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STRUCTURAL ADAPTATIONS FOR ADAPTABILITY IN SOME EXOTIC AND NATURALIZED SPECIES OF AGAVACEAE

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Abstract

A study was conducted to evaluate the structural modifications in some *Agave* (*A. americana*, *A. americana* var. *marginata*, *A. decipiens*, *A. x leopoldii*, *A. sisalana*, and *A. vera-cruz*) and *Yucca* (*Y. aloifolia, Y. aloifolia* 'Marginata', *Y. elephantipes*, and *Y. gloriosa*) species in relation to their distribution, cultivation and escape. *Agave americana* and its var. *marginata*, and *Yucca aloifolia* and its cv. Marginata had high values of root epidermis thickness and its cell area, root endodermis thickness and cell area, root cortical cell area, root vascular region area, leaf parenchyma cell area, leaf vascular bundle area, and leaf metaxylem area and thus these species show considerable adaptations to a variety of environments. Multivariate analysis supported the relationship of anatomical characteristics with morphological features to some extent. Thus, the specific anatomical features recorded in this study have considerable importance for taxonomic studies.

Introduction

Invasive plant species are more efficient in their use of resources such as water and nutrients than the species that colonize new environments (Mack, 2001). Most invasive species are generally opportunists, which exploit the environmental changes and disturbances caused by humans and natural environments (Daehler, 2003). Low-resource environments are least vulnerable to biological invasions that provide little regarding the availability of light, water or nutrients such as nitrogen and phosphorus. Limitation in one or more such resources has the potential to exclude plant species from occupying any habitat (Funk *et al*., 2008).

One plus point of invasiveness of the invading species is that while introduced into new habitats, they may have escaped from enemies like pests and diseases, and also can form unexpected beneficial associations with other organisms, which in turn, assist them in obtaining resources (Klironomos, 2002; Mitchell & Power, 2003). The loss of enemies and the gain of mutualist organisms can provide invaders with more resources than they would have obtained in their native lands (Mitchell *et al*., 2006), and this may be the major reason that invasive species outgrow native species in a wide range of habitats.

Agave L., is a large and taxonomically a complex genus of about 300 species, distributed mainly in southern USA and tropical South America (Reveal & Hodgson, 1993). *Yucca* L. comprises of 40 species, native to southern USA, Mexico and West Indies (Ji & Meerow, 2000). In Pakistan, *Agave* is is represented by six species and *Yucca* by only one, all of them are cultivated (Akhtar & Ghazanfar, 1984).

High resource-use efficiency in diverse plant groups like grasses, ferns, trees and garden ornamentals provide strong evidence that invasive plants cannot survive under low-resource conditions (Funk & Vitousek, 2007), but three species of the genus *Agave* L. were escaped from cultivation and naturalized in the Punjab plains and foothills (Akhtar & Ghazanfar, 1984). Thus, these species must have undergone some specific modifications and anatomical changes to cope with the specific environmental conditions of the regions during the long span of time they have been growing there. The present study was conducted to examine the anatomical adaptation in some *Agave* and *Yucca* species in the Punjab region.

Materials and Methods

Anatomical studies were conducted to assess the structural modifications in some *Agave* (*A. americana*, *A. americana* var. *marginata*, *A. decipiens*, *A. x leopoldii*, *A. sisalana* and *A. vera-cruz*) and *Yucca* (*Y. aloifolia, Y. aloifolia* 'Marginata', *Y. elephantipes* and *Y. gloriosa*) species in relation to their distribution, cultivation and escape, in the Punjab, Pakistan.

Double-stained permanent slides were prepared by free-hand sectioning technique. For root anatomy 2 cm piece from the root-shoot junction of the thickest root, and for leaves one cm piece from the leaf centre along the midrib were taken. The material was first preserved in FAA (formalin acetic alcohol) solution for 48 h, which contained v/v formalin 5%, acetic acid 10%, ethanol 50% and distilled water 35%. The material was then transferred in acetic alcohol solution (v/v 25% acetic acid and 75% ethanol) for long-term preservation.

The data were recorded using an ocular micrometer and photographs were taken by Carl-Ziess camera-equipped microscope. Anatomical characteristics relating to dermal, parenchymatous, mechanical, and vascular tissues were recorded during the investigation.

