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Research Article
Impact of Habitat Heterogeneity on Growth Dynamics and Physiological Responses of *Dipterygium glaucum*

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Abstract
Background and Objective: *Dipterygium glaucum*, a rangeland plant holds high ecological importance in desert conservation by providing a vegetation cover along with other species. This study investigated the impact of biotic and abiotic factors across different habitats, resulting in intraspecific variations in different ecotypes of *Dipterygium glaucum*. **Materials and Methods:** Morphological variations in different habitats were assessed using 2 way MANOVA and Principal Component Analysis (PCA) with SPSS 23.0 statistical software. Total phenolics were estimated using Folin and Ciocalteu reagent, chlorophyll content was determined using spectrophotometer method. Antimicrobial activity of the plant extract was assessed against 2 g positive and 2 g negative pathogenic bacterial strains. **Results:** Variations among populations of three habitats due to adaption to varied environmental conditions were significant. The highland variant showed robust growth compared to coastal and sand dune populations and produced 2 types of flowers white and yellow compared to only yellow flowers in other habitats. Decreased chlorophyll content and increased antimicrobial activity and total phenolics were observed under salt stress. **Conclusion:** *Dipterygium glaucum* exhibit phenotypic plasticity across different habitats resulting in intraspecific variations and exist as ecotypes.

Key words: Ecotypes, *Dipterygium*, morphometrics, chlorophyll-a and b content, phenolics, antimicrobial activity, MANOVA and Principal component analysis (PCA)

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Competing Interest: The authors have declared that no competing interest exists.

Data Availability: All relevant data are within the paper and its supporting information files.

INTRODUCTION

Plant species exposed to heterogeneity in the environment in relation to abiotic and biotic factors across different habitats, encounter selective pressures[1]. These pressures force a single genotype to produce different morphological and physiological responses when exposed to varied environmental conditions[2-4] and undergo local adaptions resulting in phenotypic plasticity[5-7] and thus exhibit intraspecific divergence[8]. These divergences among populations, over time line produce ecotypes across different habitats[9-12], representing adaptive matching through phenotypic plasticity[13], which is a commonly observed feature among many species. Species, which exhibit suitable response to varied environmental conditions have wide distributions. Among habitats, variables like temperature, humidity and salinity vary greatly and are useful indicators of how a species adapts to the local climatic conditions[14,15], in which local adaptations increase plant tolerance to stress[16,17] and produce different morphologies[13].

Oman is a subtropical dry desert country bordering the Arabian Sea and hosts diverse range of habitats. Desert prevails in the interior Oman and witness extreme high temperatures with dry and arid environmental conditions, while the coastal regions are hot and humid. *Dipterygium glaucum* Decne is one of the most common plants found among different habitats of northern and central Oman. Locally called ‘Alga’, this species is commonly sighted along roadsides, sandy plains, wadis (dry water course), rocky slopes and coastal areas where it is often found in stunted condition as a rangeland plant. In these diverse habitats *Dipterygium glaucum* exist as a xerophyte, a facultative halophyte and a highland species which suggests it is highly adaptive and has evolved suitable traits to survive the adverse arid and saline conditions. This species suffers from severe aridity, where the water scarcity and soaring temperatures affect its morphological characters[18]. It is a dominant species while in coexistence in a community and holds prime ecological importance in restoration and conservation of desert vegetation along with other species like *Acacia tortolis*, *Acacia nilotica*, *Aerva javonica*, *Leptodenia pyrotecnia*, *Zygophyllum quaterese*, *Calligonum comosum*, *Suaeda aegyptica*. The *D. glaucum* is used as soil erosion controller[19] and in rangeland cover re-establishment under grazing pressures.

In folklore medicine, several uses are enlisted for this species. It is analeptic, blood purifier, trachea dilating agent[20] used in treatment of asthma, jaundice, chronic fever, redness and irritation of skin and unhealthy patches on skin.

The medicinal value of any plant results from synergy of different secondary metabolites present in the plant. The production of these secondary compounds are influenced by environmental factors like high temperature or salinity stress that alter the metabolism in plants and show quite significant differences in their accumulation. Climate, the seasons of the year, temperature, altitude and humidity can significantly affect the quality and quantity of the bio-active compounds[21-23].

