

EDAPHIC FACTORS AS MAJOR DETERMINANTS OF PLANT DISTRIBUTION OF TEMPERATE HIMALAYAN GRASSES

KHAWAJA SHAFIQUE AHMAD¹, MANSOOR HAMEED^{1*}, FAROOQ AHMAD¹ AND BUSHRA SADIA^{2,3}

¹Lab of Plant Taxonomy, Department of Botany, University of Agriculture, Faisalabad 38040, Pakistan

²Centre of Agricultural Biochemistry and Biotechnology (CABB), University of Agriculture, Faisalabad 38040, Pakistan

³Program Chair, Biotechnology, U.S.-Pakistan Center for Advanced Studies in Agriculture and Food Security (USPCAS-AFS), University of Agriculture Faisalabad, 38000 Pakistan

*Corresponding author's email: hameedmansoor@yahoo.com

Abstract

The quantification of the comparative effect of environmental factors on species distribution can improve our knowledge of the processes that drive diversity patterns. Fifteen different habitats in Neelum valley (Kashmir), using quadrat method along altitudinal gradient were studied for the plant ecological attributes including; soil plant interaction, species composition and vegetation cover to test the hypothesis that soil factors are the major determinants of species distribution. Redundancy analysis (RDA) showed a clear impact of soil characteristics on vegetation. *Rostraria pumila*, *Pennisetum orientale*, *Sorghum nitidum* and *Arundinella* sp. had a strong association with the Kail (KL) site influenced by soil Ec. Distribution of *Lolium temulentum*, *Poa nemoralis*, and *Saccharum spontaneum*, at Chilhana (CH) site seemed to be affected by the moisture content only. Species distribution at Nagdar (NG), Kundal shahi (KS), Kairan (KR) and Dawarian (DW) site was affected by Ca²⁺ and PO₄³⁻ content respectively. Diversity pattern at Sharda, Dawarian (DW), and Lawat (LW) sites were driven by K⁺ and N⁺ content. Each grass showed a very specific relationship to environmental variables, which imitates the habitat status, ecological adaptation and degree of tolerance in species.

Key words: Edaphology, Redundancy analysis (RDA), Environmental variable, Species cover, Himalayan grasses.

Introduction

Understanding the drivers and mechanisms of changes in species distribution provides basis for making scientifically sound ecological predictions (Hegazy *et al.*, 2008). Of the numerous factors affecting species, soil has large impact on the composition and structure of plant community. Heterogeneity of soil properties, such as soil texture, moisture content, electric conductivity (Ec) and pH create niches with specific conditions, which in turn affect distribution pattern of plants (Vazquez & Givnish, 1998).

Poaceae is a species-rich family that includes many economic plants, globally with about 10,000 species and 700 genera (Crisp *et al.*, 2009; Linder & Rudall, 2005). Recent phylogenetic studies confirmed that multiple factors are involved indirectly that determine the grass diversity at large scales; Edwards & Smith 2010).

To point out the strength of environmental factors, responsible for the species distribution among ecosystems is a big task for ecologists (Hegazy *et al.*, 2008). Species diversity mainly depends on the occurrence, abundance and vegetation cover. Grasslands, in which grasses are the most important floristic component, cover about 40% of the earth surface (Peterson *et al.*, 2010).

Plant distribution is controlled on large by climate and over small scale by environmental heterogeneity (Lavers & Field, 2006). Climate affects the input of the resources needed for the plant growth, such as moisture, radiations and temperature while environmental heterogeneity (topography, aspect) determines the number of realized environmental gradient combinations in a particular landscape (Huston & De Angelis, 1994). The greater number of the combinations, the greater number of niches will available for plant growth, enable more plant species to co-exist (Tilman, 1982; Smith & Huston, 1989).

