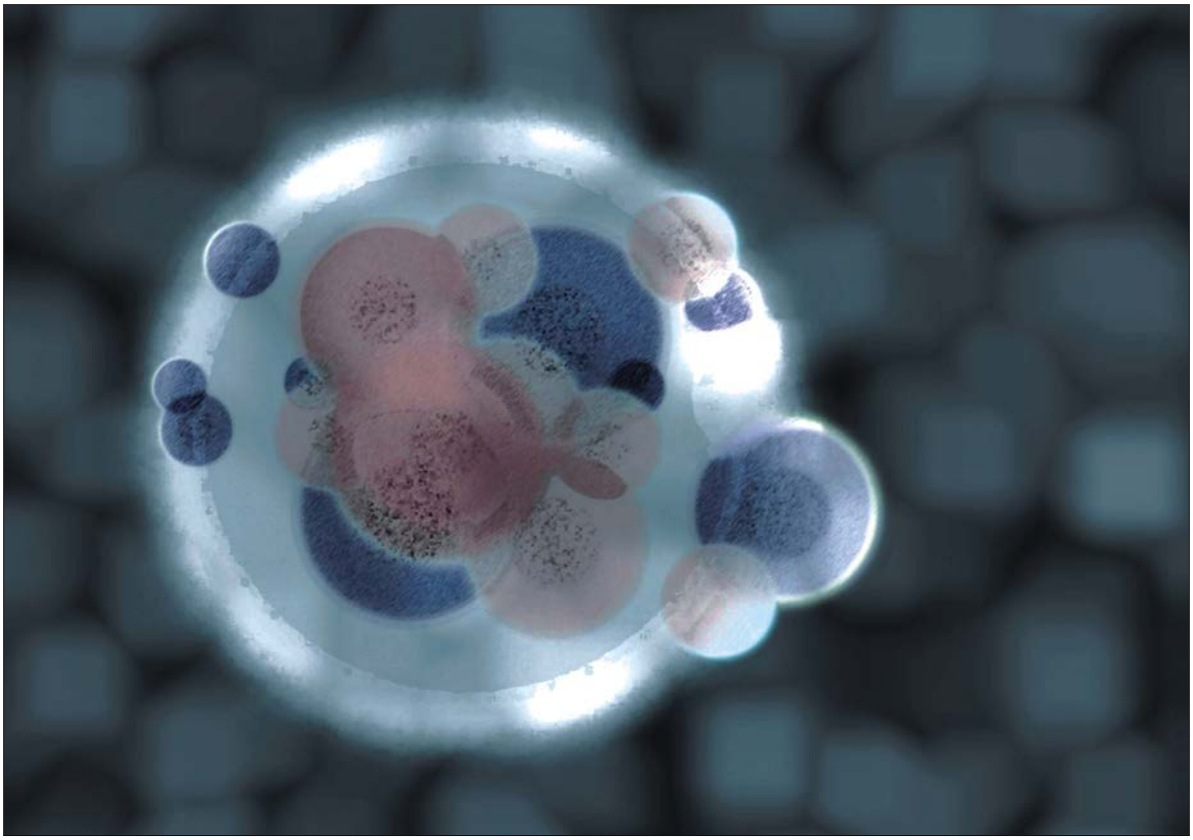

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Seasonal Trends of Chlorophylls a and b and Carotenoids in Native Trees and Shrubs of Northeastern Mexico

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Abstract: During two consecutive years, chlorophylls a and b and carotenoids contents were determined, seasonally, in foliar tissue of native Trees (T) and Shrubs (S) from Northeastern Mexico such as *Acacia rigidula* (S), *Bumelia celastrina* (T), *Castela texana* (S), *Celtis pallida* (S), *Croton cortesianus* (S), *Forestiera angustifolia* (S), *Karwinskia humboldtiana* (S), *Lantana macropoda* (S), *Leucophyllum frutescens* (S), *Prosopis laevigata* (T), *Zanthoxylum fagara* (T). Pigment determinations were carried out in a region of the State of Nuevo León, México at three county (Los Ramones, China and Linares) sites, which are grouped under a similar climatic pattern. All pigments were significantly different between years, seasons and between plants within years and seasons, except year×plant interaction for carotenoids at China site. All plants had marginal higher chlorophyll a content at Linares (0.79 mg g^{-1} f.wt.) than China (0.71) or Los Ramones (0.66) site. Chlorophyll b content followed a similar trend as chlorophyll a (0.29, 0.25 and 0.23 mg g^{-1} f.wt., respectively). Marginal differences in carotenoids content, in all plants, were found among sites being the 0.20 mg carotenoids g^{-1} f.wt. Yearly and seasonal variations in plant pigments might have been related to seasonal water deficits, excessive irradiance levels during summer and extreme low temperatures in winter that could have affected leaf development and senescence.

Key words: Chlorophylls a and b, carotenoids

INTRODUCTION

Chlorophylls and carotenoids are essential pigments of higher plant assimilatory tissues. Moreover, they play important roles in photosynthesis capturing light energy which is converted into chemical energy (Young and Britton, 1993). Chlorophylls are capable of channeling the radiant energy of sunlight into the chemical energy of organic carbon compounds through the process of photosynthesis in the cell (Sims and Gamon, 2002).

Carotenoids are a class of natural fat-soluble pigments found mainly in plants, algae and photosynthetic bacteria, where they also play a critical role in the photosynthetic process. In some non-photosynthetic bacteria, yeasts and molds, they may carry out a protective function against damage by light and oxygen (Biswal, 1995; Gitelson *et al*., 2002). Although animals appear to be unable of synthesizing carotenoids, many incorporate carotenoids from their diet. Within animals, carotenoids provide bright coloration, serve as antioxidants and can be a source for vitamin A activity (Britton, 1995). Moreover, carotenoids develop important functions in plant reproduction, through their role in attracting pollinators and in seed dispersal (Yeum and Russell, 2002).

Native shrubs and trees that grow in the semiarid regions of Northeastern Mexico are important feed resources for range ruminants and white-tiled deer (Ramirez, 1999). They also provide high quality fuelwood and timber for fencing and construction and are widely distributed in combination with other species (Reid *et al*., 1990; Fulbright *et al*., 1991); however, are affected by climatic conditions and probably causing differences in the concentrations of photosynthetic pigments (chlorophyll a and b and carotenoids) when considering effects in space (sites) and weather (seasonality). To our knowledge, this is the first study of pigment profile estimation in native woody species and leaf structures growing in Northeastern Mexico. Thus, the study was carried out with the aim of quantify and compare,

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seasonally during two consecutive years, the content of photosynthetic pigments in trees and shrubs that grow under a similar climatic pattern in Northeastern Mexico.

