SPECIES LEVEL PHOSPHORUS ACQUISITION AND INTERNAL UTILIZATION EFFICIENCY AND THEIR RELATION WITH BOTTOM-UP AND TOP-DOWN FACTORS

MANISH MATHUR[1,2]

[1]*Plant Ecology Laboratory*
Jodhpur, JNV Rajasthan, India

[2]*Central Arid Zone Research Institute*
Jodhpur, Rajasthan, India

**Corresponding author*
ravi_mm2099@yahoo.com; eco5320@gmail.com

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Abstract. Ecosystem level nutrient use efficiency (NUE) generally increases with the richness of species or life forms in a community, though, discrepancies may exist at species level. Existence of such discrepancies, phosphorus acquisition efficiency (PAE), phosphorus internal utilization efficiency (PUTIL), phosphorus use efficiency (PUE), quotient of phosphorus utilization (QUTIL) and phosphorus harvest index (PHI) were assessed at species (Corchorus depressus) level with various spatial and temporal factors within the arid area of the Thar Desert, India. These P variables were ordinate and regressed with various bottom up (species richness, relative importance of C. depressus, Shannon and Wiener index, Simpson index, evenness, seed output, percent cover of C. depressus, root length and root collar diameter) and with top down factors (soil organic carbon, nitrogen, moisture, pH and electric conductivity). The relative importance of PAE and PUTIL in the PUE as well as the QUTIL and PHI in the PUTIL were also assessed. ANOVA analysis revealed that all the factors undertaken in the present study (i.e. spatial and temporal events and their interaction) brought significant variation ($P<0.001$) in PAE, PUTIL, PUE and QUTIL. However, for PHI spatial and temporal events individually brought significant variations, their interaction was non-significant. It emerged that for PUE at low P environmental conditions, PAE was 10-37 times more important than PUTIL. Similarly for PUTIL, QUTIL was 17-56 times more important than PHI. Kaiser-Meyer-Olkin test (0.597) and Bartlett's test of sphericity indicated appropriate use of factor analysis (PCA) and significant correlation between variables in the present study, respectively. Ordination analysis showed lack of correlation between PAE and PUTIL, indicating that selection of one of these should not affect the other. Percent cover of plant, seed output, root length and root collar diameter exhibit various relationships with different P variables. Regression analysis between P variables and community factors revealed that at species level dominance of C. depressus reflects its higher P acquisition efficiency; however as the community diversity (richness, Shannon and Wiener index and evenness) increases the P internal utilization and PUE were inhibited. It can be concluded that P internal utilization and PUE of C. depressus are largely influenced by temporal factors (increase and decrease of community diversity during pulse and non-pulse events, respectively). As a result this species achieved effective nutrient use through temporal partitioning, through which it fulfilled P requirements during low resource availability. Among the soil variables soil nitrogen supported PUTIL, PUE and QUTIL, while soil moisture and soil pH favoured PHI and soil N and PHI showed negative relationship.

Keywords: *Nutrient Use Efficiency, Ecosystem level, Species Level, Ordination, Species Diversity, Plant and Soil Factors*

Introduction

Efficiency concepts in plant mineral nutrition have been defined based on the process by which plants acquire, transport, store and use the nutrient in order to produce dry matter or grain, at low or high nutrient supply (Ciarelli *et al.,* 1998). Nutrient acquisition efficiency and nutrient internal utilization efficiency are the two major components of plant nutrient use efficiency. These two components are related to the ability of the plant to acquire nutrient from the soil and to plants internal ability to produce yield units per unit nutrient in plant (Good *et al.,* 2004). Bridgham *et al.,* (1995) defined nutrient uptake efficiency as the proportion of available soil nutrients acquired by plants and the nutrient use efficiency, as total net primary productivity (PR) per quantity of nutrients acquired during the same periods. Hiremath and Ewel (2001) considered ecosystem nutrient use efficiency as the ratio of net primary productivity to soil nutrient supply. They further summarized how the ecosystem level nutrient use efficiency increases with the richness of species or life forms in a community and what the relative roles of species traits and nutrient supplying capacity of the soil in determining nutrient use efficiency are.

