

Spatio-temporal Variability in Distribution Patterns of *Tribulus terrestris*: Linking Patterns and Processes

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ABSTRACT

Spatial patterns are useful descriptors of the horizontal structure in a plant population and may change over time as the individual components of the population grow or die out. But, whether this is the case for desert woody annuals is largely unknown. In the present investigation, the variations in spatial patterns of *Tribulus terrestris* during different pulse events in semi-arid area of the Thar Desert, India, was quantified. Further ordination technique and path analysis were utilized to link the pattern and process of spatial distribution of *T. terrestris*. Dispersal indices like index of dispersal (I_D), index of clumping (I_C), Green's Index, Lloyd's mean crowding and Morisita's index of dispersion (I_δ) revealed uniform distribution pattern during non-pulse events, showing intense competition among plants for limited resources. Kaiser-Meyer-Olkin (KMO) and Bartlett's test of sphericity indicated the appropriate use of factor analysis and the significant relationships between variables. Principal Component Analysis (PCA) exhibited the significant correlation of the index of dispersion with the index of clumping and with the Lloyd index, while the Lloyd index correlated with the index of clumping and with the Morisita index. Path analysis suggested the association of soil organic carbon, nitrogen, and C/N ratio with the transition from clumped to uniform pattern. Further, lower soil phosphorus also supported the uniform distribution of this plant. Diversity indices like evenness and Simpson index are associated with uniform and clumped distribution patterns. Higher and intermediate level of percent cover and seed out-put of *T. terrestris* were also related to uniform and clumped patterns. Path analysis also indicated that salinity tolerance capacity of the species could be utilized for reclamation programme.

Keywords: Morisita index and Bartlett's test, Path analysis, Principal component analysis (PCA), Pulse events.

INTRODUCTION

The processes that generate plant spatial patterns in natural communities include plant-plant interaction (Valiente-Banuet and Verdu, 2008), environmental heterogeneity (Perry *et al.*, 2009), seed dispersal (Schurr *et al.*, 2004) and disturbance (Bisigato *et al.*, 2005; Rayburn and Monaco, 2011). There is an extensive history of observational research that has sought to explain the formation of plant spatial patterns by connecting observed patterns to ecological processes. Observational pattern studies

have tended to involve the collection of some form of spatial data on the patterns of one or more species within a community, followed by statistical analysis that seeks to describe the patterns of plants of interest. Results are then linked to the ecological processes by which the patterns are hypothesized to be formed (Rayburn, 2011).

In general, a population will have one of the three basic spatial patterns: (1) regular (or even, uniform, negative contagious) pattern in which individuals within this population are uniformly spaced; (2) random (or chance) pattern in which all individuals have an equal chance of living

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anywhere within an area, and (3) clumped (or aggregated, patchy, contagious) pattern in which individuals have a higher probability of being found in some area than in others (Yin *et al.*, 2005; Mathur and Sundaramoorthy, 2012).

For inter-specific studies, oftentimes, observed patterns have been linked to either positive or negative point interactions that have the potential to structure local plant neighborhoods (Rayburn and Monaco, 2011). For example, regular spatial patterns are often interpreted as a sign of intense competition between plants for limited resources (Stoll and Bergius, 2005). In contrast, aggregated patterns are interpreted as evidence of neutral or positive plant interactions (Valiente-Banuet and Verdu, 2008). But, for intra-specific studies (especially in arid and semi-arid regions) spatial patterns have asserted the importance of transitions among various distribution patterns of plant species (Aguar and Sala, 1999). The importance of studies of spatial pattern analysis for tree/forest communities have been explored by Salas *et al.* (2006), Law *et al.* (2009), and Basiri *et al.* (2011). Phillips and MacMahon (1981) showed that the spacing pattern of creosote bushes changes as they grow in Sonoran and Mojave Desert from a clumped pattern in established stage, then to a random one due to mortality, finally to a regular one due to competition.

In the present study, it was examined how woody annual plant *Tribulus terrestris* (Zygophyllaceae) spaced and which model may best describe its spatial pattern. Specifically the following questions were asked: (1) what is the spatial pattern of *Tribulus terrestris*? (2) how may spatial pattern changes over space and time?, and (3) what are the underlying factors associated with distribution patterns of this plant? And for this, factors such as edaphic properties (organic carbon, nitrogen, C/N ratio, moisture, pH, electrical conductivity, phosphorus), diversity parameters like richness, Shannon–Wiener index, evenness, Simpson's index and Relative Importance

Value of *T. terrestris*, and plant allocation (root length, root weight, shoot weight, R/S ratio, percent cover of plant, seed output and seed weight) were chosen to be tested.

MATERIALS AND METHODS

For the present investigation, five natural sites were selected for *T. terrestris*. Coordinates, habitat type, and other attributes are presented in Table 1. At each site, ten permanent quadrats of 5 m × 5 m abutting each other in a row were laid across the field (Kent and Cooker, 1992). Samplings were carried out during pulse (rain), inter-pulse (winter) and non-pulse events (summer) (Goldberg and Novoplansky, 1997). These events were considered as resource gradient within semi arid system. During the study period, mean annual precipitation ranged from 0.004 to 260 mm, average winter (January) temperature ranged from 10.7 to 23°C, while mean summer (June) temperature ranged from 28.7 to 42.2°C. Relative humidity ranged from 31 to 91% (Morning) and 8 to 68% (Evening). Average values of various soil, community, and plant variables are presented in Table 2.

Dispersal Indices

The following dispersal indices were quantified according to Ludwig and Reynolds (1988) by using simple Microsoft Excel Program.

Index of Dispersal (I_D)

Dispersion of a population can be classified through calculation of variance to mean ratio; namely s^2/\bar{x} . An I_D value that equals to 1.0 indicates a random distribution; zero (or < 1) indicates uniform while, more than one indicates the clumped distribution. The significance of I_D can be tested by chi-square (χ^2) test. According to Ludwig and Reynolds

Table 1. GPS locations, habitat types and other attributes of sampling sites.

