Research article

Climate and soil factors co-derive the functional traits variations in naturalized downy thorn apple (*Datura innoxia* Mill.) along the altitudinal gradient in the semi-arid environment

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ABSTRACT

Plant functional traits are consistently linked with certain ecological factors (i.e., abiotic and biotic), determining which components of a plant species pool are assembled into local communities. In this sense, non-native naturalized plants show more plasticity of morphological traits by adopting new habitat (an ecological niche) of the invaded habitats. This study focuses on the biomass allocation pattern and consistent traits-environment linkages of a naturalized *Datura innoxia* plant population along the elevation gradient in NW, Pakistan. We sampled 120 plots of the downy thorn apple distributed in 12 vegetation stands with 18 morphological and functional biomass traits during the flowering season and were analyzed along the three elevation zones having altitude ranges from 634.85 m to 1405.3 m from sear level designated as Group I to III identified by Ward's agglomerative clustering strategy (WACS). Our results show that many morphological traits and biomass allocation in different parts varied significantly ($p < 0.05$) in the pair-wise comparisons along the elevation. Likewise, all plant traits decreased from lower (drought stress) to high elevation zones (moist zones), suggesting progressive adaptation of *Datura innoxia* with the natural vegetation in NW Pakistan. Similarly, the soil variable also corresponds with the trait's variation e.g., significant variations ($P < 0.05$) of soil organic matter, organic carbon, Nitrogen and Phosphorus was recorded. The trait-environment linkages were exposed by redundancy analysis (RDA) that was co-drive by topographic (elevation, $r = -0.4897$), edaphic (sand, $r = -0.4565$ and silt, $r = 0.5855$) and climatic factors. Nevertheless, the influences of climatic factors were stronger than soil variables that were strongly linked with elevation gradient. The study concludes that *D. innoxia* has adopted the prevailing environmental and climatic conditions, and further investigation is required to evaluate the effects of these factors on their phytochemical and medicinal value.

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1. Introduction

Human activities have caused the plants to spread and propagate, resulting in a rapid rise in the distribution and quantity of alien species that progressively naturalized in non-native environments [1]. It is believed that certain plant communities are more vulnerable to being occupied by alien species due to empty or deficient resources [2]. Similarly, studies suggested that disturbance may be a prerequisite for invading alien species [3], or community characteristics such as productivity, dominance, or diversity may influence alien species' vulnerability [4]. Alien species' success is dependent not only on the invasibility of the plant community but also on the qualities; hence generalizations about community factors that drive invasion have failed [2].

Plant functional traits are attributes associated with a plant's capacity to obtain, use, and maintain available resources [5]. Leaf characteristics such as specific leaf area (SLA), specific leaf mass, and plant canopy height are often included [6]. It would be beneficial to assess plants' adaptability to changing environments to uncover plant conservation approaches and reactions to various environmental factors [7]. Furthermore, biomass is the basic quantitative characteristic that contributes to plant productivity and is the energy source that maintains the functioning of an ecosystem [6]. The plant biomass distribution law describes a plant's growth and metabolic activity rate, which determines its organs' functional qualities [8]. Environmental factors influence plant biomass distribution, affecting various plant growth processes [9]. Consequently, plant phenotypic characteristics may be potential confounders in biomass allocation analyses [10–12]. The plant must maintain a balanced biomass distribution between the shoot and the root to sustain basic physiological activities, accomplish normal development [10], and optimize resource allocation to increase its capacity with the changing environmental conditions [13,14]. In addition, the plant species produces higher biomass in native habitats under varying environmental conditions and pre-adapts species to become alien and naturalized elsewhere [15].

It is vital to note that altitudinal gradient significantly predicts microclimatic changes, determining plant functional traits [16,17]. The altitudinal gradient is linked to several factors, including reduced resource availability, shorter growing seasons, lower microbial activity, lower human population densities, and harsher climatic conditions [18]. As a result, altitudinal gradient predominately influences plants' functional qualities [5]. Plant pre-adaptation techniques include choosing stress-tolerant genotypes, progressive exposure to cold hardiness, and intraspecific hybridization with cold-tolerant species, which are important drivers of alien species over elevational gradients [19]. In addition, adaptations in an alien species' PFTs aid its capacity to live and reproduce in various climates and edaphic habitats [20–22]. The trait plasticity and adaptive divergence are common in invasive plants. However, these processes have yet to be well studied in subtropical species [23].

Datura innoxia (Mill.) Known as the downy thorn apple, one of the most ubiquitous subtropical species [24], rapidly expanding into high elevation zones, was chosen as the model plant in this research. Downy thorn apple belonging to the Solanaceae family is a naturalized species found in world dry and hot climatic regions. *Datura's* spread from North America and was limited to the United States and Mexico but recently has propagated and invaded many other regions of the world [25]. *Datura* was once classified as part of the genus *Brugmensia*, but now it is considered a distinct and medicinally important plant [26]. Along with deadly henbane, mandrake,
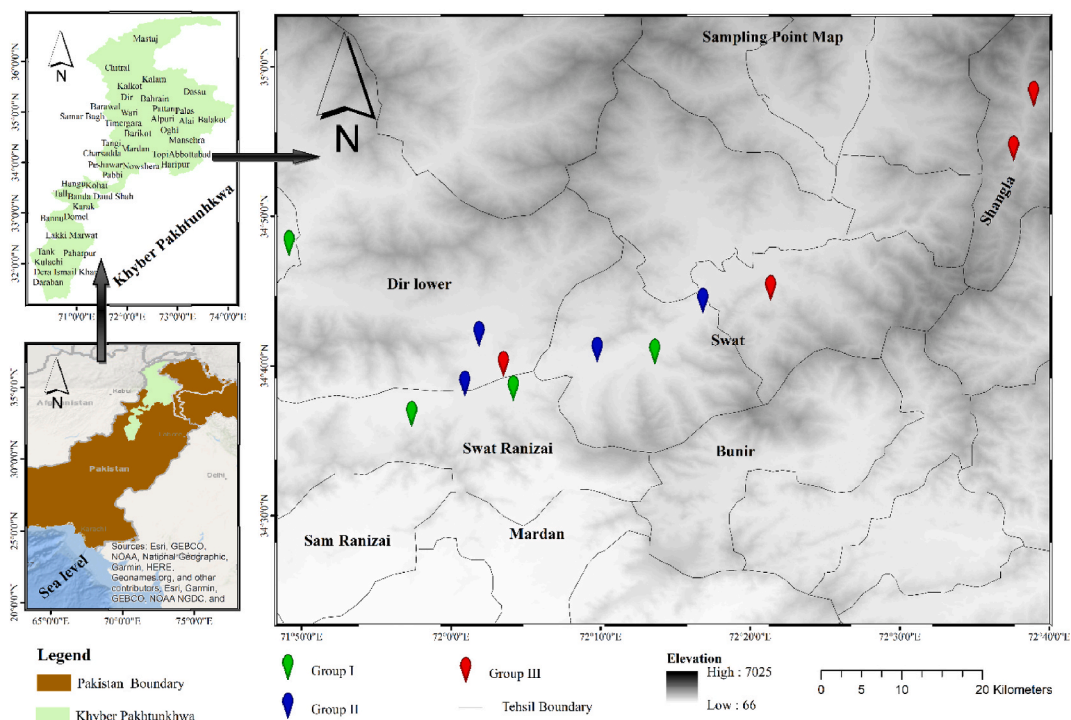

