Adaptive features in leaves of South American species of the genus *Prosopis* (Leguminosae: Mimosoideae)

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SUMMARY

This paper deals with the anatomical leaf characters of South American species of the genus *Prosopis* L. (Mimosaceae). The adaptative features of leaflets from plants growing under extreme environmental conditions have been recorded. It was found that every individual analysed is xeromorphic. The anatomical characters that exhibit a response to external environment are the following: a) number of stomata per unit area, b) pubescence, c) cuticular thickness, d) mesophyll structure.

INTRODUCTION

Prosopis is distributed in SW Asia, Africa and predominantly America, from western North America to Patagonia (Burkart 1976) and it is a dominant element in New World desert ecosystems (Simpson 1977).

The South American species of *Prosopis* are found in a wide range of environments, from dry to moist regions with a seasonal rainfall.

In areas where it grows naturally *Prosopis* species play an essential ecological role in the protection and improvement of soils and are used as a source of human food, fodder, wood, fuel, bee pasture, etc. Some species are well suited to the purpose of semi-arid land reforestation (Karlin *et al.* 1992, Lee *et al.* 1992, Wojtusik and Felker 1993) and had been recommended by FAO (1980) for forestation, agroforestry and silvopastoral systems.

The phenotypic characteristics of plants are modified by features of the physical environment, especially climate. Plants in semi-arid environments differ in shape and morphology from plants in humid areas. Changes in leaf anatomy due to external environment has been pointed out, in general, by many authors (Solbrig and Orians 1977, Smith and Nobel 1977, Böcher 1979) and in particular for individual species of *Prosopis* by Bleckmann *et al.* (1980), Vilela (1993 and 1996) and Vilela and Palacios (1995). The modification of leaf length in response to water availability has been statistically analysed by Vilela *et al.* (in press).

The main purpose of the present study is ot examine the adaptive features of leaves of South American species of *Prosopis* and their structural modifications under different environmental conditions.

MATERIALS AND METHODS

Twenty eight non-aphyllous South American species, belonging to the three American sections of the genus (Algarobia, Strombocarpa and Monilicarpa), were studied. The list of voucher specimens can be found in Vilela (1996). Mature leaves from herbarium specimens deposited at BAFC were examined.

For epidermal preparations, chemical maceration with a potassium hydroxide solution was used (D'Ambrogio de Argüeso 1986). Epidermal peels were stained with safranin and mounted in glycerine jelly.

Transverse sections were made through the middle of the lamina. Free-hand sections were stained with cresyl-blue and mounted in glycerine jelly. At least 10 stomatal and hair counts were made on each surface (abaxial and adaxial) of leaflets. Slides are deposited at BAFC. As an example of the recounts, two extreme values per species (when available in herbarium) are recorded in Table 1. *Prosopis nigra* and *P. ruscifolia* are not included in the table because data for these species has already been published by Vilela (1993) and Vilela and Palacios (1995).

Abbreviations (used under Results): st/mm^2 = stomata per mm^2; Max = maximum; Min = minimum; X = mean.

RESULTS

Epidermis in surface view

Epidermal cells are polygonal (Figure 1I). On the midrib area, the cells become more extended and stomata are almost absent. Leaflets are amphistomatic (Figure 1G and I). The number of stomata per unit area (mm^2) is always higher on the adaxial surface than on the abaxial surface (Table 1). There are four types of stomata: paracytic, anomocytic, anisocytic and actinocytic. In Sect. Monilicarpa and Algarobia, in most cases, stomata are of the paracytic type, while in Sect. Strombocarpa the frequency of anisocytic, actinocytic and anomocytic stomata is higher than in the sections mentioned above.

The highest number of stomata per unit area has been recorded on the adaxial surface of *P. affinis* (Max = 800 st/mm^2, X = 530 st/mm^2), *Prosopis alba* (Max= 768 st/mm^2, X = 708 st/mm^2) and *Prosopis elata* (Max = 750 st/mm^2, X = 673 st/mm^2).