Site No.	Coordinates		Habitat types	Soil textures			
	N	E		Clay	Silt	Sand	Gravel
1	26° 12' 33.7"	73° 4' 8.4"	Old alluvium plains	27.61	26.87	30.37	14.84
2	26° 14' 31.6"	73° 01' 21.1"	Old alluvium plain	33.35	17.83	42.77	4.99
3	26° 18' 47.0"	72° 60' 35.1"	Piedmonts area	29.5	4.23	43.02	23.25
4	26° 17' 2.5"	72° 56' 5.9"	Younger alluvium plain	27.76	3.63	56.4	7.055
5	26° 20' 58.9"	73° 3' 57.2"	Hummocky undulating terrains	30.17	10.61	61.5	2.765

Table 2. Average value of various variables during different seasonal events.

Variables	Events			
	Pulse	Inter-pulse	Non-pulse	
Soil Parameters	Electrical conductivity	0.21	0.15	0.11
	Soil organic carbon	82.82	66.82	106.50
	Moisture	10.75	0.96	0.68
	Soil pH	7.16	6.31	6.97
	Soil phosphorus	41.65	37.17	16.22
	Soil nitrogen	70.74	66.64	90.55
Community Parameters	C/N ratio	1.18	1.02	1.18
	RIV of <i>T. Terrestris</i>	51.30	32.16	15.91
	Richness	10.60	5.60	3.80
	Shannon-Wiener index	2.40	1.64	1.00
	Evenness	1.02	0.90	0.74
	Simpson Index	0.16	0.32	0.31
Plant Variables	Percent cover	0.37	0.39	1.62
	Seed Weight	0.95	1.07	1.09
	Seed out put	223.79	309.84	719.80
	R/S ratio	0.21	0.16	0.23
	Root length	15.71	22.36	14.92
	Root weight	16.00	1.96	1.97
Shoot weight	73.48	10.94	16.39	

(1988), χ^2 is a good approximation with $N-1$ degrees of freedom. If the value of χ^2 falls between the χ^2 tabular values at the 0.975 and 0.025 probability levels ($P > 0.05$), agreement with a random distribution is accepted (i.e., $s^2 = \bar{x}$). On the other hand, values of χ^2 less than the 0.975 probability level suggest a regular pattern (i.e., $s^2 < \bar{x}$), whereas χ^2 values greater than the 0.025 probability level suggest a clumped pattern (i.e. $s^2 > \bar{x}$).

Index of Clumping (I_C)

David and Moore (1954) proposed a modification of I_D , i.e. index of clumping

(I_C). The negative value of this index represents uniform distribution; the value of 0 indicates random distribution, whereas the value equal to $N-1$ indicates maximum clumping. David and Moore (1954) proposed a test for the significance of difference between samples, e.g. for the same species in two different habitats. It depends on the same number of quadrats being used in each case and takes the form of calculating

$$\omega = -\frac{1}{2} \ln \frac{v_1 \lambda_2}{\lambda_1 v_2}$$

Where, λ_1, λ_2 are the observed means and v_1, v_2 are observed variances of the two sets of data. If ω lies outside the range of $\pm 2.5/\sqrt{(N-1)}$, N is the number of quadrats in



each dataset, the difference in index of clumping is significant.

Green's Index (GI)

As compared to I_D and I_C indices, Green's index (GI; Green, 1966) better measures dispersion since it is independent of the number of individuals (Ludwig and Reynolds 1988). And it could be calculated as:

$$GI = \frac{s^2/\bar{x} - 1}{\bar{x}} = \frac{I_c}{\bar{x}}$$

Where, s^2 is variance, \bar{x} is mean (arithmetic mean obtained from the frequency of plant and the total number of individual) and N is number of quadrats.

Lloyd's Mean Crowding Index (x^*)

Mean crowding (x^*) was proposed by Lloyd to indicate the possible effect of mutual interference or competition among individuals (Moradi-Vajargah *et al.*, 2011). Theoretically, mean crowding is the mean number of other individuals adjacent to each individual in the same quadrat: $x^* = \bar{x} + s^2/\bar{x} - 1$.

As an index, the mean crowding is highly dependent upon both the degree of clumping and population density. To remove the effect of changes in density, Lloyd introduced the index of patchiness, expressed as the ratio of mean crowding to the mean. As with the variance-to-mean ratio, the index of patchiness is dependent upon quadrat size: $x^*/\bar{x} = 1$ random, < 1 regular and > 1 aggregated (Lloyd, 1967).

Morisita's Index of Dispersion

Morisita's index of dispersion (I_s) has been extensively used to evaluate the degree of dispersion/aggregation of spatial point patterns (Morisita, 1959; Tsuji and Kasuya,

2001; Rayburn, 2011). This index is based on random or regular quadrat counts, and is closely related to the simplest and oldest measures of spatial pattern, the variance: mean ratio (Dale *et al.*, 2002) and to other dispersion indices. The value of this index equal to 1 indicates random, more than one indicates aggregated, and less than one indicates uniform distribution. It can be measured as:-

$$I_s = Q \frac{\sum_{i=1}^Q n_i(n_i - 1)}{N(N - 1)}$$

Factor Analysis

To assess the suitability of factor analysis, two tests, namely, Bartlett's test of sphericity and Kaiser-Meyer-Olkin (KMO) were conducted. Exploratory factor analysis (Principal Component Analysis, PCA) was carried out as a data reduction technique. PCA was performed with Pearson correlation coefficient with the help of statistical software. Main objective of PCA analysis was to find out underlying factors associated with distribution patterns of a plant, and for this, factors such as edaphic characteristics (organic carbon, nitrogen, C/N ratio, moisture, pH, electrical conductivity, and phosphorus), diversity parameters (richness, Shannon-Wiener index, evenness, Simpson index and Relative Importance Value (RIV) of *T. terrestris*), and growth allocation parameters (root length, root weight, shoot weight, R/S ratio, seed output and seed weight) were examined. The interpretation of the correlation circle was made under the following criteria: when two variables are far from the center, then, if they are close to each other, they are significantly positively correlated (r close to 1); if they are orthogonal, they are not correlated (r close to 0); and when they are on opposite side of the center, they are significantly negatively correlated (r close to -1). Squared cosines were used to link the variable with the corresponding axis, and the greater the