Nutrient use efficiency is studied by ecologists at different scales (Mathur, 2013). At the leaf level, nutrient use efficiency is the ratio of photosynthetic rate to concentration of nutrient in the leaf lamina (Field & Mooney 1986); at the plant level, it is the ratio of growth to nutrient uptake (Hirose, 1975). Plant level nutrient use efficiency depends on productivity per unit of nutrient in the plant and mean residence time of nutrient in the plant (Berendse & Aerts, 1987). There are two ways through which nutrient use efficiency of an individual can influence nutrient use efficiency of the whole system. The first is through its influence on competitive interaction among species. Plant with high nutrient use efficiency should be able to tolerate lower nutrient availabilities: thus, they should be effective competitors in diverse communities where nutrients are in short supply (Tilman *et al.,* 1997). A system made up of such individuals should therefore have a higher productivity per unit of nutrient supplied by the soil than one made up of individuals with low nutrient use efficiencies. The second way that plant nutrient use efficiency can influence the ecosystem nutrient use efficiency is through its influence on litter nutrient return (Hobbie, 1992).

Effective uptake can be achieved through four different mechanisms (a) temporal partitioning such that one species takes up nutrients at a time when others do not (b) spatial partitioning such that one species takes up nutrients from portions of the habitat that are inaccessible to other species (c) uptake of nutrients in different proportions, or (d) uptake of different forms of the same nutrient (for example plant root absorb P as either $H_2PO_4^-$ or HPO_4^{2-}).

It follows, therefore, as suggested by Tilman *et al.,* (1997) in the context of diversity and ecosystem productivity and by Hooper (1998) in the context of diversity and nutrient retention, that ecosystem nutrient use efficiency depends upon the identification of the species making up the system, and not on a greater diversity of species per se. A complete assessment of ecosystem productivity and nutrient dynamics requires measuring the above and below ground patterns of biomass increment, nutrient content and turnover. In fact, a proper evaluation of nutrient use efficiency requires data at the whole-plant level, because patterns of aboveground utilization efficiency are not necessarily similar to whole-plant utilization efficiency (Aerts & Chapin, 2000). However most of the previous studies have focused exclusively on the nutrient utilization efficiency (NUE) of fine-litter production (Vitousek, 1984; Silver, 1994; Yasumura *et al.,* 2002; Paoli *et al.,* 2005). One whole plant NUE study from semiarid grassland in northern China was conducted by Yuan *et al.,* (2006). Destructive methods of NUE evaluation are generally criticized, therefore nutrient solution techniques have been used as important tools in short-term experiments to select and identify nutrient efficient plants (Furlani and Furlani, 1988; Ciarelli *et al.,* 1998; Spehar & Souza, 1999). In addition, these non destructive techniques might be useful for those species which have low germplasm availability in nature (Furlani *et al.,* 2002).

Woody perennials exhibit a characteristic time course of phosphorus acquisition and internal P redistribution during their life cycle (Fageria *et al.,* 2011 and White and Veneklaas, 2012). Phosphorus efficiency can be divided into P acquisition efficiency (PAE) and P utilization efficiency (PUE). PAE refers to the ability of plants to take up P from soils, whereas PUE is the ability to produce biomass or yield using the acquired P (Wang *et al.,* 2010). Enhancement of P efficiency in plants can be achieved through improving P acquisition and/or utilization. However, the contribution of PAE or PUE to plant P efficiency varies with species and environmental conditions (Wang *et al.,* 2010). A higher P internal utilization efficiency has attributed to a higher grain yield per unit of P in the grain (quotient of utilization) and to higher ability to transfer nutrient from shoot to grain, called P harvest index (Baligar & Fageria, 1997).

To check the variability in species level nutrient use efficiency and its associated variables, present study was conducted with two objectives. (1) to determine the relative importance of P acquisitions and internal utilization in the P use efficiency and relative importance of P quotient of utilization and the P harvest index, in the P internal utilization efficiency at different spatial and pulse events and (2) to find out the relationship of different efficiency variables (P acquisition efficiency, P internal utilization efficiency, P use efficiency, quotient of P utilization and P harvest index) with bottom-up (species richness, Relative Importance value of *Corchours depressus*, diversity parameters, percent cover of plant, seed output, root length and root collar diameter and top-down factors (Soil organic carbon, soil nitrogen, moisture, soil pH and electric conductivity).

