

## Interrelations Between Plants and Environmental Variables

Tavili, A.\* and Jafari, M.

Department of Rehabilitation of Arid and Mountainous Regions, Natural Resources  
Faculty, University of Tehran, P. O. Box: 31585-4314, Karaj, Iran

Received 22 July 2008;

Revised 20 Dec 2008;

Accepted 3 Jan 2009

**ABSTRACT:** Distribution and abundance of plants has been correlated with a variety of complex environmental gradients. Environmental factors affect plants growth and need to be understood by ecosystem managers. This study was carried out to examine the relationships between site factors and different vascular and non-vascular plants in north of Iran. For this purpose, vegetation and soil sampling was performed along 8 transects each with a length of 300 m in key areas of the rangeland. Also, topographic properties including elevation, slope and aspect were recorded in sampling points, too. Using TWINSpan, classification of the vegetation was performed. After grouping of the species, Multivariate technique of Principal Component Analysis (PCA) was used to analyze the relationships between vegetation and site factors. The results of classification revealed that species are classified to 6 ecological groups. The interesting result was that vascular and non-vascular plants were positioned in approximately separated groups. Also, each group according to the contained species showed different correlation with site factors. Properties of nutrient status, EC, texture and slope aspect were the most important factors that correlated strongly with the distribution of ecological groups in the study area, but the strength and weakness of the correlation was different based on the species of each group.

**Key words:** Vegetation, Site factors, Twin Span, Multivariate analysis, Iran

### INTRODUCTION

Understanding the relationships between biotic and abiotic components of an ecosystem generally has been considered as a main part of ecological studies. Finding the interactions of different plants in addition to realizing their relationships with various environmental factors could be used as guidance in vegetation improvement of forest, rangeland, and desert ecosystems. For example, assemblages of bryophytes might be used for recognition of calcareous soils (Downing and Selkirk, 1993). This means that such a habitat is suitable for calcicoles. The study of organisms forming soil bio-crusts (including lichens, mosses, algae, fungi, liverworts,...) in conjunction with associated vascular plant communities will provide a clearer picture of the functioning of ecosystems because of the difference in time scales relevant to non vascular and vascular plants (Rosentreter, 1986). Several investigators have examined the

edaphic and vascular plant community characteristics that are associated with the presence or absence of non vascular plants. Cooke (1955) examined fungi, lichens and mosses on rocks, shrubs and soil in relation to vascular plant communities in eastern Washington and western Idaho. Howarth (1983) examined perennial moss species in chenopod shrub lands, South Australia. Rosentreter (1986) used ordination to find relationships between lichens, vascular plants, and edaphic conditions in Rabbit brush communities on the Boise plateau. He found a consistent relationship among the various lichens, and soil depth, salt concentration, and associated vascular plants. Wolf (1994) studied the factors controlling the distribution of vascular and non-vascular epiphytes in Andes. Hawkes (2000) studied the interactions of bio crusts with vascular plants in a xeric Florida shrub land. Grytnesa et al. (2006) studied species richness of vascular plants,

\*Corresponding author E-mail: atavili@ut.ac.ir

bryophytes, and lichens along an altitudinal gradient in western Norway. They found that vascular plant species richness peaked immediately above the forest limit. Bryophyte species richness had no statistically significant trend, whereas lichen richness increased from the lowest point and up to the forest limit; with no trend above.

Distribution and abundance of plants has been correlated with a variety of complex environmental gradients. Environmental factors affect plants growth and need to be understood and considered by ecosystem managers. Plant growth and development are controlled by internal regulators, which are modified according to environmental conditions (Manske, 1997). Of the most ecologically important environmental factors affecting rangeland plants growth and distribution are topography (slope, aspect, and elevation) and soil properties (Jafari *et al.*, 2004). Different researches have been carried out to examine the relationships between different plants and their site factors. Danin (1989) found that life form density was apparently influenced by salt concentrations in the Judean Desert, Israel. Eldridge and Tozer (1997) used CCA to investigate effective environmental factors on the distribution of some lichens and mosses in eastern Australia.