There is a significant relationship between species diversity, distribution and moisture availability (Leathwick *et al.*, 1998). Vegetation structure in savanna and grassland regions is mainly determined by moisture content (Scholes *et al.*, 1997) and precipitation is considered to be important factor affecting the plant distribution (Cody, 1989). Soil pH directly affects the nutrients availability, nutrient toxicity, and microbial activity, as well as extending the direct effect on protoplasm of the root cells (Gould & Walker, 1999).

Himalayan ecosystems all over the world usually have very specific diverse biological communities. Although large number of review and reports are available in Indian and Nepal Himalayas but less attention has been given the western Himalaya of Pakistan due to remoteness of the area (Tanner *et al.*, 1998). Keeping in mind the need and importance of ecological indicators for the conservation and management of wild plant resource, the present work was designed to explore the relationship between soil factors and species cover over a large distributional area.

Materials and Methods

Study area: The Neelum Valley (Kashmir) a temperate Himalayan region, situated at an altitude of 900-6,325 m above sea level (a.s.l.), lies between 73-75° E longitude and 32-35° N latitude. The climate is characterized by cold winter (average 1-4°C) and moderate summer (average temperature (22-30°C). The average rainfall is 165 cm annually. Soil is loamy and sandy loam, adept to hold moisture and suitable for the growth of forests (Ahmad *et al.*, 2012).

Soil variables and data analysis: Soil samples were taken from 15 sampling points to analyze the 9 soil variables for physicochemical characteristics. The area location and altitude were determined with the help of Global Positioning System (GPS) and the slope gradient and slope aspects were measured using a compass. Soil moisture was calculated by way of drying, and pH and electrical conductivity by using a pH/Ec meter (WTW series InoLab pH/Cond 720). Soil organic matter was determined by $K_2Cr_2O_7-H_2SO_4$ oxidation method of Walkley-Black, total nitrogen content was determined by diffuse method, available P was determined by Bray-P method. The flame photometric method was used to estimate K^+ and Ca^{2+} cations. Cl^- content was measured with the help of chloride meter (Jenway, PCLM).

Vegetation sampling: The vegetation was sampled by quadrat method and 1 m² quadrat were used at five sampling points along a straight transect line, and each sampling point was selected 20 m away from subsequent quadrat. At each sampling point 25 quadrat were laid perpendicular to a straight transect line for the vegetation study to record the data for percent cover of each species in each quadrat.

Statistical analysis: Analysis of variance for soil variables and ecological parameters was determined (Steel *et al.*, 1997) and the means were compared by applying the LSD test. The Redundancy Analysis (RDA) technique used to evaluate the impact of different ecological variables on species distribution using Canoco Computer Package for Windows [Version 4.5].

Results

Soil physiochemical characteristics: Most of the soil characteristic varied significantly at $p < 0.005$ except soil organic matter and Ca^{2+} showed non-significant difference among the all study sites. The soil moisture content seemed to be closely related to the physical properties of the soil as well as to vegetation type. The main factor affecting soil moisture was precipitation. The pH of the soil varies from 4.6 to 8.2 mostly acidic and tends to be slightly basic with low content of exchangeable cations at Chilhana (CH) and Jura (JR) sites. A significant difference was also observed in Ec, saturation percentage and ionic contents of the soil in the analysis (Table 1).

Taxonomic diversity and percentage cover: A total of 52 species of grasses belonging to 10 tribes and 28 genera were recorded from 15 sampling sites in Neelum Valley. Poaceae was the largest tribe (12 spp.); followed by Andropogoneae (11 spp.); Aveneae (9 spp.); Paniceae (8 spp.); Aristideae and Brachypodieae (3 spp. each), whereas, rest of the 5 tribes represents 2 or 1 species. Dodonial was species rich site with 15 species (28.85%), followed by Dawarian, Sharda, and Taobut (12 spp.), Kairan, Nagdar and Halmat with 11 species (Table 2).

