Full Length Research Paper

Among and within population variation in growth dynamics and floral sex ratios in *Inula racemosa;* a critically endangered medicinal herb of N. W. Himalayas

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The purpose of the present study was to determine the extent to which different morphological and reproductive characteristics of a critically endangered, Himalayan herb (*Inula racemosa*) varied along an altitudinal gradient. To this end, seven populations growing at different altitudes (1595 - 2800 m asl) across the Kashmir Himalaya were assessed. ANOVA expressed significant differences (P=0.05) in all growth parameters as a function of altitude. The highest difference between the populations was apparent in the stem height and in all populations patterns in the foliar and floral number and dimensions closely followed those in plant height. In four out of the seven populations, significant variation in floret number per head was detected among plants within all seven populations. Only 19-34% of variation was found within plants and in contrast 38-72% variation was found among plants. As compared to total ovule number per capitulum the species show low percentage of reproductive success (59-72% seed set). However, increasing altitude resulted in a decrease in relative and absolute allocation of biomass to reproductive structures in the form of decreasing dry weight of individual capitula as well as in the form of absolute declining of total number of capitula produced. There was also a trend for increased relative allocation to below-ground rhizome with increasing altitude, even though altitude did not affect absolute allocation to below-ground and vegetative structures.

Key words: Altitude, floral sex ratio, growth, *Inula racemosa,* phenotypic variability, reproductive success.

INTRODUCTION

Plants grow in a modular manner and are indeterminate in their growth which allows them to be highly plastic in both morphology and reproduction. Moreover, because buds act as the germ, any mutations acquired will be passed along through subsequent cell divisions. It is this mode of growth that allows the large degree of morphological plasticity, characteristic of plant growth, resulting in wide intraspecific differences in many features of plant architecture (Silvertown and Lovett Doust, 1993).

Whether this variation is genetic or environ-mental can be debated, however it is most certainly mediated physiologically (Waller, 1988). However, plant growth pattern influences a number of important traits that affect fitness, including pollination and dispersal (Waller, 1988). It can also provide phylogenetic infor-mation (Walton and Hufford, 1994). Moreover, plant growth and allocation patterns are influenced by a complex suite of potentially-interacting factors, providing a mechanism by which, over the long term, adaptive associations among external

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factors and the various morphological traits can occur. However, morphological variation is not necessarily due to an evolved response and precise causal mechanisms for architectural variation is yet to be established for most species (Waller, 1988).

Altitudinal system presents strong, multidimensional environmental gradients (Korner, 2003) and plants at different positions along these gradients face distinct growth conditions. Each of these factors may influence plants directly and also indirectly by altering plant response to other factors. Different altitudinal ranges are therefore excellent model systems for studying plant responses to environmental variation over small geographical scales. Elevational gradients are thus convenient scenarios to investigate such responses and key traits for plant functioning vary in a clinal fashion along elevation gradients. For instance, the reduction in overall plant size is the most conspicuous structural alteration observed along elevational gradients (Korner et al., 1989).

Flower size does not seem to be affected in a proportional way and therefore alpine plant species are often believed to invest relatively more in reproductive structures (Fabbro and Korner, 2004). For perennial plants absolute allocation to reproduction usually increases with size (Clauss and Aarssen, 1994). However, the proportional reproductive allocation, that is, reproductive effort has been found to increase (Aarssen and Taylor, 1992), decrease (Waite and Hutchings, 1982) or be independent of plant size (Pickering, 1994). Such varied effects of plant size on reproductive effort may be genetically or environmentally induced (Schmid and weiner, 1993) and/or result from different morphological/developmental constraints (Geber, 1990).

In this study, we used four years of field observations to explore within and among population variation and/or adaptive plasticity in phenotypic traits and reproductive success of perennial herb *Inula racemosa* Hook.f. (Asteraceae). The species has a limited distribution in Hindukush Himalayan region across Afghanistan, Pakistan, India and Nepal and is primarily found in open temperate meadows and forest margins of North-western Himalayan mountainous regions between 2100 and 2800 m in altitude. The species is known for its potent medicinal properties (Wani et al., 2006), is facing ruthless over-exploitation and is at the verge of extinction. Once being considered as critically endangered, the species is now drawing favourable attention in various conservation programmes.