squared cosine, the greater the link. However, in order to determine basic soil, vegetation diversity, and growth allocation variables sustaining these interrelationships, the concept of component defining variables (CDV) was employed which stipulates the selection and subsequent naming of variables with the highest component loading (correlation coefficient) as variables that provide the best relationships (Iwara *et al.*, 2011). Appropriate regression equations were selected on the basis of probability level significance and higher R^2 value. This path analysis was made by Curve Expert software (2001).

RESULTS AND DISCUSSION

During non-pulse event, all indices indicated uniform pattern of spatial distribution. This showed the intense competition between individual plants for limited resources. At Site 5, no temporal variation in distribution types was recorded; plants at this site exhibited uniform

distribution pattern (Table 3). Both the indexes of dispersion and of clumping exhibited that plants at Sites 1 and 5 showed no changes in spatial pattern during various events. At these two sites, plants showed uniform distribution during all temporal events. At Sites 2 and 4, transitions from uniform to clumped pattern from the pulse to inter-pulse event and, conversely, from clumped to uniform from the inter-pulse to non-pulse event were recorded. However at Site 3, random pattern produced during pulse event and then transferred to uniform pattern during inter-pulse and non-pulse events. Departure from randomness (χ^2 test) revealed regular pattern at all sites during all events as the value of χ^2 were less than the 0.975 probability level (Table 3). Index of clumping ranged from -0.704 to 1.52. Test of significance (Table 4) indicated that most of the values were lower than ω values, indicating the significance of I_C index.

During the inter-pulse event, Green, Lloyd, and Morisita indexes exhibited clumped/aggregated distribution patterns for the plant species, suggesting habitat

Table 3. Various distribution indices at different sites during various temporal events.

Events	Sites	Indices					
		Index of dispersion	χ^2 ^a	Index of clumping	Green	Lloyd's	Morisita
Pulse	Site 1	0.99	0.112	-0.21	0.025	1.25	1.58
	Site 2	0.74	0.05	-0.65	0.007	1.55	0.987
	Site 3	1.000	0.111	0.000	0.000	1.000	1.050
	Site 4	0.697	0.077	-0.303	-0.009	0.900	0.937
	Site 5	0.444	0.049	-0.556	-0.022	0.780	0.818
Inter-pulse	Site 1	0.580	0.047	-0.147	0.008	1.580	1.280
	Site 2	1.250	0.028	0.874	0.007	1.780	1.780
	Site 3	0.741	0.082	-0.259	-0.009	1.910	1.979
	Site 4	2.523	0.280	1.523	0.054	1.570	1.634
	Site 5	0.443	0.049	-0.557	-0.037	0.650	0.695
Non-pulse	Site 1	0.877	0.040	0.240	-0.024	0.784	1.580
	Site 2	0.582	0.074	0.874	-0.120	0.870	1.740
	Site 3	0.296	0.033	-0.704	-0.031	0.704	0.738
	Site 4	0.687	0.076	-0.313	-0.015	0.850	0.899
	Site 5	0.585	0.065	-0.415	-0.019	0.810	0.857

^a Tabular value of χ^2 at 0.95 levels (N-1) is 3.325.

**Table 4.** Test for significance of index of clumping.

Event types		Site 1	Site 2	Site3	Site 4
Pulse	Site 2	0.368	-	-	-
	Site 3	0.525	0.427	-	-
	Site 4	0.508	0.728	0.477	-
	Site 5	0.797	0.497	0.654	0.741
Inter-pulse	Site 2	0.61	-	-	-
	Site 3	0.43	0.254	-	-
	Site 4	0.23	0.145	0.741	-
	Site 5	0.44	0.244	0.684	0.542
Non-pulse	Site 2	0.331	-	-	-
	Site 3	0.541	0.391	-	-
	Site 4	0.487	0.546	0.715	-
	Site 5	0.741	0.523	0.222	0.756

$$\omega = \pm 2.5/\sqrt{(N-1)} = 0.83$$

heterogeneity. During the pulse event at Site 1, these three indices indicated clumped distribution pattern, while at Site 2, the above three indices showed random, clumped, and uniform over time, respectively. Similarly, at Site 3, these indices showed random, random and clumped patterns, respectively.

Studies like King and Woodell (1973), Phillips and MacMahon (1981) and Skarpe (1991) revealed that the regular pattern generally occurred during intense competition for limited resources, such as water or soil resources. The random pattern may be a direct result of ecological processes such as habitat heterogeneity (Tirado and Pugnaire 2003) or may emerge temporarily when the aggregated pattern shifts to the regular pattern because of density-dependent mortality (Prentice and Werger, 1985). The intra-specific clumped or aggregated has been attributed to environmental heterogeneity (Perry *et al.*, 2009), seed dispersal (Schurr *et al.*, 2004), and plant-plant interaction (Phillips and MacMahon, 1981).