Agrostis pilosa and *Agrostis viridis* showed high percent cover at Athmuqam and Kundal Shahi respectively. *Apluda mutica* showed high cover at Dawarian and Halmat. *Aristida cynantha* occupied high cover area at Jura and Dodonial. *Aristida funiculata* showed high frequency at Kundal shahi but it was present at Halmat with low frequency. *Aristida mutabilis* showed high cover at Athmuqam. *Arthraxon prionodes* showed high cover area at Kail. *Arundinella nepalensis* and *Arundinella* sp., showed its maximum cover area at Nagdar and Kail sites respectively. *Avena byzantina* and *Avena fatua* showed their maximum cover Athmuqam and Janwai and Tao butt respectively. *Bothriochloa bladhi* showed the maximum cover at Janawai and *Bothriochloa pertusa* was present at Nagdar and Tao butt. Both *Brachypodium distachyon*, and *Brachypodium* sp., showed their consistent presence at four study sites where *Brachypodium* sp., showed relatively low cover at Dodonial. *Brachypodium sylvaticum* and *Capillipedium parviflorum* showed their maximum cover at Kundal Shahi and Chilhana sites. *Cenchrus pennisitiformis* showed low cover values at Dodonial. *Cynodon dactylon* grass showed its maximum maximum cover at Dodonial, with moderate cover at Sharda. *Digitaria cruciata* was the only grass that showed high cover at Kundal Shahi, Nagdar and Sharda (SH). *Eleusine indica* was present at Kairan with high cover. *Festuca Kashmiriana* showed high cover at Sardari and *F. levengei* was present at Sharda with moderate cover. *Festuca simlensis* showed its maximum cover at Sharda. *Heteropogon contortus* showed maximum cover at Dodonial. *Hordeum glaucum* showed moderate cover value at Kairan and *Hordeum marinum* was present at Chilhana with high cover. *Koeleria cristata* showed low cover area at Kairan and *K. macrantha* showed high cover at Nagdar. *Lolium perenne* showed its maximum cover at Tao butt whereas, *temulentum* was the only grass that showed its maximum cover at Kail and Halmat. *Milium effusum* was present at Nagdar with moderate cover. *Panicum atrosanguineum* was present at Jura and Sardari with moderate cover. *Panicum decompositum* showed its moderate cover at Dodonial, Halmat and Taobutt. *Parapholis incurva* was moderately present at Jura. *Pennisitum orientale* was with high cover at Sardari. *Poa argunensis*, *Poa attenuata* and *Poa falconeri* showed their maximum cover at Sharda, Sardari and Lawat respectively. *Poa infirma* and *P. nemoralis* was present with moderate and high cover at Kairan and Chilhana respectively. *Polypogon monspeliensis* was present with high cover at Athmuqam. *Rostraria clarkeana* showed high cover at Jura and low at Sharda. *Rostraria pumila* showed high cover at Kail and relatively low cover at Jura, Athmuqam and Dawarian. *Saccharum filifolium* showed its maximum cover at Kairan whereas *Sacchrum spontaneum* was with high cover at Chilhana. *Schizachyrium impressum* showed moderate cover at Athmuqam with relative low cover at Athmuqam, Lawat and Dawarian. *Setaria pumila* showed low cover at Kundal Shahi. *Sorghum arundinaceum* showed high cover at Janawai and low cover at Dodonial. *Sorghum nitidum* was present at Kail (KI) with relatively very high cover area (Table 3).

Table 1. Soil physico-chemical characteristics of study sites of Neelum Valley, Azad Jammu and Kashmir.

