

# Plant Biomass Trait Values and their Trade-offs: Temporal Dynamics and Their Governing Factors

MANISH MATHUR

Central Arid Zone Research Institute (ICAR), Jodhpur 342003, Rajasthan, India.

Email: [eco5320@gmail.com](mailto:eco5320@gmail.com)

## ABSTRACT

Plant trait based approaches provide a mechanistic framework to understand and predict its potential survival and role within the community. *Tephrosia purpurea* is a perennial leguminous erect short-lived underscrub abundantly present on the wastelands of the Indian hot arid and semi arid region. In this study, its temporal biomass trait values and the trade-off with total biomass and among its different compartments were quantified. Impact of different bottom-up and top-down factors on the magnitude of all trait and trade-off values were also assessed. Contrary to several other such studies conducted from different eco-regions of the world, impacts of heat index, net radiation, extraterrestrial and incoming solar radiation, actual vapor pressure, species physiological attributes (maintenance respiration, NPP and GPP), community variables (richness and Relative importance value) were identified as significant factors by Canonical Correlation Analysis. Partial Least Squares (PLS) test suggested that various exploratory factors are working significantly and in random fashion and for this species and with this experimental set-up only two species variables i.e. leaf biomass trait and trade-off between capsule and stem can be mathematically explained with different factors.

Key Words: *Tephrosia purpurea*; Compartments; Biomass Allocation; Solar Energy; Canonical Correlation Analysis

## INTRODUCTION

Plant biomass patterns are the reflection of a plant's morphological, growth and reproductive attributes and its association with metabolism, CO<sub>2</sub> assimilation, and carbon sequestration as well (Reekie and Bazzaz 2005 and Allaie et al. 2006). By virtue of such important tasks, biomass allocation patterns is a fundamental point to figure out its inter- and intra-community roles. Allocation of belowground and aboveground biomass has been exercised both in *in-vitro* and *in-vivo* experiments. Root to shoot (R/S) ratio plays an important role in carbon cycle models (Wu et al. 2013) and this varies with environmental conditions. With response to environmental conditions, plant species have a dynamic shifting pattern for biomass allocations (Patty et al. 2010) and are quantified through trait plasticity and trade-off patterns (Bradford and D'Amato 2012). Trade-offs also occurs between vegetative biomass and reproductive biomass, as well as non-photosynthetic

organs biomass and leaf biomass (Wang et al. 2017). Allocation patterns and their relationship with environmental factors have been explored with different perspectives; habitat and land use and some of them are grassland vegetation of semi arid China (Liu et al. 2014), biomass allocation of stoloniferous and rhizo-matous plants (Xie et al. 2016), warming effects on allocation in an alpine meadow (Xu et al. 2016), belowground plant biomass allocation in tundra (Wang et al. 2016) and drought effects (Eziz et al. 2017). Such studies established relationships between biomass allocation patterns and environmental variables and suggested some possible mechanisms. However, such relative studies are not conducted for species inhabiting Indian hot arid zone. In the Indian hot arid and semi arid areas, water availability work as "pulse" and this denotes the rainy seasons, while inter-pulse period represents small and erratic episode of rains particularly occurring during winter season while the long dry period is referred to as non-pulse period (summer). Such yearly periodicities

have the potential to affect plant attributes as these variations bring drastic changes in morphological, physiological and ecological behaviour of a species. However, from this region, these temporal dynamics are not fully explored for the biomass traits and trade-off of perennial evergreen undershrub.

*Tephrosia purpurea* is a leguminous erect short-lived undershrub, prefers dry, gravelly/ rocky and sandy soils. Ecosystem services of this species include regulatory (checks the soil-erosion and nitrogen fixation), provisional (leaves are used as fodder, seeds can be used as a substitute for coffee, shoots for broom making) and cultural (medicinal properties) (Mathur 2016). Earlier different ecological aspects of this species have been investigated such as germination ecology (Sunita et al. 2014), allelopathic interactions (Yadav and Yadav 2014), nitrogen fixation capacity (Mohammed and Fredan 2011) and association studies (Mathur and Sundaramoorthy 2013).

The present study was made with two objectives in the perspective of the above knowledge and gap: (a) study the seasonal pattern of the biomass trait value and trade-off for *Tephrosia purpurea* and (b) how environmental (solar, soil and community dynamics) and species physiological attributes affect them.

## STUDY SITES

The study was carried out at five different arid wastelands namely, Jalamand (26° 12' 48.4" N and 73° 4' 7.8" E), Kudi (26° 11' 33.4" N and 73° 3' 6.1" E), Mandor (26° 21' 54.5" N and 73° 03' 48.9" E), JNVU campus (26° 14' 12.4" N and 73° 01' 24.2" E) and Basni sites (26° 14' 47.01" N and 73° 0.0' 58.9" E) located at Jodhpur, Rajasthan, India.

These wastelands are located on older alluvial plain habitat with higher proportion of sand (43.3%) and gravel (33.5%). Data were collected in two consecutive years (2004-2005) during three different seasons, namely rainy season (July to October), winter (November to February) and summer (March to June). Different meteorological parameters were collected from meteorological section of Central Arid Zone Research Institute, Jodhpur. During the study period, mean annual precipitation ranged from 0.004 to 260 mm, average winter (January) temperature ranged from 10.7 °C to 23 °C, and mean summer (June) temperature ranged from 28.7 °C to 42.2 °C. Relative humidity ranged from 31% to 91% in the morning and from 8% to 68% in the evening.

## METHODS

### Soil and Vegetation Analysis

Soil samples were collected up-to 30 cm depth from three different locations at all wastelands during each season. All soil parameters were quantified in triplicate. Soil moisture (%) was estimated in non-dried soil through gravimetric method (Black 1965) while other physical and chemical parameters were estimated in air-dried and sieved (2mm) soil samples (Pandeya et al. 1968). Electric conductivity (mS m<sup>-1</sup>) and soil pH were measured in water-soil suspension (5:1) by Systronics digital meters 304 and 802 respectively. Soil organic carbon, total nitrogen and available phosphorus were quantified by standard methodologies of Jackson (1973) and Allen et al. (1976). At each land and during each season, nested quadrat technique was utilized wherein 10 quadrats of 10 x 10m abutting each other in a row were laid across the field (Kent and Coker 1992) for woody perennials. Relative Importance Value was calculated through relative frequency, abundance and density (Kent and Cooker 1992). Diversity indices were calculated as per standard methodology (Ludwig and Reynold 1999). The species richness is defined as the total number of species per sampling unit (Bhattarai et al. 2004). Shannon-Weaver's diversity index generally ranges from 1.5 to 3.5 and rarely up to 4.5. Its higher value indicates high diversity while the lower value represents the dominance of a few species (Mathur and Sundaramoorthy 2008).