The results of Neave *et al.* (1994) research on vegetation – site factors relationships in southern coast of New South Wales suggested that soil chemical properties is the main reason of vegetation changes. De Blois *et al.* (2002) investigated factors affecting plant species distribution in hedgerows of southern Quebec. Hejcmanova Neerkova and Hejcman (2006) investigated the effect of environmental variables on the structure of woody vegetation within one geomorphologic unit (500 ha) in Niokolo Koba National Park in Senegal. The results demonstrated that soil type and topography were the main factors affecting woody vegetation of the locality. Abiotic factors determining vegetation patterns in a semi-arid Mediterranean landscape was studied by Pueyo and Alados (2007). They found that gypsum substrate determines strongly the plant community patterns in a semi-arid Mediterranean landscape, as it can be observed by the strong response of gypsophile vegetation to the relaxation of the rigors of gypsum soils with topography. The current study was carried out to

find the relationships between vascular and non vascular plants of Alagol region rangelands with environmental factors.

## MATERIALS & METHODS

Study area, rangelands next to Alagol wetland, is located in Golestan province, northern Iran (37° 18' to 37° 22' N and 54° 32' to 54° 40' E). The climate of the study area can be classified as arid. A 20 year period meteorological data shows that the mean annual precipitation of area is less than 250 mm. January and February have the highest rainfall while the lowest rainfall occurs in June and July. Mean daily temperature is estimated 17.4°C. Absolute maximum and minimum temperature are 42.8°C and -5.36°C, respectively. The elevation of the study area ranges between 15–50 MSL. Based on field surveys, key areas of the rangeland were selected for sampling. According to the extent (8560 hectares) and hilly shape of the study area, eight transverse transects with a length of 300 m, each including fifteen 1 m<sup>2</sup> quadrates were established. Four transects were put in south to north aspect (along altitudinal gradient) and the other four transects were laid from west to east of the hills. In total, 120 quadrates were used for vegetation data collection. Elevation, slope and slope aspect (direction) of quadrates were recorded.

Vegetative sampling method was randomized – systematic. Canopy cover percentage related to each of vascular and non vascular species within quadrates was recorded. Unknown species were gathered, coded and identified in the laboratory.

A total number of 60 soil samples were taken from 0-10 cm depth. Samples were air-dried at laboratory and passed through a 2 mm sieve to get ride of gravel and boulders. Soil texture was determined by the hydrometer analysis (Bouyoucos, 1962), and the results were used to calculate the percentage of sand, clay and silt. Soil reaction (pH) and electric conductivity (EC) were evaluated using pH-meter and electric conductivity meter, respectively. Walkey and Black titration method (Black, 1979) was used to determine organic carbon (OC) content. Kjeldhal method for estimation of N, EDTA titration for soluble Ca and Mg, AgNO<sub>3</sub> titration for soluble Cl (Sparks, 1996), Olsen *et al.* (1954) for

phosphorus, and flame photometer for soluble sodium and potassium measurements were applied.

After data collection, a matrix including plants and environmental variables was made. The Windows (Ver. 3.0) of PC-ORD (McCune and Mefford, 1997) was used for classification and ordination of vascular and non vascular plants in gradient of site factors. Data were analyzed by a series of multivariate techniques such as TWINSPLAN (Two Way Indicator Species Analysis) and PCA (Principal Component Analysis). In classification of species the basic idea is that a characteristic species combination (or at least a group of differentiated species) should gather samples containing these species into clusters of similar samples. Ordination is used to reduce the dimensionality of a data matrix by extracting axes.

**RESULTS & DISCUSSION**

In total 41 taxa were found in the investigation area including 26 vascular species mainly annuals from Compositeae and Gramineae, 4 mosses from Pottiaceae and 11 lichens from different families. Obtained eigenvalues from divisions of TWINSPLAN classification based on Van-der-Maarel (1979) numerical scale resulted in six different homogenous ecological groups as follows:

Group 1: *Psora decipiens*, *Buellia zohari*, *Aloina bifrons*, and *Aloina aloides*.

The two first species are lichens and the two latter ones are mosses.

Group 2: *Tortula revolvens*, *Diploschistes muscorum*, *Diploshistes diacapsis*, *Fulgensia fulgens*, *Fulgensia subbracteata*, and *Squamarina cartilaginea*.