The data were subjected to analysis of variance (ANOVA) in completely randomized design (CRD) for the comparison of means following Steel *et al*., (1997). The anatomical data were also subjected to multivariate (cluster) analysis using Minitab statistical software (version 11) to assess the relationship between anatomical and morphological characteristics and significance of anatomical characteristics in distributional pattern and taxonomy of the species of Family Agavaceae recorded from the Punjab.

Results

Root anatomy: Epidermis thickness and its cell area in *Agave americana* and its var. *marginata* were significantly higher than those recorded in other species and cultivars (Table 1). Endodrmis thickness and its cell area, however, was greater in *Yucca* than *Agave* species and cultivars. *Yucca aloifolia* showed the maximum of these characteristics. Variation regarding cortical cell area was quite high in all the species, but its maximum in *A. americana* and *Y. aloifolia.* The variety and cultivar of these species also showed large cortical cells. All the *Yucca* species/cultivars showed much higher sclerification than that in *Agave* species, the maximum of this parameter being in *Y. aloifolia* 'Marginata'.

Table 1. Anatomical characteristics of some species/cultivars of family Agavaceae from the Punjab, Pakistan.

	Agave americana	*Agave americana* var. *marginata*	*Agave decipiens*	*Agave x leopldii*	*Agave sisalana*	*Agave vera-cruz*	*Yucca aloifolia*	*Yucca aloifolia* 'Marginata'	*Yucca elephantipes*	*Yucca gloriosa*
	Root anatomical parameters									
Epidermis thickness (μm)	571.921e	490.233d	326.863c	326.845c	163.432a	163.487a	245.139b	326.831c	326.897c	326.865c
Epidermis cell area (mm^2)	0.110e	0.126f	0.042c	0.031b	0.010a	0.010q	0.031b	0.063d	0.021b	0.021b
Endodermis thickness (μm)	81.725a	81.767a	81.772a	81.788a	81.765a	81.770a	163.423b	163.451b	163.419b	81.748a
Endodermis cell area (mm^2)	0.016b	0.010a	0.016b	0.010a	0.016b	0.016b	0.042e	0.031d	0.031d	0.021c
Cortical cell area (mm^2)	0.252g	0.210f	0.126d	0.031d	0.094b	0.094b	0.252g	0.220f	0.105c	0.184e
Sclerenchyma thickness (μm)	326.820a	408.545b	735.392e	571.938d	490.221c	490.271c	898.774f	1062.127g	817.003f	898.726f
Sclerenchyma cell area (mm^2)	0.031a	0.047a	0.063b	0.047a	0.047a	0.047a	0.105c	0.131d	0.189e	0.131d
Vascular region area (mm^2)	7.049g	5.307e	0.472a	0.839a	2.622b	4.384d	6.293f	2.360b	2.407b	3.147c
Metaxylem area (mm^2)	0.105a	0.294b	0.294b	0.189b	0.184b	0.184b	0.955e	0.692d	1.028f	0.577c
Phloem area (mm^2)	0.105b	0.220d	0.210d	0.084a	0.157c	0.157c	0.288d	0.519e	0.184c	0.629f
	Leaf anatomical parameters									
Cuticle thickness (μm)	122.554e	40.850a	122.554c	81.725b	81.725b	122.554c	122.554e	81.725b	122.554c	81.725b
Epidermis thickness (μm)	245.139a	326.863b	326.863f	245.139a	245.139a	408.597c	326.863b	326.863b	408.597c	326.863b
Epidermis cell area (mm^2)	0.047b	0.042b	0.084c	0.047b	0.016a	0.079c	0.042b	0.042b	0.079c	0.042b
Parenchyma cell area (mm^2)	0.472d	0.420d	0.294b	0.184a	0.378c	0.472d	0.220b	0.378c	0.220b	0.252a
Vascular bundle area (mm^2)	7.049g	5.307e	0.472a	0.839a	2.622b	4.384d	6.293f	2.360b	2.407b	3.147c
Metaxylem area (mm^2)	0.047c	0.047c	0.005a	0.005a	0.021b	0.005a	0.021b	0.047cb	0.021b	0.021b
Adaxial stomatal density	37.433c	15.450a	63.981b	25.775b	27.944b	17.931a	115.566e	69,881cd	34.952e	110.890e
Abaxial stomatal density	16.371a	29.921b	35.349c	23.375b	25.918b	23.345b	118.402f	95.438e	25.882b	67.234d
Adaxial stomatal area (mm^2)	0.079c	0.031a	0.042a	0.094d	0.094d	0.189e	0.079c	0.052b	0.079e	0.063b
Abaxial stomatal area (mm^2)	0.063b	0.052b	0.063b	0.105d	0.094e	0.210e	0.052b	0.031a	0.031a	0.063b