Phenolic compounds play an important role in protecting the plants under a biotic stress conditions, particularly the oxidative injury[24,25]. Under a saline habitat enhanced salinity results in an ionic imbalance and hyperosmotic stress effecting the cellular membranes and the photosynthetic system due to harmful effect of reactive oxygen species[26].

A common but ecologically and medicinally important species like *Dipterygium glaucum* with a wide distribution under varied habitats, adapts itself to different environmental conditions and exhibit phenotypic plasticity and thus shows physiological, morphological, genetic differences and exist as ecotypes.

There are no reports yet on effect of different habitats on the physiological and the morphological variations in *Dipterygium glaucum*. In this study it investigated how different habitats impact *Dipterygium glaucum* differently and how these variations are expressed morphologically and physiologically in the plant. This study contributes to the knowledge of various survival tactics adapted by plant species, to thrive under stressful conditions.

MATERIALS AND METHODS

The study was conducted during the period January-July, 2017.

Study site: The study area was located at 3 different habitats spread across Muscat region, the north-eastern part of Oman in Arabia Peninsula. The habitats are, Seeb/Al Hail beach, 23.6284° N, 58.2669° E, Al Sifah highlands, (400 m above sea level) 23.268° N, 58.4652° E and Bowsher sand plains-23.5821° N, 58.0271° E. For each of the 3 habitats, 3 sites were selected randomly, thus a total of 9 sites which are distributed across northeastern Oman. Each species was sampled along one transect at each of the 9 sites (Fig. 1).

Plant material: Healthy *Dipterygium glaucum* Decne, plants growing wild in different habitats were collected between February 15th and 15th March, 2017 (Fig. 2). Voucher

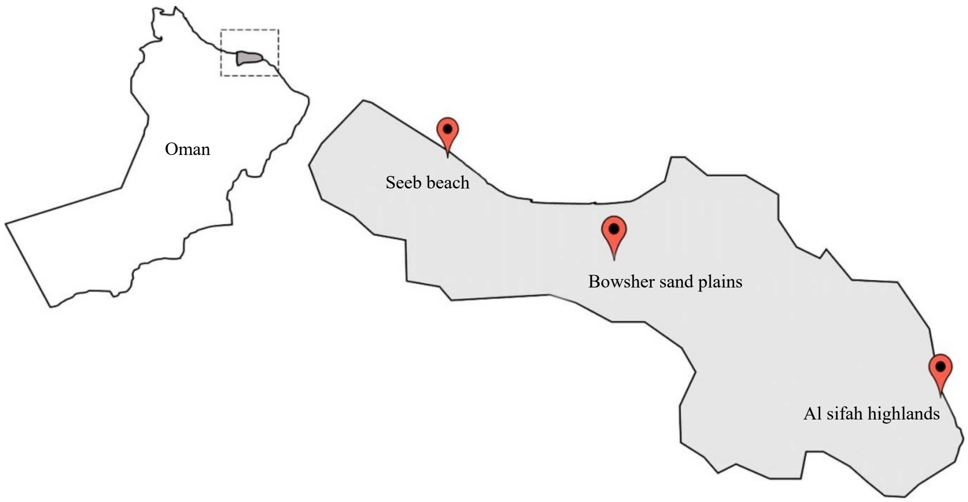

Fig. 1: Map of Oman and the sites of sample collection
Al Seeb/Al Hail beach, 23.6284° N, 58.2669° E, Al Sifah highlands, (400 m above sea level) 23.268° N, 58.4652° E and Bowsher sand plains- 23.5821° N, 58.0271° E

Fig. 2: *Dipterygium gluacum* in natural habitat and in flowering

specimens were compared with the herbarium sheets at Herbarium, Department of Biology, Sultan Qaboos University, Oman.

For morphometric analysis 10 plants from each habitat were assessed and morphological data was recorded on the height of the mature plant, branch length, diameter of the stem, length of root, diameter of root, total number of leaves, total number of flowers, total number of fruits, size of the flower and internode length.

Chemicals: All the chemicals that used were of analytical grade purchased from Sigma (Sigma-Aldrich, Germany) and Merck (Darmstadt, Germany).