The first species is a moss and the rest are lichens.

Group 3: *Artemisia scoparia*.

This is a vascular plant.

Group 4: *Collema tenax* (lichen), *Barbula trifaria* (moss), and *Poa bulbosa* (grass).

Group 5: Annual forbs, Annual grasses, and *Peganum harmala* (a perennial forb).

Group 6: *Fulgensia bracteata* (lichen), *Salsola* sp., and *Artemisia sieberi* (2 prennial brushes).

As it is seen in groping of the species, non-vascular and vascular plants are separated and positioned in different groups when classification is applied. (Table 1). shows the means of different site factors in 6 ecological groups. The results of PCA ordination is given in (Table 2). According to (Table 2). eigenvalues demonstrate that 64.92% and 24.3% of variance is accounted by the first and second principal components (PC1 and PC2), respectively. PC1 and PC2 together accounted for 89.22% of the total variance in data set. So, the first 2 axes of the ordination provide information useful for interpreting the environmental gradients that influence the group's distribution.

**Table 1. Environmental characteristics of 6 ecological groups**

Group Factor	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6
Clay (%)	10.72	10.4	13.5	10	10.21	15.13
Loam (%)	43.4	42.43	40.72	42.6	42.15	43.78
Sand (%)	45.55	46.53	45.5	46.9	47.69	48.01
pH	7.55	7.65	7.9	7.66	7.63	7.84
Ec (ds/m)	0.82	.089	.048	0.83	0.82	0.81
Ca (meq/l)	14.27	13.87	8.82	13.96	13.76	13
Mg (meq/l)	2.83	2.96	2.63	2.9	2.85	3.03
Cl (meq/l)	1.17	1.51	0.9	1.2	1.4	1.09
Na (meq/l)	0.84	0.86	0.74	0.87	1.06	0.74
K (mg/kg)	20.1	20.93	16.91	21.74	21.6	24
P (mg/kg)	0.51	0.49	0.39	0.52	0.52	0.48
N (%)	0.082	0.08	0.062	0.082	0.08	0.072
OC (%)	1.32	1.35	0.98	1.36	1.34	1.08
Elevation (m)	31	34.5	30	35	35.5	34
Slope (%)	20.5	19.5	14.5	18	19	16
Slope aspect	N	N	S	N	N	W

**Table 2. PCA applied to the correlation matrix of the environmental factors**

Axis	Eigenvalue	% of Variance	Cum.% of Var.	Broken-stick Eigenvalue
1	11.037	64.92	64.92	<b>3.44</b>
2	4.13	24.29	<b>89.22</b>	<b>2.44</b>
3	1.23	7.23	96.45	1.94
4	0.367	2.15	98.61	1.60
5	0.236	1.39	100	1.35
6	0	0	100	1.15
7	0	0	100	0.99
8	0	0	100	0.84
9	0	0	100	0.72
10	0	0	100	0.61

Factor	PC 1	PC2	PC3	PC4	PC5	PC6
Clay	-0.2299	<b><u>0.3087-</u></b>	-0.0098	0.0464	0.3045	-0.2440
Loam	0.1618	0.3698	0.3320	0.1581	0.0819	0.4656
Sand	0.1290	<b><u>0.432</u></b>	-0.1711	0.0117	-0.1906	-0.2728
pH	-0.2707	0.1382	-0.2877	-0.0900	-0.1815	0.3580
Ec	<b><u>0.2776</u></b>	0.1742	-0.0090	-0.2546	0.0219	0.1862
Ca	<b><u>0.2886</u></b>	0.1241	0.1140	0.0586	0.0136	0.0684
Mg	0.1790	0.3747	-0.1351	-0.3349	-0.1106	-0.4380
Cl	0.2538	-0.0498	-0.2899	-0.5859	0.4581	0.0835
Na	0.2116	-0.2035	-0.3671	0.5093	0.5588	0.0392
K	0.1669	<b><u>0.3854</u></b>	-0.2137	0.2411	-0.0797	0.0457
P	<b><u>0.2921</u></b>	0.0778	0.0114	0.2876	-0.1033	-0.1651
N	<b><u>0.2966</u></b>	-0.0125	0.1271	0.0266	-0.1870	-0.1265
OC	<b><u>0.2901</u></b>	-0.1189	0.0295	-0.0039	-0.2234	0.0870
Elevation	0.2079	0.1319	-0.5920	0.0622	-0.2829	0.1747
Slope	0.2768	-0.0842	0.2855	-0.1274	0.2833	0.0802
Aspect	-0.2006	<b><u>0.3596</u></b>	-0.0878	0.1072	0.1847	-0.3098