During each event and from each site, 15 random individual plants were uprooted. Leaf-area index was calculated by using LICOR- 3000 area meter. GPP was calculated from the total NPP plus the total respiration. Total NPP (g C m<sup>-2</sup>) was determined as the sum of aboveground net primary production (ANPP) and the belowground net primary production (BNPP). Carbon content was determined by modified Walkley and Black's method, and the total nitrogen was estimated by micro-Kjeldahl method (Jackson 1973).

### Energy used in Transpiration

The energy necessary to evaporate water at the mean temperature during the growing season was calculated by using Harrison equations, as follows:

$$\lambda_v = 597.3 - 0.564T$$

where  $\lambda_v$  is the latent heat of vaporisation (cal g<sup>-1</sup>) and  $T$

is the mean temperature in the growing season ( $^{\circ}\text{C}$ ). Transpiration ( $T_R$ ) was estimated by partitioning evapo-transpiration into evaporation and transpiration, as follows:

$$T_R = \text{AET} [1 - \exp(-0.82F)],$$

where AET is the actual evapo-transpiration and F is the leaf area index. The actual evapo-transpiration (mm) during the growing season was calculated by following equation:

$$\text{AET} = P - \exp\left(\frac{\text{PET}}{P}\right)$$

where P is the mean annual precipitation (mm) and PET is the potential evapo-transpiration (mm) during the growing season, calculated from Thornthwaite's method, as follows:

$$\text{PET} = 16 \left(\frac{L}{12}\right) \left(\frac{N}{30}\right) \left[\frac{10T}{I}\right]^G$$

where T is the waverage temperature ( $^{\circ}\text{C}$ ) during the particular pulse event, L is the average day-length (h) during the pulse events, N is the number of days and I is the heat index. The heat index was calculated as

$$I = \sum_{i=1}^n \left(\frac{T_i}{5}\right)^{1.514}$$

where  $T_i$  is the average temperature during the pulse event; a was calculated as

$$a = 0.49239 + 0.0179I - 0.000077I^2 + 0.000000675 I^3.$$

### Determination of Solar Radiation

To evaluate the percentage of the energy utilised by the plant in photosynthesis and transpiration, incoming solar radiation and net solar radiation were determined. Net radiation ( $R_n$ ,  $\text{MJ m}^{-2} \text{day}^{-1}$ ) was estimated by an equation provided by Allen et al (1998), as follows:

$$R_n = R_{ns} - R_{nl},$$

where  $R_{ns}$  is the incoming net shortwave radiation and  $R_{nl}$  is the outgoing net long-wave radiation.

$$R_{nl} = (1 - \alpha) \times R_s,$$

where  $\alpha$  is the albedo or canopy reflection coefficient

(0.23) and  $R_s$  is the incoming solar radiation ( $\text{MJ m}^{-2} \text{day}^{-1}$ ) which was determined as follows:

$$R_s = \left[0.25 + 0.5 \left(\frac{n}{N}\right)\right] \times R_a$$

where n is the actual duration of sunshine (h), N is the maximum possible duration of sunshine r daylight hours (h) obtained from

$$N = \frac{24\omega_s}{\pi}$$

where  $\omega_s$  is the sunset hour angle and it is calculated as

$$\omega_s = \arccos[-\tan(w) \tan(d)],$$

where w is the latitude (red) and d is the solar decimation (red), calculated as

$$\delta = 0.409 \left(\frac{2\pi}{365} J - 139\right)$$

where J is the number of days in the particular pulse event and  $R_a$  is the extraterrestrial radiation ( $\text{MJ m}^{-2} \text{day}^{-1}$ ).

$$R_a = \frac{24(60)}{\pi} G_{sc} d_r [\omega_s \times \sin(\varphi) \times \sin(\delta) + \cos(\varphi) \times \cos(\delta) \times \sin(\omega_s)]$$

where  $G_{sc}$  is the solar constant ( $0.082 \text{ MJ m}^{-2} \text{min}^{-1}$ ), and  $d_r$  is the inverse relative distance earth-sun, as follows:

$$d_r = 1 + 0.033 \cos\left(\frac{2\pi}{365} J\right)$$

The outgoing net long-wave radiation was determined as

$$R_{nl} = \sigma \left[ \frac{T_{\max,k}^4 + T_{\min,k}^4}{2} \right] (0.34 - 0.14 \sqrt{e_a} (1.35 \frac{R_s}{R_{so}} - 0.35))$$

where  $\sigma$  is the Stefan-Boltzmann constant ( $4.903 \times 10^9 \text{ MJ K}^{-4} \text{m}^{-2} \text{day}^{-1}$ ),  $T_{\max,k}$  and  $T_{\min,k}$  are daily maximum and minimum absolute temperatures (K), respectively,  $e_a$  is the actual vapour pressure (kPa).

$$R_{so} = (0.75 + 2X \times 10^{-5} z) \times R_a$$

$$e_a = 0.6108 \exp \left[ \frac{17.27T}{T + 237.3} \right]$$

where z is the elevation above sea level (m) and  $\exp = 2.7183$  (base of natural logarithm) raised to the power.

## Trait values and their Trade-off

### Compartment biomass trait value

$$TraitValue = \frac{(1 - Min_{BC})}{(1 - Max_{BC})}$$

### Trade off compartment biomass with total biomass

$$TraitValue = \frac{\frac{(1 - Min_{BC})}{TB}}{\frac{(1 - Max_{BC})}{TB}}$$

### Trade off among different compartments

$$TraitValue = \frac{(1 - Min_{RC})}{(1 - Max_{RC})}$$

BC=Biomass of a compartment; TB= Total Biomass and RC is the ratio of biomass of two compartment.