	CH	JR	KS	AT	KR	NG	LW	DW	DD	SH	KL	JW	SR	HL	TB	F ratio	LSD (5%)
Soil pH	8.2 ^a	6.9 ^{ab}	5.8 ^{bcd}	4.6 ^{bcd}	5.7 ^{bcd}	6.2 ^{abcd}	4.9 ^{def}	5.4 ^{cdef}	5.7 ^{ef}	7.0 ^{abcde}	6.3 ^{cdef}	5.6 ^f	7.2 ^{abcd}	7.9 ^{abcde}	7.4 ^{abc}	2.71**	1.3146
S (%)	46.64 ^b	26.93 ⁱ	38.76 ^{fe}	46.32 ^{bc}	30.64 ^h	43.49 ^{cd}	30.85 ^h	40.38 ^{ef}	30.52 ^h	52.34 ^a	40.06 ^{de}	37.15 ^g	47.87 ^b	47.06 ^{bc}	45.05 ^{bcd}	58.9**	2.8850
ECe (dS m ⁻¹)	8.8 ^a	8.7 ^a	6.6 ^{efg}	5.8 ^{gh}	6.8 ^{def}	8.0 ^{abc}	6.8 ^{def}	7.6 ^{bcd}	8.4 ^{ab}	8.6 ^a	5.7 ^h	7.4 ^{cde}	7.7 ^{bc}	6.4 ^{efg}	6.8 ^{def}	13**	0.8241
K ⁺ mg L ⁻¹	8.47 ^d	8.97 ^{cd}	9.93 ^{bc}	9.43 ^{bcd}	9.04 ^{cd}	8.66 ^d	9.1 ^{bcd}	8.45 ^d	8.67 ^d	10.02 ^b	8.58 ^d	8.98 ^{cd}	11.22 ^a	9.44 ^{bcd}	8.89 ^d	4.6*	0.9704
Ca ²⁺ L ⁻¹	4.18 ^a	3.7 ^b	4.58 ^{ab}	3.67 ^a	4.34 ^{ab}	3.78 ^b	4.52 ^{ab}	4.86 ^{ab}	4.22 ^{ab}	4.46 ^{ab}	3.97 ^{ab}	4.42 ^b	4.82 ^{ab}	3.67 ^b	3.55 ^{ab}	0.72ns	1.8851
PO ₄ ³⁻ (mg L ⁻¹)	92.14 ^a	83.52 ^f	92.01 ^a	88.66 ^c	80.93 ^{gh}	81.22 ^g	77.45 ⁱ	71.08 ^k	80.06 ^h	87.67 ^d	84.02 ^f	86.04 ^e	78.06 ^j	90.56 ^b	79.07 ⁱ	356**	0.9254
Cl ⁻ (mg L ⁻¹)	0.6de ^f	0.8 ^{cdef}	0.4 ^{ef}	1.1 ^{bcd}	1.3 ^{bcd}	1.8 ^{ab}	0.9 ^{cdef}	1 ^{cdef}	1.2 ^{bcd}	2.0 ^a	1.5 ^{abc}	0.8 ^{cdef}	0.3 ^f	0.4 ^{ef}	0.7 ^{def}	4.08*	0.7209
TN (%)	0.118 ^b	0.105 ^b	5.55 ^a	0.111 ^b	0.109 ^b	0.099 ^b	0.107 ^b	0.121 ^b	0.10 ^b	0.104 ^b	0.116 ^b	0.096 ^b	0.112 ^b	0.103 ^b	0.122 ^b	1007**	0.1293
OM (%)	2.38 ^a	2.09 ^a	2.03 ^a	2.36 ^a	2.22 ^a	2.06 ^a	2.04 ^a	1.84 ^a	2.13 ^a	2.42 ^a	1.92 ^a	1.98 ^a	1.88 ^a	2.27 ^a	1.98 ^a	0.34ns	0.9563
Soil texture	SCL	SCL	SL	SL	L	CL	SL	CL	L	SL	L	CL	L	CL	CL		

S (%) = saturation percentage, ECe = Electric conductivity, TN = Total nitrogen, OM = Organic matter, SCL = sandy clayey loam, SL = sandy loam, L = loam, CL = clayey loam

Study sites: Chiliahana (CH), Jura (JR), Kundal Shahi (KS), Athmuqam (AT), Kairan (KR), Lawat (LW), Dawarian (DW), Dodonial (DD), Sharda (SH), Kail (KL), Janawai (JW), Sardari (SD), Halmat (HM), Tao but (TB).