Corchorus depressus (Linn.) belongs to family Tiliaceae, distributed in almost all parts of the world. It is a prostrate, woody perennial with branches radiating from a woody crown, closely addressed to the ground, and the plant is regarded as a good sand binder in the desert (Mathur, 2005). Fruit is a capsule, 8 to 15-mm long, often curved upward from the underside of the branches, cylindrical, beaked, four-valve, and septet between the seeds. Seeds are minute and brown colored. Various medicinal uses of this plant for general weakness, gonorrhea, diabetes, treachery troubles, and improve sexual vigour have been reported (Chopra and Nayar, 1956; Shekhawat, 1986; Kumar *et al.,* 2003). The clinical validation, phytodiversity, and phytochemistry studies have been carried out by Mathur (2005).

Material and Methods

Site selection and their status

Five different sites were selected with-in in the 16 km radius of the Jodhpur city of the Rajasthan state, Indian (*Table 1*). Each site differing in respect of soil composition, land uses and vegetation status. During the study period mean annual precipitation ranged from 0.004 to 260 mm, winter (December) temperature varied from 10.7 to 23^0C, summer (May) temperature varied from 28.7 to 42.2°C and relative humidity ranges from 31 to 91% (Morning) and 08 to 68% (Evening).

Biomass estimation

The above and below-ground biomass of the *C. depressus* was estimated by collecting random samples from different sites. Fifteen plants were uprooted and gently washed under tap water. The plants were air-dried and weighed using an electronic balance (accuracy 0.001 g.). As per the resources hypothesis (Goldberg & Novoplansky, 1997) the sampling were carried out during rainy (July), winter (December) and summer (May) periods for evaluation of the impacts of pulse, inter-pulse and non-pulse events.

Nutrient Quantification

Phosphorus was estimated by spectroscopic method (Allen *et al.,* 1976) based on the development of molybdenum blue color. The standard was prepared with KH_2PO_4.

Nutrient Efficiency Indices

Different nutrient efficiency indices were calculated following Parentoni and Junior-Souza, (2008). Two groups of efficiency variables were obtained for each site in each pulse event. The first group comprised of the variables P acquisition efficiency (PAE) and P internal utilization efficiency (PUTIL), which were used to obtain the P use efficiency (PUE). While, the second comprised of two variables, quotient of utilization and P harvest index

(1) Phosphrus Acquisition Efficiency (PAE)

$$\mathrm{PAE} = \frac{\mathit{Phosphorus\ in\ Plant}}{\mathrm{Phosphorus\ in\ soil}}$$

(2) Phosphorus Internal Utilization Efficiency (PUTIL)

$$\mathrm{PUTIL} = \frac{\mathit{Seed\ dry\ matter\ produced\ (Seed\ Biomass)}}{\mathrm{Phosphorus\ in\ Plant}}$$

(3) Phosphorus Use Efficiency (PUE)

$$\mathrm{PAE\ X\ PUTIL}$$

(4) Quotient of Phosphorus Utilization (QUTIL)

$$\mathrm{QUTIL} = \frac{\mathrm{Seed\ Biomass}}{\mathit{Phosphorus\ in\ Seed}}$$

(5) Phosphorus Harvest Index

$$\mathrm{PHI} = \frac{\mathrm{Phosphorus\ in\ Seed}}{\mathit{Phosphorus\ in\ Plant}}$$

The relative importance of PAE and PUTIL over PUE was investigated according to Moll *et al.,* (1982). This methodology was developed to investigate the relative importance of two variables (PAE and PUTIL), obtained experimentally, over a third variable (PUE) which is obtained by the multiplication of PAE and PUTIL. This information could be valuable for comparative evaluation of each of two variables (PAE and PUTIL) that to be used in selection program related with P use efficiency. The same also exercised for two variables related with P internal utilization efficiency and PHI

The analysis of variance (ANOVA) was carried out in a two way strip – plot design, which sacrifices precision on the main effects of both factors. The interaction is measured more accurately by this method compared to randomized complete block or split-plot design (Gomez & Gomez, 1984).

Multivariate Analysis

Bartlett's test of sphericity and Kaiser-Meyer-Olkin (KMO) were carried out to assess the suitability of factor analysis. Principal Component Analysis (PCA) was carried out as a data reduction technique. PCA was performed with Pearson correlation coefficient. The main objective of PCA was to find out relationship of different efficiency variables (PAE, PUTIL PUE, QUTIL of P utilization and P harvest index) with bottom-up (species richness, Relative Importance value of *C. depressus*, diversity parameters, percent cover of plant, seed output, root length and root collar diameter) and top-down factors (Soil organic carbon, soil nitrogen, moisture, soil pH and electric conductivity).