Chlorophyll extraction: Chlorophyll was extracted from 1 g fresh leaves using 10 mL of 80% acetone[27], filtered and the final volume adjusted to 100 mL. The absorbance of the solution was read at 480, 645 and 663 nm against the solvent (acetone) blank. The amounts of photo-synthetic pigments were expressed as mg g^{-1} fresh weight.

Calculations were done according to following equations:

- **Total chlorophyll:** 20.2 (A645)+8.02 (A663)
- **Chlorophyll a:** 12.7 (A663)-2.69 (A645)
- **Chlorophyll b:** 22.9 (A645)-4.68 (A663)

$$\text{Carotenoid: } A480+(0.114(A663)-(0.638\text{-}A645)\times\frac{V}{1000}\times W$$

Determination of total phenolics: The amount of total phenolic content was determined spectrophotometrically[28] by folin-ciocalteu reagent. About 0.5 mL of methanol extract of *Dipterygium glaucum* was mixed 2.5 mL of 10% Folin-Ciocalteu reagent and 2.5 mL of sodium carbonate (7.5%), the mixture was allowed to stand for 15 min in parafilm covered tubes. Absorbance of the mixture was recorded at 765 nm against a blank, composed of methanol, folin-ciocalteu and sodium carbonate. Gallic acid was used as a standard. The total phenolic contents were expressed as milligrams of gallic acid equivalents per gram (mg GAE g^{-1} extract).

Preparation of extract: Shade dried plant material was grounded to fine powder , 100 g of the powder was extracted for 24 h in 300 mL 100% methanol in a rotatory shaker at room temperature. The residue was re-extracted under the same conditions three times. Extract was filtered and evaporated to dryness using a rotary evaporator. Finally, the residue was re-suspended in dimethyl sulfoxide (DMSO) to yield 100 mg mL^{-1} extract.

Micro-organisms: Bacterial strains used in the investigation were the ATCC cultures of: *Staphylococcus aureus* (ATCC 29213) *Escherichia coli* (ATCC 9637), *Pseudomonas aeruginosa* (ATCC 10231) and *Bacillus subtilis* (ATCC 6633).

Disc diffusion method: The antibacterial activity of the extract was determined by the disc diffusion method. Different strains of bacteria were cultured in a nutrient broth at 37°C for 24 h. About 6 mm sterilized discs were soaked with 100 µL of the test solution and placed on the agar plates inoculated with different bacteria. Ampicillin (1 mg $disc^{-1}$) was employed as a positive control and DMSO as a negative control. Plates were incubated for 24 h at 37°C and the antibacterial activity was assessed by measuring the inhibition zones in millimeters. The experiment was run in triplicate.

Statistical analysis: Statistical analyses were done using SPSS 23.0. Two-way MANOVA was applied to test for intraspecific differences in the morphometric characters among the different habitat ecotypes. Means were compared using *post hoc* Tukey's HSD at $\alpha = 0.05$. Descriptive statistics were generated, listing the mean, standard deviation and coefficient of variation for each morphological character. Spearman's ρ correlation coefficient was calculated to check correlation between mean of different growth parameters. Principal component analysis (PCA) was performed using the correlation matrix on the morphometric data in order to understand the patterns of variations within the populations from different habitats. The principal component axes were extracted according to the eigenvalues and biplot of scores of first two axes of principal component analysis was used to identify the best suited habitat and study the interrelationship among different habitats.

RESULTS

Morphological variations among growth parameters

MANOVA analysis: Morphological variations among populations were high. The MANOVA analysis for variables showed significant differences between growth parameters of plants collected from different habitats (Wilks <0.01) (Table 1).

Highly significant differences among populations were observed in plant height, branch length (Fig. 3a), stem diameter, flower size, fruit size (Fig. 3b), number of flowers and fruits (Fig. 3c). All of these characters were highly expressed under Al Sifah highland conditions followed by beach and least expressed in water stressed sand plains. The flower size in highland variants was 6 times as compared to desert morphotype. Further highland morphotypes bear two flower colors, yellow and white, while only yellow flowers were observed at other habitats. Similar trend was seen in fruit size where an average fruit in highland variant was double the size of a desert morphotype,

Roots were longer in desert morphotype, where *Dipterygium glaucum* was growing as a xerophyte in water limited environment as compared to beach and highland