Pubescence is not a constant feature for a species. The highest number of hairs per unit area has been found in the psammophilous species *P. argentina* (Max = 714 hairs/mm^2, X = 501 hairs/mm^2). In most cases, individuals belonging to the Ser. Cavenicarpae (*P. ferox* and *P. tamarugo*) and Ser. Ruscifoliae (*P. ruscifolia*, *P. fiebrigii*, *P. vinalillo* and *P. hassler*) are glabrous, while in Ser. Chilenses (*P. chilensis*, *P. nigra*, *P. alba*, *P. caldenia*, *P. flexuosa*, *P. alpataco* and *P. pugionata*) some individuals are glabrous and others hairy (Table 1).

The distribution of hairs on each surface varies among species and individuals. *Prosopis argentina* has comparatively few hairs on the abaxial side, while *P. rojasiana* and *P. alba* have few on the adaxial surface (Table 1).

In *P. caldenia*, wax occurs as a covering on the epidermis.

Transverse section

Both the upper and lower epidermis consist of a single layer of cells (Figure 1A). The epidermal cells have a very thick cuticle, sometimes as thick as the diameter of the cell (Figure 1C). In some cases the abaxial cuticle is thinner than the adaxial one, in others they are almost equal (Table 2).

A cross section through a stomatal region shows that in most cases the guard cells are sunken below the level of the subsidiary cells. The thick cuticle of the subsidiary cells forms an outer chamber. The wall of the guard cells has cuticular thickenings (Figure 1B). Hairs are 1-cellular, erect, with thick walls and sharp tips (Figure 1H). Mesophyll is dorsiventral (Figure 1A). The photosynthetic tissue between the upper and lower epidermis consists of palisade parenchyma; the palisade cells are elongated.

Vascular bundles are colateral and enclosed in a bundle sheath. Large tetrahedric crystals occur chiefly in this bundle sheath (Figure 1E). Fibers are associated with vascular tissues (Figure 1F). They occur as a bundle cap adjacent to the phloem and lower part of the xylem. In larger veins, sclerenchyma is found on both dorsal and ventral sides.

Thin-walled mucilaginous cells often occur in the mesophyll (Figure 1D). The size and number of these cells varies. They may be located beneath the upper and the lower epidermis (*P. alpataco*, *P. nigra* and *P. strombulifera*) or in the center of the mesophyll (*P. ruizleali*, *P. argentina*).

CONCLUSIONS

Prosopis inhabits a wide range of environments. Twenty four of the species studied grow in Argentina, where the water deficit increases from E to W (rainfall: 1,200 to 80 mm/year). During summer months the water balance is negative (more evapo-transpiration than precipitation) in most parts of the area of distribution of *Prosopis* in Argentina, except for the provinces of Corrientes, and E of Formosa, Chaco and Santa Fe. Some species, like *P. nigra* and *P. alba*, are distributed in areas where the water balance is positive and others where the water deficit is very severe. However, independent of their place of origin, every individual analysed is xeromorphic. We may conclude that the leaflets of *Prosopis* species possess a number of specialized adaptations promoting efficient utilization and retention of water it acquires, such as sunken stomata, higher number of stomata on the adaxial surface, thick cuticles, palisade dorsiventral chlorenchyma, large quantities with fibers associated to vascular bundles and mucilaginous cells.

By midday plants are under great moisture stress. In order to avoid water loss some species fold their leaves, due to the action of pulvinus. In this way, most stomata are protected against water vapor removal and a lower vapor pressure deficit produced a decrease in transpiration.

The pubescence is not a fixed character for a species, so it cannot be used to discriminate taxa. *Prosopis ruizleali*, *P. chilensis*, *P. nigra*, *P. flexuosa* and *P. alba* have been described as glabrous species (Burkart 1976), while in Table 1 we can see that some individuals are hairy.

In addition to precipitation and evapo-transpiration, differences in soil also contribute to a differential absorption of water. Vilela and Palacios (1995) describe the influence of salty soil on the anatomical features of *Prosopis ruscifolia*. In *P. argentina* (G 1338 and K 6180) and *P. ruizleali* (1643) we can observe the influence of sandy soils on the presence of hairs.