Mean within rows sharing same letter are non-significant at p<0.05 level (n=3)

* ** = significant at 0.05 and 0.001 levels, respectively. Ns = non-significant

Table 2. Meteorological and topographical data of sampling sites in Neelum Valley Azad Jammu & Kashmir.

Sampling sites	Coordinates	Altitude (m)	Slope (%)	Aspect	Observed taxa	%age
Chiliahana	34° 23' 56.1" N 73° 46' 29.5" E	1100	60-70	Eastern	9	17.31
Jura	34° 29' 26.9" N 73° 50' 04.8" E	1290	55-65	Western	11	21.15
Kundal Shahi	34° 33' 03.6" N 73° 50' 52.2" E	1318	40-50	North-eastern	8	15.38
Athmuqam	34° 35' 33.9" N 73° 55' 0.72" E	1403	20-35	Western	13	25.00
Kairan	34° 38' 54.3" N 73° 56' 57.1" E	1499	20-25	Northern	11	21.15
Nagdar	34° 40' 24.7" N 73° 57' 20.0" E	1555	50-60	North-western	11	21.15
Lawat	34° 41' 15.9" N 73° 58' 11.3" E	1579	40-50	Southern	11	21.15
Dawarian	34° 43' 25.1" N 74° 59' 58.1" E	1807	35-45	Northern	12	23.08
Dodonial	34° 41' 58.78" N 74° 06' 03.09" E	2774	20-30	Southern	15	28.85
Sharda	34° 47' 03.9" N 74° 10' 47.6" E	2014	25-35	East-western	12	23.08
Kail	34° 48' 58.2" N 74° 25' 09.7" E	2047	15-25	North-western	9	17.31
Janawai	34° 47' 23.0" N 74° 33' 56.0" E	2187	30-40	Western	8	15.38
Sardari	34° 45' 44.1" N 74° 38' 17.3" E	2239	15-20	South-eastern	10	19.23
Halmat	34° 46' 42.6" N 74° 40' 28.9" E	2267	5-15	Eastern	11	21.15
Tao butt	34° 43' 42.7" N 74° 43' 26.3" E	2300	5-10	East-western	12	23.08

RDA analysis: RDA ordination biplot (Fig. 1) indicated a strong effect of soil characteristics on distribution of grasses at different habitats. *Rostraria pumila*, *Pennisetum orientale*, *Sorghum nitidum*, and *Arundinella* sp. showed a strong association with the KL site with strong influence of soil Ec. Distribution of *Lolium temulentum*, *Poa nemoralis*, and *Saccharum spontaneum*, at CH site was seemed to be affected by the moisture contents. Distribution of *Heteropogon contortus*, *Parapholis incurva*, *Setaria pumila*, *Agrostis viridis*, *Capillipedium parviflorum*, *Panicum humile*; *Koeleria cristata*, *Bothriochloa pertusa*, *Digitaria cruciata*, *Aristida funiculata*, *Hordeum glaucum*, and *Eleusine indica* species, strongly associated to the NG, KS, KR sites, were affected by Ca^{2+} content. *Bothriochloa bladhii* at PW site was controlled by PO_4^{3-} content. Presence of *Festuca kashmiriana*, *Poa argunensis*, *Poa falconeri*, *Sorghum arundinaceum* species at SH, DD, LW sites seemed to be influenced by K^+ and N^+ content. *Aristida cyana*, *Aristida mutabilis*, *Cenchrus* sp., *Poa attenuata*, were more associated with SR whereas, *Panicum atrosanguineum* with JR, and *Agrostis pilosula* and *Avena byzantine* were associated with AT site. Distribution of *Aristida funiculata*, *Koeleria macrantha* species at TB site was not influenced by any of the soil factor.

Discussion

Mechanism for species turnover is still poorly understood due to dispersal limitation and environmental variables that are considered to shape the distribution of species (Davidar *et al.*, 2007). Soil nutrients which are related to moisture can play a major role in species distribution (Phillipse, 2003). Among all, clay soils with greater amount of nutrients and water availability have higher support for thick vegetation cover (Schuur & Matson, 2001).