MATERIALS AND METHODS

Study area: This study was carried out at three sampling sites situated in the state of Nuevo Leon, Mexico. The first site was located at El Abuelo Ranch in Los Ramones county (25° 40' N; 99° 27' W) with an elevation of 200 m. The climate is semiarid with warm summer. Annual mean air temperature is about 22°C. Average annual rainfall is approximately 700 mm. The second site was located at Zaragoza ranch in China county (25° 31' N and 99° 16' W). It has an elevation of 200 m. The climate is dry and warm throughout the year. Average total annual rainfall ranges from 400 to 600 mm with an annual mean air temperature of 22°C. The third site was located at the Experimental Station of Facultad de Ciencias Forestales, Universidad Autónoma de Nuevo León (24° 47' N; 99° 32' W; elevation of 350 m) located at Linares county. The climate is subtropical and semiarid with warm summer. Monthly mean air temperature ranges from 14.7°C in January to 22.3°C in August, although daily high temperatures of 45°C are common during summer. Average annual precipitation is about 805 mm with a bimodal distribution. In this study, registered seasonal mean air temperatures (°C) and rainfall (mm) are shown in Table 1. In general, the three sites are grouped under a similar climatic pattern with peak rainfall during May, June and September. The main type of vegetation is known as the Tamaulipan Thornscrub or Subtropical Thornscrub Woodlands (SPP-INEGI, 1986). The dominant soils are deep, dark-gray, lime-gray, lime-clay Vertisols, with montmorillonite, which shrink and swell noticeably in response to changes in soil moisture content.

Plant material and tissue sampling procedures: Plant species such as *Acacia rigidula* Benth. (Fabaceae, shrub), *Bumelia celastrina* H. B. K. (Sapotaceae; tree), *Castela texana* Torr and Gray (Verbenaceae; shrub), *Celtis pallida* Torr. (Ulmaceae; shrub), *Croton cortesianus* Kunt. (Euphorbiaceae; shrub), *Forestiera angustifolia* Torr. (Oleaceae; tree), *Karwinskia humboldtiana* Roem et Schult. (Rhamnaceae; shrub), *Lantana macropoda* Torr., (Simaroubaceae; shrub), *Leucophyllum frutescens* Berl. (Scrophulariaceae; shrub), *Prosopis laevigata* (Willd) M.C. Johnst. (Fabaceae; tree) and *Zanthoxylum fagara* L. (Rutaceae; tree), that are the most representative of the native vegetation of the Northeastern Mexico and the subtropical savanna ecosystems of southern Texas, USA (Reid *et al*., 1990), were selected for pigment analysis.

Terminal shoots with fully expanded leaves from different plants per species were randomly chosen from a 50×50 m representative and undisturbed thornscrub plot located in each site. Collections were undertaken, seasonally during two consecutive years: in summer, 2004 (August 28); fall, 2004 (November 28); winter, 2005 (February 28); spring, 2005 (May 28); summer, 2005 (August 28); fall, 2005 (November 28); winter, 2006 (February 28) and spring, 2006 (May 28). Shoots were excised and sampled from the middle side of four plants (replications) of each species. Leaves were placed into plastic bags and stored on ice under dark condition using a chest insulator. Cooled samples were then transported to laboratory for pigment analyses which were performed within 12 h after collections.

Determination of chlorophylls and carotenoids: Quadruplicate leaf tissue samples (1.0 g of fresh weight) of each plant species were used for analyses. The chlorophylls a and b and carotenoids were extracted in 80% (v/v) aqueous acetone and vacuum filtered through a Whatman No. 1 filter paper. Pigment measurements were quantified spectrophotometrically using a Perkin-Elmer Spectrophotometer (Model Lamda 1A). Absorbance of chlorophylls a and b and carotenoids extracts were determined at wavelengths of 663, 645 and 470 nm, respectively. Concentrations (mg g^{-1} f.wt.) of pigments were calculated by equations of Lichtenthaler and Wellburn (1983).

Table 1: Seasonal mean air temperatures (°C) and rainfall (mm) at research sites in Northeastern Mexico

	Site					
	Los Ramones		China		Linares	
Season	Temperature	Rainfall	Temperature	Rainfall	Temperature	Rainfall
Summer 2004	22.8	294	23.6	457	23.6	447
Fall 2004	17.7	96	19.4	31	22.1	95
Winter 2005	10.1	98	11.3	74	13.4	133
Spring 2005	16.5	96	18.2	140	20.5	94
Summer 2005	23.1	322	24.5	486	23.4	465
Fall 2005	17.2	194	19.5	101	19.0	316
Winter 2006	8.7	4	11.5	14	9.7	9
Spring 2006	18.8	158	19.9	150	19.6	79

Statistical analyses: Data of chlorophylls and carotenoids were statistically analyzed using one-way analysis of variance with a multi-factorial arrangement being years (2), seasons (4), plant species (11) the factors. Where the F-test was significant ($p<0.05$), differences were validated using the Tukey´s honestly significant difference. Assumptions of normality of data were tested using the Kolmogorov-Smirnov test (Steel and Torrie, 1980). To compare pigment content between Fabaceae and non Fabaceae and shrubs versus trees plant species, the t-test was performed (Steel and Torrie, 1980). Simple correlation analyses between pigment content and mean temperature and cumulative rainfall registered at each season was also computed. In addition, climate variables were used as covariates to adjust pigment data (Steel and Torrie, 1980). All applied statistical methods were computed using the SPSS package (Version 9).

RESULTS

Chlorophyll a content was significantly different between years, seasons and between plants within years and seasons (Table 2). During the first year, at Los Ramones site, chlorophyll a content in shrub *A. rigidula* (summer 2004) was lower (0.3 mg g^{-1} f.wt.) and in the tree *P. laevigata* (spring 2005; Table 3) was higher (1.1 mg g^{-1} f.wt.). Conversely, in second year, lower values (0.3 mg g^{-1} f.wt.) were found in *L. macropoda* in winter 2006 and higher (0.9 mg g^{-1} f.wt.) in *C. pallida* during summer 2005. At China site (Table 3) *C. cortesianus* (fall 2004) and *L. macropoda* (spring 2005) achieved lower (0.4) and higher (1.8) chlorophyll a content, respectively. During the second year, *C. cortesianus* (winter 2006) and *A. rigidula* (summer 2005) acquired lower (0.3) and higher (1.2) content, respectively. In Linares (Table 3), during the first year, higher (0.3) and lower (1.2) contents were registered in *P. laevigata* during fall 2004 and *B. celastrina* in winter 2005, respectively. However, during the second year, *L. macropoda* and *P. laevigata* resulted with lower (0.4) and higher (1.4) contents of chlorophyll a during winter 2006 and spring 2006, respectively. At Los Ramones and China sites, chlorophyll a content, in all plants, resulted higher in the first year than the second year. Conversely, at Linares, the second year was higher. It appears, that all plants had marginal higher chlorophyll a content at Linares (overall mean = 0.79 mg g^{-1} f.wt.) than China (0.71) or Los Ramones (0.66).