Fig. 1. Distribution of the sampling sites along an altitudinal gradient in the study area.

and nightshade, *Datura* is a typical "witches' herb," well-known for its critical ingredient in magical potions and witches' brews [27]. Chemically, all *Datura* plants include atropine alkaloids (i.e., hyoscyamine, atropine, and scopolamine), primarily found in their seeds and flowers and have been used as hazardous material and narcotics in some communities [28]. There would be 5:1 poison diversity among the plants, and the toxic quality of a specific plant would be determined by its age, environment, and existing climatic conditions. Datura is exceedingly dangerous as a medication but also has various medical benefits; e.g., in many traditional civilizations, its usage is deemed essential due to specific alkaloids [27]. *D. innoxia* (atropine alkaloid) and *D. ferox* (scopolamine 98–100% alkaloids), which are toxic to cattle, are the most frequent species generally found in South America and Europe [29]. However, research on its ecological relationships, distribution patterns, and functional trait variations is scarce.

Life-history features, herbivory sensitivity, and other similarities between native and invasive species are projected to enhance efficient resource utilization in naturalized species [30]. Therefore, this research explored plant functional traits of naturalized *D. innoxia* with elevation in the Malakand division of Khyber Pakhtunkhwa, Pakistan. The plant's morphological and biomass parameters were analyzed under the hypothesis that plant functional traits correlate with resource acquisition and conservation, as well as being influenced by environmental factors. This suggests that specific critical ecological variables may affect variations in functional traits along the altitudinal gradient. As a result, we predicted features like biomass allocation to various plant organs and morphological traits that reflect resource efficiency. Our aims were 1) to assess the communities and related environmental variables associated with *D. innoxia* population and morphological traits, 2) to assesses the association between plant traits and environmental factors along a steep elevation gradient coupled with environmental and climatic factors, 3) to find out whether local climatic conditions act as barrier, making some traits non-viable and therefore preventing the establishment of certain naturalized plant species present in the regional pool.

2. Materials and methods

2.1. Study area

The study was conducted in the Malakand division, which has seven districts and is one of the major divisions in Khyber Pakhtunkhwa (KP), Pakistan (Fig. 1). The area lies at latitude of 34°32′26.18″N to 36°38′5.88″N and at longitude of 70°1′36.36″E to 71°36′36.41″E. The area spans largest division of the province occupying 40% of the land and 25% of the population [31]. A semi-arid climate characterized the sampling sites, with an annual average temperature ranging from 4 °C to 40.5 °C and rarely below 1 °C or above 44 °C, and average annual precipitation of 71 mm (Fig. 2). Similarly, the relative humidity ranges from 50 to 65%, with maximum recorded in July and August while minimum in May and June (Fig. 2). The sampling sites selected were found to be dominated by *D. innoxia,* in association with *Cannabis sativa, Parthenium hysterosporus, Mirabilis jalapa, Xanthium strumarium,* and *Medicago denticulate.* In order to conduct sampling in the study area, three elevation zones were designated. These were categorized as follows: Group I represented lower elevation zones (634.85 ± 27 m above sea level), encompassing plain areas with sub-tropical conditions. Group II denoted middle elevation zones (924.4 ± 18.49 m asl), characterized by a transition from sub-tropical to temperate conditions. Group III comprised higher elevation zones (1405.3 ± 59 m asl), predominantly consisting of temperate areas (see Fig. 3).**2.2 Experimental design and sampling procedure**.

The study recorded twelve morphological, biomass parameters and their variations in *D. innoxia* at various elevation zones of the Malakand division by selecting 120 permanent plots (each of $10 \times 10 = 100$ m^2). Initially, we classified the 120 plots distributed in 12 vegetation stands into three groups using Ward's agglomerative cluster comprising 40 plots ($4 \times 10 = 40$ plots) in each group (Fig. 4). One hundred and twenty plants were randomly marked for biomass and morphological traits measurements by selecting forty individuals at each elevation zone (group). Based on the elevation gradient *D. innoxia* population in the sample, three ($5 \times 5 = 25$ m^2) quadrates were established in each stand for collecting phytosociological data by following Bürzle et al. [32], to calculate the structural attributes, including the importance value index (IVI). The community traits, i.e., height, cover, and aboveground biomass, were determined using a measuring tape and electrical balance of accuracy of 0.01g. The biomass for each parameter was measured by
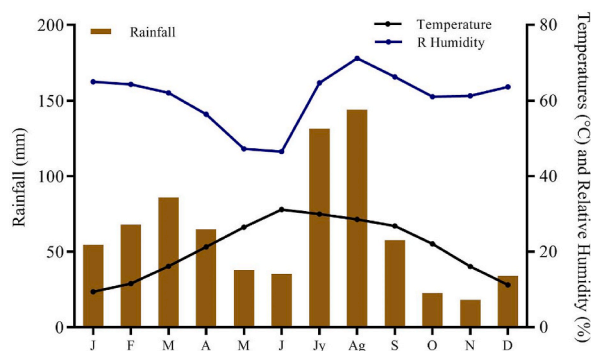

Fig. 2. Climatic diagram exhibited mean annual rainfall (mm), mean monthly temperature (C°) and relative humidity (%) records at the sampling sites (data presented is taken from Swat, Dir, Timergara and Malakand meteorological stations (1965–2021).
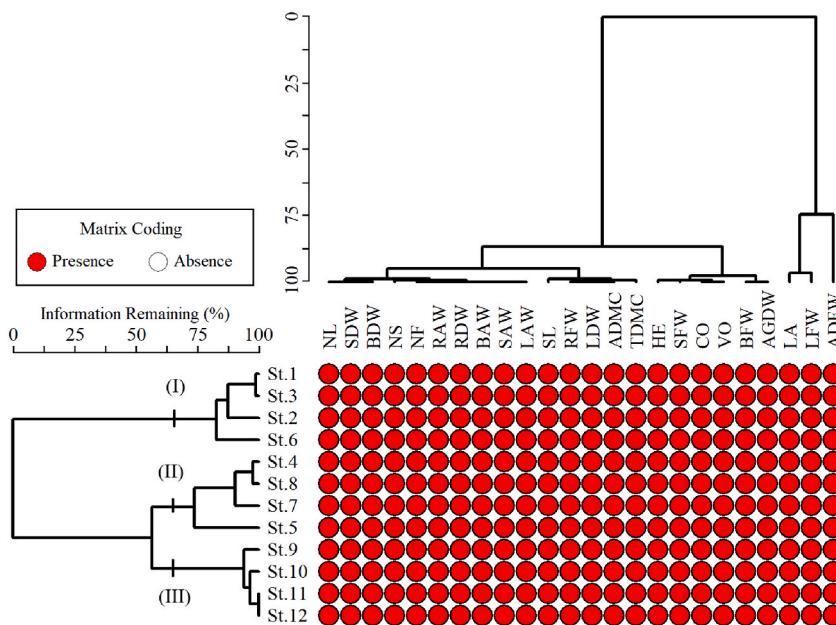
Fig. 3. Dendrogram of *Datura innoxia* dominated plots: Group-I – *Datura-Parthenium community*, Group-II– *Datura-Xanthium community,* and Group-III – *Datura-Cynodon community*. Numbers enclosed in parentheses signify the groupings used in analysis (see Materials and methods section).