### Multivariate Analysis

Canonical Correlation Analysis (CCorA) and Partial Least Squares (PLS) are well-known techniques for feature extraction from two sets of multidimensional variables. The fundamental difference between them is that CCorA maximizes the correlation while PLS maximizes the covariance (i.e it measure of how much two random variables vary together). CCorA is a multivariate statistical model that facilitates the study of interrelationships among sets of multiple dependent and multiple independent variables. In this analysis, redundancy test determine the magnitude of the variance in one set of variables that is accounted for by the other set of variables. Partial least squares regression is an extension of the multiple linear regression model in which multidimensional direction in the exploratory variables (X) space explains the maximum multidimensional variance direction in the dependent (Y) space. This latent type regression is particularly suited when the matrix of X has more variables than observations. Significant relationships between species biomass variables and exploratory variables obtained from CCorA were further treated with PLS. This test was carried out to know the random relationships between variables and to find the mathematical relationships between them. Both these multivariate technique were carried out by using Xlstat (2008).

## RESULTS

During the study period values of different solar, physiological, plant community and soil attributes are presented in Table 1. Among solar energy variables heat index, PET, Rnl, ea were recorded higher during summer period while AET, transpirations and Rn were recorded higher during rainy period. Except NPP, all species physiological parameters were recorded higher during summer. Richness and species diversity (Shannon-Weaver Index) were recorded maximum during rainy and winter seasons, respectively. While RIV of this species gradually increase from rain to winter and was maximum during summer period. Soil parameters like organic carbon and nitrogen were recorded higher during summer while other parameters were recorded maximum during rainy period.

Among the different compartments, maximum biomass trait for root (0.56) and for capsule (0.43) were recorded during winter period (Figure 1). While, for both these parts almost similar biomass trait value were recorded during rainy and summer periods. For stem (0.52) and leaf (0.62) higher biomass trait values were recorded during summer period. For stem, gradual increase was recorded from rainy to winter to summer, however, for leaf a slight decrease was recorded during winter period.

Seasonal trade-off values for different compartments with total biomass are presented in Figure 2. Higher trade-off with total biomass was recorded for stem (0.82) during winter period followed by leaf (0.80) and root (0.71), while for the capsule higher value (0.41) was recorded during summer and minimum (0.15) during rainy period. Compared to other compartments, capsule trade-off with total biomass was recorded less during all the seasons. For stem and leaf similar trade-off trends were recorded during rainy and summer seasons.

Results of trade-off among different compartments are presented in Figure 3. Highest was recorded between Leaf and stem (25.67) during summer period. Trade-off between root to stem, root to leaf, root to capsule, capsule to stem and root to leaf were recorded maximum during summer period. Minimum values for leaf to stem, capsule to stem, capsule to stem and capsule to leaf were recorded during winter period.

Results of canonical correlation analysis are presented in Table 2 and Figure 4. Axes 1 and 2 together approached 100% variabilities with their cumulative variance of 50 % each. Reduancy coefficient results showed that high proportions of the variabilities of the

Table 1. Values of different attributes during the study period

Attributes Types	Variable Name	Temporal Events		
		Rain	Winter	Summer
Solar Energy Variables	Heat Index	5774.5	3326	6433
	PET	6.68	7.6	7.7
	AET	227.8	153.1	142.93
	Transpiration	11.82	7.195	4.64
	Lambda Latent Heat of Vaporization ( $\lambda$ ; cal g <sup>-1</sup> )	2332	2342	2319
	Rn (Net Radiation (MJ m <sup>-2</sup> day <sup>-1</sup> ))	10.2	8.99	9.39
	Rns (Incoming net shortwave radiation)	13.75	15.92	14.52
	Rnl (Outgoing Net Long wave Radiation)	4.315	5.975	5.13
	Ra (Extraterrestrial radiation, MJ m <sup>-2</sup> day <sup>-1</sup> )	21.37	22.74	21.35
	Ea (Actual Vapor Pressure, kPa)	2.55	1.84	2.65
Species Physiological Parameters	Rs (Incoming Solar radiation,(MJ m <sup>-2</sup> day <sup>-1</sup> ))	17.63	18.85	19.9
	Maintenance Respiration (MR)	19.07	30.73	42.120
	Respiration Cost (RC)	7.8	7.96	10.1
	NPP	156.38	213.46	139.56
	GPP	183.25	252.15	191.78
	Plant Community Parameters	Richness	15	12
Relative Importance Value of species (RIV)		10.59	25.5	45.37
H index		1.28	1.54	1.41
Soil Parameters	Organic Carbon (SOC)	67.25	161.95	181.84
	Phosphorus (SP)	38.98	29.66	12.42
	Nitrogen (SN)	45.89	63.80	80.48
	Soil pH	8.50	7.30	7.058
	Electrical Conductivity (EC)	0.46	0.21	0.15
	Moisture (Smoi)	9.75	1.42	0.93

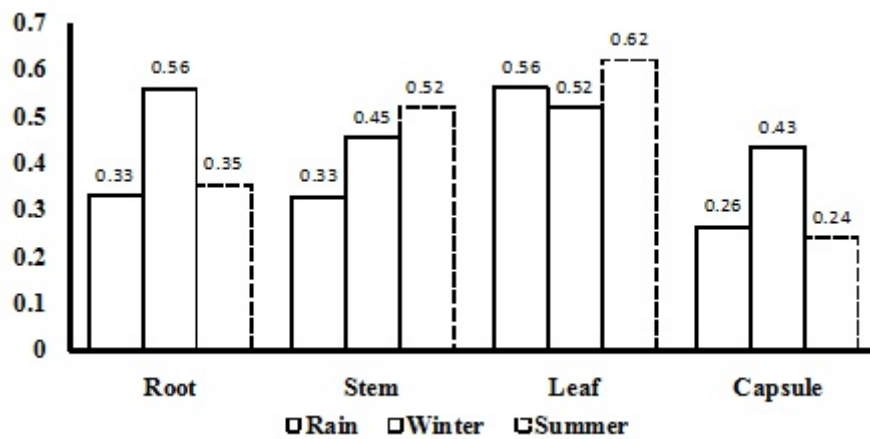


Figure 1. Seasonal biomass trait values of different compartments

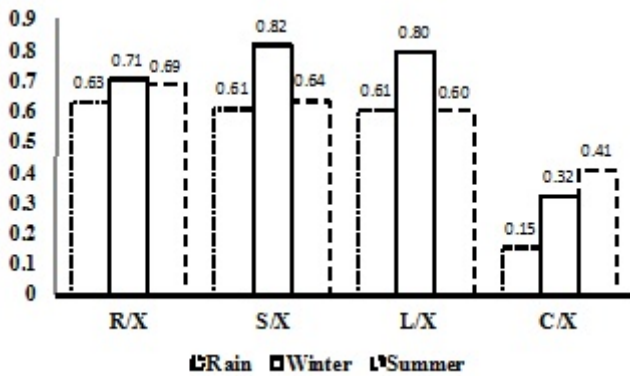


Figure 2. Seasonal trade-off values for different compartments with total biomass