It seems that during fall (overall mean = 0.73 mg g^{-1} f.wt.) and winter (0.72) chlorophyll a was higher than summer (0.68) or spring (0.69). In general, it appears that Fabaceae plants showed higher (0.74 mg g^{-1} f.wt.) contents of chlorophyll a than non Fabaceae species (0.68; Table 4). In addition, trees were higher (0.76 mg g^{-1} f.wt.) than shrubs (0.68; Table 5).

Table 2: Calculated mean square values from the statistical analysis corresponding to data collected between summer 2004 and spring 2006 of eleven plant species at Northeastern Mexico

		Chlorophyll a			Chlorophyll b			Carotenoids		
Sites	Sources of variation	MS	F-value	Sig	MS	F-value	Sig	MS	F-value	Sig
Los Ramones	Years	0.30	25	***	0.20	152	***	0.02	21	***
	Seasons	0.10	6	***	0.10	63	***	0.10	96	***
	Plant Species	0.10	11	***	0.01	5	***	0.03	34	***
	Y×S	0.30	28	***	0.10	35	***	0.02	20	***
	Y×PS	0.04	4	***	0.01	5	***	0.001	1	**
	S×PS	0.10	7	***	0.01	8	***	0.01	5	***
	Y×S×PS	0.10	8	***	0.01	4	***	0.01	5	***
	Error	0.01			0.002			0.001		
China	Years	0.20	15	***	0.20	53	***	0.01	9	***
	Seasons	0.03	3	*	0.20	61	***	0.10	79	***
	Plant Species	0.40	33	***	0.10	14	***	0.10	108	***
	Y×S	0.10	11	***	0.02	8	***	0.01	22	***
	Y×PS	0.10	10	***	0.01	5	***	0.01	8	ns
	S×PS	0.10	8	***	0.01	3	***	0.01	11	***
	Y×S×PS	0.10	11	***	0.01	4	***	0.01	6	***
	Error	0.01			0.003			0.001		
Linares	Year	0.60	38	***	0.02	6	**	0.04	31	***
	Season	0.10	6	***	0.20	51	***	0.10	70	***
	Plant Species	0.20	13	***	0.10	18	***	0.04	36	***
	Y×S	1.00	47	***	0.10	44	***	0.04	32	***
	Y×PS	0.10	9	***	0.01	4	***	0.01	5	***
	S×PS	0.10	9	***	0.02	7	***	0.01	6	***
	Y×S×PS	0.10	6	***	0.02	7	***	0.01	4	***
	Error	0.01			0.003			0.001		

MS = Mean Square; Y = Years; S = Seasons PS = Plant Species; Sig = Significant level; *: ($p<0.05$); **: ($p<0.01$); ***: ($p<0.001$); ns = not significant

Table 3: Seasonal contents (mg g^{-1} f.wt.) of chlorophyll a at Los Ramones, China and Linares sites in eleven native trees and shrubs

			Plant species													
Site	Year	Season	*Cro. cor.*	*Leu. fru.*	*Kar. hum.*	*Aca. rig.*	*Bum. cel.*	*Pro. lae.*	*Cel. pal.*	*Zan. fag.*	*For. ang.*	*Lan. mac.*	*Cas. ere.*	Mean	SE	p-value
Los Ramones	1	Sum-04	0.55	0.78	0.71	0.32	0.69	0.42	0.62	0.71	0.49	0.64	0.63	0.60	0.01	<0.001
		Fall-04	0.54	0.82	0.85	0.77	0.74	0.66	0.62	0.93	0.44	0.52	0.52	0.67	0.02	<0.001
		Win-05	0.60	0.69	0.57	0.91	0.96	0.58	0.88	0.80	0.87	0.82	0.79	0.78	0.02	0.002
		Spr-05	0.83	0.58	0.73	0.73	0.85	1.09	0.58	0.68	0.58	0.93	0.50	0.73	0.02	<0.001
		Mean	0.64	0.71	0.71	0.70	0.82	0.68	0.68	0.78	0.61	0.74	0.61	0.70		
	2	Sum-05	0.63	0.48	0.69	0.63	0.85	0.57	0.89	0.81	0.55	0.63	0.48	0.66	0.02	<0.001
		Fall-05	0.55	0.55	0.74	0.88	0.85	0.82	0.79	0.65	0.50	0.76	0.77	0.71	0.01	<0.001
		Win-06	0.53	0.47	0.78	0.84	0.71	0.63	0.57	0.48	0.48	0.28	0.56	0.58	0.02	<0.001
		Spr-06	0.64	0.53	0.54	0.47	0.65	0.65	0.67	0.55	0.51	0.77	0.51	0.59	0.01	0.002
		Mean	0.59	0.51	0.69	0.70	0.76	0.67	0.73	0.62	0.51	0.61	0.58	0.63		
China	1	Sum-04	0.52	0.78	0.65	0.45	0.80	0.95	0.64	0.67	0.56	0.80	0.39	0.67	0.01	<0.001
		Fall-04	0.35	0.80	0.89	1.00	0.67	0.79	0.64	1.08	0.74	0.79	0.46	0.74	0.02	<0.001
		Win-05	0.94	0.81	0.76	0.94	0.65	0.70	0.84	0.81	0.63	0.82	0.58	0.77	0.02	0.002
		Spr-05	0.58	0.78	0.63	0.76	0.74	1.09	0.46	0.42	0.69	1.79	0.44	0.75	0.01	<0.001
		Mean	0.58	0.79	0.72	0.82	0.71	0.88	0.66	0.77	0.66	1.01	0.47	0.73		
	2	Sum-05	0.43	0.67	0.65	1.19	0.70	0.79	0.74	0.69	0.91	0.66	0.45	0.71	0.02	<0.001
		Fall-05	0.41	0.71	0.51	1.01	0.86	0.72	0.64	0.83	0.57	0.96	0.68	0.72	0.02	<0.001
		Win-06	0.30	0.66	0.90	0.68	0.92	0.61	0.34	0.59	0.76	0.51	0.59	0.62	0.01	<0.001
		Spr-06	0.54	0.81	0.57	0.60	0.77	0.75	0.57	0.88	0.88	0.72	0.39	0.68	0.02	<0.001
		Mean	0.42	0.71	0.66	0.87	0.81	0.72	0.57	0.75	0.78	0.71	0.53	0.68		
Linares	1	Sum-04	0.57	0.92	0.63	0.62	1.02	0.60	0.57	0.46	0.35	0.72	0.48	0.62	0.03	0.001
		Fall-04	0.45	0.66	1.01	0.69	0.92	0.25	0.60	0.52	0.51	0.55	0.55	0.60	0.03	<0.001
		Win-05	0.84	0.90	0.98	0.53	1.19	0.72	0.86	0.69	0.77	1.03	1.02	0.86	0.02	<0.001
		Spr-05	0.61	0.83	0.71	0.91	0.45	0.66	0.55	0.49	0.59	0.86	0.62	0.66	0.02	<0.001
		Mean	0.62	0.82	0.83	0.67	0.92	0.57	0.65	0.54	0.57	0.79	0.64	0.69		
	2	Sum-05	0.67	0.67	0.76	0.82	1.24	1.06	0.99	0.67	0.85	0.65	0.53	0.81	0.02	<0.001
		Fall-05	0.77	0.93	1.24	0.78	0.98	0.61	1.07	1.17	0.68	1.21	0.56	0.91	0.02	<0.001
		Win-06	0.50	0.95	0.87	0.76	0.69	0.82	0.63	0.59	0.55	0.48	0.72	0.69	0.02	<0.001
		Spr-06	0.84	0.56	0.48	0.68	0.84	1.40	0.63	0.74	0.74	0.57	0.54	0.73	0.02	<0.001
		Mean	0.70	0.78	0.84	0.76	0.94	0.97	0.83	0.79	0.71	0.73	0.59	0.78		