The present investigation revealed that distribution patterns of *T. terrestris* were site and event specific. At Site 5 a constant uniform distribution pattern indicated large niche availability and high niche occupancy. At Sites 4 and 5, reverse back transitions

occurred, i.e. uniform–clumped–uniform. The emergence of clumped pattern between two uniform patterns can be explained by the finding of Molles (1999) who suggested that clumped pattern occurs when dispersal is limited because the seed dispersal of *T. terrestris* is associated with animal activity which occurred less during semi pulse event (winter). The less dispersal occurred during winter season and thus produced the clumped pattern, while the reverse back transition from clumped to uniform can be explained by the steady mortality during non-pulse event. However, at Site 3, three types of the transitions of spacing patterns have been recorded: random–uniform–uniform (as indicated by the index of clumping, the index of dispersion and the Green index), random–clumped–uniform (by Lloyd index), and clumped–clumped–uniform (by Morisita index).

For *T. terrestris*, higher level of uniform distribution can be explained by its long distance seed dispersal mechanism (Mathur, 2005). Uniformity of regular pattern at Site 5 during all the events can be explained by high space availability as well as higher amount of sand content compared to the other sites (Table 1). However, at Site 4, the appearance of clumped distribution pattern in between two successive uniform patterns may be associated with winter rainfall that

led to the low distance dispersal (Mathur and Sundaramoorthy, 2013). At Site 3, the presence of random distribution during the pulse event can be explained by density dependent mortality.

According to Aguiar and Sala (1999), such spatial transitions are unidirectional, i.e., clumped–random-uniform (with depleting resources). They further stated that the competition among neighboring plants is the most common explanation for such unidirectional intra-specific transitions, which will lead to density-dependent growth and survival and hence plants that are closer together will be smaller and more likely to die; the competition will therefore convert clumped (aggregated) distribution into random one and random distribution into regular one. The present study partially supports the findings of Aguiar and Sala (1999). To answer the difference of the present study from their study, the distribution data along with soil, diversity, and plant allocation were analyzed with multivariate analysis (PCA; Tables 4 and 5). The *KMO* measure of sampling adequacy is an index used to examine the appropriateness of factor analysis (Table 5). A high value (between 0.5 and 1.0) indicates factor analysis is appropriate, while the value below 0.5 indicates the inappropriate use of factor analysis. In present study, *KMO* was 0.526, which indicated appropriate use of factor analysis. For Bartlett's test of sphericity, there are two levels to interpret this test (a) H_0 : There is no correlation significantly different from 0 between the variables, and (b) H_a : at least one of the correlations between the variables is significantly different from 0. As the computed *P*-value is higher than the significance level= 0.05, one should reject the null hypothesis H_0 and accept the alternate. Present study showed that there were significant relationships between the variables.

Table 5. Bartlett's sphericity and Kaiser-Meyer-Olkin sampling adequacy tests.

Chi-square (Critical value)	315.749
DF	276
p-value	0.090
Alpha	0.05
<i>KMO</i>	0.526

According to Li *et al.* (2008), PCA was considered useful if the cumulative percentage of variance approached 80%. In present study, as to the cumulative percentage, the first four axes together accounted for 82.09% of variability in the data set (Table 6) with their individual contribution being 34.94, 21.65, 15.75, and 9.74%, respectively. For each component, the variables with loading value ≥ 0.70 were identified as significant and used for path analysis and for discussion (Iwara *et al.*, 2011). Results revealed that 20 out of 24 variables were significant. Correlation circle (Figure 1) revealed that the Index of dispersion significantly correlated with the index of clumping ($r= 0.811^{**}$, $P < 0.01$) and Lloyd index ($r= 0.528^*$, $P < 0.05$). The Lloyd index showed significant relationships with the index of clumping ($r= 0.536^*$, $P < 0.05$) and the Morisita index ($r= 0.662^*$, $P < 0.05$).

Path Analysis

Spatial Indices and Soil Parameters

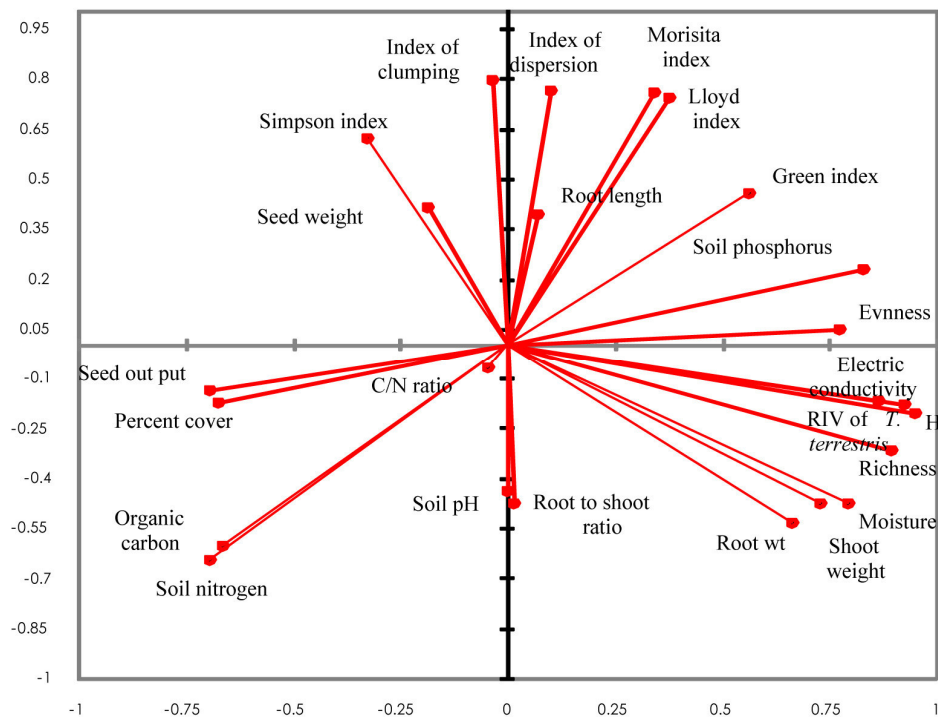
Both soil organic carbon [Lloyd Index= $1.851 - (0.0013 \text{ soil organic carbon}) - 7.94E - (0.5 \text{ soil organic carbon}^2)$, $R^2 = 0.609 \pm 0.35$, Figure 2-a] and soil nitrogen [Soil nitrogen= $3.024 - (0.024 \text{ Lloyd index})$, $R^2 = 0.767^{**} \pm 0.281$, Figure 2-b] showed negative relationships with Lloyd index on both quadratic and linear scales. Similarly, these soil parameters both were linearly and negatively related to Morisita index [Morisita index= $2.856 - (0.0194 \text{ soil organic carbon})$, $R^2 = 0.810^{**} \pm 0.258$, Figure 2-c]; [Morisita index= $2.6144 - (0.0192 \text{ soil nitrogen})$, $R^2 = 0.590 \pm 0.356$, Figure 2-d]. Also, *C/N* ratio revealed a polynomial relation with Morisita index [Morisita index= $7.781 - (10.64 \text{ C/N ratio}) + (4.163 \text{ C/N ratio}^2)$, $R^2 = 0.537 \pm 0.038$, Figure 2-e]. Soil nitrogen exhibited negative relationships with the index of dispersion (Index of dispersion= $31660.03 \exp(-0.160 \text{ soil nitrogen})$, $R^2 = 0.910^{**} \pm 0.688$, Figure 2-f), and with the Green index [Green index= $0.127 - (0.0018 \text{ soil nitrogen})$, $R^2 = 0.634 \pm 0.030$, Figure 2-g] in exponential and liner scales, respectively.