Vascular bundle area was the maximum in *A. americana,* which was closely followed by that recorded in *Y. aloifolia* and *A. americana* var. *marginata.* Metaxylem and phloem area were generally greater in *Yucca* species, where the metaxylem area was maximum in *Y. elephantipes* and phloem in *Y. gloriosa.*

Intensive sclerification in the vascular region was recorded in *A. americana*, *A.* x *leopoldii* and *Y. aloifolia* (Fig. 1). However, in *A. americana* var. *marginata, A. decipiens, A. vera-cruz* and *Y. gloriosa,* sclerification was restricted to metaxylem vessels only. In *Agave* species, prominent sclerification was recorded outside the endodermis, but in *A.* x *leopoldii,* the sclerification was much more prominent. In *Yucca* species, thick-walled sclerenchyma was recorded in *Y. elephantoides* and *Y. gloriosa.*

Leaf anatomy: Five species, *A. americana*, *A. decipiens*, *A. vera-cruz*, *Y. aloifolia*, and *Y. elephantipes* possessed thick cuticles (Table 1). Epidemal thickness and its cell area were the maximum in *A. vera-cruz* and *Y. elephantipes.* Large parenchymatous cells were recorded in *A. americana* and its var. *marginata* and *A. vera-cruz.*

Variations regarding vascular bundle area were huge among all the species and cultivars studied, where the maximum of this parameter was recorded in *A. Americana,* which was closely followed by that in *Y. aloifolia* and *A. americana* var. *marginata*. Metaxylem area was the maximum in three species, *A. Americana,* its variety *A. americana* var. *marginata* and *Y. aloifolia* 'Maginata'.

Vascular region in three species, *A. americana, A. americana* var. *marginata* and *Y. aloifolia,* was intensively sclerified (Fig. 1). Metaxylem vessels, however, were more prominent in *A. americana* and its var. *marginata* and *Y. aloifolia* 'Marginata'.

All the species and cultivars showed great diversity in stomatal density and area of stomatal complex (Table 1). Stomatal density was the maximum in *Y. aloifolia* on both adaxial and abaxial leaf surfaces. Its area, however, was the maximum in *A. vera-cruz* on both leaf surfaces.

Multivariate analysis: Dendrogram of morphological data presented two distinct groups, in which *Y. aloifolia* and its cultivar 'Marginata' clustered very close to each other. Both the other species of *Yucca* also were related closely to them (Fig. 2). All the *Agave* species were clustered under the same group, however, *A. americana, A. sisalana, A. vera-cruz* and *A. americana* var. *marginata* were relatively more closer.