Data are means from four independent measurements per plant species. *Croton cortesianus* (*Cro. cor.*), *Leucophyllum frutesceus* (*Leu. fru.*), *Karwiuskia humboldtiana* (*Kar. hum.*), *Acacia rigidula* (*Aca. rig.*), *Bumelia celastrina* (*Bum. cel.*), *Prosopis laevigata* (*Pro. lae.*), *Celtis pallida* (*Cel. pal.*), *Zanthoxyllum fagara* (*Zan. fag.*), *Forestiera angustifolia* (*For. ang.*), *Lantana macropoda* (*Lan. mac.*) and *Castela erecta* (*Cas. ere.*). Sum-04 = Summer 2004; Win-05 = Winter 2005; Spr-05 = Spring 2005; Sum-05 = Summer 2005; Win-06 = Winter 2006; Spr-06 = Spring 2006. Means, standard errors (SE) and p-values are provided

Chlorophyll b content was significantly different between years, seasons and between plants within years and seasons (Table 2). During the first year, at Los Ramones site (Table 6), chlorophyll b content in the shrub *A. rigidula* (summer) was lower (0.2 mg g^{-1} f.wt.) and in *L. frutescens* (summer) was higher (0.4). Moreover, in second year *A. rigidula* (winter) was lower (0.03) and *C. cortesianus* (spring) was higher (0.4). At China (Table 6) lower values (0.1) were detected in *C. texana* in spring and higher (0.6) in *L. macropoda* in spring too. During the second year, chlorophyll b content followed a similar pattern as the first year. At Linares (Table 6), during the first year, lower (0.1) and higher (0.6) values were observed in *F. angustifolia* and *L. frutescens* during summer 2004, respectively. Conversely, in the second year, *C. pallida* in winter 2005 was higher (0.1) and *K. humboldtiana* in autumn was lower (0.6). In all plants, annual and seasonal contents of chlorophyll b followed a similar trend as chlorophyll a; Linares was marginal high (0.29 mg g^{-1} f.wt.) than Los Ramones (0.25) or China (0.23).

It seems that during spring, summer and fall chlorophyll b (0.28 mg g^{-1} f.wt.) resulted higher than in winter (0.19). In general, Fabaceae species showed very similar (23 mg g^{-1} f.wt.) chlorophyll b content than non Fabaceae (0.26; Table 4). In addition, shrubs were very similar (0.26 mg g^{-1} f.wt.) than trees (0.24; Table 5).

With exception of interaction year*plant species at China site, carotenoids content was significantly different between years, seasons and between plants within years and seasons (Table 2). At Los Ramones site (Table 7), during the first year, lower (0.1 mg g^{-1} f.wt.) and higher (0.3 mg g^{-1} f.wt.) values were detected in *P. laevigata* (summer) and *K. humboldtiana* (fall), respectively. In second year, lower (0.1) and higher (0.4) values were observed in *A. rigidula* (spring) and *K. humboldtiana* (winter), respectively. During first year, at China (Table 7), *C. texana* (summer) and *K. humboldtiana* (winter) were lower (0.1) and higher (0.5), respectively. Moreover, in second year, *C. texana* (spring) was lower (0.03) and *K. humboldtiana* (winter) higher (0.5). In Linares

Table 4: Seasonal contents (mg g^{-1} f.wt.) of chlorophyll a, chlorophyll b and carotenoids at Los Ramones, China and Linares sites between native trees and shrubs belonging to the Fabaceae and non Fabaceae family

			Chlorophyll a			Chlorophyll b			Carotenoids		
Site	Year	Season	Fabaceae	Non Fabaceae	p-value	Fabaceae	Non Fabaceae	p-value	Fabaceae	Non Fabaceae	p-value
Los Ramones	1	Sum-04	0.37	0.65	<0.001	0.26	0.33	0.006	0.09	0.17	<0.001
		Fall-04	0.71	0.66	0.264	0.26	0.24	0.353	0.24	0.22	0.197
		Win-05	0.74	0.79	0.531	0.24	0.24	0.642	0.21	0.23	0.143
		Spr-05	0.89	0.70	<0.001	0.24	0.27	0.126	0.20	0.19	0.824
	2	Sum-05	0.60	0.67	0.136	0.20	0.23	0.054	0.17	0.16	0.316
		Fall-05	0.85	0.68	<0.001	0.23	0.24	0.365	0.23	0.21	0.026
		Win-06	0.73	0.54	<0.001	0.12	0.12	0.531	0.24	0.23	0.158
		Spr-06	0.56	0.59	0.256	0.24	0.25	0.600	0.11	0.14	0.012
China	1	Sum-04	0.74	0.65	0.120	0.25	0.32	0.002	0.16	0.17	0.046
		Fall-04	0.90	0.71	0.009	0.29	0.29	0.940	0.25	0.20	0.001
		Win-05	0.84	0.75	0.215	0.22	0.22	0.843	0.23	0.24	0.442
		Spr-05	0.93	0.71	<0.001	0.24	0.29	0.018	0.22	0.20	0.173
	2	Sum-05	0.99	0.65	<0.001	0.22	0.25	0.109	0.22	0.17	<0.001
		Fall-05	0.87	0.68	<0.001	0.24	0.26	0.104	0.25	0.21	0.001
		Win-06	0.64	0.62	0.562	0.07	0.13	<0.001	0.23	0.24	0.765
		Spr-06	0.68	0.68	0.957	0.22	0.29	0.006	0.17	0.14	0.024
Linares	1	Sum-04	0.61	0.63	0.683	0.19	0.32	<0.001	0.17	0.14	0.014
		Fall-04	0.47	0.63	0.021	0.28	0.27	0.872	0.20	0.19	0.823
		Win-05	0.62	0.92	<0.001	0.22	0.28	0.001	0.17	0.26	<0.001
		Spr-05	0.79	0.64	0.004	0.29	0.30	0.739	0.23	0.18	0.001
	2	Sum-05	0.95	0.78	0.001	0.25	0.26	0.543	0.20	0.18	0.028
		Fall-05	0.69	0.96	<0.001	0.23	0.39	<0.001	0.27	0.27	0.867
		Win-06	0.79	0.67	0.023	0.19	0.15	0.022	0.24	0.22	0.209
		Spr-06	1.04	0.66	<0.001	0.31	0.29	0.125	0.21	0.17	0.061