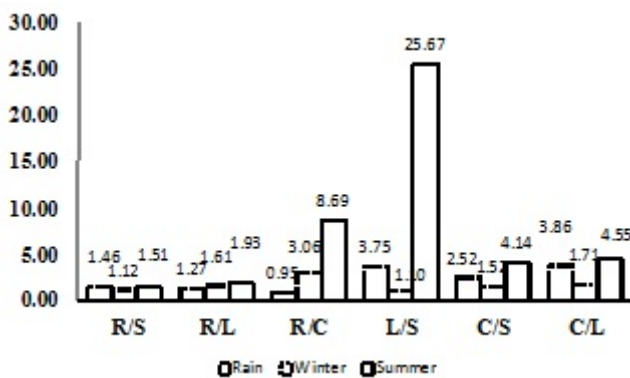


Figure 3. Trade-off among different compartments

environmental and species attributes were predicted by CCorA. Such results are also verified with canonical variable adequacy coefficients which were 0.57 and 0.56 for environmental and species variables at axes 2 and axes 1, respectively. Factor loading scores of different variables are presented in Table 3. Among community variables, Shannon-Weaver diversity index (H) and species richness, and were located on axes one and two, respectively. RIV was located opposite to species richness while, among soil parameters phosphorus and nitrogen were located close and on opposite side of the species richness, respectively. Soil electrical conductivity, pH and moisture were located on the axes two however; soil organic carbon was located to opposite to soil moisture.

Among the physiological parameters, NPP and GPP were located on axes one. Construction and maintenance respiration were associated negatively at axes two. Rn, Rnl and Ra and AET, RN solar variables were located on

axes one and two, respectively. Heat index was located to Rn. Species variables likes root, capsule, S/X and L/X were located on axes one while, R/S and C/L were located opposite to them. R/X and Leaf were located opposite to each other.

Table 2. Canonical Correlation Analysis Variables

Variables	F1	F2
Eigenvalue	1.000	1.000
Variability (%)	50.000	50.000
Cumulative %	50.000	100.00
Redundancy coefficients (Y1)	0.424	0.576
Redundancy coefficients (Y2)	0.564	0.436
Canonical variable adequacy coefficients (Y1)	0.424	0.576
Canonical variable adequacy coefficients (Y2)	0.564	0.436

Table 3. Factor loading of environmental (Y1) and species variables (Y2)

Environmental Variables (Y1)	F1	F2	Species Variables (Y2)	F1	F2
Heat Index	-0.957	-0.291	Root (R)	1.000	0.000
PET	0.503	-0.864	Stem (S)	0.268	-0.963
AET	-0.485	0.875	Leaf (L)	-0.749	-0.662
Transpiration	-0.255	0.967	Capsule (C)	0.978	0.207
Lambda	0.77	0.638	R/X	0.749	-0.662
Rn	-0.811	0.584	S/X	1.000	-0.029
Rns	0.965	-0.262	L/X	0.995	0.104
Rnl	0.913	-0.408	C/X	0.283	-0.959
Ra	0.994	0.105	R/S	-0.977	-0.211
Rea	-0.98	-0.199	R/L	0.115	-0.993
Rs	0.137	-0.991	R/C	-0.164	-0.986
MR	0.099	-0.995	L/S	-0.505	-0.863
RC	-0.36	-0.933	C/S	-0.731	-0.682
NPP	0.952	0.306	C/L	-0.947	-0.322
GPP	1	-0.021			
Richness	0.051	0.999			
RIV	0.01	-1.000			
H index	0.909	-0.418			
SOC	0.438	-0.899			
SP	0.078	0.997			
SN	0.113	-0.994			
pH	-0.438	0.899			
EC	-0.403	0.915			
Smoi	-0.537	0.844			