Considering (Table 2). confirms that the overriding factors of PC1 are Ec, N, P, Ca, and OC. PC2 is correlated to sand, clay, K and aspect. According to the correlations between site factors and components, it seems that PC1 represents soil characteristics of nutrients (different minerals) and salinity while PC2 is related to texture, potassium and slope aspect. The latter site factor affects some other environmental variables like moisture. As it is shown in (Fig. 1). the location of groups resulted from TWINSpan is different in four quarters. The distance between the indicator points of the vegetation groups on the diagram shows the degree of similarity and dissimilarity of groups in the environmental factors. According to (Fig. 1). four completely different ecological groups are separated based on their relations to the environmental variables. One ecological group comprised of the primary groups of 1, 2, and 4. These are located in fourth quarter of the axes and including non vascular plants of the study area,

except for *Poa bulbosa* in group 4. The rest three groups (3, 5 and 6) are comforted in quarters third, fourth and second, respectively. These groups contain vascular plants of the study area except to *Fulgensia bracteata* (group 6), which is lichen. The relationships between groups and environmental factors (axes 1 and 2) is interpreted considering the angle between groups and axes, the length of vectors, and positive or negative sign of correlation coefficients of the environmental factors (Table 2). Fig. 1 and Table 2 help us to interpret the relationships. All of the groups are affected by the site properties related to PC1 and PC2 but the strength and weakness of their correlation is different. For instance, group 5 is equally affected by PC1 and PC2 factors, that is, texture, electrical conductivity, nutrients of N, P, K, Ca and OC in addition to aspect are of relatively equal importance for presence of group 5 species in the study area. The direct or indirect relationship between species and environmental variables are

taken from Table 2 based on variables signs. For example, because of wind erosion in the study area, sand percentage of soil texture is higher. Therefore, species of group 5 prefer sandy soils and show a strong correlation with sand.

According to (Fig. 1). groups 1, 2, and 4 (non-vascular plants) are highly correlated with EC, nutrients, and OC (PC1) and the second most important factors in the occurrence and distribution of mentioned species in the study area are texture and aspect. In south Australia, Downing and Selkirk (1993) reported that conductivity, nutrient status, soil texture, pH, light level, leaf litter (organic matter), and fire frequency played a significant part in determining bryophyte distribution. Most of these factors are of high importance in our study, too. Canonical Correspondence Analysis (CCA) revealed that bryophytes and lichens were related to annual rainfall, pH, calcium carbonate levels, plant cover and organic carbon in semi-arid eastern Australia (Eldridge and Tozer, 1997).

As it was referred about group 5 species, sandy or loamy-sand texture of study area is preferred by bryophytes and lichens. This is supported by Bond and Harris (1964) who suggested that bio-crusts develop on sandy soils. Of course it should be noted that trend to sandy soils is not a general rule for all lichens and mosses. Each species has an especial ecological need. Graetz and Tongway (1986) based on their research in Australia believed that biological crusts are associated with fine-textured soils.