Fabaceae plant species: *Acacia rigidula* and *Prosopis laevigata*. Non Fabaceae plant species: *Croton cortesianus*, *Leucophyllum frutescens*, *Karwinskia humboldtiana*, *Bumelia celastrina*, *Celtis pallida*, *Zanthoxyllum fagara*, *Forestiera angustifolia*, *Lantana macropoda* and *Castela erecta*. Sum-04 = Summer 2004; Win-05 = Winter 2005; Spr-05 = Spring 2005; Sum-05 = Summer 2005; Win-06 = Winter 2006; Spr-06 = Spring 2006. Mean and p-values of the t-test are provided

Table 5: Seasonal contents (mg g^{-1} f.wt.) of chlorophyll a, chlorophyll b and carotenoids at Los Ramones, China and Linares sites between native plant species grouped as shrubs and trees

			Chlorophyll a			Chlorophyll b			Carotenoids		
Site	Year	Season	Shrubs	Trees	p-value	Shrubs	Trees	p-value	Shrubs	Trees	p-value
Los Ramones	1	Sum-04	0.59	0.60	0.611	0.31	0.34	0.076	0.16	0.15	0.440
		Fall-04	0.63	0.76	0.001	0.25	0.24	0.548	0.21	0.23	0.235
		Win-05	0.78	0.77	0.810	0.24	0.24	0.657	0.22	0.23	0.777
		Spr-05	0.68	0.87	<0.001	0.25	0.29	0.021	0.19	0.21	0.174
	2	Sum-05	0.62	0.74	0.005	0.22	0.24	0.035	0.16	0.17	0.279
		Fall-05	0.69	0.77	0.018	0.24	0.23	0.269	0.21	0.21	0.912
		Win-06	0.56	0.61	0.279	0.14	0.08	<0.001	0.22	0.27	<0.001
		Spr-06	0.58	0.61	0.259	0.27	0.20	<0.001	0.13	0.13	0.857
China	1	Sum-04	0.61	0.81	<0.001	0.33	0.26	0.001	0.17	0.19	0.045
		Fall-04	0.70	0.85	0.023	0.28	0.32	0.338	0.20	0.22	0.050
		Win-05	0.79	0.72	0.108	0.23	0.18	<0.001	0.25	0.21	0.004
		Spr-05	0.75	0.75	0.503	0.29	0.24	0.001	0.21	0.19	0.165
	2	Sum-05	0.70	0.73	0.762	0.26	0.21	0.002	0.18	0.19	0.519
		Fall-05	0.69	0.80	0.005	0.25	0.27	0.216	0.21	0.23	0.018
		Win-06	0.59	0.71	0.001	0.13	0.11	0.061	0.23	0.25	0.132
		Spr-06	0.63	0.80	<0.001	0.28	0.27	0.697	0.14	0.18	0.001
Linares	1	Sum-04	0.61	0.67	0.156	0.32	0.24	0.009	0.14	0.17	0.042
		Fall-04	0.61	0.56	0.305	0.29	0.23	0.061	0.19	0.20	0.408
		Win-05	0.86	0.87	0.998	0.27	0.26	0.121	0.25	0.23	0.075
		Spr-05	0.71	0.54	<0.001	0.30	0.29	0.682	0.20	0.16	0.011
	2	Sum-05	0.74	0.99	<0.001	0.25	0.30	0.012	0.18	0.22	<0.001
		Fall-05	0.91	0.92	0.830	0.37	0.35	0.247	0.27	0.28	0.380
		Win-06	0.68	0.70	0.686	0.17	0.13	0.022	0.21	0.24	0.067
		Spr-06	0.63	0.99	<0.001	0.27	0.37	<0.001	0.16	0.23	0.001

Shrub plant species: *Acacia rigidula*, *Croton cortesianns*, *Leucophyllum frutescens*, *Karwinskia humboldtiana*, *Celtis pallida*, *Forestiera angustifolia*, *Lantana macropoda* and *Castela erecta*. Tree plant species: *Bumelia celastrina*, *Prosopis laevigata* and *Zanthoxyllum fagara*. Sum-04 = Summer 2004; Win-05 = Winter 2005; Spr-05 = Spring 2005; Sum-05 = Summer 2005; Win-06 = Winter 2006; Spr-06 = Spring 2006. Mean and p-values of the t-test are provided

Table 6: Seasonal contents (mg g^{-1} f.wt.) of chlorophyll b at Los Ramones, China and Linares sites in eleven native trees and shrubs