The present study aimed to present a comparative study of within and among-population variation in various morphological and reproductive traits. A specific aim of this research project was to quantify and contribute to the body of knowledge of the phenotypic variability and allocation pattern for an individual species and its interactions with its environment. To achieve these aims, data were collected from naturally growing populations across a wide geographic range. Specifically, we search for trends in trait variation reflecting the changes along a steep altitudinal gradient. We focus on variation in growth morphology and architectural traits, reproductive success and changes in allocation patterns and their relation to the environmental conditions along the altitudinal gradient. This paper also presents an attempt to make a formal quantitative analysis of the floral composition in populations of *I. racemosa* growing over the wide range of different altitudinal gradients. Here we reported observations of total floret numbers and percentage female ray and hermaphrodite disc florets per capitulum and the variation within and among individuals within different studied populations of *I. racemosa.*

MATERIALS AND METHODS

Study species

I. racemosa Hook. f. (Asteraceae); endemic to North West Himalaya and its adjoining areas is a long lived herbaceous perennial species found in moderately-moist, shady and sloppy habitats of North Western Himalayas at an altitudinal range of 2100 to 2800 m-asl. Plants produce multiple stems each year, about 1-2 m tall. Mature flowering individuals are about 60 to 200 cm tall with a terminal raceme of yellow flowers visited by bumblebees (Shabir et al., 2013). Mean date of flowering (first flower) is about 15 July in our study site. Flowers are arranged in terminal discoid capitula of 5-8 cm in diameter, with 5-30 capitula per stem. Fruit ripening (small achene) occur in September.

Study sites

Six natural populations of *I. racemosa* were studied for four consecutive years (2009-2012). Study populations were located along an altitudinal gradient representing a wide range of geographical and environmental conditions across the Kashmir Himalaya (Table 1). The geographical co-ordinates of these sites were recorded using geographical positioning system (GPS). Because of the difficult access to the wild populations, one additional transplanted population at KUBG was maintained to have a ready access to the germplasm and to acclimatize the plants at low altitude conditions. Comprehensive field notes on habit, habitat, growth dynamics, floral sex ratio and reproductive success were recorded.

Plant morphological characterization

In order to address the overall morphology of the species and to capture the variability in floral and vegetative traits within and among populations of *I. racemosa*, a series of traits for 30 individuals per population were measured at peak flowering time. The different readily identified characters were chosen for morphological measurements which include: plant height, leaves number, foliar dimensions, floral density and floral dimensions (Table 2). Differences among populations in various morphological features were analysed by one-way ANOVA using SPSS.

Floral sex ratios and reproductive success

Heads at peak flowering from all the selected populations of *I. racemosa* were collected during all the four seasons and each

Table 1. Salient features of selected sites for the collection of *I. racemosa.*

Study site	Altitude (m-asl)	Latitude and longitude	Climatic zone	Habitat	Threat factor
Gulmarg	2650	34°03'N 74^{0}22'E	Temperate	Moist open slope	Grazing, extraction and habitat destruct
Drung	2150	34°4' N 74°35'E	Temperate	Moist open slope	Grazing, extraction and habitat destruct
Harwan	1800	34°9' N 74°54'E	Temperate	Moist open slope	Grazing with partial landslides
Sonamerg	2800	34°20′N 75°20′E	Temperate	Moist open field	Grazing and habitat destruction
Dawar Guraz	2580	34°63′N 74°83′E	Temperate	Roadside	Heavy land slides
Kanzalwan	2580	34°63′N 74°83′E	Temperate	Roadside	Heavy land slides
KUBG[+]	1595	34°5'N 74°35'E	Temperate	Moist open field	Nil

Table 2. Morphological variations recorded among seven different populations of of *I. racemosa*