A strong association can be observed in grasses such as, *Rostraria pumila*, *Pennisetum orientale*, *Sorghum nitidum*, and *Arundinella* sp. with the KL site. The distributional pattern of these species seemed to be strongly influenced by soil Ec. Occurrence of *Lolium temulentum*, *Poa nemoralis*, and *Saccharum spontaneum*, at CH site was likely to be affected by the moisture contents. Moisture contents of the soil depends upon the composition of the soil, availability of nutrients and topography of the area (Michael *et al.*, 2002).

Agrostis viridis, *Capillipedium parviflorum*, *Panicum humile*, *Koeleria cristata*, *Bothriochloa pertusa*, *Digitaria cruciata*, *Aristida funiculata*, *Hordeum glaucum*, *Eleusine indica*, strongly associated to the NG, KS, KR sites, were together affected by Ca^{2+} content. *Bothriochloa bladhii* strongly associated with PW rather than DW was affected by PO_4^{3-} content. Study sites SH, DD, LW were strongly associated with the distribution of *Festuca kashmiriana*, *Poa argunensis*, *Poa falconeri*, *Sorghum arundinaceum* species and K^+ and nitrogen of the soil seemed to influence the distribution pattern of the species over these sites. Nitrogen in inorganic and extractable form had little impact on species distributions (Ros *et al.*, 2011).

Aristida cyanatha, *Aristida mutabilis*, *Cenchrus* sp., *Poa attenuata*, *Panicum atrosanguineum*, *Agrostis pilosula* and *Avena byzantine* were more associated with SR, JR, and AT sites. The distribution of these grasses over these sites was under the influence of soil pH and Cl^- content. Among the soil properties affecting the species distribution,

soil pH, electric conductivity (EC) and moisture content may play the most important role (Pausas & Austin, 2001). Species response to pH varies from vegetation structure in savanna and grassland regions is mainly determined by moisture content (Scholes *et al.*, 1997) and precipitation is considered to be one factor effecting the plant distribution (Cody, 1989). Soil pH directly affects the nutrients availability, nutrient toxicity, and microbial activity, and extends the protoplasm of the root cells (Marschner, 1986; Gould & Walker, 1999).

TB site is strongly associated with the distribution of the *Aristida funiculata*, and *Koeleria macrantha*. This site was not influenced by any of the soil physico-chemical characteristics. These outcomes indicate the role of other environmental gradients such as temperature and radiation, pattern of rainfall and availability of nutrient which may have a combined effect of plant distribution. Vegetation patterns is controlled by many environmental gradients as a one dimensional environmental gradient is meaningless until defined in the term of other environmental conditions, and generalization about one gradient is conditional upon other variables (Austin & Heyligers, 1989).

Along altitudinal gradient a significant decrease in vegetation cover can be observed. Elevation as an environmental factor has a multifaceted influence on the distribution patterns of plant species (Zhao & Fang, 2006). The pragmatic decrease in species distribution is due to deforestation, human interaction, and quick disappearance of annual plants because of cold conditions (Malik *et al.*, 2007). Areas with high altitude are the hotspot for biodiversity with large number of species due to human impact (Nogues *et al.*, 2008). Himalayan high altitude plains above the tree line are cold (Nautiyal *et al.*, 2004), and dry hyper optimal habitats with varying phytodiversity (Sharma *et al.*, 2009; Grytnes & Vetaas, 2002).

Digitaria cruciata, *Cynodon dactylon*, *Arthraxon prionodes*, *Heteropogon contortus*, *Apluda mutica*, *Cenchrus pennisetiformis*, *Festuca simlensis*, and *Saccharum filifolium* are the grasses with broad range of distribution over various sites. DD had the maximum species cover, followed by AT, DW, TB and SH sites. A strong correlation between species cover and environmental factors has been reported (Lavers & Field, 2006). Different species have different need for moisture, soil nutrient content and amount of radiation received. The distribution of the species within any ecosystem is the function of numerous biotic and abiotic factors which makes it difficult to investigate the effect of single environmental factor. Different species respond differentially to environmental factors. The maximum species can be found in the sites with high temperature, intermediate rainfall, low radiation and high nutrient levels (Minchin, 1989; Gould & Walker, 1999).