			Plant species													
Site	Year	Season	*Cro. cor.*	*Leu. fru.*	*Kar. hum.*	*Aca. rig.*	*Bum. cel.*	*Pro. lae.*	*Cel. pal.*	*Zan. fag.*	*For. ang.*	*Lan. mac.*	*Cas. ere.*	Mean	SE	p-value
Los Ramones	1	Sum-04	0.34	0.40	0.29	0.15	0.35	0.37	0.26	0.30	0.31	0.38	0.32	0.32	0.01	<0.001
		Fall-04	0.24	0.28	0.28	0.34	0.30	0.19	0.23	0.30	0.21	0.20	0.21	0.25	0.01	0.002
		Win-05	0.17	0.26	0.24	0.25	0.27	0.22	0.23	0.22	0.32	0.23	0.25	0.24	0.01	0.003
		Spr-05	0.30	0.22	0.29	0.22	0.27	0.26	0.19	0.33	0.22	0.34	0.23	0.26	0.01	<0.001
		Mean	0.26	0.29	0.28	0.24	0.28	0.26	0.23	0.29	0.27	0.28	0.25	0.26		
	2	Sum-05	0.23	0.21	0.22	0.19	0.26	0.22	0.28	0.24	0.19	0.20	0.20	0.22	0.01	0.008
		Fall-05	0.22	0.20	0.30	0.25	0.23	0.20	0.28	0.25	0.17	0.32	0.20	0.24	0.01	0.001
		Win-06	0.17	0.15	0.12	0.15	0.18	0.09	0.06	0.01	0.23	0.13	0.16	0.12	0.01	<0.001
		Spr-06	0.41	0.24	0.28	0.30	0.20	0.18	0.22	0.21	0.24	0.27	0.19	0.25	0.01	<0.001
		Mean	0.26	0.20	0.23	0.22	0.21	0.17	0.20	0.16	0.21	0.23	0.19	0.21		
China	1	Sum-04	0.27	0.46	0.42	0.25	0.28	0.25	0.28	0.25	0.36	0.43	0.18	0.31	0.01	<0.001
		Fall-04	0.23	0.31	0.31	0.31	0.28	0.27	0.35	0.41	0.28	0.33	0.16	0.29	0.02	0.266
		Win-05	0.25	0.24	0.29	0.24	0.17	0.19	0.30	0.18	0.16	0.23	0.16	0.22	0.01	<0.001
		Spr-05	0.33	0.26	0.32	0.26	0.26	0.23	0.22	0.22	0.25	0.59	0.15	0.28	0.01	<0.001
		Mean	0.27	0.31	0.33	0.27	0.25	0.23	0.29	0.27	0.26	0.38	0.16	0.27		
	2	Sum-05	0.32	0.28	0.24	0.26	0.20	0.19	0.28	0.24	0.29	0.22	0.16	0.24	0.01	<0.001
		Fall-05	0.26	0.26	0.22	0.31	0.31	0.16	0.23	0.34	0.21	0.33	0.21	0.26	0.01	<0.001
		Win-06	0.07	0.18	0.20	0.09	0.18	0.06	0.11	0.08	0.21	0.14	0.05	0.12	0.01	<0.001
		Spr-06	0.30	0.43	0.29	0.24	0.24	0.19	0.21	0.38	0.25	0.24	0.28	0.28	0.01	<0.001
		Mean	0.24	0.29	0.23	0.23	0.23	0.15	0.21	0.26	0.24	0.23	0.16	0.22		
Linares	1	Sum-04	0.40	0.64	0.30	0.24	0.40	0.15	0.36	0.19	0.14	0.31	0.21	0.30	0.01	<0.001
		Fall-04	0.31	0.17	0.34	0.36	0.21	0.19	0.34	0.27	0.18	0.36	0.23	0.28	0.01	0.016
		Win-05	0.25	0.29	0.35	0.25	0.37	0.19	0.26	0.20	0.21	0.30	0.29	0.27	0.01	<0.001
		Spr-05	0.28	0.45	0.33	0.28	0.30	0.30	0.22	0.27	0.27	0.35	0.23	0.30	0.01	0.002
		Mean	0.30	0.39	0.34	0.28	0.33	0.22	0.29	0.23	0.20	0.33	0.24	0.29		
	2	Sum-05	0.33	0.26	0.26	0.24	0.36	0.26	0.31	0.24	0.23	0.19	0.15	0.26	0.01	<0.001
		Fall-05	0.37	0.38	0.56	0.27	0.46	0.19	0.44	0.40	0.25	0.35	0.34	0.36	0.01	<0.001
		Win-06	0.14	0.34	0.19	0.18	0.10	0.20	0.07	0.09	0.10	0.19	0.12	0.16	0.01	<0.001
		Spr-06	0.32	0.21	0.28	0.24	0.38	0.39	0.35	0.35	0.29	0.27	0.19	0.30	0.01	<0.001
		Mean	0.29	0.30	0.32	0.23	0.33	0.26	0.29	0.27	0.22	0.25	0.20	0.27		

Data are means from four independent measurements per plant species. *Croton cortesianus* (*Cro. cor.*), *Leucophyllum frutesceus* (*Leu. fru.*), *Karwiuskia humboldtiana* (*Kar. hum.*), *Acacia rigidula* (*Aca. rig.*), *Bumelia celastrina* (*Bum. cel.*), *Prosopis laevigata* (*Pro. lae.*), *Celtis pallida* (*Cel. pal.*), *Zanthoxyllum fagara* (*Zan. fag.*), *Forestiera angustifolia* (*For. ang.*), *Lantana macropoda* (*Lan. mac.*) and *Castela erecta* (*Cas. ere.*). Sum-04 = Summer 2004; Win-05 = Winter 2005; Spr-05 = Spring 2005; Sum-05 = Summer 2005; Win-06 = Winter 2006; Spr-06 = Spring 2006. Means, Standard Errors (SE) and p-values are provided

Table 7: Seasonal contents (mg g^{-1} f.wt.) of carotenoids at Los Ramones, China and Linares sites in eleven native trees and shrubs

			Plant species													
Site	Year	Season	*Cro. cor.*	*Leu. fru.*	*Kar. hum.*	*Aca. rig.*	*Bum. cel.*	*Pro. lae.*	*Cel. pal.*	*Zan. fag.*	*For. ang.*	*Lan. mac.*	*Cas. ere.*	Mean	SE	p-value
Los Ramones	1	Sum-04	0.15	0.15	0.24	0.10	0.17	0.07	0.17	0.20	0.14	0.16	0.13	0.16	0.01	<0.001
		Fall-04	0.16	0.18	0.31	0.28	0.22	0.21	0.23	0.29	0.24	0.18	0.17	0.22	0.01	0.001
		Win-05	0.20	0.15	0.27	0.24	0.24	0.18	0.28	0.27	0.23	0.23	0.22	0.23	0.01	0.001
		Spr-05	0.20	0.16	0.30	0.17	0.19	0.23	0.17	0.20	0.18	0.21	0.13	0.20	0.01	<0.001
		Mean	0.18	0.16	0.28	0.20	0.21	0.18	0.22	0.24	0.20	0.20	0.16	0.20		
	2	Sum-05	0.16	0.11	0.23	0.22	0.18	0.12	0.21	0.20	0.13	0.12	0.11	0.16	0.01	<0.001
		Fall-05	0.19	0.15	0.23	0.27	0.21	0.18	0.20	0.24	0.17	0.26	0.19	0.21	0.01	<0.001
		Win-06	0.15	0.16	0.37	0.28	0.21	0.21	0.23	0.37	0.21	0.13	0.18	0.23	0.01	<0.001
		Spr-06	0.13	0.11	0.18	0.09	0.14	0.13	0.15	0.12	0.13	0.17	0.11	0.13	0.01	0.001
		Mean	0.16	0.13	0.25	0.21	0.18	0.16	0.20	0.24	0.16	0.17	0.15	0.18		
China	1	Sum-04	0.14	0.13	0.41	0.13	0.15	0.19	0.17	0.21	0.09	0.19	0.09	0.17	0.01	<0.001
		Fall-04	0.10	0.19	0.31	0.25	0.15	0.24	0.18	0.27	0.22	0.18	0.13	0.20	0.01	<0.001
		Win-05	0.25	0.21	0.46	0.25	0.18	0.21	0.23	0.24	0.23	0.21	0.16	0.24	0.01	<0.001
		Spr-05	0.15	0.15	0.30	0.21	0.18	0.23	0.19	0.17	0.20	0.36	0.11	0.20	0.01	<0.001
		Mean	0.16	0.17	0.37	0.21	0.16	0.22	0.20	0.22	0.19	0.23	0.12	0.21		
	2	Sum-05	0.10	0.14	0.25	0.25	0.16	0.19	0.21	0.20	0.20	0.17	0.14	0.18	0.01	<0.001
		Fall-05	0.11	0.18	0.28	0.27	0.21	0.22	0.22	0.26	0.18	0.23	0.17	0.21	0.01	<0.001
		Win-06	0.13	0.20	0.49	0.26	0.24	0.21	0.16	0.29	0.20	0.18	0.24	0.24	0.01	<0.001
		Spr-06	0.10	0.10	0.23	0.14	0.14	0.21	0.14	0.19	0.20	0.15	0.03	0.15	0.01	<0.001
		Mean	0.11	0.16	0.31	0.23	0.19	0.21	0.18	0.24	0.19	0.18	0.15	0.20		
Linares	1	Sum-04	0.03	0.15	0.18	0.21	0.21	0.14	0.12	0.14	0.12	0.19	0.11	0.15	0.01	<0.001
		Fall-04	0.12	0.23	0.28	0.20	0.24	0.19	0.21	0.18	0.18	0.17	0.12	0.19	0.01	0.001
		Win-05	0.22	0.24	0.36	0.15	0.30	0.19	0.26	0.20	0.25	0.25	0.25	0.25	0.01	<0.001
		Spr-05	0.16	0.16	0.28	0.25	0.10	0.21	0.17	0.18	0.18	0.21	0.16	0.19	0.01	<0.001
		Mean	0.14	0.20	0.28	0.20	0.21	0.18	0.19	0.18	0.19	0.21	0.16	0.19		