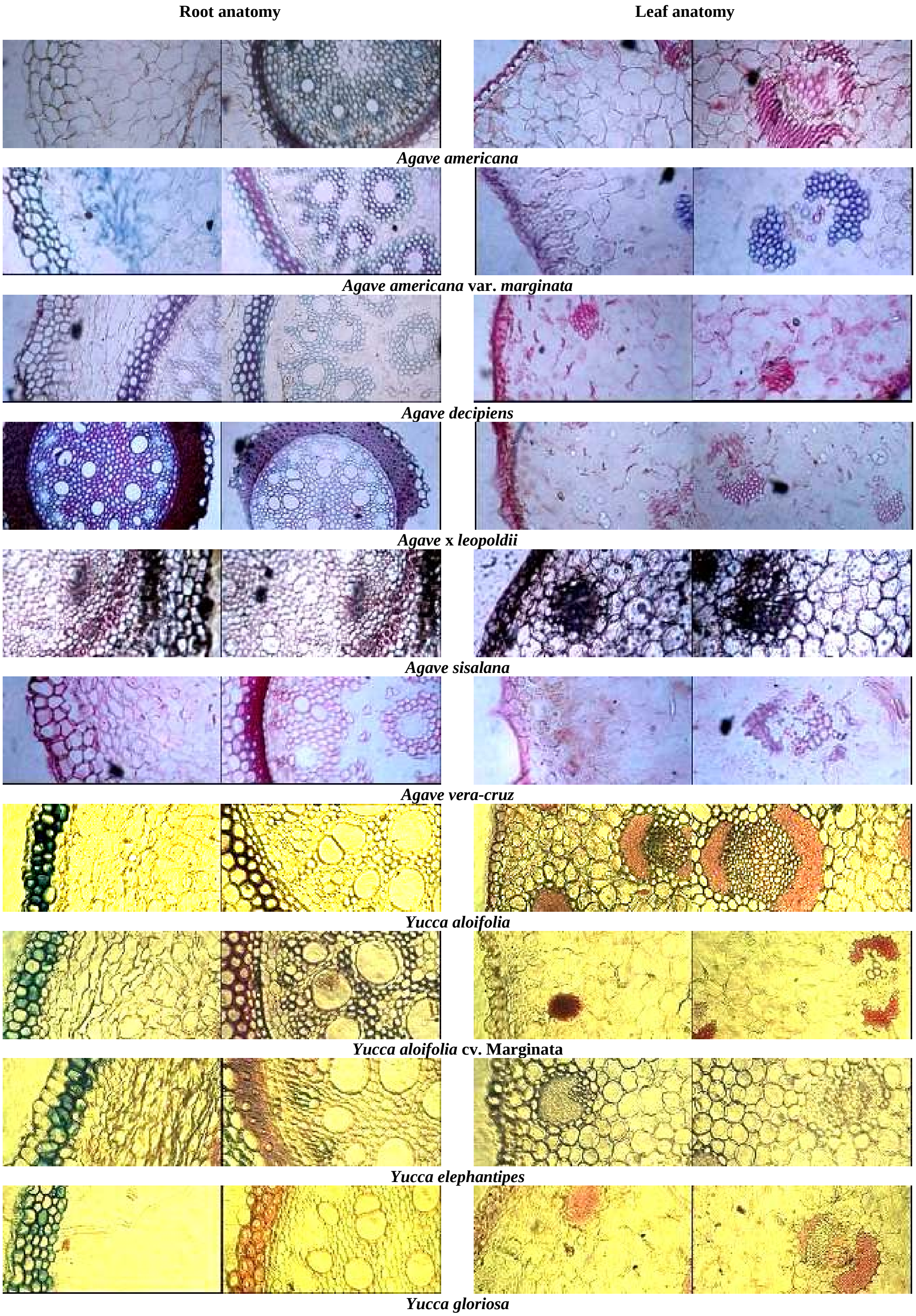

Fig. 1. Transverse section of root and leaves in some species/cultivars of family Agavaceae from the Punjab, Pakistan