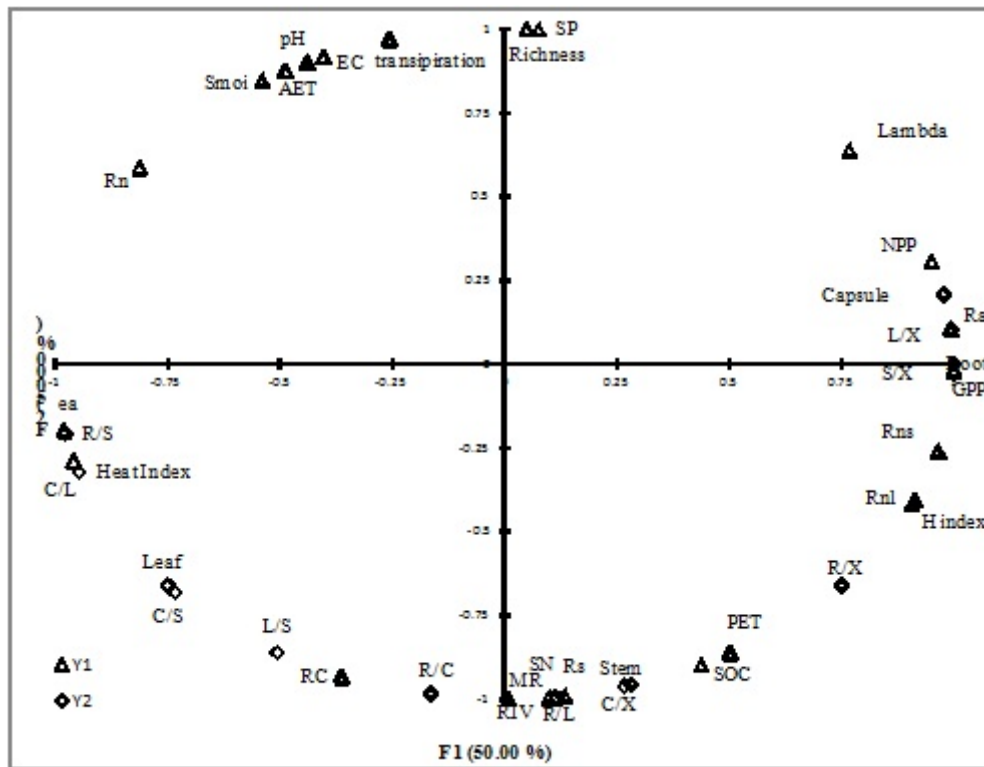


Figure 4. Bi-plot of canonical Correlation Analysis

Table 4. Results of Canonical Correlations and Partial Least Squares Analysis

Variables	Root	Stem	Leaf	Capsule	R/X	S/X	L/X	C/X	R/S	R/L	R/C	C/S	C/L
Heat Index	-0.957	0.024	0.910	<b>-0.996</b>	-0.524	-0.948	-0.982	0.008	<b>0.997</b>	0.179	0.444	0.898	<b>0.999</b>
Transpiration	-0.255	<b>-1.000</b>	-0.450	-0.049	-0.831	-0.283	-0.153	<b>-1.000</b>	0.045	<b>-0.990</b>	-0.912	-0.473	-0.071
Lambda	0.770	-0.408	<b>-0.999</b>	0.886	0.155	0.751	0.833	-0.393	-0.888	-0.545	-0.755	<b>-0.998</b>	-0.935
Rn	-0.811	-0.781	0.221	-0.673	<b>-0.995</b>	-0.828	-0.746	-0.790	0.670	-0.674	-0.443	0.195	0.580
Ra	<b>0.994</b>	0.166	-0.815	<b>0.995</b>	0.676	0.991	<b>1.000</b>	0.181	<b>-0.994</b>	0.010	-0.267	-0.799	-0.975
ea	-0.980	-0.071	0.866	<b>-1.000</b>	-0.603	-0.974	<b>-0.995</b>	-0.087	<b>1.000</b>	0.085	0.357	0.852	<b>0.992</b>
Rs	0.137	<b>0.991</b>	0.554	-0.071	0.758	0.166	0.033	0.989	0.075	<b>1.000</b>	0.955	0.576	0.190
MR	0.099	0.985	0.585	-0.109	0.733	0.128	-0.005	0.982	0.113	<b>1.000</b>	0.965	0.606	0.227
NPP	0.952	-0.040	-0.916	<b>0.995</b>	0.510	0.942	0.979	-0.024	<b>-0.995</b>	-0.195	-0.458	-0.905	<b>-1.000</b>
GPP	<b>1.000</b>	0.288	-0.735	0.974	0.763	<b>1.000</b>	0.992	0.304	-0.973	0.136	-0.143	-0.717	-0.940
Richness	0.051	-0.949	-0.699	0.257	-0.623	0.021	0.154	-0.943	-0.260	-0.986	<b>-0.993</b>	-0.718	-0.370
RIV	0.010	0.966	0.654	-0.197	0.670	0.040	-0.094	0.962	0.201	<b>0.995</b>	0.985	0.674	0.312
SP	0.078	-0.940	-0.719	0.283	-0.602	0.049	0.181	-0.934	-0.287	-0.981	<b>-0.996</b>	-0.737	-0.395
SN	0.113	0.987	0.573	-0.095	0.743	0.142	0.009	0.985	0.099	<b>1.000</b>	0.962	0.595	0.213
EC	-0.403	<b>-0.990</b>	-0.304	-0.205	-0.908	-0.430	-0.305	<b>-0.992</b>	0.201	-0.955	-0.837	-0.330	0.086
PLS													
R2	0.485	0.255	<b>0.994</b>	0.689	0.002	0.455	0.589	0.241	0.692	0.401	0.676	<b>0.998</b>	0.793
Std. deviation	0.128	0.119	0.005	0.083	0.058	0.117	0.100	0.159	0.168	0.360	3.219	0.093	0.954
MSE	0.01	0.005	0.000	0.002	0.001	0.005	0.003	0.008	0.009	0.043	3.453	0.003	0.304
RMSE	0.074	0.069	0.003	0.048	0.033	0.068	0.058	0.092	0.097	0.208	1.858	0.054	0.551*