Table 7: Continued

			Plant species													
Site	Year	Season	*Cro. cor.*	*Leu. fru.*	*Kar. hum.*	*Aca. rig.*	*Bum. cel.*	*Pro. lae.*	*Cel. pal.*	*Zan. fag.*	*For. ang.*	*Lan. mac.*	*Cas. ere.*	Mean	SE	p-value
	2	Sum-05	0.14	0.13	0.24	0.19	0.26	0.22	0.22	0.17	0.20	0.16	0.13	0.19	0.01	<0.001
		Fall-05	0.21	0.22	0.51	0.29	0.28	0.25	0.29	0.31	0.22	0.23	0.20	0.27	0.01	<0.001
		Win-06	0.17	0.27	0.35	0.24	0.27	0.23	0.17	0.21	0.17	0.14	0.20	0.22	0.01	<0.001
		Spr-06	0.20	0.15	0.23	0.17	0.22	0.25	0.12	0.21	0.18	0.13	0.11	0.18	0.01	0.013
		Mean	0.18	0.19	0.32	0.22	0.26	0.24	0.20	0.23	0.19	0.16	0.16	0.21		

Data are means from four independent measurements per plant species. *Croton cortesianus* (*Cro. cor.*), *Leucophyllum frutesceus* (*Leu. fru.*), *Karwiuskia humboldtiana* (*Kar. hum.*), *Acacia rigidula* (*Aca. rig.*), *Bumelia celastrina* (*Bum. cel.*), *Prosopis laevigata* (*Pro. lae.*), *Celtis pallida* (*Cel. pal.*), *Zanthoxyllum fagara* (*Zan. fag.*), *Forestiera angustifolia* (*For. ang.*), *Lantana macropoda* (*Lan. mac.*) and *Castela erecta* (*Cas. ere.*). Sum-04 = Summer 2004; Win-05 = Winter 2005; Spr-05 = Spring 2005; Sum-05 = Summer 2005; Win-06 = Winter 2006; Spr-06 = Spring 2006. Means, Standard Errors (SE) and p-values are provided

(Table 7), during the first year, minimum (0.03) and maximum (0.4) concentrations were registered in *C. cortesianus* (summer) and *K. humboldtiana* (winter). During second year, *C. texana* (spring) was lower (0.1) and *K. humboldtiana* (fall) was higher (0.5). Low marginal differences were found in all plants among research sites being the overall mean of 0.20 mg carotenoids g^{-1} f.wt.

It appears that during fall (0.22 mg g^{-1} f.wt.) and winter (0.23) carotenoids was higher than summer (0.17) or spring (0.17). In general, it appears that Fabaceae and non Fabaceae species showed similar (0.20 mg g^{-1} f.wt.; Table 4) carotenoids content. In addition, shrubs resulted similar than trees (0.20; Table 5).

DISCUSSION

Chlorophylls and carotenoids absorb light energy and transfer it into the photosynthetic apparatus of leaves; therefore, determinations of leaf pigments content can provide a valuable tool to integrate and understand the physiological and biochemical function of leaves (Sims and Gamon, 2002). Results of this study suggest that chlorophylls a and b and carotenoids content of plant species varied between years, seasons and between plants within years and seasons. This finding confirm the importance to address research on these native plants, with ecological and forage potential value, in order to understand the function that, plant pigments, may play in ecosystem productivity and the influence of drought and extreme temperatures that prevails during winter and summer seasons in this region (González *et al*., 2000).

It has been established that productivity of higher plants is mediated by leaves and adaptations of plants to the environment involve leaf traits (Valladares *et al*., 2000). Native vegetation in Northeastern Mexico, composed mainly by shrubs and small trees, is characterized by low biomass productivity (about 3.2 kg DM ha^{-1} $year^{-1}$; Villalón, 1989) because during dry seasons native plants have to deal with soil water deficits, high temperatures and high irradiance levels (González *et al*., 2004). Furthermore, these plants have low tissue water potential because are exposed to low temperatures (-3 to 5°C) during winter and dry and warm whether in spring and summer seasons (González *et al*., 2000, 2004). Under such environmental conditions, photosynthesis may be limited by temperature, stomatal control and light energy damage. In addition, chlorophylls content and the chlorophyll a/b ratio, in some plants, are affected by temperature (Ottander *et al*., 1995) and prevailing shade characteristics (Castrillo *et al*., 2001).