Table 1: Results of the multi-variate analysis of variance (MANOVA) in *Dipterygium glaucum* using eleven morphological traits as dependent variables and three habitats as independent factors

	Multi-variate tests[a]							
Effects	Value	F-value	Hypothesis df	Error df	Significant	Partial Eta squared	Noncent. Parameter	Observed Power[d]
Intercept								
Pillai's trace	1.000	29627.393[b]	11.000	2.000	0.00	1.000	325901.323	1.000
Wilk's lambda	0.000	29627.393[b]	11.000	2.000	0.00	1.000	325901.323	1.000
Hotelling's trace	162950.661	29627.393[b]	11.000	2.000	0.00	1.000	325901.323	1.000
Roy's largest root	162950.661	29627.393[b]	11.000	2.000	0.00	1.000	325901.323	1.000
Habitats								
Pillai's trace	1.986	37.864	22.000	6.000	0.00	0.993	833.005	1.000
Wilk's lambda	0.000	771.663[b]	22.000	4.000	0.00	1.000	16976.579	1.000
Hotelling's trace	257749.689	11715.895	22.000	2.000	0.00	1.000	257749.689	1.000
Roy's largest Root	257680.753	70276.569[c]	11.000	3.000	0.00	1.000	773042.258	1.000

a: Design: Intercept+Habitats, b: Exact statistic, c: Statistic is an upper bound on F-value that yields a lower bound on the significance level, d: Computed using alpha = 0.05

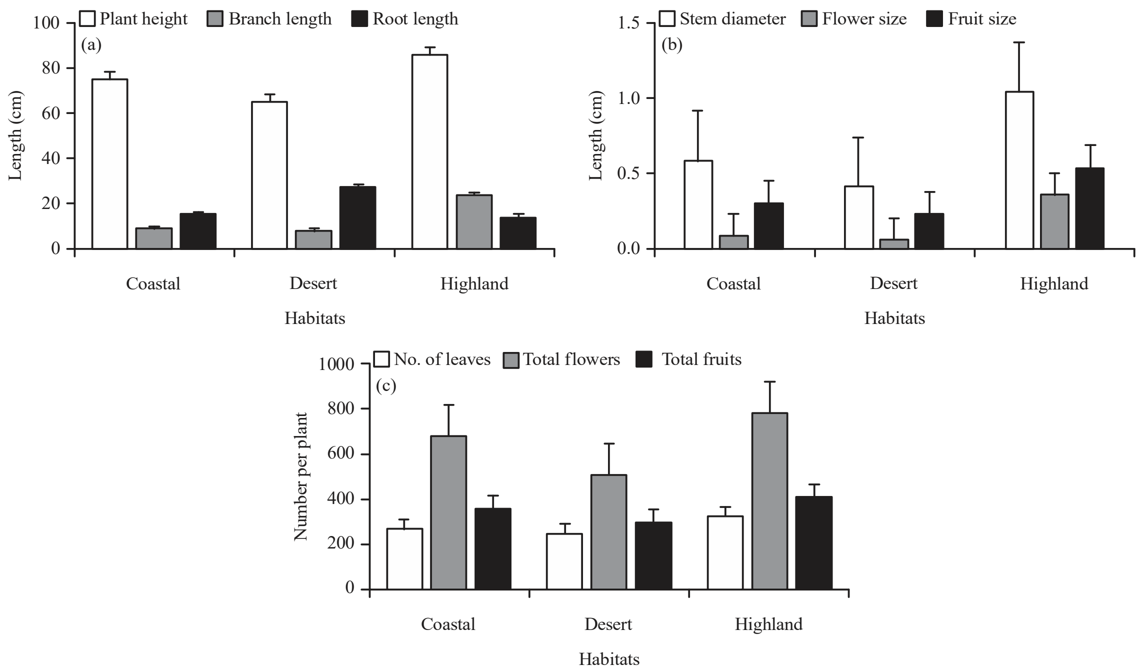

Fig. 3(a-c): Morphological variations (mean±SD) in *Dipterygium glaucum* populations recorded at three different habitats, (a) Plant height, branch length and root length in coastal, desert and highland habitats, (b) Variation in flower, fruit size and (c) Variation in number of leaves, flowers and fruits per plant