In this study soil moisture was not directly investigated but it is clear that aspect affects the moisture of soil. Seasonal amounts of soil moisture at a site are usually inferred from elevation and aspect (West *et al.*, 1978). Although elevation was not significantly correlated with distribution of the species but in contrast aspect (northern aspect) showed a strong correlation. So, soil moisture could be considered as a site factor that affects the presence of the species. The role of soil moisture, as a key element in the distribution

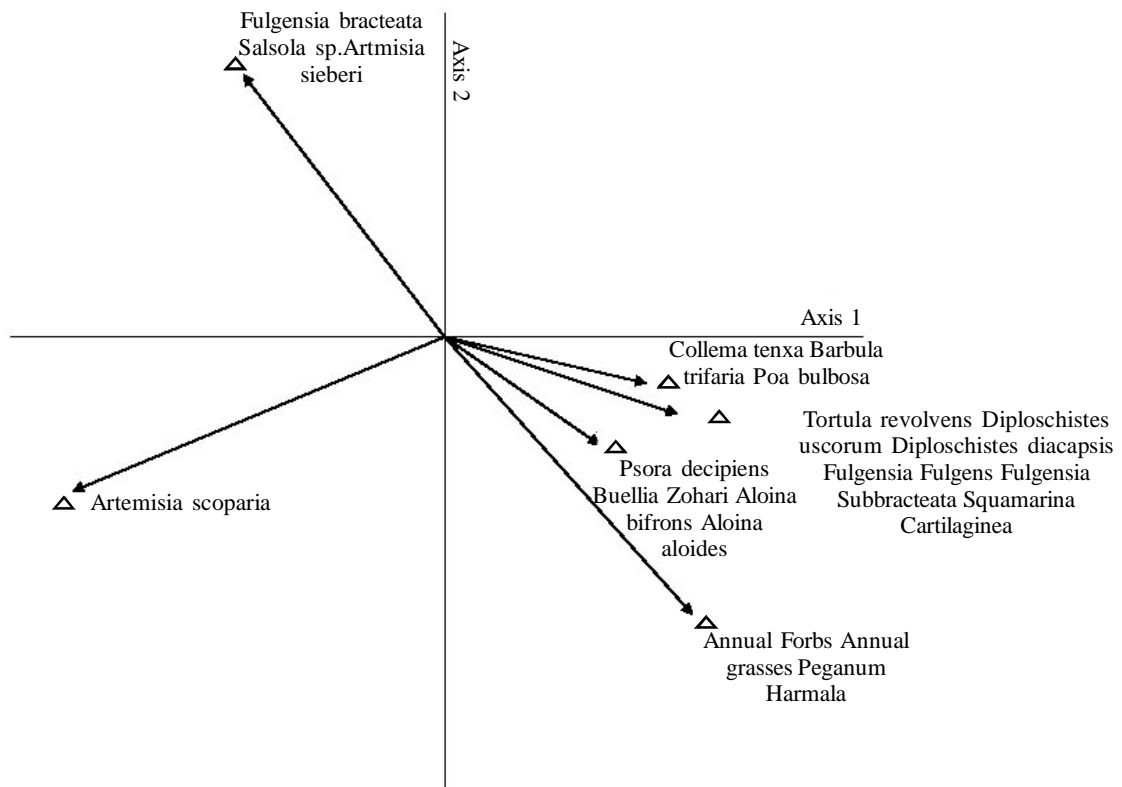


Fig.1. Distribution of 6 ecological groups species defined by the first two axes of PCA

of plants is described by El-Sheikh and Yousef (1981). In countries located on northern hemisphere (like Iran) northern aspects contain higher levels of soil moisture compared to southern one (Moghaddam, 2000). Eldridge and Tozer (1997) in their study in semi-arid eastern Australia found that rainfall (moisture) with affecting nutrient availability is a primary determinant in distribution of bryophytes and lichens. JANIŠOVÁ (2005) states that bryophyte growth is controlled mostly by moisture conditions. Field surveys in different seasons revealed that the cryptogam abundance in general fluctuated significantly between seasons reaching maximum in autumn and spring. This shows their dependency to moisture condition.

No correlation was observed between vascular or non-vascular plants and topographic characteristics of slope and elevation. The elevation of the study area ranges between 15–50 MSL This small range of altitudinal changes associated with thin slope variation has not had any significant influence on species distribution. Tavili *et al.* (2008) found no correlation between plants distribution and topographic properties due to small changes in elevation, aspect and slope of Zereshkin rangelands.

## CONCLUSION

According to the results of classification of species in 6 separated groups containing bio crusts and non-bio crusts in different groups, it finds out that although understudy vascular and non-vascular plants are related to the same habitat with the same environmental variables, but each one shows different behavior against site factors. The strength and weakness of group's relationships with environmental factors depends on the species of each group and their ecological needs.