Bold and highlighted numbers are the significant correlations

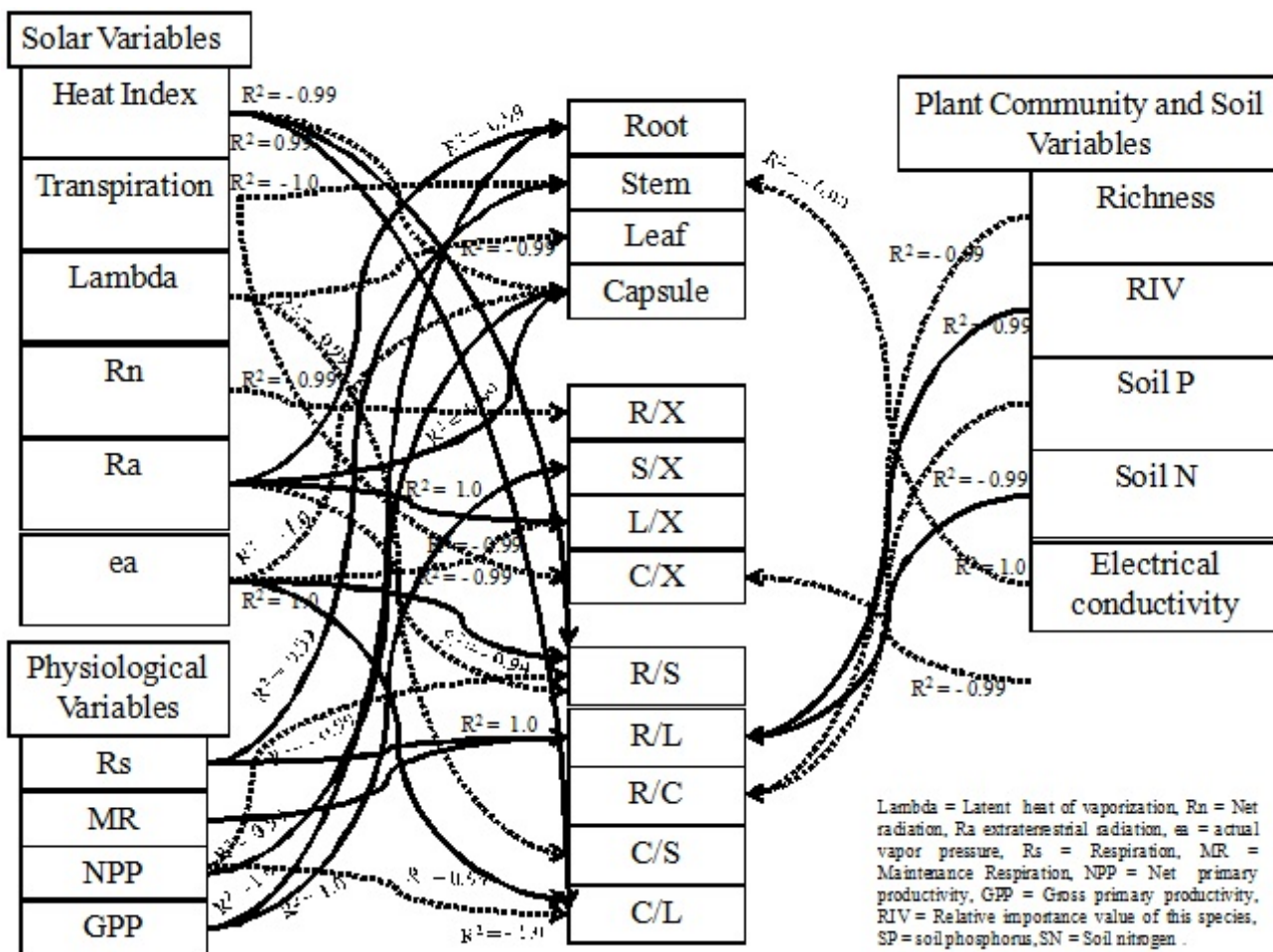


Figure 5. Flow-diagram pertaining to environmental variables and their impact on species traits and trade-off.

Results of correlation matrix between environmental and species variables are presented in Table 4 and Figure 4. Among eleven solar variables only six were significantly related with species attributes. Variables like heat index, Ra and ea were showed significant impact on capsule biomass trait value and R/S. Further, Ra and ea significantly linked with L/X. Transpiration showed negative significant relationships with stem biomass trait value and with C/X and R/L while lambda showed similar relationships with leaf and C/S. Physiological parameters like Rs, MR, NPP and GPP had have relationships with root, stem, capsule, S/X, R/S, R/L, C/L. Among them R/S and C/L were negatively related with NPP. Community parameters like richness and RIV showed positive and negative relationships with R/L and R/C, respectively. Similar trends were also recorded with soil nitrogen and soil

phosphorus, respectively. Electrical conductivity was also negatively and significantly related with stem and L/X. Thus, community diversity and soil organic carbon, pH and moisture were not related with trait values and trade-off pertains to this species. Significant relationships were further summarized into flow diagram (Figure 5) where in positive and negative relationships were symbolized with complete and dashed arrow, respectively.

Results of Partial Least Square (PLS) are presented in Table 4. Through this analysis, only two significant relationships were established as compared to CCorA from which 31 significant relationships existed between 13 plant variables and 15 exploratory variables. Two significant relationships pertain to leaf and C/S and their equations are as follows:

Leaf Biomass =

$$2.03 + 3.9E-06 * \text{Heat Index} - 7.0E-04 * \text{transpiration} - 5.9E-04 * \text{Lambda} + 3.3E-03 * \text{Rn} - 7.41E-03 * \text{Ra} + 1.4E-02 * \text{ea} + 2.9E-03 * \text{Rs} + 3.0E-04 * \text{MR} - 1.6E-04 * \text{NPP} - 1.4E-04 * \text{GPP} - 1.0E-03 * \text{Richness} + 2.3E-04 * \text{RIV} - 3.3E-04 * \text{SP} + 2.0E-04 * \text{SN} - 9.27E-03 * \text{EC}, \text{ and}$$

C/S =

$$41.50 + 1.0E-04 * \text{Heat Index} - 1.8E-02 * \text{transpiration} - 1.5E-02 * \text{Lambda} + 8.8E-02 * \text{Rn} - 0.19 * \text{Ra} + 0.37 * \text{ea} + 7.7E-02 * \text{Rs} + 8.1E-03 * \text{MR} - 4.4E-03 * \text{NPP} - 3.8E-03 * \text{GPP} - 0.02 * \text{Richness} + 6.1E-03 * \text{RIV} - 8.8E-03 * \text{SP} + 5.2E-03 * \text{SN} - 0.2 * \text{EC}.$$

Thus, with PLS approach the relative trend of leaf biomass and trade off among different compartments (i.e. C/S) can be predicted by using studied variables.

## DISCUSSION

Biomass allocation is the key strategy of plant to adapt to environmental conditions (Guo et al. 2016). Among various theories explaining the patterns of plant biomass allocation, two of them are most popular, i.e., optimal partitioning and allometric partitioning (Yang and Luo 2011). Under optimal partitioning theory (OPT), plants should allocate additional biomass to the organ that takes up the resource that most limits growth. For example, under low light, most plant species increase leaf area through some combination of increasing biomass allocation to leaves and producing thinner leaves (e.g., Grubb et al. 1996, Portsmouth and Niinemets 2007). Similarly, increased root biomass under low soil nutrients has been interpreted as evidence of a plastic allocation response to capture limiting soil resources (Portsmouth and Niinemets 2007). According to allometric partitioning theory (APT), different plant structures usually grow asymmetrically, and a power allometric relationship between shoot and root, which is insensitive to local environmental conditions (Enquist and Niklas 2002). In the present temporal study no such trends were recorded with respect to OPT and APT. During the rainy period when soil moisture and phosphorus were in adequate supply *T. purpurea* invest more in their photosynthetic part and least in reproductive part. During summer period when soil moisture was low but with adequate soil organic carbon and nitrogen, this species also invest more in their leaf followed by stem and root. Thus, for this species

compartment biomass trait value governed by other factors like solar and community variables and also by the random interactions of several variables. Inconsistency of OPT theory with root biomass under low nutrient conditions was also reported by Kobe et al. (2011) where they reported role of nonstructural carbohydrates (TNC) for such results. Both these theories also have drawbacks as OPT does not consider the size of the individual plant (Marcelis and Heuveling 2007), while APT does not provide quantitative descriptions about how environmental factors affect biomass allocation and how the mechanism how photosynthesis are allocated to different organs (Genard et al. 2008).