Table 2: Proportion of explained variance (%) of growth parameters of *Dipterygium glaucum* along different axis of principal component analysis

Total variance explained								
Initial eigenvalues			Extraction sums of squared loadings			Rotation sums of squared loadings		
Total	Variance (%)	Cumulative (%)	Total	Variance (%)	Cumulative (%)	Total	Variance (%)	Cumulative (%)
8.065	73.323	73.323	8.065	73.323	73.323	4.827	43.881	43.881
1.047	9.522	82.845	1.047	9.522	82.845	4.286	38.964	82.845
0.914	8.311	91.155						
0.531	4.829	95.984						
0.207	1.881	97.865						
0.137	1.244	99.110						
0.050	0.457	99.567						
0.024	0.214	99.780						
0.012	0.111	99.892						
0.010	0.092	99.984						
0.002	0.016	100.000						

Extraction method: Principal component analysis

types. While a reverse trend was observed for root diameter where roots of coastal plants were 6 times thicker than the desert plants (Fig. 4a and b).

PCA analysis: The PCA after varimax rotation, extracted two PC factors with eigenvalues >1 explaining 82.845% of the variance (Table 2). The PCs plots by sampling site for the different morphological characters for the two PCs are shown in Table 3. The PCI which showed 73.323% of the total variation was highly positively correlated with traits such as total height, stem diameter, fruit size, number of leaves, except the root length which was negatively correlated with PC 1. Loadings on PC 2 which showed 9.522% (Table 2) of the total variation was positively correlated with traits like root length and flower size and negatively with root diameter.

The biplot of the PCA, clearly segregates the three distinct ecosystems (Fig. 5) as they formed non-overlapping groups and showed a considerable phenotypic variability. The high and positive loading of Al Sifah highland variants on PC1 (Fig. 5), which is positively correlated (Table 3) with most

Table 3: Scores of variance of morphological characters along the first two principal axes of a PCA

	Component	
Component matrix[a]	1	2
Fruit size	0.966	0.086
Height of plant	0.965	-0.122
Stem diameter	0.948	0.123
Internode length	0.935	0.231
Total leaves	0.927	0.099
Branch length	0.914	0.184
Flowers	0.902	0.036
Root diameter	0.846	-0.420
Root length	-0.706	0.533
Fruits	0.608	-0.325
Flower size	0.579	0.588

Extraction method: Principal component analysis, a: 2 components extracted

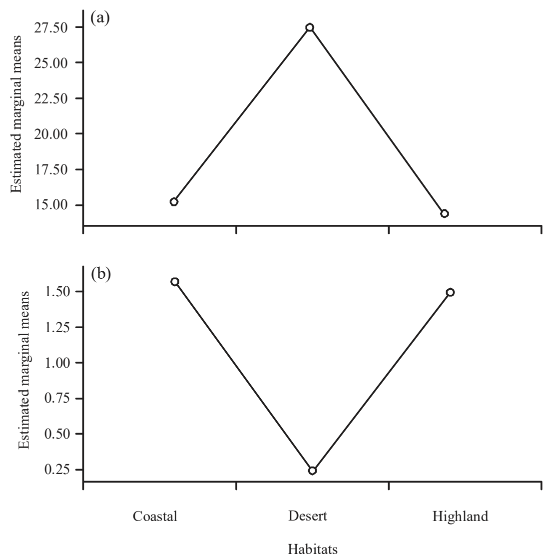

Fig. 4(a-b): Variations in estimated marginal means of (a) Root length and (b) Root diameter from coastal, desert and highland populations

of the growth parameters suggested *D. glaucum* thrived best in this particular habitat and produced robust individuals. Negative values on PC1 for the water stressed desert morphotypes makes this habitat the least favorable for most of the vegetative and reproductive traits except for root length, which was positively correlated with PC2. The loading of coastal morphotypes on the lower positive and negative sides of the PC1 suggested this habitat is not as favorable as highland conditions.

As the correlation among the growth parameters in the biplot is indicated by the directional vectors, clearly a strong correlation (Fig. 5) between the plant height, total flowers, total fruits, number of leaves, stem diameter, branch length can be observed as the angles between the directional vectors were at <90°. Root length was negatively correlated with most of other growth parameters as the angles among the directional vectors are at >90°. The PCA revealed that most of the morphological characters showed the highest value in the Al Sifah highland, except for the root diameter, which was the thickest in coastal morphotypes and root length which was longest in desert plants.