Mucilaginous cells are considered a storage tissue that apparently may actually serve as a source of reserve water during drought. In *P. tamarugo* they have been described by Hull and Bleckmann (1977).

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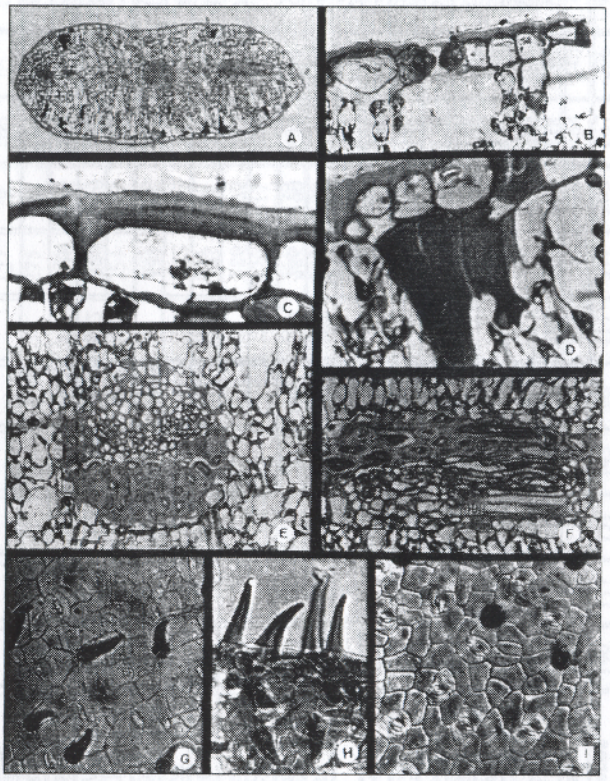
Figure 1. *Prosopis alpataco* (leaflet). A - Cross section; B - stomata; C - epidermal cell; D - mucilaginous cell; E - central bundle; G - adaxial surface; H - hairs; I - abaxial surface.



Sect./Ser./Species	Hairs						Stomata					
	Adaxial			Abaxial			Adaxial			Abaxial		
	Max	Min	X	Max	Min	X	Max	Min	X	Max	Min	X
Sect. Strombocarpa												
Ser. Strombocarpae												
P. strombulifera 1637	301	159	213	397	238	286	286	222	238	190	48	98
P. strombulifera 1590	-	-	-	S	S	S	286	206	240	195	63	119
P. torquata 1434	-	-	-	-	-	-	286	254	271	159	79	116
P. torquata 1713	-	-	-	-	-	-	175	127	148	63	32	54
P. abbreviata G 1719	-	-	-	31	6	14	222	143	178	150	63	101
P. abbreviata S 793	-	-	-	-	-	-	150	100	124	127	79	109
P. burkartii 1574	S	S	S	S	S	S	413	333	356	206	127	157
P. burkartii BP	-	-	-	S	S	S	302	143	225	175	95	114
P. reptans B 5935	190	127	160	270	95	189	365	286	330	349	127	213
P. reptans R 6680	254	175	209	206	95	155	286	190	259	254	79	160
Ser. Cavenicarpae												
P. ferox B 360	-	-	-	-	-	-	286	175	233	127	79	100
P. ferox M 22650	-	-	-	-	-	-	175	95	127	79	48	59
P. tamarugo 1576	-	-	-	-	-	-	222	143	190	79	48	68
P. tamarugo 1585	-	-	-	-	-	-	143	95	110	63	16	40
Sect. Monilicarpa												
P. argentina G 1338	714	333	501	508	365	432	270	159	205	143	79	114
P. argentina K 6180	507	127	238	222	111	175	238	143	181	175	95	117
Sect. Algarobia												
Ser. Ruscifoliae												
P. fiebrigii 547	-	-	-	-	-	-	683	556	617	317	238	278
P. fiebrigii 1516	-	-	-	-	-	-	476	349	409	238	175	198
P. vinalillo 547	-	-	-	-	-	-	508	333	435	238	111	151
P. vinalillo 483	-	-	-	-	-	-	381	254	294	143	95	119
P. hassleri 803	-	-	-	-	-	-	436	300	356	248	176	223
P. hassleri 676	-	-	-	-	-	-	248	164	213	124	76	92