Thus, it can be interpreted that the lower level of soil organic carbon, nitrogen, as well as *C/N*

**Table 6.** Eigen value analysis and other attributes obtained from Principal Component Analysis.

Parameters	F1	F2	F3	F4	F5
Eigenvalue	9.086	5.631	2.796	2.014	1.538
Variability (%)	34.946	21.658	15.754	9.740	5.917
Cumulative %	34.946	56.604	72.350	82.098	88.05
ID	0.029	0.792	0.057	0.083	0.055
Ic	0.036	0.032	0.029	0.106	0.766
Gi	0.713^a	0.106	0.003	0.034	0.085
L	0.093	0.776	0.023	0.002	0.069
Morisita	0.176	0.736	0.077	0.040	0.006
Electrical conductivity	0.700	0.072	0.026	0.011	0.005
Soil organic carbon	0.715	0.196	0.081	0.034	0.004
Moisture	0.746	0.125	0.033	0.009	0.010
Soil pH	0.000	0.207	0.121	0.364	0.012
Soil phosphorus	0.713	0.016	0.021	0.022	0.002
Soil nitrogen	0.755	0.093	0.037	0.015	0.060
C/N ratio	0.004	0.017	0.769	0.057	0.048
RIV of <i>T. Terrestris</i>	0.842	0.093	0.001	0.012	0.010
Richness	0.725	0.187	0.000	0.035	0.014
Shannon-Wiener index	0.795	0.084	0.000	0.001	0.021
Evenness	0.727	0.000	0.016	0.001	0.127
Simpson Index	0.064	0.785	0.177	0.056	0.061
Percent cover	0.772	0.012	0.076	0.149	0.027
Seed Weight	0.024	0.144	0.149	0.346	0.000
Seed out put	0.783	0.004	0.005	0.001	0.005
R/S ratio	0.001	0.179	0.321	0.172	0.009
Root length	0.012	0.167	0.582	0.060	0.102
Root weight	0.771	0.062	0.004	0.018	0.000
Shoot weight	0.746	0.326	0.182	0.004	0.002

^a Variables bold with eigenvectors (coefficients) $\geq \pm 0.70$ are considered.