Chlorophyll content: A smaller leaf area and a seasonal leaf fall in dry conditions in this plant is compensated by occurrence of a photosynthesizing chlorenchyma tissue below the epidermis of stem. The content of total chlorophyll varied among different habitats and was 1.24 mg g^{-1} of the leaf fresh weight in highland plants, 1.127 mg g^{-1} in desert plants and 1.06 mg g^{-1} of the leaf fresh weight in coastal plants under increased salinity.

The content of chlorophyll-a was significantly greater than that of chlorophyll-b in all variants. Increased salinity at beach marginally decreased the chlorophyll-b content as compared to highland and desert conditions.

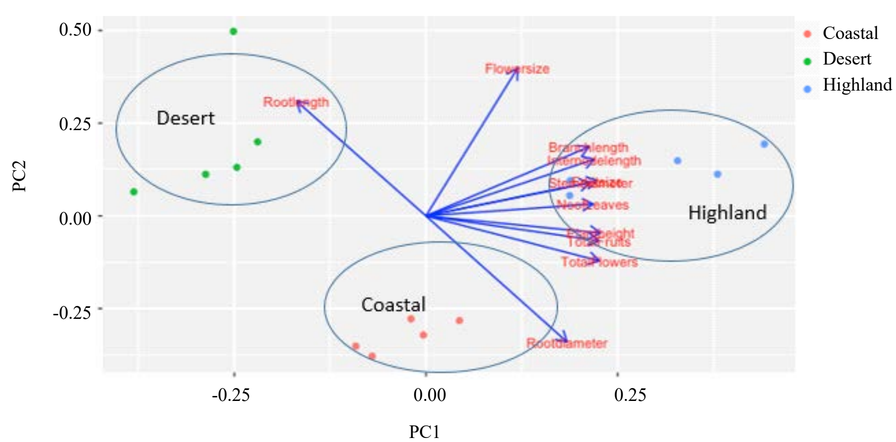

Fig. 5: Biplot representation of the scores on the first two axes of the principal component analysis of 11 morphological characters of *Dipterygium gluacum* across coastal, desert and highland habitats

Table 4: Antibacterial activity of *Dipterygium gluacum* against 4 bacterial strains

	Inhibition zones (mm)			
	Gram-positive		Gram-negative	
Habitat	*Bacillus subtilis*	*Staphylococcus aureus*	*Pseudomonas aeruginosa*	*Escherichia coli*
Coastal	20 mm	0	30 mm	0
Desert	10 mm	0	10 mm	0
Highland	17 mm	0	25 mm	0

Total phenolic content: The total phenolic content of the methanolic extract of the plants collected from desert was 65.78 and 68.35 mg g^{-1} GAEs for highland plants, while for coastal plants an increased total content of 73.2 mg g^{-1} GAEs was observed.

Antimicrobial activity: The antimicrobial activity of the extracts of *Dipterygium glaucum* was studied against four pathogenic bacterial strains (Table 4), 2 Gram-positive (*Bacillus subtilis*, *Staphylococcus aureus*) and 2 Gram-negative (*Escherichia coli* and *Pseudomonas aeruginosa*). Methanolic plant extracts from different habitats exhibited antibacterial activity against *B. subtilis* and *P. aeruginosa* (Table 4). Variation in inhibition zones was observed across habitats, where coastal ecotypes exhibited maximum inhibition and least was observed in Al Sifah highlands. Inhibition was more for Gram-negative *P. aeruginosa* as compared to Gram-positive *B. subtilis*. No inhibition was observed against both *S. aureus* and *E. coli.*

DISCUSSION

By exhibiting phenotypic plasticity, a plant species produces different morphotypes according to prevailing environmental conditions. The adaptive role of phenotypic plasticity in various plant species has been recognized by different studies[29,30]. A range of suitable habitats for the growth of *Dipterygium glaucum* has been revealed by this study and this species exhibited variability in its morphological characters under the influence of varied environmental conditions.