With reference to the individual compartment trade-off with total biomass, present results are in agreement with OPT theory where in maximum value for root to total biomass trade-off was recorded during summer period. Stem and leaf pulled more from total biomass during winter, while almost similar trend for both these parts were observed during remaining periods. High trade-off for leaf and stem with total biomass during winter season representing the optimal mechanism of this species for photosynthesis and the storage of photosynthesis product, respectively. While higher values for root trade-off with total biomass during rainy and summer period indicating the species mechanism for supporting nutrient acquisitions. Such seasonal compartment trade-offs with total biomass were reported with Rieger et al. (2015). Porter et al. (2012) in their meta-analysis of biomass allocation also reported large amount of variations in allocation pattern and compartment trade off in natural habitats and which are probably due to ecosystem and landuse type, and species associations. Among different compartment, great trade-off was observed between leaf and stem during summer period. Such result was expected as this species is a perennial evergreen one. This followed by trade off between root and capsule during similar seasons. Root and stem showed similar trade-off during different seasons, while trade off between root and stem and capsule and leaf showed slight decrease during winter period.

Various exploratory-dependent relationships were established with canonical correlation analysis and such relationships are within the agreement of several previous studies indicating that precipitation and temperature (Liu et al. 2014), salinity and transpiration (Lambers et al. 2008), soil compaction (Coutand et al. 2008), temperature (Wang et al. 2017) and light intensity

(Xie et al. 2016) are affecting plant biomass trait values and their trade-offs. In present study, impacts of heat index, net radiation, extraterrestrial and incoming solar radiation, actual vapor pressure, species physiological attributes (maintenance respiration, NPP and GPP), community variables (richness and Relative importance value) were also quantified. This ordination technique indicated that such relationships are existed in a pair i.e. exploratory-dependent manner. However, under natural conditions such pair wise associations are difficult to interpret. Thus, the significant relationships from CCorA were further funneled with PLS which suggested that various factors are working significantly and in random fashion and for this species and with this experiment set-up only two species variables i.e. leaf biomass trait and trade-off for C/S can be mathematically explained. Such step wise use of both these multivariate techniques has also been advocated by Sun et al. (2009).

## CONCLUSION

Plant species biomass traits and their trade-off patterns are the key features to understand their role in different ecosystem services. Present study suggests that for such species variables, different bottom-up and top-down factors work in random fashion. Thus, species-specific studies at various landuse and landforms are essential for understanding the species functional diversity i.e.. range and value of organism traits that influence ecosystem properties.

## ACKNOWLEDGEMENTS

I am thankful to former Director, CAZRI, Jodhpur for granting me study leave for this research work. I am also thankful to Prof. S. Sundaramoorthy, JNV University, Jodhpur for his scientific guidance.

## REFERENCES

- Allaie, R.R.; Reshi, Z. and Wafai, B.A. 2006: Demographic plasticity in relation to growth and resource allocation pattern in *Anthemis cotula* - an alien invasive species in Kashmir Himalaya, India. *Applied Ecology and Environmental Research* 4(1): 63-74.
- Allen, R.G.; Pereira, L.S.; Raes, D. and Smit, M. (1998) *Crop Evapotranspiration Guidelines for Computing Crop Water Requirements*. FAO Irrigation and Drainage Paper 56. Food and Agriculture Organisation of the United Nations, Rome, Italy. 300 pages
- Allen, S.E.; Grimshaw, H.M.; Parkinson, J.A.; Quarmby, C. and Roberts, J.D. 1976. Chemical analysis. Pages 411-466, In: Chapman, S.B. (Editor) *Methods of Plant Ecology*. Blackwell Scientific Publications, Oxford
- Bhattarai, K.R.; Vetaas, O.R. and Grytnes, J. A. 2004. Relationship between plant species richness and biomass in arid sub-alpine grassland of the central Himalayas Nepal. *Folia Geobotanica* 39: 57-71
- Black, C.A. 1965. *Methods of Soil Analysis: Part I Physical and Mineralogical Properties*. American Society of Agronomy, Madison, Wisconsin, USA. 1188 pages.
- Bradford, J.B. and D'amato, A.W. 2012. Recognizing trade-offs in multi-objective land management. *Frontiers in Ecology and the Environment* 10(4): 210-216.
- Coutand, C.; Dupraz, C.; Jaouen, G.; Ploquin, S. and Adam, B. 2008. Mechanical stimuli regulate the allocation of biomass in trees: demonstration with young *Prunus avium* tree. *Annals of Botany* 101: 1421-1432.
- Enquist, B.J. and Niklas, K.J. 2002. Global allocation rules for patterns of biomass partitioning in seed plants. *Science* 295: 1517-1520.
- Eziz, A.; Yan, Z.; Tian, D.; Han, W.; Tang, Z. and Fang, J. 2017. Drought effect on plant biomass allocation: a meta-analysis. *Ecology and Evolution* 7: 11002-11010.
- Genard, M.; Dauzat, J.; Frank, N.; Lescouret, F.; Moitrier, Vaast, P. and Vercambre, G. 2008. Carbon allocation in fruit trees: from theory to modeling. *Trees* 22: 269-282.
- Grubb, P.J.; Lee, W. G.; Kollman, J. and Wilson, J. B. 1996. Interaction of irradiance and soil nutrient supply on growth of ten European tall-shrub species and *Fagus sylvatica*. *Journal of Ecology* 84: 827-840.
- Guo, H.; Bo, X.U.; Yan, W.U.; Shi, F.; Cong, W.U. and Ning, W.U. 2016. Allometric partitioning theory versus optimal partitioning theory: the adjustment of biomass allocation and internal C-N balance to shading and nitrogen addition. *Polish Journal of Ecology* 64: 189-199.
- Jackson, M. L. 1973. *Soil Chemical Analysis*. Prentice Hall, Englewood Cliffs, NJ, USA. 498 pages.
- Kent, M. and Coker, P. 1992. *Vegetation Description and Analysis. A Practical Approach*. Belhaven Press, London. 363 pages.
- Kobe, R.K.; Iyer, M. and Walters, M. B. 2007. Optimal partitioning theory revisited: nonstructural carbohydrates dominate root mass responses to nitrogen. *Ecology* 91(1): 166-179.
- Lambers, H.; Chapin, F.S. and Pons, T.L. 2008. *Plant Physiological Ecology*. Springer, New York, USA. xxix+ 605 pages.
- Liu, M.; Liu, G.; Gong, L.; Wang, D. and Sun, J. 2014. Relationships of biomass with environmental factors in the grass area of Hulunbuir, China. *PLoS ONE* 9(7): e102344. doi:10.1371/journal.pone.0102344.
- Ludwig, J.A. and Reynolds, J.F. 1999. *Statistical Ecology: A Primer on Methods and Computing*. John Wiley, New York. 337pages.
- Marcelis, L.F.M. and Heuvelink, E. 2007. Concepts of modeling carbon allocation among plant organs. Pages 103-111, In: Vos, J.; Marcelis, L.F.M.; Visser, P.H.Bd; Struik, P.C. and Evers,