**Figure 1.** Bi-Plot of principal component analysis.

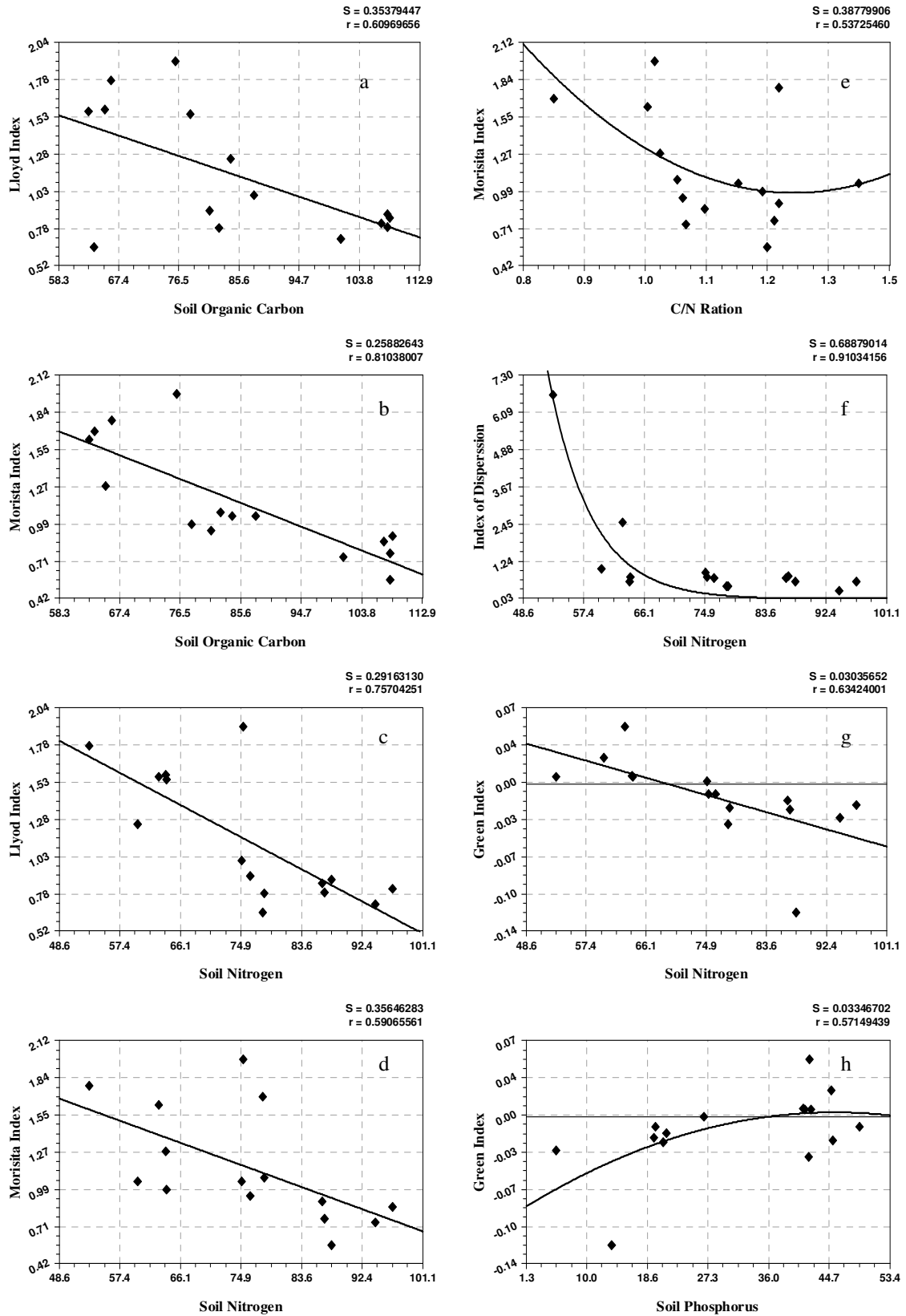


Figure 2. Path Analysis between various variables (a to l).

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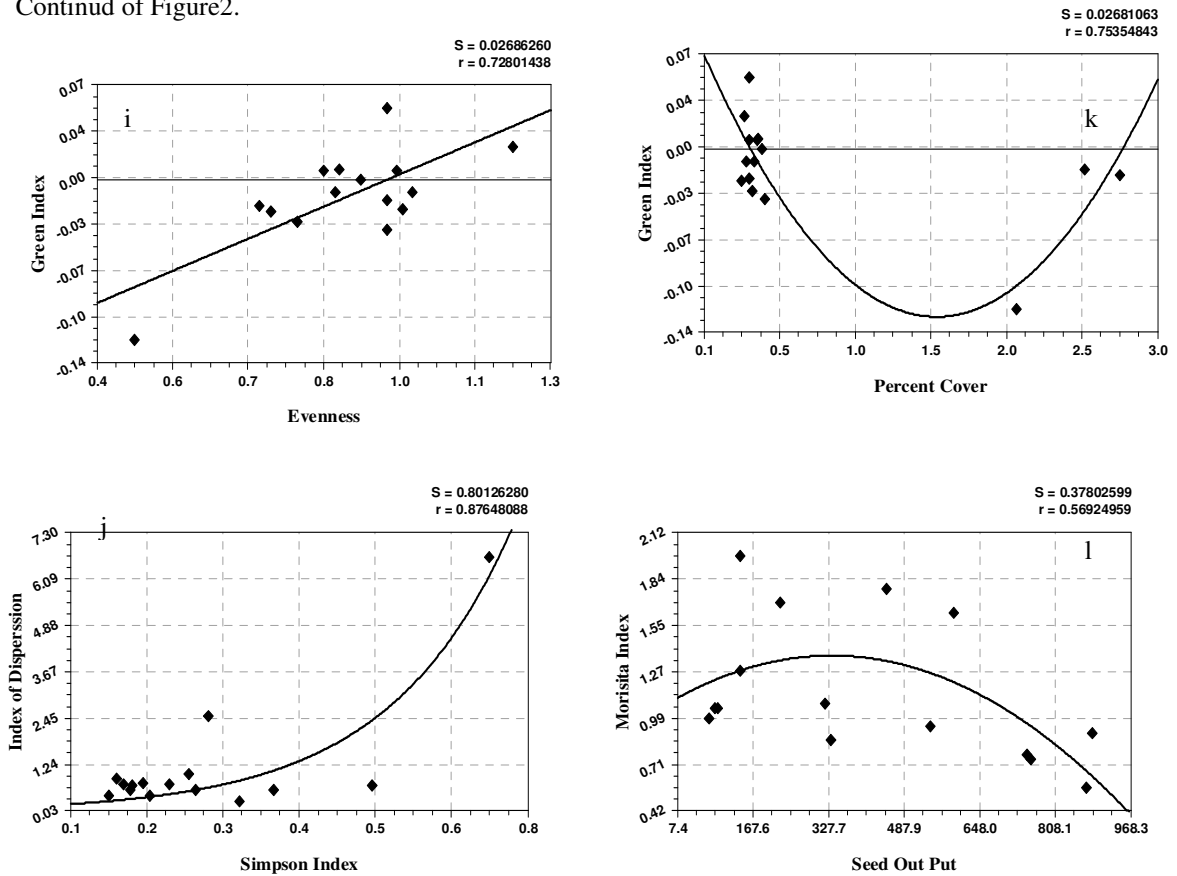


Figure 2. Path Analysis between various variables (a to l).

Table 7. Path analysis summary between soil parameters and community dynamics.