Fig. 4. *Datura innoxia* well grown in bloom stage (A) and stand of sampling (B).

selecting 10 well-growing *D. innoxia* plants in each stand after measuring the phytosociological traits. The aboveground parts (i.e., stem, branches, leaves, flowers, and fruits) were cut off and put into numbered, tagged, or labeled envelopes following [33]. Plant biomass in the plot was measured after sorting the parts into different categories in the oven for 72 h at 65 °C.

2.2. Measurement of leaf traits profile

The leaf area of *D. innoxia* was measured using a measuring tape. The specific leaf area (SLA) was computed using the following equation:

$$SLAi = \frac{DWi}{Li * Wi}$$

Where *SLA*i is the specific leaf area of the *i*th leaf (g/cm^2), *DW*i, *L*i, and *W*i are dry weight (g), length (cm), and width (cm), respectively, of each rectangular leaf section. Finally, the leaves were packed into an envelope and dried in an oven for 72 h at 65 °C, and the dry weight was recorded. The SLA was expressed as the ratio of LALA to leaf dry weight [34].

2.3. Soil analysis and climate data acquisition

Soil samples were collected from root zone of all the twelve sites from the center of each 10 × 10 m plots at a depth of 30 cm and mixed thoroughly to obtain three replicates (*n = 3*) per site. The samples were dried and sieved through a mesh (pore size: 2 mm) to

remove roots and other debris and transported to the laboratory for soil textural and physiochemical (i.e., soil nutrients) properties. After completing the process, wilting point (cm^3), field capacity (mm/m), electrical conductivity (mm/hr), available water, saturation, and soil bulk density ($g.cm^{-3}$) were calculated. The pH of soil samples was determined using 1:5 soil water suspensions described by Ref. [35]. A hydrometer was used to measure the percent of silt, sand, and clay following [36]. Acid-base neutralization was used to assess the lime concentration in soil [37]. The concentration of phosphorus ($mg.Kg^{-1}$) was calculated following [38], whereas the $K_2Cr_2O_7$ technique was used to determine the amount of organic matter in the soil [39]. Total nitrogen (TN %) was assessed using the micro-Kjeldahl method, which comprises digestion with concentrated H_2SO_4 and determination of NH_3 using the indophenol blue method on an auto-analyzer (Kjeltec TM 2100, FOSS, Sweden) [40]. The NaOH fused flame spectrum technique was used to determine total potassium (TK %) (Digital Flame Analyzer, Model 2655–00, Cole-Parmer Instrument, Chicago, USA). For precise spatial location and other important topographical variables (i.e., elevation, slope, and aspect), we used the RedHen DX-GPS system, altimeter, and magnetic compass, respectively.

2.4. Statistical analysis

One-way analysis of variance (ANOVA) followed by Tukey's HSD means comparisons were used for testing differences in the plant functional traits and associated environmental variables. The significance level at $P < 0.05$ was settled for testing the significant variation. The linear regression model investigated the relationship between elevations and plant functional traits following [41]. The discriminant plant functional characteristics and relationships of topographic, soil physiochemical, and bioclimatic factors were studied using redundancy analysis (RDA). The RDA was applied to the previously selected discriminant morphological traits and the environmental and bioclimatic variables (Bio-1 to Bio-19) extracted in the compatible format using spatial location data of each vegetation stand from the Worldclim database (http://www.worldclim.org/current). With the step function in the vegan package [42], non-significant bioclimatic variables were sequentially removed for robust results. We used PC-ORD ver.6.0 software [43] to analyze the relationship between morphological traits and environmental variables.

3. Results

3.1. Vegetation analysis and

Three vegetation groups were identified in the stands where *Datura innoxia* was abundant in NW Pakistan (Table 1). The recognized vegetation groups corresponded well with particular environments differing in ecological conditions and, consequently, floral diversity (Fig. 4). Group I was formed by *the Datura-Parthenium* community, Group II represent*ed the Datura-Xanthium* community*,* and Group III *represented the Datura-Cynodon* community. According to the surveyed vegetation, 20 species belonging to 14 families and 15 genera coexisted with *D. innoxia*. Among the associated species, four exotic invasive species–*Cannabis sativa* L., *Parthenium hysterophorus* L., *Cynodon dactylon* (L.) Pers. and *Xanthium strumarium* L. were consistently present. Other neighbor species with importance values (IV) less than 5% in the vegetation stands were *Chenopodium album* L., *Persicaria maculosa* S·F.Gray, *Heliotropium indicum* L., *Silybum marianum* (L.) Geartn, *Verbesina encelioides* (*Cav.*) *Benth. & Hook. f. ex A. Gray, Chenopodium album* L., *Ajuga bracteosa* Wall. ex Benth., *Origanum vulgare* (Linn), and *Tagetes minuta* L. vegetation stands dominated by the *Datura-Parthenium* community (Group I) were the species-poor habitats, where only 7 coexisting species were recorded. In contrast, the highest numbers of the coexisting

Table 1
Importance value index (IVI) of plant species distributed in three major vegetation groups of *Datura innoxia*.

Plant Botanical names	Group I	Group II	Group III
Datura innoxia (Mill.)	47.39 ± 6.0	44.75 ± 1.61	43 ± 4.77
Cannabis sativa L.	9.78 ± 1.34	6.8 ± 2.5	5.20 ± 2.3
Parthenium hysterosporus L.	16 ± 5.35	5.9 ± 4.3	10.3 ± 7.8
Chenopodium album L.	2.1 ± 2.1	5.93 ± 3.4	3.94 ± 3.9
Amaranthus viridis L.	*-	1.34 ± 1.3	*-
Heliotropium indicum L.	*-	2.28 ± 2.1	1.95 ± 0.77
Cynodon dactylon (L.) Pers.	14.8 ± 1.95	9.81 ± 1.5	13.47 ± 5.0
Persicaria maculosa S·F.Gray	2.53 ± 2.5	1.57 ± 1.5	*-
Silybum marianum (L.) Geartn	*-	2.44 ± 0.81	*-
Xanthium strumarium L.	7.25 ± 4.62	11.93 ± 4.6	*-
Ajuga bracteosa Wall. ex Benth.	*-	*-	3.89 ± 3.8
Origanum vulgare (Linn)	*-	*-	2.26 ± 2.2
Artemisia capillaris Thunb.	*-	*-	1.54 ± 1.5
Chenopodium album L.	*-	1.14 ± 1.1	*-
Verbesina encelioides (Cav.) Benth.& Hook.f. ex A. Gray	*-	3.68 ± 2.7	*-
Sonchus asper (L.) Hill	*-	1.31 ± 0.7	*-
Rumex hastatus D. Don	*-	*-	1.97 ± 1.9
Tagetes minuta L.	*-	*-	4.98 ± 2.2
Plantago lanceolata	*-	*-	1.44 ± 0.9
Heliotropium indicum L.	*-	*-	5.92 ± 2.5

Note: values are presented as Mean ± Standard Error; *- (Absence of a species).

species (13 species each) were observed in Groups II and III, respectively.