Attribute	Gulmarg	Drung	Harwan	Sonamerg	Dawer	Kanzalwan
Plant height	164.85±16.06	189.43±17.34	181.19±14.78	161.25±14.21	166.02±12.41	165.29±18.33
Leaf no.	15.21±2.09	17.41±2.31	17.99±3.22	15.26±3.29	15.33±2.88	15.41±2.01
Max. leaf length (cm)	57.61±7.41	57.14±8.32	66.52±6.59	56.29±7.22	52.21±8.29	53.64±7.16
Max. leaf breadth (cm)	14.36±2.21	12.67±1.86	15.29±2.11	13.34±2.01	14.55±1.99	14.92±1.85
Capitulum number	14.81±2.85	16.51±2.87	18.29±3.21	14.55±2.02	15.52±2.25	16.01±1.87
Capitulum diameter (cm)	7.49±1.62	7.54±1.41	6.92±2.03	7.89±1.88	7.82±1.38	7.09±1.19
Ray floret number	55.06±6.57	55.11±4.45	54.24±5.41	55.92±6.07	55.61±4.99	54.99±5.33
Disc floret number	415.21±23.26	416.61±26.52	431.45±31.29	445.92±37.34	401.66±23.11	429.24±29.66
Achene number (per capitulum)	342.34 ±8.38	317.67 ±11.76	321.24±12.22	338.29±10.51	313.72±17.64	326.77±12.28
Achene length (mm)	3.11±0.31	3.15±0.64	3.62±0.91	3.94±0.23	3.66±0.35	3.54±0.22
Achene width (mm)	0.41±0.01	0.44±0.01	0.48±0.11	0.49±0.02	0.45±0.04	0.47±0.02

collection involved selecting plants at regular intervals (1-2 m, depending on the population sampled) along a transect. We sampled 20 plants in each population and two heads were collected arbitrarily from scattered positions on each plant. In total, we collected 280 flower heads per season. The heads were dissected under a bifocal magnifying glass and the number of counted to examin and disc flowers wi

populations. In late September mature fruiting heads were similarly collected from all the selected populations. On each head we determined the percent seed set, expressed as the ratio of developed achenes to the total number of florets per capitulum. Developed seeds could easily be distinguished from undeveloped ones because the former are black and hard while the later are soft and empty. The data were analysed using ANOVA, followed by calculations of the percentage variation at each level (Sokal and Rohlf, 1995).

Reproductive allocation

To determine resource allocation pattern, 15 individuals of each population were dug up and separated into rhizomes, stems, leaves and inflorescence. The flower fraction contains all flowers including their involucres, whereas stems and flower stalks form the stem fraction and the leaves with their petioles included form the leaf fraction. In cases of clonal, multistemmed individuals, the sampling unit was a ramet, also referred to as flowering shoot. All plant material was dried to a constant mass in an oven at 60°C and weighed. Reproductive effort was calculated from dry weight of the different parts of individual plants, that is, dry weight or biomass allocated to reproductive and vegetative structures (Abrahamson and Gadgil, 1973).

$$R.E = \frac{\text{Dry weight of the inflorescence}}{\text{Total dry weight of the above ground tisssues}} \times 100$$

RESULTS

Growth attributes

I. racemosa is a perennial ascending hairy herb with 100-200cm grooved orthotropic stem and rhizome that grows 5-10 cm below the soil surface. Leaves are winged petiolate with an elliptical-lanceolate lamina (average length 30-50 cm) and having villous lower surface. In all reproductive plants varying number of 5-30 inflorescences per plant emerge per growing season. Inflorescence is capitula which are 4-8cm in diameter. Involucral bracts are 4-5 seriate. Marginal ray florets are ligulate, pistillate and 2-3 toothed while central florets are tubular, perfect and 5 toothed.

The populations of *I. racemosa* analysed in this field survey varied considerably in their morphological features showing an admirable phenotypic variation both at inter and intra-population level (Table 2). There were highly significant differences among populations in stem height, leaf dimensions, capitulum size and capitulum number (Table 2). Based on the means of the thirty plants per population, the strongest difference between the populations was apparent in the shoot size which was almost 1.5 times as high in Harwan (189.43±17.34; P=0.03) as in Sonamerg (161.25±14.21; P=0.001) with an average decrease of 2.74% between 1800 and 2800 m-asl (Table 2). The other growth parameters that followed the similar trend as shown by the plant height