Independent Variables	Dependent Variables	Relation Type	Equations
Electric conductivity	RIV of <i>T. terrestris</i>	Linear	Relative importance value of <i>T. terrestris</i> = $8.81 + (264.22 \text{ electrical conductivity})$, ($R^2 = 0.847^{**} \pm 8.59$)
Moisture	RIV of <i>T. terrestris</i>	Linear	Relative importance value of <i>T. terrestris</i> = $21.76 + (2.75 \text{ soil moisture})$ ($R^2 = 0.857^{**} \pm 8.33$)
Soil phosphorus	RIV of <i>T. terrestris</i>	Linear	Relative importance value of <i>T. terrestris</i> = $7.560 + (0.8069 \text{ soil phosphorus})$, ($R^2 = 0.719^{**} \pm 11.24$)
Electrical conductivity	Species richness	Linear	Richness = $-1.3840 + (50.71 \text{ electrical conductivity})$, ($R^2 = 0.802^{**} \pm 1.84$)
Moisture	Species richness	Linear	Richness = $4.21 + (0.593 \text{ moisture})$, ($R^2 = 0.913 \pm 1.33$)
Soil Phosphorus	Species richness	Linear	Richness = $2.199 + (0.141 \text{ soil phosphorus})$, ($R^2 = 0.620^* \pm$
Electrical conductivity	Shannon-Wiener Index	Linear	Shannon-Wiener diversity index = $-0.0326 + (10.78 \text{ electrical conductivity})$, ($R^2 = 0.829^{**} \pm 0.377$)
Moisture	Shannon-Wiener Index	Wiener	Shannon-Wiener diversity index = $1.234 + (0.1077 \text{ moisture})$, ($R^2 = 0.804^{**} \pm 0.400$)
Soil phosphorus	Shannon-Wiener Index	Wiener	Shannon-Wiener diversity index = $1.434 - (0.0374 \text{ soil phosphorus}) + 0.00121 \text{ soil phosphorus}^2$, ($R^2 = 0.7466^{**} \pm 0.467$)
Electrical conductivity	Evenness	Linear	Evenness = $0.556 + (2.070 \text{ electrical conductivity})$ ($R^2 = 0.630^* \pm 0.132$).
Moisture	Evenness	Linear	Evenness = $0.800 + (0.203 \text{ moisture})$, ($R^2 = 0.601^* \pm 0.136$)
Soil Phosphorus	Evenness	Linear	Evenness = $0.620 + (0.0083 \text{ soil phosphorus})$, ($R^2 = 0.706^{**} \pm 0.120$)

** : $P < 0.01$, * : $P < 0.05$.

ratio supported the clumped distribution pattern of this plant, while as these soil factors increase during the non-pulse event, they support its transition from random to uniform distribution (as shown by Green, Lloyd and Morisita indexes).

On the other hand, the soil phosphorus was correlated with Green Index in a positive polynomial fashion (Green index = $-0.088 + 0.0040 \text{ soil phosphorus} - 4.50E-005 \text{ soil phosphorus}^2$, $R^2 = 0.571 \pm 0.033$, Figure 2-h). According to this equation, the higher level of soil phosphorus (pulse event) did not give any clear indication about the distribution pattern, but its lower value (non-pulse event) indicated the uniform distribution.

Spatial Indices and Diversity Parameters

In the present investigation, both Simpson's evenness and dominance indexes showed positive relationships with Green index [Green index = $-0.160 + (0.1674 \text{ evenness})$, $R^2 = 0.7280 \pm 0.0268$, Figure 2-i] and with index of dispersion [Index of dispersion = $0.155e^{\text{exp}(5.271 \text{ Simpson's index})}$, $R^2 = 0.876 \pm 0.801$, Figure 2-j] in linear and exponential fashions, respectively. Lower evenness (i.e., with few species being dominant) supports the uniformity while intermediate evenness supports clumped pattern. For Simpson's dominance index, both its lower and higher values largely supported the uniformity, while an intermediate dominance supported clumped distribution at a few sites.

Spatial Indices and Plant Attributes

There were polynomial relationships between the Green Index and percent cover of *T. terrestris* [Green Index = $0.0839 - (0.266 \text{ percent cover}) + (0.084 \text{ percent cover}^2)$, $R^2 = 0.753 \pm 0.0268$, Figure 2-k] and between the Morisita index and seed output (Morisita index = $1.101 + (0.00161 \text{ seed output}) - 2.41E-$

$(006 \text{ Seed Output}^2)$, $R^2 = 0.569 \pm 0.378$, Figure 2-l]. Thus, higher and intermediate levels of percent cover and seed output are associated with uniform and clumped spatial pattern, respectively.

Soil Parameters and Community Dynamics

Regression analysis revealed that, among soil parameters, the electrical conductivity, moisture, and phosphorus were the major controlling factors of community dynamics parameters including relative importance value of *T. terrestris*, richness, Shannon-Wiener index and evenness. The same three soil parameters showed positive linear relationships with these community parameters (Table 7). This is because both exploratory (dependent) and responding (independent) variables were higher during pulse event and lower during non-pulse event (Table 3). This finding suggested that the plant had high salinity tolerance (higher RIV during higher electrical conductivity) and could be utilized for reclamation programme.

Soil Parameters and Plant Variables

Path analysis showed that both soil organic carbon and nitrogen were associated with the percent cover and seed out-put of *T. terrestris* in polynomial positive fashions (Table 8). This is because both exploratory and responding variables were higher during similar event (non-pulse). The electrical conductivity showed a negative power relation to the seed out-put, and the organic carbon exhibited polynomial relationships with both the root and shoot weight. Here it can be interpreted that the high level of both root and shoot weight was observed at an intermediate level of the soil organic carbon. Similarly, the soil phosphorus also exhibited positive relationships with root and shoot weight but in exponential manner, and the electrical conductivity showed positive