3.2. Environmental and soil variables

The elevation of the habitats sampled ranges from 634.85 ± 27 m to 924.4 ± 18.49 m in the three contrasting habitats (Group I to III) and varied significantly across the elevation gradient (F = 141, P < 0.05). However, the spatial variable, i.e., Latitude and Longitude, did not vary significantly, showing less variation while the aspect degree ranges from $105.75 \pm 41°$ to $144.5 \pm 52.9°$. In the soil variables, silt particles vary significantly compared to sand and clay (ANOVA; $F = 3.35, P \leq 0.08$). The soil nutrients organic matter (ANOVA; $F = 5.19, P \leq 0.03$), organic carbon (ANOVA; $F = 5.18, P \leq 0.03$), nitrogen (ANOVA; $F = 4.98, P \leq 0.03$) and phosphorus (ANOVA; $F = 4.01, P \leq 0.06$) varies significantly coupling with elevation gradient to sustained *D. innoxia* communities in the region (Table 2). Similarly, the quantities of organic matter, organic carbon, Nitrogen and Phosphorus were higher in Group I, followed by Group II and III (Table 2).

3.3. Morphological and biomass traits

The average height, volume, and cover of the *D. innoxia* population showed a decreasing trend across the elevation. It decreased by 4.42%, 10.35%, and 8.96%, respectively, with changes in elevation from Group I-III, while density gradually increased by 38.48% (Table 3). Similarly, the leaf area, aboveground dry biomass, and dry root biomass decreased by 13.05%, 40.32%, and 26.30%, respectively. The number of leaves increased by 39.60%, while stem length, the number of flowers, leaf length, leaf width, and leaf area increased firstly and then decreased by 16.17%, 18.99%, 27.70%, 6.65%, and 30.05 %, respectively. The biomass allocation of organs in *D. innoxia* was significantly different ($P \leq 0.05$), having higher shoot biomass than root (Table 3). The traits displayed relationship with the elevation gradient, some of which shows significant relation i.e. number of leaves/plant (Adj $R^2 = 0.15$, P < 0.05), stem length/plant (Adj $R^2 = -0.08$, P < 0.05), leaf area/plant (Adj $R^2 = -0.08$, P < 0.05), plant height/plant (Adj $R^2 = 0.06$, P < 0.05), leaf width/leaf (Adj $R^2 = 0.28$, $P < 0.05$), root dry weight (Adj $R^2 = 0.06$, P < 0.05), stem dry weight/plant (Adj $R^2 = 0.06$, P < 0.05), below ground dry weight/plant (Adj $R^2 = 0.32$, P < 0.05), leaves dry weight/plant (Adj $R^2 = 0.04$, $P < 0.05$), above-ground dry weight/plant (Adj $R^2 = 0.11$, P < 0.05) and total dry weight/plant (Adj $R^2 = 0.15$, P < 0.05) as depicted in Fig. 5. All the vegetative traits showed the maximum mean value at 500 m and minimum at 1500 m altitude.

3.4. Morphological-biomass traits linkages with the abiotic environment

The traits of *D. innoxia* were influenced by environmental and soil variables showing 82.5 percent of the total variance (Table 4 & Fig. 6). The major contributing axis is axis explaining 60.1%, followed by axis 2, which has 15.5% and 9.9% of the ecological variation, respectively. The eigenvalues for axis 1, 2, and 3 were 14.41, 3.73, and 2.37, respectively. Therefore, the information explained by axes 1, 2, and 3 was used to analyze the relationship between plant functional traits and environmental factors. The elevation had the highest negative correlation on the first axis in the RDA ordination, followed by the sand percentage, with correlation coefficients of

Table 2
Characteristics of abiotic factors of the sampling sites (i.e., topographic, edaphic, and soil) of the three groups based on elevation gradient. Given are arithmetic means and the standard errors (SESE). The different alphabet superscript letters indicate significant differences in the means (one-way ANOVA test, $P < 0.05$).

Variable	Unit	Codes	Group-I Mean ± SE	II Mean ± SE	III Mean ± SE	F-value	p-value
Latitude	(°)	Lat	34.68 ± 0.41	34.68 ± 0.01	34.78 ± 0.04	2.40	0.15
Longitude	(°)	Long	72.02 ± 0.06	71.92 ± 0.15	71.79 ± 0.24	0.42	0.67
Elevation	M	Elev.	634.85 ± 27^a	924.4 ± 18.49^b	1405.3 ± 59^c	141.51	0.00
Aspect angle	(°)	AA	144.5 ± 52.9	119.25 ± 14.61	105.75 ± 41	0.24	0.79
Clay	%	Cl	7.9 ± 1.37	9.3 ± 3.71	3.9 ± 1.68	1.27	0.33
Silt	%	Si	63.8 ± 4.99^a	41.3 ± 11.67 ab	31.6 ± 12.18^b	3.35	0.08
Sand	%	Sa	28.05 ± 6.2	49.4 ± 13.76	54.5 ± 10.87	2.65	0.12
pH	–	pH	7.75 ± 0.11	8.1 ± 0.12	7.97 ± 0.14	1.70	0.24
Organic Matter	%	OM	0.52 ± 0.1^a	$0.50 \pm 0.13a$	0.095 ± 0.06^b	5.19	0.03
Organic Carbon	%	OC	0.3 ± 0.07^a	$0.29 \pm 0.075a$	0.05 ± 0.03^b	5.18	0.03
Lime	%	Lim	6.62 ± 3.03^a	5 ± 3.36^a	3.7 ± 1.16	0.29	0.76
Nitrogen	mg.Kg^{-1}	Ni	0.025875^a	0.025 ± 0.006^a	0.005 ± 0.003^b	4.98	0.03
Phosphorus	mg.Kg^{-1}	P	12.49 ± 1.2^a	9.286 ± 2.07^a	6.37 ± 1.06^b	4.01	0.06
Potassium	mg.Kg^{-1}	K	114 ± 25.59	110.5 ± 19.9	106 ± 33.1	0.02	0.98
Electrical Conductivity	mm/hr	EC	359.31 ± 30	354.9 ± 85.32	566.15 ± 138	1.59	0.26
Total Dissolve Solid	ppm	TDS	229.95 ± 19	226.98 ± 54.51	362.33 ± 88	1.59	0.26
Wilting Point	cm^3	WP	0.069 ± 0.01	0.089 ± 0.011	0.071 ± 0.01	0.54	0.60
Field Capacity	mm/m	FC	0.27 ± 0.009	0.23 ± 0.03	0.21 ± 0.03	1.58	0.26
Bulk Density	g.cm^{-3}	BD	1.52 ± 0.03	1.57 ± 0.07	1.7 ± 0.09	1.72	0.23
Saturation Point	g.cm^{-3}	SP	0.42 ± 0.014	0.41 ± 0.03	0.36 ± 0.03	1.72	0.23
Available Water	g.cm^{-3}	AW	2.16 ± 0.079	1.68 ± 0.25	1.66 ± 0.23	1.92	0.20

Table 3
Variation in morphological traits of *Datura innoxia* along the environmental gradient. For the same morphological traits, means followed by different letters (i.e., superscript a and b) are significantly different (*P*-value <0.05), Tukey's contrasts test for multiple comparisons of means, SE =Standard error).