across the study sites include leaf number, leaf dimensions and capitula number. Plants flowered for a period of 8-10 weeks and the highest percentage of flowering plants and the largest mean number of capitula per plant were reached between late-July and early-August. Log (capitulum number) per individual also decreased significantly and substantially with altitude (by an average of 14% between 1800 m and 2800 m a.s.l.) with a mean capitulum number ranging from 14.55±2.02 to 21.31±2.79, (P=0.05) across populations. This decline in capitulum number might partly be related to decreasing plant size with altitude, since log (capitulum number) is correlated with stem height across all species and regions (r = 0.61, 0.001). Contrary to patterns among natural populations, KUBG plants were almost 2 times larger than plants in the natural populations. In addition, plants from the cultivated population also show the highest values of foliar and floral dimensions (Table 2).

Floral sex ratio and reproductive success

A significant reduction in both total floret number and ray floret number per capitulum occurred with increased altitude (Table 2), however, the reduction in ray floret number was minor relative to total floret number. In four out of seven populations, significant variation in floret number per head was detected, and among plants within all seven populations (Table 3). Only 19-34% of variation was found within plants and in contrast 38-72% variation was found among plants. The added variance component within plants in the proportion of disc florerts was significant for only transplanted KUBG population while a significant variation in this variable did exist among different sampled populations, and 36-54% of total variation occurred among populations (Table 3). In all sampled populations, most of the variation in total floret number was among plants (58-77%). Percentage seed set per capitulum also varied along altitudinal gradient and lowest seed set was observed in transplanted KUBG population (59.94%). A significant variation was observed in achene number per head among the plants within all the seven populations (Table 2).

Reproductive statistics for the seven studied populations of *I. racemosa* (Table 3), which includes the estimation of number of ovules developing per capitulum and the percentage of reproductive success showed that the species showed 59-72% of seed set. Multiplying the mean number of achenes per capitulum by the mean number of capitula per stem gives the estimate of seed-reproductive capacity per stem as shown in Table 2. The number of capitula per stem varied with overall plant height, from zero on small stems to over 30, with a mean of 14-30 across populations. In addition, the number of ramets per rhizome varied from one to seven, and thus represents a great plasticity in numbers of capitula per stem and thus the reproductive success.

Table 3. Distribution of variation in total flower number and percentage of disc flowers and achene number per head among and within p opulations an

| Population	No. of heads per plant	No. of plants per population	Percentage of variation in flower number per head		Percentage of variation in disc flowers per head		P
			Within plants	Among plants	Within plants	Among plants	W
Gulmarg	5	10	24.9	45.8**	18.3	32.2*	
Drung	5	10	34.6***	57.3**	26.1	48.8*	
Harwan	5	10	19.2	38.6***	16.4	34.5**	
Sonamerg	5	10	28.7**	61.5***	30.8	56.9***	
Qanzalwan	5	10	26.8**	45.3*	44.1	37.5**	
Dawer	5	10	22.1	52.6**	27.9	45.6*	
KUBG	5	10	31.3**	72.3*	52.7**	56.1***	

Reproductive allocation at flowering

For the studied species, plant size varied across altitudes, the total resource pool thus varied over several orders of magnitude and a significant difference was observed in total above ground dry weight biomass, dry weight of different vegetative structures and the total reproductive effort among the plants of studied populations, growing at different altitudes. Allocation of biomass to different organs was size dependent for plants in all sites (Figure 1) and at lower altitudes, mean plant biomass was approximately 1.5 to 2 times higher than at higher altitude. Plant size decreased with increasing altitude (r = 0.91). However, increasing altitude resulted in a decrease in relative and absolute allocation of biomass to reproductive structures in the form of decreasing dry weight of individual capitula (r=0.81) as well as in the form of absolute declining of total number of capitula produced (r=0.79). There was also increase in relative allocation to below-ground rhizome with increasing altitude, even though altitude did not affect absolute allocation to below-ground and vegetative structures. On average, flowering individuals of high altitude, Sonamerg population