- J.B. (Editors). Functional Structural Plant Modeling in Crop Production. Springer, Dordrecht.
- Mathur, M. and Sundaramoorthy, S. 2008. Distribution pattern and growth assessment of *Corchorus depressus* in semi arid Indian desert. *Tropical Ecology* 49: 69-71.
- Mathur, M. 2016. Spatial distribution of *Tephrosia purpurea* on different habitats in relation to soil, community and site factors. *Range Management and Agroforestry* 37 (2): 148-154.
- Mathur, M. and Sundaramoorthy, S. 2013. Inter-specific association of herbaceous vegetation in semi arid Thar desert, India. *Range Management and Agroforestry* 34: 26-32.
- Mohammed, A.A. and Fredan, A.L. 2011. Nitrogen fixing legumes in the plant communities. *American Journal of Environmental Sciences* 7: 166-172.
- Pandeya, S.C.; Puri, G.S. and Singh, J.S. 1968. *Research Methods in Plant Ecology*. Asia Publishing House, Bombay. 272 pages.
- Patty, L.; Halloy, S.R.P.; Hiltbrunner, E. and Korner, C. 2010. Biomass allocation in herbaceous plants under grazing impact in the high semi-arid Andes. *Flora* 205(10): 695-703.
- Poorter, H.; Niklas, K.J.; Reich, P.B.; Oleksyn, J.; Poot, P. and Mommer, L. 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist* 193: 30-50.
- Portsmouth, A. and Niinemets, U. 2007. Structural and physiological plasticity in response to light and nutrients in five temperate deciduous woody species of contrasting shade tolerance. *Functional Ecology* 21: 61-77.
- Reekie, E.G. and Bazzaz, F.A. 2005. *Reproductive Allocation in Plants*. Elsevier Academic Press; Burlington, MA, USA. 264 pages.
- Rieger, I.; Kowarik, I. and Cierjacks, A. 2015. Drivers of carbon sequestration by biomass compartment of riparian forests. *Ecosphere* 6 (10): 1-16.
- Sun, L.; Ji, S.; Yu, S. and Ye, J. 2009. On the equivalence between canonical correlation analysis and orthonormalized partial least squares. *Proceedings of the 21<sup>st</sup> International Joint Conference on Artificial Intelligence*: 1230-1235. Morgan Kaufmann Publishers, San Francisco, CA. USA.
- Sunita, K.; Srivastava, M. and Abbasi, P. 2014. Response of *Tephrosia purpurea* to salinity stress in relation to germination carotenoid content and proline content. *Biolife* 21: 276-281.
- Wang, J.; Gao, J.; Wu, Y.; Sun, J.; Xu, B.; Shi, F.; Bisht, N.; Xu, J. and Wu, N. 2017. Biomass allocation and trade-offs of *Pedicularis longiflora* Rudolph. At two slope aspects in an alpine meadow of the eastern Tibetan Plateau. *Applied Ecology and Environmental Research* 15 (3): 51-65.
- Wang, P.; Heijmans, M. M. P.D.; Mommer, L.; Ruijven, J. V.; Maximov, T. C. and Berendse, F. 2016. Belowground plant biomass allocation in tundra ecosystem and its relationships with temperature. *Environmental Research Letters* 11: 055003.
- Wu, J.B.; Hong, J.T.; Wang, X.D.; Sun, J.; Lu, X.Y. Fan, J.H. and Cai, Y. J. 2013. Biomass partitioning and its relationship with the environmental factors at the alpine steppe in northern Tibet. *PLoS ONE* 8 (12): e81986.
- Xie, X.F.; Hu, Y.K.; Pan, X.; Liu, F.H.; Song, Y.B. and Dong, M. 2016. Biomass allocation of stoloniferous and Rhizomatous plant in response to resource availability: a phylogenetic meta-analysis. *Frontiers in Plant Science*. 7: 603. doi: 10.3389/fpls.2016.00603
- Xu, M.; Liu, M.; Xian, X. and Zhai, D. 2016. Warming effects on plant biomass allocation and correlation with the soil environment in an alpine meadow, China. *Journal of Arid Land* 8 (5): 773-786.
- Yadav, P. and Yadava, R.N. 2014. Allelopathic effects of some leguminosae plants. *International Journal of Science and Research* 3: 441-442.
- Yang, Y. and Luo, Y. 2011. Isometric biomass partitioning pattern in forest ecosystem: evidence from temporal observation during stand development. *Journal of Ecology* 99: 431-437.

Received 23 January 2018

Accepted 5 July 2018