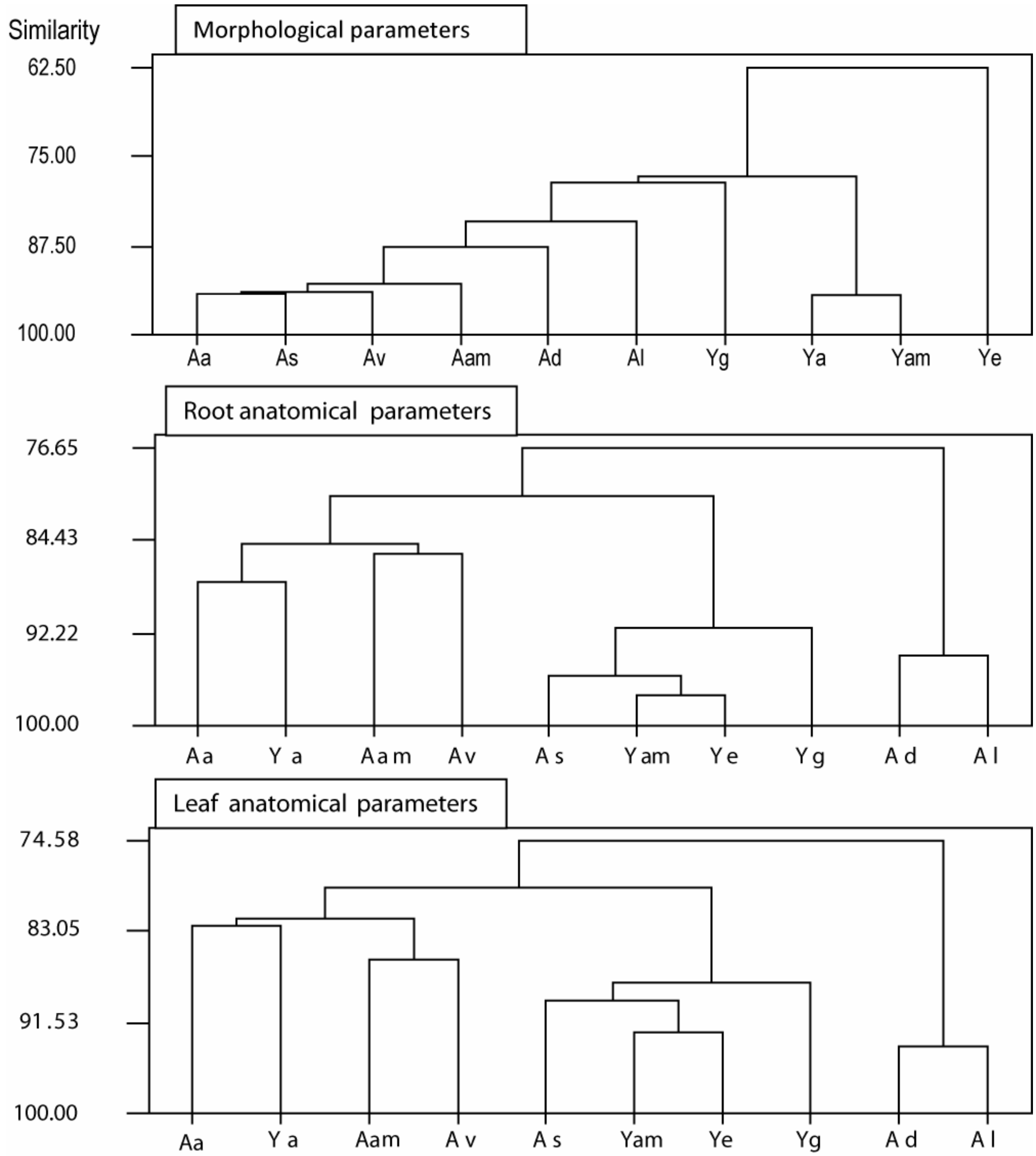

Fig. 2. Dendrogram of morphological and anatomical parameters in *Agave* and *Yucca* species from the Punjab, Pakistan.

The dendrogram of root anatomical data presented three distinct groups, in which *A. decipiens* and *A.* x *leopoldii* clustered very close to each other. The second cluster consisted of *A. sisalana,* and three species of *Yucca* (*Y. aloifolia* 'Marginata', *Y. elephantipes,* and *Y. gloriosa*). The third cluster had two distinct sub-clusters, one of *A. americana* and *Y. aloifolia,* and the other of *A. americana* var. *marginata* and *A. vera-cruz.* The dendrogram of leaf anatomy followed the similar pattern, as was recorded in the case of root anatomy. However, percent similarity in case of leaf anatomy was relatively higher than that of root anatomy.

Discussion

All the species/cultivars of *Agave* and *Yucca* are leaf succulents. Three species of *Agave, A. americana*, *A. americana* var. *marginata,* and *A. vera-cruz* were escaped from cultivation and naturalized quite well in the Salt Range and foothills of Rawalpindi district (Akhtar & Ghazanfar, 1984). *Agave sisalana*, and *A. decipiens* were commonly cultivated species in the region, however, *A. x leopoldii* was relatively rare. All *Yucca* species were cultivated commonly, but *Y. elephantipes* was relatively rare in the region.