Code	Group-I	II	III	*F*-value	*p*-value
	Mean ± SE	Mean ± SE	Mean ± SE		
$X_{NL/P}$	25.0 ± 2.1[a]	29.6 ± 2.1[a]	34.9 ± 2.5[b]	4.81	0.03
$X_{SL/P}$	37.4 ± 11.2	46.6 ± 12.6	31.3 ± 9.6	0.47	0.64
$X_{NF/P}$	12.9 ± 3.7	8.97 ± 1.4	10.4 ± 1.6	0.63	0.56
$X_{LL/L}$	25.0 ± 3.5	18.1 ± 0.9	18.1 ± 0.9	3.71	0.06
$X_{LW/L}$	18.1 ± 1.8	16 ± 0.96	16.1 ± 1.1	0.76	0.49
$X_{LA/L}$	203.8 ± 19	208 ± 24	177.2 ± 12	0.73	0.51
$X_{PHg/P}$	63.7 ± 7.6	64.9 ± 0.8	60.9 ± 2.05	0.23	0.80
$X_{PCov/P}$	82.5 ± 8.6	62.3 ± 13	75.1 ± 5.3	1.11	0.37
$X_{PVol/P}$	74.7 ± 9.7	56.4 ± 12	67.0 ± 5.16	0.93	0.43
$X_{Pden/S}$	1346.6 ± 27	1414 ± 41	1864.9 ± 63	0.37	0.69
$X_{RDW/P}$	16.9 ± 0.8[a]	13.4 ± 0.5[b]	12.4 ± 0.29[c]	16.21	0.001
$X_{RL/P}$	20.1 ± 1.1	14.5 ± 0.73	13.87 ± 0.4	17.38	2.46E-07
$X_{SDW/P}$	26.2 ± 0.8[a]	21.4 ± 2.1[a]	17.5±2 b	6.02	0.02
$X_{BDW/P}$	32.4 ± 0.8[a]	26.7 ± 1.1[b]	20.3 ± 0.69c	45.69	0
$X_{LDW/P}$	55.2 ± 1.9[a]	36.3 ± 1.2[b]	30.0 ± 1.1c	75.69	0
$X_{RSr/P}$	0.62 ± 0.01	0.59 ± 0.01	0.77 ± 0.01	29.23	5.05E-11
$X_{AGDW/P}$	113.9 ± 2.4[a]	84.5 ± 2.9[b]	67.9 ± 2.7c	74.87	0
$X_{TDW/P}$	91.9 ± 0.84[a]	73.7 ± 1.7[b]	56.5 ± 1.55c	38.80751	3.76E-05

Note: $X_{NL/P}$ (number of leaves/Plant); $X_{SL/P}$ (stem length/Plant); $X_{NF/P}$ (number of flowers/Plant); $X_{LL/L}$ (leaf length/Leaf); $X_{Lw/L}$ (leaf width/Leaf); $X_{LA/L}$ (leaf area/Leaf); $X_{PHg/P}$ (plant height/Plant); $X_{Cov/P}$ (plant cover/Plant); $X_{PVol/P}$ (plant volume/Plant); $X_{pden/S}$ (plants density/Site); $X_{RDW/P}$ (root dry weight/P); $X_{RL/P}$ (root length/P); $X_{SDW/P}$ (stems dry weight/Plant); $X_{BFW/P}$ (branches dry weight/Plant); $X_{LDW/P}$ (leaves dry weight/Plant); X_{RSr} (roots hoot ratio); $X_{AGDW/P}$ (aboveground dry weight/Plant); $X_{TDW/P}$ (total dry weight/Plant).

−0.48 and −0.45, respectively (Table 5). The first axis was positively correlated with silt percentage and phosphorus, with correlation coefficients of 0.58 and 0.59. In the ordination biplot, plant morphological traits and bioclimatic variables are separated. Higher elevation sites were mostly on the right of the ordination plot. They were present under the influence of bioclimatic layers. *D. innoxia* had the most leaves near the origin of the sorting axis, indicating that NL was less affected by environmental factors. Environmental factors significantly impacted the traits LA, LAW, SAW, RFW, SDW, NF, and SL.

In bioclimatic variables, Annual Mean Temperature (Bio-1), Temperature Annual Range (Bio-7), Precipitation Seasonality (Coefficient of Variation) (Bio-15), Precipitation of Wettest Quarter (Bio-16), and Precipitation of Warmest Quarter (Bio 18) were the significant contributors that affect the morphological and biomass traits negatively. Similarly, the climatic variable displays negative correlation along altitude i.e. MYT ($R = -0.92$, $P = 0.01$), AYH ($R = -0.83$, $P = 0.01$) and DLH ($R = -0.81$, $P = 0.01$). In contrast soil variables show non-significant correlation across the elevation gradient except OM % ($R = -0.61$, $P = 0.01$). Likewise, LL/L shows a non-significant correlation across the elevation gradient in plant vegetative traits. Pearson's correlation revealed that the environmental and bioclimatic factors show significant relationships, as depicted in the heat map (Fig. 7). The elevation showed a significant negative correlation with Bio-1, 5, 10, 11, organic matter, and organic carbon (P < 0.05). In addition, the Bio-15 shows a significant negative correlation with Bio-8, 14, 17, 12, 18, 19 and longitude (P < 0.01). Similarly, soil electrical conductivity (EC) significantly correlates with clay percentage, saturation point (SP), field capacity (FC), and available water (AW). In contrast, Bio-4 showed a significant positive correlation with Bio-5, 10, and 11, respectively.

4. Discussion

In the current study, morphological traits plasticity and biomass allocation were assessed along the elevation gradient in changing environmental and soil conditions. These information's provide suitable habitats for the propagation, growth, and collection of such plants for phytochemical and medicinal uses. Our results show that in naturalized habitats where *D. innoxia* is abundant; having variable environmental conditions indicates wide gradients of these factors. However, the communities and associated species were more specific floristically, i.e., having only twenty associated species. We recognized three groups *Datura-Parthenium* community (Group I), *Datura-Xanthium* community (Group II)*, and Datura-Cynodon* community (Group III), which could be distinguished ecologically as well as floristically. The most common co-occurring species in all groups of *D. innoxia* were *Cannabis sativa, Parthenium hysterosporus, Cynodon dactylon,* and *Xanthium strumarium.* The study found that most co-dominant associated species in *D. innoxia* communities were invasive, such as *C. sativa*, *P. hysterosporus*, and *X. strumarium*; the only non-invasive co-dominant species was *Cynodon dactylon*. There have been reports of *Xanthium-Cannabis* communities from neighbouring districts like Mardan Khyber Pakhtunkhwa [44] and the Pothwar region [45]. Moreover, these invasive species have co-dominated other communities, e.g. Refs. [45, 46], reported *P. hysterosporus* and *X. strumarium* growing together in the Boren zone of Ethiopia. Researchers like [47,48], and [49] suggested that invasive plants have led to a decline in species richness and biodiversity in general which provides strength and verify our findings as we have only recorded twenty-two species with the naturalized downy thorn apple in this region.