weighed 191.47 ± 18.0 g, while the KUBG population growing at lower altitude had mean individual/ramet weights of 244.85 ± 38.24 g, that is, were 1.5 times heavier. However, mean flower mass fraction (flower mass/total shoot mass) was larger in higher altitude Sonamerg (0.19) population than in lowland populations (0.21 in KUBG). The stem mass fraction differed in the opposite direction and was almost two times lower at high (0.37, p≤0.01) than at low altitude (0.58, p≤0.04). The leaf mass fraction of shoots did not differ significantly between altitudes. In terms of biomass, reproductive effort increased significantly with altitude (26.93 in Gulmarg, Figure 1) while at lower altitude populations (20.85 in KUBG, Figure 1), reproductive effort varied inversely with plant size. Further, the percentage allocation to reproductive parts, that is, reproductive effort was more towards maleness (0.32±0.21 to 0.27±0.09) than femaleness (0.16±0.43 to 0.15±0.07), which suggests an outbreeding nature of the species.

DISCUSSION

In this study, we found distinct directional trends in
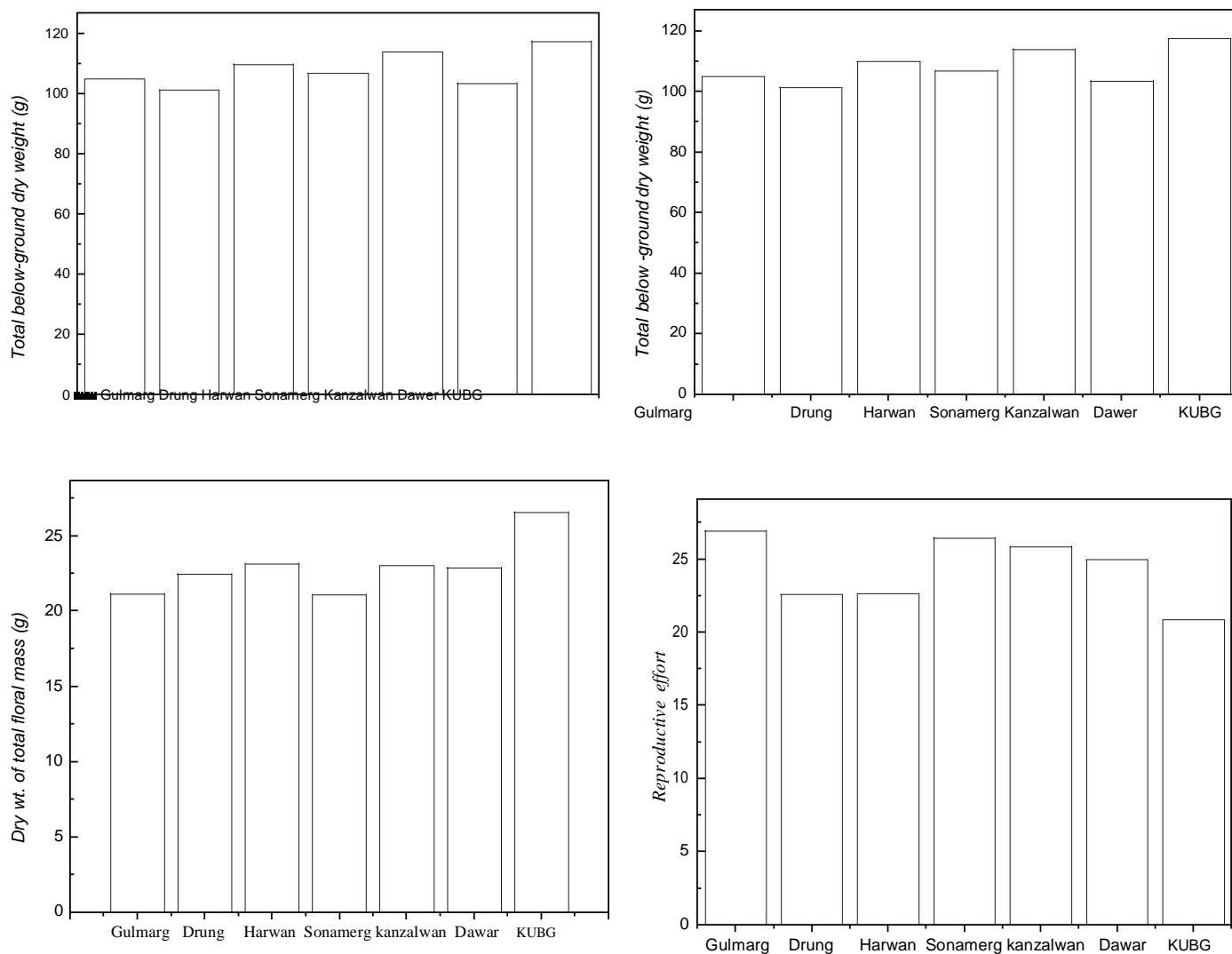
Figure 1. (a) Total above-ground dry weight, (b) total below ground dry weight, (c) dry weight of total floral mass, (d) reproductive effort.