Root anatomy: Root epidermis plays a critical role in controlling water movement through root, as it connects the root with external environments (Bahaji *et al.,* 2002; Saleem *et al*., 2010). Thicker epidermis in *Agave americana* and its var. *marginata* may provide these species an ecological benefit for their adaptability to a variety of environmental types.

Under water limited environments, the endodermis plays a central role, as it is a barrier for radial movement of water and nutrients in roots (Vasellati *et al*., 2001; Pena-Valdivia *et al*., 2010). Thick endodermis in *Y. aloifolia* and its cultivar 'Marginata' might be one of the key factors responsible of wide cultivation of these species in a variety of environments.

Cortical region is structurally and functionally the important component of root that serves as a storage area of water and nutrients (Lux *et al*., 2004; Hameed *et al*., 2009). Large cortical cells may provide ecological success to *A. americana* and its var. *marginata, Yucca aloifolia* and its cv. Marginata for the adaptability to cope with environmental stresses (Zwieniecki & Newton, 1995), and, hence their wide range of distribution.

Sclerenchyma thickness and its cellular area were generally higher in *Yucca* species/cultivars than those in *Agave*, therefore the *Yucca* are probably more adaptable to arid or semi-arid environments. Intensive sclerification is essentially useful for drought prone enevironments, as was earlier reported in *Paspalidium dilatatum* (Vasellati, 2001), *Cenchrus ciliaris* (Nawazish *et al*., 2006) and *Imperata cylindrica* (Hameed *et al*., 2009).

Yucca species and cultivars generally had greater metaxylem area and phloem area. It is well documented that wider vessels conduct water with lower resistance than do the smaller vessels (Nicotra *et al*., 2002). On this basis, it can be concluded that *Yucca* species/cultivars are more adaptable to environmental heterogeneity than those of *Agave*.

Leaf anatomy: Leaf succulence is generally related to osmotic stress tolerance. All the species studied in the present study are leaf succulents. Leaf anatomy showed quite a variable pattern in all these, however, three *Agave* species (*A. americana*, *A. decipiens* and *A. vera-cruz*) and two *Yucca* specis (*Y. aloifolia* and *Y. elephantipes*) had thicker cuticle along with thick epidermis, and these species seem to be of more drought loving nature than the others. Earlier, Hameed *et al*., (2009) reported thicker cuticles under physiological droughts.

Larger parenchyma cell area seems to be more efficient in water storage that is essential for survival under harsh climates. Large parenchymatous cells in *A. americana* and its cultivar *A. americana* var. *marginata* and *A. vera-cruz* are the indication of their wide distribution in a variety of different environmental conditions, as earlier reported by Zwieniecki and Newton (1995) and Baloch *et al.,* (1998).

Stomatal density and area presented a similar pattern in family Agavaceae on both leaf surfaces. This must be the reason that the orientation of the leaves in this family is more or less perpendicular to the soil surface, and therefore, there were non-significant differences on both adaxial and abaxial leaf surfaces. However, stomatal density was relatively higher in *Yucca* species and cultivars, but the area was in *Agave* species. Stomatal density is the key factor in controlling water loss through leaf surfaces, and therefore, vital for the degree of tolerance of plant species to environmental stresses (De Villers *et al*., 1996; Naz *et al*., 2010).

In general, on the basis of anatomical characteristics, *Agave americana* and its var. *marginata*, and *Yucca aloifolia* and its cv. Marginata seem to be more adaptable to a variety of environments, as was confirmed by their large scale distribution throughout the world. These species had high values of root epidermis thickness and its cell area, root endodermis thickness and cell area, root cortical cell area, root vascular region area, leaf parenchyma cell area, leaf vascular bundle area, and leaf metaxylem area.

On the basis of multivariate analysis, it can be predicted that for taxonomical studies, anatomical characteristics do not completely support the morphological features. More reliably, it is suggested that most of the anatomical characteristics were adaptive in nature to various environmental conditions, like high sclerenchyma ratio to drought and salinity, large cortical or parenchyma (succulence) to drought, thick epidermis and cuticle to different abiotic stresses, large metaxylem vessels to limited moisture environment. However, some clusters for morphology and anatomy were closely related, and therefore, the validity of anatomical data cannot be ignored in the taxonomic studies.

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