The morphological features of root, stem, leaves, number of leaves, and biomass components exhibited considerable variations
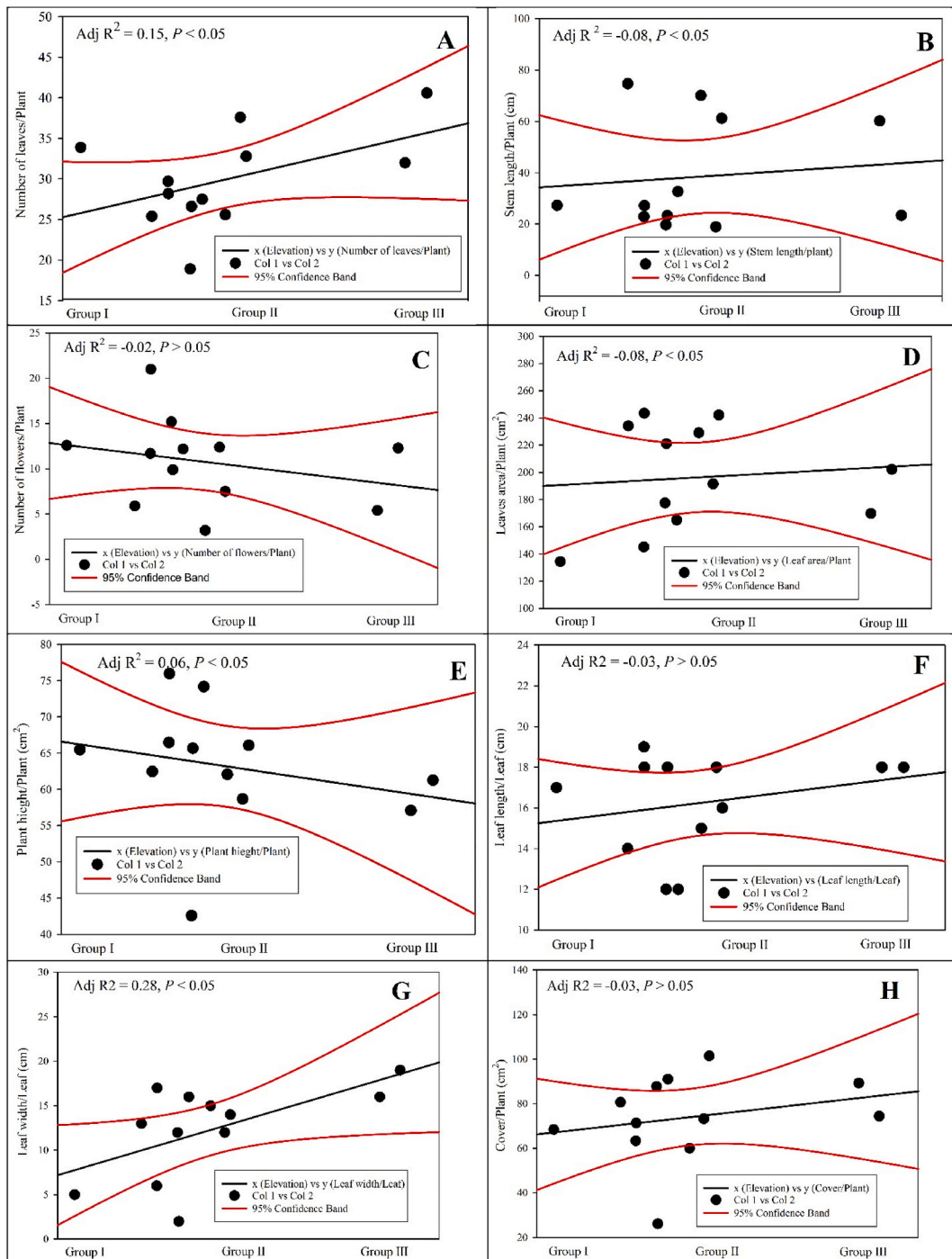
Fig. 5. Linear regression model of *Datura innoxia* functional traits across the elevation gradient. Note: A-O represent the figure Panels

(Table 3). However, the variation degree was substantial for biomass components. We may infer that climate and environmental variables play an essential role in *D. innoxia*'s phenotypic plasticity, which confers a considerable capacity to adjust to ecological challenges [50–52]. The detected hierarchical inconsistency of trait variations may reflect intraspecific genetic variation, as has been shown by Ref. [53]. Since the observed variability has a heritable component, quantitative genetic studies can also investigate the variation in morphological and biomass traits. Total dry and aboveground and stem dry biomass was shown to have the most overall intraspecific variability (Table 3). The species' wide range of morphological features and biomass allocation might be advantageous in
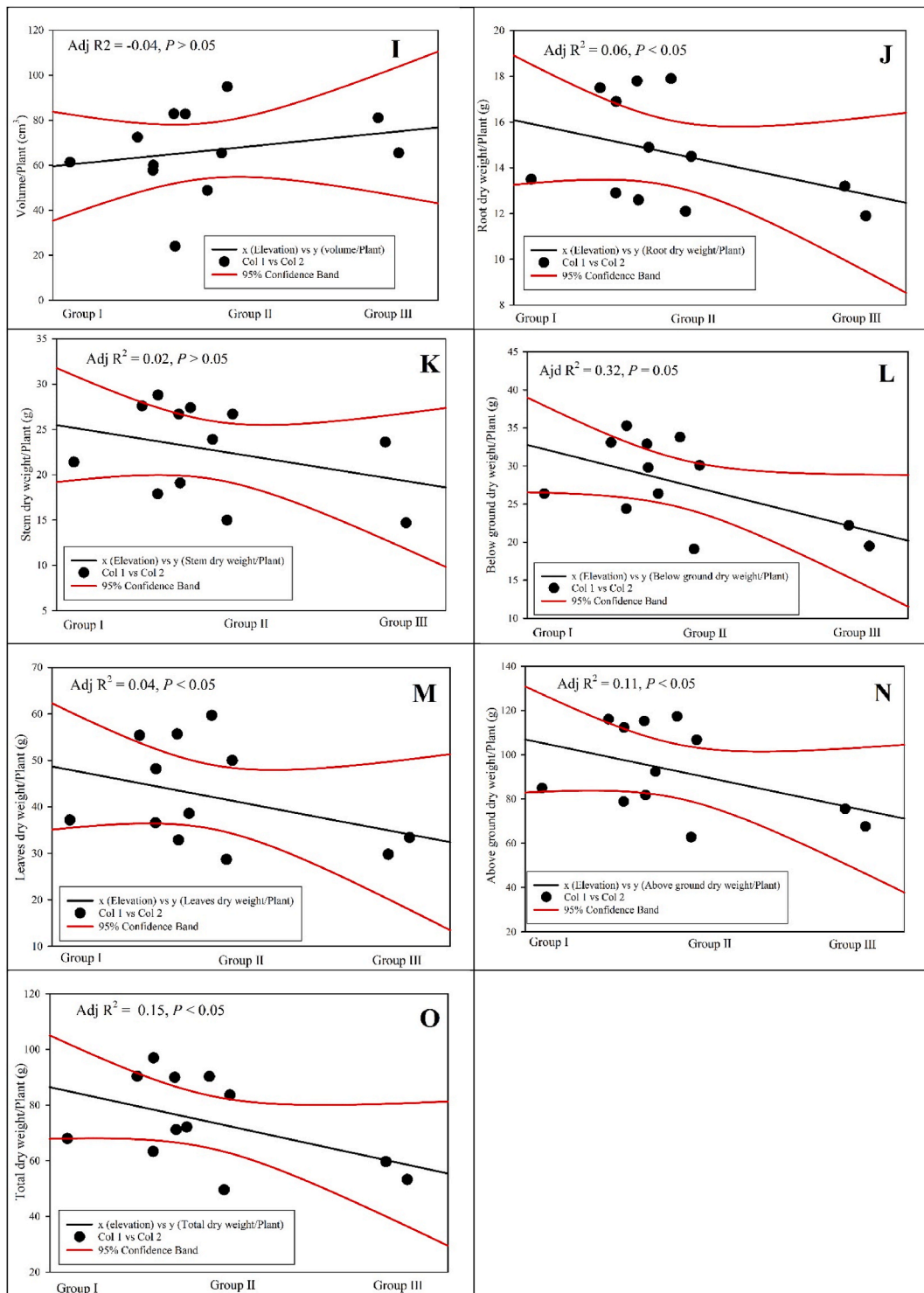
Fig. 5. (*continued*).