**Table 8.** Path analysis summary between soil parameters and plant variables.

Independent variables	Dependent variables	Relation type	Equations
Soil organic carbon	Percent cover	Polynomial	Percent cover = $9.297 - (0.238 \text{ organic carbon}) + (0.001 \text{ organic carbon}^2)$, ($R^2 = 0.753^{**} \pm 0.626$)
Soil nitrogen	Percent cover	Polynomial	Percent cover = $6.840 - (0.206 \text{ soil nitrogen}) + (0.001 \text{ soil nitrogen})$, ($R^2 = 0.653^{**} \pm 0.722$)
Soil organic carbon	Seed out-put	Polynomial	Seed output = $4263.27 - (102.48 \text{ organic carbon}) + (0.647 \text{ organic carbon}^2)$, ($R^2 = 0.748^{**} \pm 213.40$)
Soil nitrogen	Seed out-put	Polynomial	Seed output = $1550 - (43.46 \text{ soil nitrogen}) + (0.365 \text{ soil nitrogen}^2)$, ($R^2 = 0.554^* \pm 267.566$)
Electrical conductivity	Seed out-put	Power	Seed output = $5.16 \text{ electric conductivity}^{-2.221}$, ($R^2 = 0.642^{**} \pm 236.81$)
Soil organic carbon	Root weight	Polynomial	Root weight = $-170.81 + (4.321 \text{ organic carbon}) - (0.025 \text{ organic carbon}^2)$, ($R^2 = 0.627^* \pm 7.59$)
Soil phosphorus	Root weight	Exponential	Root weight = $0.0061 \exp(0.171 \text{ soil phosphorus})$, ($R^2 = 0.830^{**} \pm 5.21$)
Electric conductivity	Root weight	Polynomial	Root weight = $8.472 - (146.94 \text{ electrical conductivity}) + (780.80 \text{ electrical conductivity}^2)$, ($R^2 = 0.705^{**} \pm 6.90$)
Soil organic carbon	Shoot weight	Polynomial	Shoot weight = $(-720.60 \text{ organic carbon}) - (0.105 \text{ Organic Carbon}^2)$, ($R^2 = 0.729^{**} \pm 23.38$)
Soil phosphorus	Shoot weight	Exponential	Shoot weight = $0.380 \exp(0.111 \text{ soil phosphorus})$, ($R^2 = 0.667^{**} \pm 24.44$)
Electrical Conductivity	Shoot weight	Linear	Shoot weight = $-44.59 + (492.63 \text{ electrical conductivity})$, ($R^2 = 0.777^{**} \pm 20.63$)

** : $P < 0.01$, * : $P < 0.05$.

relationships with the root and shoot weight in polynomial and linear fashions, respectively (Table 8).

CONCLUSIONS

Murrell *et al.*, (2001) and Rayburn and Monaco (2011) have pointed out that most of the spatio-temporal theories remain untested by either empirical observations or experimental studies. They further cited the rare validation of spatial theories by Stoll and Prati (2001). Their validation explained that spatial pattern of an individual plant species might alter the competitive interaction in plant communities and facilitate co-existence. The quantitative measures of pattern used in the present study provide a useful basis for further and more generalized comparison of the spatial patterns of individual plants in the semi-arid Thar region in India. Environmental and habitat heterogeneity may have acted individually or in concert with other

processes to produce the spatial patterns detected in this study. Analysis revealed that, contrary to other studies, the uniform distribution was the predominant spatial pattern (particularly during non-pulse event), however, other spatial transition between various events were also observed.

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تغییرات زمانی-مکانی الگوی پراکنش *Tribulus terrestris*: ارتباط دادن الگوها با

فرایندها

م. ماتور

چکیده

الگوهای پراکنش گیاه توصیف گرهای مفیدی از ساختار افقی در یک جمعیت گیاهی هستند که ممکن است به تدریج که اجزای منفرد جمعیت گیاه رشد میکنند یا میمیرند تغییر کنند. اما این که آیا این پدیده در مورد گیاهان چوبی یکساله بیابانی هم رخ میدهد دانسته نیست. در پژوهش حاضر، تغییرات مکانی الگوی تریبولوس ترستریس طی وقایع نوسانی (pulse events) در منطقه نیمه خشک بیابان تار در هند، به صورت کمی و رقمی برآورد شد. برای ارتباط دادن بین الگوهای پراکنش مکانی **تریبولوس ترستریس** با فرایندها از روش های دسته بندی و تحلیل مسیر (path analysis) استفاده شد. شاخص هایی مانند شاخص پراکندگی، (I_D)، شاخص انبوهی (I_C (index of clumping)، شاخص گرین، شاخص میانگین تراکم لوید، و شاخص پراکندگی مورسیتا (Morisita's index of dispersion)، I_δ ، الگوی توزیع یکنواختی را در خارج از وقایع نوسانی گواه دادند که رقابت شدید بین گیاهان برای منابع محدود را نشان میدهد. آزمون های کایزر-میر-اولکین (KMO) و بارتلت

در مورد کرویت (sphericity) حاکی از مناسب بودن کاربرد تجزیه عاملی (factor analysis) و رابطه معنی دار بین متغیرها بود. تجزیه به مولفه های اصلی (PCA) همبستگی معنی داری بین شاخص پراکندگی با شاخص انبوهی و شاخص لوید نشان داد در حالی که شاخص لوید با شاخص انبوهی و شاخص مورسیتا همبستگی داشت. نتایج تجزیه مسیر، همراهی ماده آلی خاک، نیتروژن خاک و نسبت کربن به نیتروژن را با انتقال از الگوی انبوهی به الگوی یکنواخت نشان میداد. افزون بر این، کم بودن فسفر خاک نیز حاکی از الگوی یکنواخت این گیاه بود. شاخص های تنوع همچون همسانی عددی گونه ها و شاخص سیمپسون با الگو های توزیع یکنواخت و انبوه همراه بود. زیاد بودن یا مقدار متوسط درصد پوشش گیاهی و تولید بذر تریبولوس ترستریس نیز با الگوی یکنواخت و انبوه مربوط بودند. نیز، تجزیه مسیر چنین اشاره داشت که تحمل شوری این گونه گیاه می تواند در برنامه های بهسازی خاک مورد استفاده قرار گیرد.