Sect./Ser./Species	Hairs						Stomata					
	Adaxial			Abaxial			Adaxial			Abaxial		
	Max	Min	X	Max	Min	X	Max	Min	X	Max	Min	X
Ser. Denudantes												
P. denudans 1667	-	-	-	-	-	-	175	95	137	95	63	84
P. denudans 2511	-	-	-	-	-	-	127	79	100	95	48	73
P. ruizleali 1643	150	25	75	50	0	30	275	100	213	175	100	140
P. ruizleali 1645	-	-	-	-	-	-	175	100	158	150	100	115
P. castellanosii 1774A	175	48	109	95	16	46	206	127	160	159	63	116
P. calingastana M 5844	190	111	154	127	79	105	254	127	195	190	127	152
P. calingastana C24352	111	63	97	127	32	71	190	45	149	127	79	106
Ser. Humiles												
P. rojasiana 1501	302	175	229	397	222	300	524	397	468	270	127	208
Ser. Pallidae												
P. rubriflora 1579	-	-	-	-	-	-	429	317	376	222	111	160
P. campestris C 513	95	48	68	95	16	67	365	270	317	222	95	160
P. affinis 2036	304	240	266	180	124	155	800	400	530	176	132	154
P. affinis 463	-	-	-	-	-	-	555	333	444	270	159	214
P. elata 2151	625	100	243	400	100	220	500	200	370	275	125	190
P. elata 1402	425	150	275	475	300	362	650	375	560	400	200	328
Ser. Chilenses												
P. chilensis V. 175	112	48	82	80	48	62	576	416	499	256	128	176
P. chilensis B. 257	-	-	-	-	-	-	400	288	352	176	80	130
P. caldenia L115549	-	-	-	-	-	-	432	316	366	168	104	140
P. caldenia M 7137	-	-	-	-	-	-	312	268	291	136	88	115
P. flexuosa 1734	396	228	254	288	224	257	544	336	464	240	144	206
P. flexuosa A53	190	111	151	143	63	111	317	206	267	206	95	156
P. alpataco 1651	198	124	145	150	108	129	325	100	243	225	125	188
P. alpataco A34	-	-	-	-	-	-	317	206	268	111	63	84
P. alba 1244	288	212	250	368	288	320	768	324	708	496	352	422
P. alba 2041	-	-	-	-	-	-	412	316	364	180	124	161
P. pugionata 1640	250	125	173	250	100	193	450	300	390	300	200	233
P. pugionata 1736	111	48	78	159	80	127	381	254	304	190	95	162

Table 2. Cuticular thickness (μm)

Species	Adaxial surface	Abaxial surface
P. strombulifera 1603	*8.6*	*6.9*
P. strombulifera 1628	*4.0*	*4.9*
P. torquata 1707	*9.6*	*10.4*
P. torquata 1714	*7.5*	*7.5*
P. ferox M 22650	*12.0*	*12.2*
P. ferox F 2491	*13.8*	*16.0*
P. argentina H 20262	*6.4*	*4.7*
P. argentina K 6180	*7.2*	*6.4*
P. ruizleali 1643	*6.9*	*4.9*
P. ruizleali 1644	*6.9*	*5.1*
P. ruizleali 1645	*8.4*	*7.7*
P. elata 1402	*8.4*	*7.8*
P. elata 1502	*7.6*	*5.8*
P. elata 2151	*7.2*	*7.6*
P. alpataco 1651	*7.9*	*6.2*
P. alpataco 1655	*7.3*	*6.6*
P. pugionata 1640	*5.2*	*4.0*
P. hassleri 1386	*11.9*	*10.9*
P. hassleri 803	*12.4*	*8.4*
P. hassleri 676	*10.3*	*8.7*