the selection and domestication processes since distinct 'ideotypes,' or subtypes can be identified to satisfy various utilization demands [54–57].

The elevation is an essential factor in determining the community's composition and brings variations in morphological features [58]. For example, Pauchard & Alaback [59] revealed that naturalized plants are restricted to lowland environments because of the

Table 4

Correlation between sample scores for an axis derived from the response variables (main matrix) and the sample scores that are linear combinations of the predictors (second matrix).

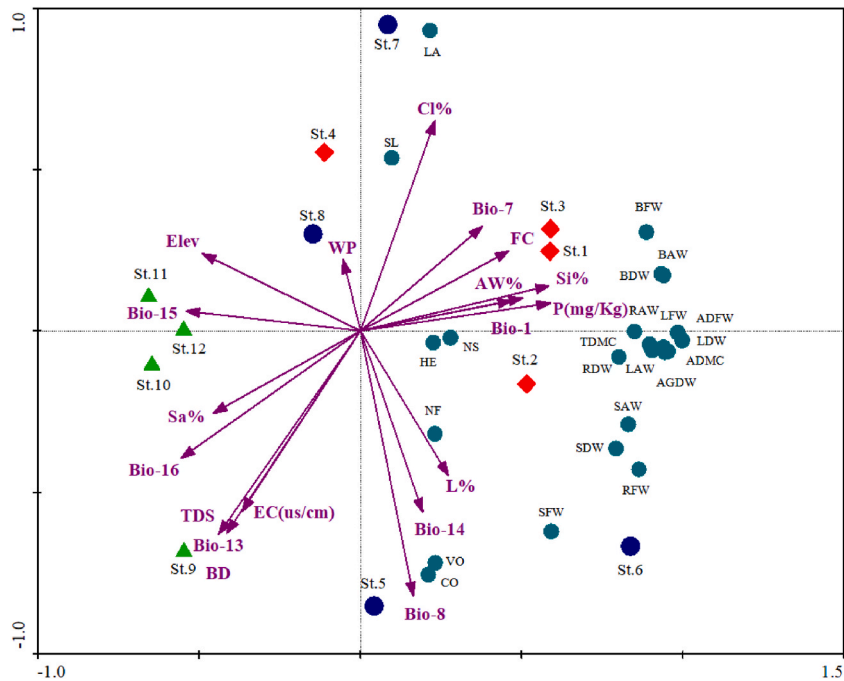| Variables	Axis I	Axis II	Axis III
Eigenvalue	0.738	0.165	0.040
% of variance explained	60.1	15.5	9.9
Cumulative % explained	60.1	75.6	82.5
Pearson Corr., Response-Pred.*	1	1	0.999
Kendall Corr., Response-Pred.	1	1	1

Fig. 6. RDA-biplot of an environmental variable showing important factors affecting different biomass.

Table 5

Redundancy analysis of different environmental and bioclimatic variables influencing biomass allocation pattern and plant functional traits of *Datura innoxia*.

| Variables	Correlation			
	Axis I	Axis II	Axis III	Axis IV
Elevation	**−0.4897**	0.2397	−0.0955	−0.0146
Sand %	**−0.4565**	−0.2546	0.3488	0.0929
Clay %	0.2311	**0.6512**	−0.3871	−0.1236
Silt %	**0.5855**	0.1403	−0.2092	0.1542
Lime %	0.2729	**−0.4479**	−0.1292	0.1032
Phosphorus (mg/kg)	**0.5887**	0.086	−0.2665	0.2787
Electrical conductivity (μs/cm)	**−0.3673**	**−0.5587**	0.1806	0.1194
Total dissolved solids (ppm)	**−0.3672**	**−0.5591**	0.1806	0.119
Wilting Point %	−0.0532	0.2208	0.1774	−0.5512
Field Capacity %	**0.4603**	0.248	−0.283	−0.122
Bulk Density (g/cm)	**−0.4144**	**−0.6269**	0.3122	0.0438
Available Water %	**0.4686**	0.0933	−0.2576	−0.0938
Bio-1 (Annual Mean Temperature)	**0.503**	0.1018	0.2688	0.0795
Bio-7 (Temperature Annual Range)	**0.3784**	**0.324**	0.0134	−0.1815
Bio-8 (Mean Temperature of Wettest Quarter)	0.164	**−0.8212**	0.0309	−0.1807
Bio-13 (Precipitation of Wettest Month)	**−0.4396**	**−0.6298**	−0.0168	0.1408
Bio-14 (Precipitation of Driest Month)	0.1927	**−0.5615**	−0.0255	−0.5315
Bio-15 (Precipitation Seasonality)	**−0.5407**	0.0619	−0.0159	0.615
Bio-16 (Precipitation of Wettest Quarter)	**−0.5553**	−0.3942	0.038	0.323
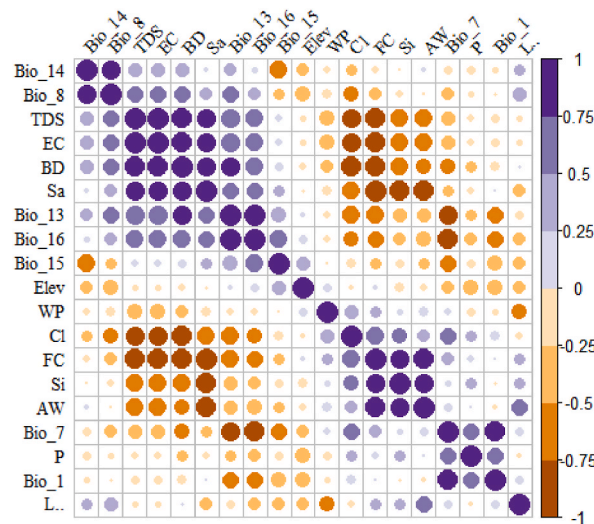
Fig. 7. Heat diagram of the discriminant climatic, topographic and soil variables governing *Datura innoxia* functional traits. For bioclimatic factors (BIO-1 to BIO-19, see Table 1) and for topographic and soil variables see Table 3.

harsh temperature and resource limitations at higher altitudes. Except for the number of leaves and plant density, *D. innoxia* plant functional parameters (morphological and biomass) exhibited significant declines along the increasing elevation gradient. Plant-available resources are typically restricted due to physical or geometric crowding (plant density) influences, which may disrupt the balance in the distribution and composition of plant-available resources [60,61]. In this sense, many researchers have observed similar trends in trait variation, such as [62]studied seed biomass in *Saussurea* species of the Asteraceae [63]; analyzed flower morphology in *Impatiens textori,* [64], investigated growth dynamics in *Ferula jaeschkeana* [65]. studied the life history of *Ageratina adenophora* and revealed that altitudes play a vital role in invasive species biomass distribution. The decrease in plant height is one characteristic that allows the plant to maintain its population at higher altitudes under extreme conditions. The plant is protected from wind and cold stress by decreasing aboveground plant height [66]. As the plant comes closer to the ground, heat buildup in the leaf canopy rises, which may aid seed germination [66].