mean difference for capitula number was observed between the transplanted population of KUBG and the population of Sonamerg. These findings suggest that plants growing at lower altitudes are distinctly more vigorous, much taller and bearing larger number of leaves and inflorescences as compared to plants growing at higher altitudes as also previously revealed by Johnson and Cook (1968) and Hickman (1975). Also, the relationships between plant size and reproduction, that is, increased allocation to reproduction (number of capitula) with plant size; is in conformity with the observations of Ohlson (1988), Aarssen and Taylor (1992), Kudo (1993) and Clauss and Aarssen (1994).

In the seven populations of *I. racemosa* considered in this study, variation in total flower number per head was often evident. However, the floral sex ratio remained within narrow limits despite much variation (interpopulation) in floret count across populations. Specifically,

large plants bore significantly more flowers per head than small plants in all studied populations. Of the seven studied populations, significant variation in total floret number was found in four populations and it accounted for a significant amount of the variation in proportion of ray and disc florets across populations.

Knowledge of the resource allocation pattern of plants is beneficial to understand the life history strategy operative in the species. Of the total resource pool, reproductive allocation is often determined by plant size (Lacey, 1986; Samson and Werk, 1986; Saulinier and Reekie, 1995) and thus reflects the reproductive potential of a species. Studied populations of *I. racemosa* significantly differed in proportional biomass partitioning, with high altitude plants having low biomass allocation to stem, leaves and inflorescences and high to belowground rhizome. At lowest altitude, plants dry mass partitioning averaged 27% for rhizome (P=0.0001), 19% for stems

(P=0.008), 16% for leaves (P=0.089) and 13% for inflorescences (P=0.002). At the highest altitude population, these values averaged 29% for rhizome (P=0.0001), 18% for stems (P=005), 17% for leaves (P=024) and 11% for inflorescences (P=0.0001). The study revealed that the flower size did not seem to be affected in a proportional way and high altitude Dawar population allocated more of their percentage aboveground biomass to floral structures than lowland KUBG population, while the shoot mass fraction allocated to stems decreased in high altitude populations.

Therefore, alpine plant species are often believed to invest relatively more in reproductive structures. This suggests that alpine plants have enough resources to allocate more proportional aboveground biomass to flowers. It also implies a clear prioritizing of reproduction over growth at high altitude. These results suggest that environmental selective forces could result in variation of reproductive strategies in the species (Silverton and Lovett-Doust, 1993). Studies of other plant species have also shown that reproductive effort decreases significantly with increasing plant size (Klinkhamer et al., 1990). In addition, sub-division of reproductive resources among floral parts e.g. stamens and carpels are also variable with more allocation towards male (0.27±0.09 to 0.32±0.21) than carpels (0.15±0.07 to 0.16±0.43). Such increased strategies in the biomass allocation to male reproductive structures suggest an outbreeding nature of the species (Huang et al., 2004).

In summary, analysis of the growth responses of *I. racemosa* along the altitudinal gradient indicates significant effects on several characters measured (P < 0.001). The altitude showed positive correlation with below-ground biomass (r = 0.84) and negatively correlated with the plant height (r = -0.91) number of leaves, number of capitula and above ground biomass (r = -0.59). Negative correlation of all morphological parameters to the increasing altitudes indicates better growth performance of this species at lower elevations.

ACKNOWLEDGEMENT

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