Schlerf *et al*. (2003) studied seasonality of pigments in spruce needles; however, they found higher values than those found in this study. It has been suggested that variation of pigments could be related to phenological phases of plant species such a flowering and production of sprouts (Arthur *et al*., 1987). Other studies have revealed that loss of pigment content might have been associated with reduction in nitrogen flux into leaf tissue, alterations in the activity of enzyme systems such as nitrate reductase (Morilla *et al*., 1973) or nitrogenase in legumes (Engin and Sprent, 1973). In this study, Fabaceae species showed higher content in chlorophyll a than non Fabaceae species (Table 4). Differences might have related to the capability of symbiotic nitrogen fixation potential of *A. rigidula* and *P. laveigata* (Zitzer *et al*., 1996) since these species achieved higher leaf nitrogen content (1.7% dry mass) than non Fabaceae (1.4%) (unpublished nitrogen analyses results of studied species). It is clear that nitrogen is an essential element of the chlorophyll structure (Goodwin and Mercer, 1988). Similarly, other studies have also shown higher content of chlorophyll in Fabaceae than non Fabaceae (Northup *et al*., 2005; Hughes *et al*., 2007). In this study, however, chlorophyll b and carotenoids contents remained the same across families.

In this study, chlorophylls in all plants were higher than carotenoids. Moreover, a significant positive linear relationship was found between carotenoids and chlorophyll a content (Fig. 1). Chlorophyll a content explained about 32% (China; ($p<0.001$), 39% (Los Ramones; ($p<0.001$) and 45% (Linares; ($p<0.001$) of the total seasonality of carotenoids. These finding are in

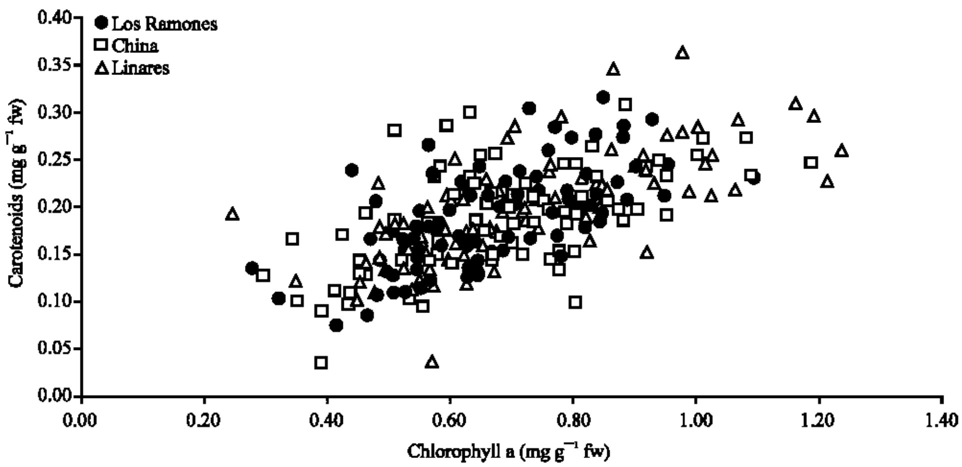

Fig. 1: Relationship between leaf carotenoids content and chlorophyll a for all leaf tissue samples in 11 native trees and shrubs at four sampling seasons and two consecutive years. Plotted data points are means from four independent measurements per plant species per season per year

agreement with Sims and Gamon (2002), who studied the relationships between leaf pigment content and spectral reflectance across a wide range of plant species. Relationships between carotenoids and chlorophyll a content included a range of healthy leaves and stressed leaf tissue due to drought and extreme temperatures (Table 1). During winter of 2006 a temperature of -5°C was registered in the region causing a reduction of chlorophyll b content at the three sites. However, the seasonal pattern of chlorophyll a content was more variable than chlorophyll b or carotenoids in all plants.

Evaluated plants are characterized by a wide range of taxonomic groups exhibiting differences in growth patterns, leaf life spans, textures, growth dynamics and phenological development (Reid *et al*., 1990; McMurtry *et al*., 1996; Northup *et al*., 1996). In general, tree species had higher contents of chlorophyll a than shrubs. In contrast, contents of chlorophyll b and carotenoids did not differ among growth forms. Perennial plants such as *Bumelia celastrina*, *Celtis pallida*, *Karwinskia humboldtiana* and *Zanthoxylum fagara* had higher (mean = 0.7 mg g^{-1} f.wt.) chlorophyll a than deciduous species such as *Forestiera angustifolia*, *Castela texana* and *Croton cortesianus* (0.6). Variations in chlorophyll content between plants have been related to leaf development and senescence (Gamon and Surfus, 1999; Carter and Knapp, 2001). Furthermore, Valladares *et al*. (2000) reported that chlorophyll content was higher in shade leaves that sun leaves, whereas carotenoids content and nonphotochemical quenching increased with light. In addition, Niinemets (1997) argued that decreased solar irradiance enhanced chlorophyll synthesis.

Studies on carotenoids composition of sun leaves of plants with different life forms have revealed that sun leaves contained greater amounts of the components of the xanthophyll cycle violaxanthin, antheraxanthin and zeaxanthin as well as of β-carotene than the shade leaves (Demmig-Adams and Adams, 1992). However, in the present study, it remains unclear whether lower or higher chlorophyll content at a given season is related to shade or sun leaves, since a pooled leaf sample was taken from each individual species. Kyparissis *et al*. (1995) have indicated that reduction of chlorophylls does not result from severe photoinhibitory damage, instead, it may be an adaptive response against the adverse conditions of the Mediterranean summer. This rationale could be extended to Northeastern Mexico ecosystems, since water availability, as in Mediterranean field conditions (Kyparissis *et al*., 2000; Valladares *et al*., 2000; Oliveira and Peñuelas, 2001), is the most limiting factor controlling plant growth, survival and distribution in dry climates (Newton and Goodin, 1989). In this study, even though, there was not a clear relationship between pigment content and seasonal mean temperatures and rainfall, the great diversity of native plants in Northeastern Mexico reflects the plasticity of how trees and shrubs species deal with seasonal water deficits, extreme temperatures (frost or heat) and excessive irradiance levels as main multiple stresses that may co-occur either during the winter or summer seasons.

IMPLICATIONS

Results of the present study suggest that, even though, all plants differed in pigment content and followed a seasonal pattern, during adequate or adverse conditions such as extreme temperatures and water shortages, they still could play important roles in maintaining the productivity of dry rangeland ecosystems. However, studies on leaf tissue at morphological, anatomical, biophysical, biochemical, physiological and molecular level should be addressed to elucidate the underlying mechanisms employed by these trees and shrubs to adapt to this ecosystem and to deal with prolonged drought periods, high temperatures and high irradiance levels, with the purpose to identify fundamental mechanisms that increase or reduce pigment concentration and how they are related to photochemical efficiency, photoinhibition and tissue water relations. These questions could be focused at both leaf and chloroplast (thylakoid) level. Thus, thornscrub ecosystems in Northeastern Mexico provide a good opportunity to investigate the ecophysiology and photoprotective capacity of native trees and shrubs that traditionally have been used as a forage source for domestic livestock and wildlife.

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