On the other hand, pollinators are more attracted to plants at lower altitudes, which assure reproductive fitness [5]. The reduction in RDW with elevation was in contrast to Ref. [64]. They reported an increase in root biomass with elevation, which may be attributed to species' internal genetics and physiological capabilities coupled with changes in environmental conditions. Furthermore, since distinct mountain ranges may have different connections between height and environmental elements, area-specific patterns may result in varied elevation impacts on plant traits [67]. Elevation changes affect soil qualities that may contribute to variations in plants' morphological and biomass characteristics [68–70]. Electrical conductivity and pH increased with an increase in elevation. In contrast, TK, OM, TP, TN, and Lime decreased, which may play an important role in variations of the plant morphological and biomass characteristics [71–73]. Our research found that increased biomass allocation to aboveground components, including total and vegetative parts, and decreased leaf number in *D. innoxia* may be due to improved nutrient availability at altitudes below 600 m. In addition [74], reported that soil nutrient availability and chemical composition are either directly or indirectly governed by a plant species' potential to invade. Moreover, Vasquez et al. [75] reported that invasive species can use available soil nutrients that determine their growth progression or decline.

Redundancy analysis (RDA) indicated statistically significant relationships between discriminant morphological descriptors of *D. innoxia* with bioclimatic and environmental parameters, which explained a substantial portion of the variance observed between individuals (82.5%). Bioclimatic and environmental conditions considerably influence the variability of discriminating morphological and biomass descriptors across and within elevation zone. The impact of topography and soil characteristics (such as soil type, moisture content, and nutrient content) on *D. innoxia* may also be significant because they vary across the elevation and comply with [76]. [77,78] have believed that such variations may be possible sources of phenotypic diversity and influence plant communities. However, additional studies are needed to distinguish the effects of climate and soil on the morphological diversity of these species. This study did not investigate anthropogenic variables and other factors that might have a role in the morphological differentiation of the species and was advocated by Ref. [79]. For example, human disturbances (like fire and pruning), chronic grazing by herbivores (livestock animals), and insect defoliation may contribute to species trait diversity, especially given that the studied populations do not exist inside protected areas. Plant morphology and functional features have been demonstrated to be affected by grazing and fire in several studies e.g. Refs. [80–82], in addition to environmental factors. Our findings indicate that rainfall (rainfall seasonality (Bioclim-, rainfall of the wettest quarter (Bioclim-) is the most critical climatic driver of phenotypic diversity in the species under consideration. The wettest quarter's precipitation and the wettest month's precipitation had an essential role in determining phenotypic variety. High values in the low elevation zone were associated with excellent or high leaf biomass weight/total dry biomass performance. Other species such as *Vitex doniana* Sweet [78] and *Adansonia digitata* L. [83], as well as [84] in Mali and Burkina Faso,

have revealed favorable associations between rainfall and morphological features. However, some studies, such as those conducted by Ref. [55] in Niger, indicated a negative association between rainfall and fruit size for the *Balanites aegytiaca* Delile. in these studies, and more significant fruit sizes were seen in drier circumstances. These incongruent findings show that rainfall has a species-specific influence on morphological features. This impact may be attributed to species-specific adaptations to environmental circumstances in response to rainfall. Temperature-related bioclimatic indicators (mean annual temperature (Bio-19), annual temperature range (Bio-12), mean temperature (Bio-21), and temperature seasonality (Coefficient of variation) were also significant predictors of plant morphological and biomass descriptors. As previously reported for *V. doniana* in Benin [78], a similar link between excessive temperature and precipitation and morphological variability has been observed. Likewise, previous research has found significant effects of climatic conditions on the morphological traits of several other species, including *Afzelia africana* Sm. [85], *Afzelia digitata* [86], *Detarium microcarpum* Guill. & Perr. [87], and *Viola paradoxa* [88].

This research offers evidence in favor of a high degree of variability in the physical features of the species and the significant role of climatic and environmental factors in determining this variability, despite the limited geographic coverage of our data. However, it is necessary to collect data from a broader geographic range to understand better the function of climatic and environmental factors and other variation sources in determining the species' morphology. Indeed, given the species' wide geographic range, data collected only in Khyber Pakhtunkhwa (a small portion of the species' total longitudinal expansion) may not provide sufficient information on the role of climate and environmental factors in determining the morphological characteristics of the species population. Furthermore, future research of this kind should include as many ecological aspects as feasible, such as anthropogenic disturbance, plant invasion, and other associated issues.

5. Conclusions

Morphological traits and biomass distribution patterns in *D. innoxia* significantly varied across the elevation gradient. A small and thin leaf pattern at a higher altitude may lead to decreased root length due to less availability of nutrients. The biomass allocation strategy with an average root-to-shoot ratio was favored in the *Datura-Parthenium* community (Group I). *D. innoxia* tends to have the intermediate leaf pattern with the highest stem, the slender root morphology pattern with the longer root length, and the biomass allocation strategy with the lowest root-to-shoot ratio in the *Datura-Xanthium* community (Group II). The low stem length, high thickness, thick root pattern with minimum root length, and biomass allocation strategy with the highest root-to-shoot ratio tended to prevail in the *Datura-Cynodon* community (Group III). The current research found that the morphological characteristics and biomass distribution patterns of non-native plants vary greatly across elevations, which may be influenced by environmental conditions like soil characteristics and bioclimatic layers. The results suggested that lower elevation plants produce more biomass and may be helpful for the collection and utilization of phytochemicals and medicinal purposes. In addition, quantitative genetic research will help determine how much of the observed variability is a heritable characteristic and its improvement.

Data availability statement

The dataset used in this study can be obtain from the corresponding author upon a reasonable and justified request.

CRediT authorship contribution statement

Nasrullah Khan: Writing – original draft, Methodology, Formal analysis, Conceptualization. **Rafi Ullah:** Writing – original draft, Methodology, Formal analysis, Data curation. **Mohammad K. Okla:** Writing – review & editing, Visualization, Validation, Supervision, Funding acquisition. **Mostafa A. Abdel-Maksoud:** Writing – review & editing, Methodology, Formal analysis. **Ibrahim A. Saleh:** Visualization, Software, Formal analysis. **Hashem A. Abu-Harirah:** Project administration, Methodology, Formal analysis. **Tareq Nayef AlRamadneh:** Writing – review & editing, Visualization, Validation, Software. **Hamada AbdElgawad:** Writing – review & editing, Methodology, Formal analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.heliyon.2024.e27811.

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