Studies of distribution and richness patterns along different environmental gradients have demonstrated that vascular plants, bryophytes, and lichens, often show different patterns (Slack, 1984; Pausas, 1994; Anderson *et al.*, 1995; Dirkse and Martakis, 1998; Molau and Alatalo, 1998; Pharo *et al.*, 1999; JANIŠOVÁ, 2005). Herben (1987) suggests the explanation of different behavior of bryophytes and vascular plants. According to him, bryophytes have an opportunistic strategy and

respond to factors of much shorter duration and greater fluctuations than vascular plants. Vascular plants respond slower to environmental factors thus reflecting more conveniently the long-term ecological regime of the stand.

Totally, in addition to general result obtained from the current study (emphasizing on different behavior of vascular and non-vascular plants related to ecological properties), also it could be concluded that presence of few perennial vascular species and frequent different annual vascular plants beside cryptogams in the study area shows that still soil is not mature. So, bryophytes and lichens- as pioneers- are preparing the conditions for more occurrences of vascular plants, especially perennial ones.

## REFERENCES

- Anderson, D. S., Davis, R. B. and Janessen, J. A. (1995). Relationships of bryophytes and lichens to environmental gradients in Maine peatlands. *Plant Ecology*, 120(2), 147-159.
- Black, C. A. (1979). Methods of soil analysis. *American Society of Agronomy*, 2, 771-1572.
- Bond, R. D. and Harris, J. R. (1964). The influence of the microflora on physical properties of soils. I. Effects associated with filamentous algae and fungi. *Australian Journal of Soil Research*, 2, 111-122.
- Bouyoucos, G. Y. (1962). Director for making mechanical analyses of soils by the hydrometer methods. *Soil Science*, 42, 225-228.
- Cooke, W. B. (1955). Fungi, lichens and mosses in relation to vascular communities in eastern Washington and adjacent Idaho. *Ecological Monography*, 25, 119-180.
- Danin, A. (1989). The impact of prevailing winter winds on the distribution of vegetation in the Judean Desert, Israel. *Journal of Arid Environment*, 17, 301-305.
- de Blois, S., Domon, G. and Bouchard, A. (2002). Factors affecting plant species distribution in hedgerows of southern Quebec. *Biological Conservation*, 105, 355– 367.
- Dirkse, G. M. and Martakis, G. F. P. (1998). Species density of phanerogams and bryophytes in Dutch forests, *Biodiversity Conservation*, 7, 147–157.
- Downing, A. J. and Selkirk, P. M. (1993). Bryophytes on the calcareous soils of Mungo National Park, an