The results of MANOVA confirmed that environmental factors influenced the morphological differences between the three populations of *D. glaucum* across its range. According to earlier studies[31-34], plant species demonstrated local adaptation along latitudinal and elevation gradients. The PCA revealed that the Al Sifah high altitude conditions were more favorable to most of the growth parameters (i.e., both vegetative and reproductive), there by indicating better growth conditions in terms of moisture availability and slightly lower temperatures. The MANOVA results further revealed that the coastal habitat conditions were relatively better for the growth of *D. glaucum* as compared to the inland sand dunes, where most of the characters were minimally expressed. Plasticity plays an important role in adaptive responses to the changing environment as it allows a plant to express maximally in terms of phenotype under optimal conditions and tolerate the harsh environment as suboptimal conditions[35,36].

The results of principal component analysis supports the fact that the differences recorded in the multi-variate analysis (MANOVA) were real differences that did not occur simply by randomized chance. Striking phenotypic and physiological differences between two ecotypes has been recorded and documented by numerous studies[37-40].

Though *Dipterygium glaucum* is a sand dune-forming species of high ecological importance in view of desert vegetation restoration and conservation, species suffers from severe aridity, where the lack of water and very high temperature can affects its growth performance as compared to coastal and highland variants. Different plant species under water stress recorded reduction in stem diameter[41]. On the contrary, root length was almost double in sand plain habitats as compared to beach and highland ecotypes. Arid desert plants develop taproots that descend to deeper soil layers to gather water that is far down, producing few lateral roots within top 1m of soil with fine small lateral roots produced in deeper soil layers[42]. Longer root length under water stress conditions has been observed in previous studies[42,43]. Root diameter increased profoundly under salinity stress due to succulence of cortex, resulting in increased volume of vacuoles which permits accumulation of larger amount of water and dissolved ions[44]. Similar halophytic response has been recorded by earlier studies[45].

Decrease in chlorophyll content per unit of leaf area under increased salinity was observed in our study. There is an overwhelming evidence of salinity stress affecting the photosynthetic enzymes, chlorophyll and carotenoids content[45-47]. Accumulation of ions of different salts induces an inhibitory effect on the biosynthesis of the different fractions of chlorophyll thereby reducing the overall chlorophyll and carotenoids content[48].

Higher total phenolic content was recorded in *D. glaucum* coastal plants as compared to the other ecotypes. Accumulation of phenolic compounds under salt stress in plants is reported by many studies[49-53]. In order to overcome oxidative stress due to accumulation of reactive oxygen species under salt stress, plants develop adaptive mechanisms in order to reduce the oxidative damage. The mechanism involves production of phenolic compounds to in order to scavenge the free radicals.

The plant extract from different habitats possess antibacterial activity against some of the tested organisms. Previous studies have documented antimicrobial activity in *Dipterygium glaucum*[20,54]. The diameter of inhibition zones varied among different ecotypes suggesting different phytoconstituents accumulated under different environmental conditions under different habitats. Maximum inhibition was observed for coastal morphotype suggesting more bio-active compounds being produced by the plants under salinity stress. Variation in antimicrobial activity in plant extracts across different habitats has been documented by many studies[55,56].

CONCLUSION

Significant morphological plasticity among ecotypes of *Dipterygium glaucum* exist along different habitats. This species exist under a range of habitats but highland conditions are favorable to most of the vegetative and reproductive traits indicating better growth conditions at this habitat as compared to the salinity stressed coastal habitat and water stressed sand plains. Under the influence of various abiotic stresses, this species undergo morphological and physiological adaptations in order to survive.

SIGNIFICANCE STATEMENT

This study reinforced and justified the use of this species as a herbal remedy in traditional medicine as the methanolic extract of the plant exhibited antimicrobial activity against *B. subtilis* and *P. aeruginosa* and an adequate amount of total phenolics were observed. Being part of diet of important rangeland animals like Gazelle and an important species of community structure involved in the restoration of desert vegetation this study suggests that *Dipterygium gluacum* is morphologically and physiologically accustomed to variation in water and temperature and adapts itself to diverse environment conditions. This study will provide useful insight to researchers to understand the adaptations undergone by plants of arid zones to survive under harsh environmental conditions and aid in conservation of the flora of arid zones.

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