The findings of the present study revealed that edaphic factors are likely to be of particular importance in investigating the pattern of vegetation dynamic and response of the species toward particular soil variable. These patterns differ considerably are related to different adaptation strategies of the species to soil conditions. Therefore, it can be concluded that soil factors are not only the key drivers for the distribution of species over various habitats. It is likely to be governed by the combined effect of soil structure and composition, soil moisture, available nutrients and other environmental variables over the distribution of individual species.

Acknowledgement

The presented work in manuscript is a part research work conducted by PhD scholar Kh. Shafique Ahmad, 2011-ag-17, at the Department of Botany, University of Agriculture Faisalabad. The first author is highly indebted to Prof. Dr. Muhammad Ashraf, Chairman Pakistan Science Foundation for his moral and technical support.

References

- Ahmad, K.S., R. Qureshi, M. Hameed, F. Ahmad and T. Nawaz, 2012. Conservation assessment and medicinal importance of some plant resources from Sharda, Neelum Valley, Azad Jammu and Kashmir, Pakistan. *Int. J. Agric. Biol.*, 14: 997-1000.
- Austin, M.P. and P.C. Heyligers. 1989. Vegetation survey design for conservation grad sect sampling of forests in north eastern New South Wales, Australian developments in conservation evaluation. (Ed.): C.R. Margules. *J. Biol. Conserv.*, 50: 13-32.
- Cody, M.L. 1989. Growth form diversity and species community structure in desert plants. *J. Arid Environ.*, 17: 199-209.
- Crisp, M.D., M.T.K. Arroyo, L.G. Cook, M.A. Gandolfo, G.J. Jordan, M.S. McGlone and P.H. Weston. 2009. Phylogenetic biome conservatism on a global scale. *Nature*, 458: 754-756.
- Davidar, P., B. Rajagopal, D. Mohandass, J.P. Puyravaud, R. Condit, S.J. Wright and E.G. Leigh Jr. 2007. The effect of climatic gradients, topographic variation and species traits on the beta diversity of rain forest trees. *Global Ecol. Biogeogr.* 16: 510-518.
- Edwards, E.J. and S.A. Smith. 2010. Phylogenetic analyses reveal the shady history of C₄ grasses. *Proc. Natl. Acad. Sci.*, 107: 2532-2537.
- Edwards, E.J., C.P. Osborne, C.A.E. Strohmer and S.A. Smith. 2010. The origins of C₄ grasslands: Integrating evolutionary and ecosystem science. *Science*, 328: 587-591.
- Gould, W.A. and M.D. Walker. 1999. Plant communities and landscape diversity along a Canadian arctic river. *J. Veg. Sci.*, 10: 537-548.
- Grytnes, J.A. and O.R. Vetaas 2002. Species richness and altitude: A comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. *Am. Nat.*, 159: 294-304.
- Hegazy, A.K., J. Lovett-Doust, O. Hammouda and N.H. Gomma. 2008. Vegetation distribution along the altitudinal gradient in the northwestern Red Sea region. *Comm. Ecol.*, 8: 151-162.
- Huston, M.A. and De Angelis. 1994. Competition and coexistence: The effect of resource transport and supply rate. *Am. Natur.*, 144: 954-977.
- Lavers, C. and R. Field. 2006. A resource-based conceptual model of plant diversity that reassesses causality in the productivity-diversity relationship. *Global Ecol. Biogeogr.*, 15: 213-224.
- Leathwick, J.R., B.R. Burns and B.D. Clarkson. 1998. Environmental correlates of tree alpha diversity in New Zealand primary forests. *Ecography*, 21: 235-246.