- arid area of southern central Australia. *Great Basin Naturalist*, **53**, 13-23.
- Eldridge, D. J. and Tozer, M. E. (1997). Environmental factors relating to the distribution of terricolous bryophytes and lichens in semi-arid eastern Australia. *The Bryologist*, **100**(1), 28-39.
- El-Sheikh, A. M. and Yousef, M. M. (1981). Halophytic and xerophytic vegetation near Al-Kharg springs. *Journal of Colloid Science*, **12**(1), 5-12.
- Graetz, R. D. and Tongway, D. J. (1986). Influence of grazing management on vegetation, soil structure and nutrient distribution and the infiltration of applied rainfall in a semi-arid chenopod shrubland. *Australian Journal of Ecology*, **11**, 347-360.
- Grytnesa, J. A., Heegaarda, E. and Ihlenb, P. G. (2006). Species richness of vascular plants, bryophytes, and lichens along an altitudinal gradient in western Norway. *Acta Oecologia*, **29** (3), 241-246.
- Hawkes, C. (2000). Interaction of soil crust with vascular plants in a xeric Florida shrubland. Ph.D. Dissertation. University of Pennsylvania, Philadelphia. USA.
- Hejmanova-Neerkova, P. and Hejman, M. (2006). A canonical correspondence analysis (CCA) of the vegetation–environment relationships in Sudanese savannah, Senegal. South Africa. *Journal of Botany*, **72**, 256–262.
- Herben, T. (1987). Bryophytes in grassland vegetation sample plots: what is their correlation with vascular plants? *Folia Geobot. Phytotax.*, **22**, 35–41.
- Howarth, L. (1983). The ecology of perennial moss species in chenopod shrublands on Middleback Station, South Australia. Ph.D. Thesis. Department of botany. University of Adelaide. South Australia.
- Jafari, M., Zare Chahouki, M. A., Tavili, A., Azarnivand, H. and Zahedi Amiri, Gh. (2004). Effective environmental factors in the distribution of vegetation types in Poshtkouh rangelands of Yazd province (Iran). *Journal of Arid Environments*, **56**, 627-641.
- JANIŠOVÁ, M. (2005). Vegetation-environment relationships in dry calcareous grassland. *Ekológia (Bratislava)*, **24**(1), 25-44.
- Manske, L. L. (1997). Effects from environmental factors of light, temperature, and precipitation on range plants in the Dickinson, North Dakota, region. NDSU Dickinson Research Extension Center. Range Research Report DREC 97-1015. Dickinson, ND. 22p.
- McCune, B. and Mefford, M. J. (1997). PC\_ORD. Multivariate Analysis of Ecological Data Version 3.0. MjM software design. Glenden Beach, OR.
- Moghaddam, M. R. (2000). Range and range management. Tehran University Press.
- Molau, U. and Alatalo, J. M. (1998). Responses of subarctic-alpine plant communities to simulated environmental change: biodiversity of bryophytes, lichens and vascular plants, *Ambio* **27**, 322–329.
- Neave, I. A., Davey, S. M., Russell, S. M., Smith, J. J. and Florence, R. G., (1994). The relationships between vegetation patterns and environment on the south coast of New South Wales. *Journal of Forest Ecology and Management*, **72**, 71-80.
- Olsen, S. R., Colw, C. W., Watanabe, F. S. and Dean, L. A. (1954). Estimation of available phosphorus in soils by extraction with sodium bicarbonate. U. S. Department of Agriculture. ARC publication.
- Pausas, J. G. (1994). Species richness patterns in the understory of Pyrenean *Pinus sylvestris* forest, *Journal of Vegetation Science*, **5**, 517–524.
- Pharo, E. J., Beattie, A. J. and Binns, D. (1999). Vascular plant diversity as a surrogate for bryophyte and lichen diversity, *Conservation Biology*. **13**, 282–292.
- Pueyo, Y. and Alados, C. L. (2007). Abiotic factors determining vegetation patterns in a semi-arid Mediterranean landscape: Different responses on gypsum and non-gypsum substrates. *Journal of Arid Environments*, **69**, 490–505.
- Rosentreter, R. (1986). Compositional patterns within a rabbitbrush-chrysothamnus community of the Idaho Snake River Plain. In: E. D. McArthur and L. W. Bruce (eds). Proceedings symposium on the biology of Artemisia and Chrysothamnus, Provo UT. Technical Report. INT- 200. USDA Forest Service.
- Slack, N. G. (1984). A new look at bryophyte community analysis: field and statistical methods. *Journal of Hattori Botany*, **55**, 113–132.
- Sparks, D. L. (1996). Methods of soil analysis. Part 3, chemical methods. Soil Society of America, Inc. American Society of Agronomy Inc.
- Tavili, A., Biniáz, M. and Zare Chahouki, M. A. (2008). plant – site factors relationship in Zereshkin

rangelands, Iran. *Journal of Balkan Ecology*, **11(1)**, 83-91.

Van-der-Maarel, E. (1979). Transformation of cover – abundance values in phytosociology and it's effects on community. *Vegetation*, **39**, 97-114.

West, N. E., Tausch R. J., Rea K. H. and Tueller, P. T. (1978). Taxonomic determination, distribution, and ecological indicator values of sagebrush within the pinyon juniper woodlands of the Great Basin. *Journal of Range Management*, **31**, 87-92.

Wolf, J. H. D. (1994). Factors controlling the distribution of vascular and non-vascular epiphytes in the northern Andes. *Vegetatio*, **112**, 15-28.