- Linder, H.P. and P.J. Rudall. 2005 "The Evolutionary History of Poales," *Annual Reviews in Ecol. Syst.*, 36: 107-124.
- Malik, N.Z., M. Arshad and S.N. Mirza. 2007. Phytosociological Attributes of different plant communities of Pir-Chinasi Hills of Azad Jammu and Kashmir. *Int. J. Agric. Biol.*, 4:569-574.
- Marschner, H. 1986. Mineral nutrition of higher plants. Academic press, London.
- Michael, F., L.C. Laporte, Duchesne and S. Wetzel. 2002. Effect of rainfall patterns on soil surface CO₂ efflux, soil moisture, soil temperature and plant growth in a grassland ecosystem of northern Ontario, Canada: implications for climate change. *B.M.C. Ecol.*, 2: 10.
- Minchin, P.R. 1989. Montane vegetation of the Mt. Field Massif, Tasmania: a test of some hypotheses about properties of community patterns. *Vegetatio*, 83: 97-110.
- Nautiyal, M.C., B.P. Nautiyal and V. Prakash. 2004. Effect of Grazing and Climatic Changes on Alpine Vegetation of Tungnath, Garhwal Himalaya, India. *The Environmentalist*, 24: 125-134.
- Noguez, D.B., M.B. Araujo, T. Romdal and C. Rahbek. 2008. Scale effects and human impact on the elevational species richness gradients. *Nature*, 453: 216-219.
- Pausas, J.G. and M.P. Austin. 2001. Patterns of plant species richness in relation to different environments. *Appl. J. Veg. Sci.*, 12: 153-166.
- Peterson, P.M., K. Romaschenko and G. Johnson. 2010. A classification of the Chloridoideae (Poaceae) based on multi-gene phylogenetic trees. *Mol. Phylogen. Evolution*, 55: 580-598.
- Phillips, O.L. 2003. Habitat association among Amazonian tree species: a landscape scale approach. *J. Ecol.*, 91: 757-775.
- Ros, G.H., E.J.M. Temmingh and E. Hoffland. 2011 Nitrogen mineralization: A review and meta-analysis of the predictive value of soil tests. *Eur. J. Soil. Sci.*, 62(1): 162-173.
- Scholes, R.J., G. Pickett, W.N. Ellery and A.C. Blackmore. 1997. Plant functional types in African Savanna and Grassland, Cambridge University press, Cambridge. p. 255-270.
- Schuur, E.A.G. and P.A. Matson. 2001. Net primary productivity and nutrient cycling across a mesic to wet precipitation gradient in Hawaiian Montane Forest. *Oecologia*, 128: 431-442.
- Sharma, C.M., S. Suyal, S. Gairola and S.K. Ghildiyal. 2009. Species richness and diversity along an altitudinal gradient in moist temperate forest of Garhwal Himalaya. *J. Am. Sci.*, 5(5): 119-128.
- Smith, T.M. and M.A. Hutson. 1989. A theory of spatial and temporal dynamics of plant communities. *Vegetatio*, 83: 49-69.
- Steel, R.G.D., J.H. Torrie and D. Dickey. 1997. Principles and Procedure of Statistics. A Biometrical Approach 3rd Ed. McGraw Hill Book Co. Inc., New York. pp. 352-358.
- Tanner, E.V.J., P.M. Vitousek and E. Cuevas. 1998. Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecol.*, 79: 10-22.
- Tilman, D. 1982. Resource competition and community structure. Princeton university press, Princeton.
- Vazquez, J.A.G. and T.J. Givnish. 1998. Altitudinal gradients in tropical forest composition, structure and diversity in the sierra de Manantlan, Jalisco, Mexico. *J. Ecol.*, 86: 999-1020.
- Zhao, S. and J. Fang. 2006. Patterns of species richness for vascular plants in China's nature reserves. *Diver. Distrib.*, 12: 364-372.

(Received for publication 3 March 2015)