Appropriate regression equations were selected on the basis of probability level significance and high R^2 value. Path analysis was carried out with Curve Expert software, 2001.

Results and Discussion

Most of the sites were located on the older alluvial plains (with higher proportion of sand), followed by younger alluvial plain, and piedemonts (*Table 1*). Herbaceous covers were dominated by *Dactyloctenium aegyptium, Eragrostis ciliaris, Aristida funiculata,* grasses that represent the sub-climax stage of habitats (Saxena & Aggarwal, 1983). Different plant, soil and community parameters are presented in *Table 2*. Coefficient of variance of biomass data at five sites and during different seasonal events indicates that at most of the sites comparatively higher biomass was recorded during pulse event except at site 2 where it was recorded maximum during non-pulse event (*Figure 1*). The greatest P concentration was recorded in seed collected from site 1 during the pulse event. The analysis of variance revealed that the factors studied in the present investigation caused P to vary at the 99% probability level (*Table 3*).

A significant proportion of P released in the present study is probably due to effects of drying and rewetting on the microbial biomass as reported by the Sparling *et al.,* (1985) and Qiu & Mccomb (1995). Qiu & Mccomb (1995) attributed the entire increase in soil P on air-drying to killed microbial cells. He & Zhu (1998) reported that of the adsorbed P transformed by microbes from soil, 17-34% was water soluble and available P. This clearly indicates microbial turnover to be the cause of increase in available P during wet season. The results are in agreement with those reported by Rao & Tarafdar (1992) where maximum available P was recorded during pulse event in soils.

PUTIL, which exhibit the relationships between seed dry matter productions with relation to P in plant, exhibits higher during inter-pulse events followed by non-pulse event. Thus, during medium and low resources conditions, compared to other modules, plant invests their resources more in their reproductive part.

The result revealed that PUE is largely affected with spatial factor. At site 1, 2 and 3 higher PUE was recorded during non-pulse event, while at remaining sites it was recorded maximum during inter-pulse event (*Table 4*). Thus these results revealed that at moderate to low resource condition nutrient uptake of this species seems better.

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

Site No.	Coordinates		Habitat types	Soil Textures				Sub-Climax species (arrange in descending order of RIV)
	N	E		Clay	Silt	Sand	Gravel	
1	$26^0\ 12^{'}\ 48.4^{''}$	$73^0\ 4^{'}\ 7.8^{''}$	Old alluvium plains	26.39	17.89	35.58	20.13	*Dactyloctenium aegyptium* *Eragrostis ciliaris*
2	$26^0\ 11^{'}\ 33.4^{''}$	$73^0\ 3^{'}\ 6.1^{''}$	Younger alluvium and river bed terrain	17.09	25.43	23.53	33.54	*E. cilliaris, Lepidagathis cristata*
3	$26^0\ 14^{'}\ 47.01^{''}$	$73^0\ 0.0^{'}\ 58.9^{''}$	Old alluvium plains	28.72	21.31	31.29	18.80	*D. sindicum ,I. cordifolia*
4	$26^0\ 14^{'}\ 12.4^{''}$	$73^0\ 01^{'}\ 24.2^{''}$	Old alluvium plains protected	29.18	18.56	43.3	10.26	*E. cilliaris*
5	$26^0\ 21^{'}\ 54.5^{''}$	$73^0\ 03^{'}\ 48.9^{''}$	Younger alluvium and river bed terrace	25.35	15.48	37.46	21.47	*E. cilliaris, A.funiculata*

***Table 2.** Various parameters at C. depressus locations during study period*

Parameters		Range
Plant Variable	Percent Cover of *C. depressus* (Sq. M)	0.061-0.645
	Seed Output	10.98-28.34
	Root Length (Cm)	7.5-31.18
	Root Collar Diameter (Cm)	0.5-2.07
Soil Compositions	Organic Carbon (mg $100g^1$)	61.4-432.5
	Total Nitrogen (mg $100g^1$)	18.95-112.65
	Moisture	0.59-12
	pH	7.32-9.08
	Electric Conductivity	0.11-1.202
Community Composition (1X1 m) quadrate	Richness	4-12
	Shannon Weiner Index (H')	1.19-2.38
	Relative Importance Value of *C. depressus*	6.25-49.17
	Evenness	0.77-1.202
	Simpson Index	0.008-0.33

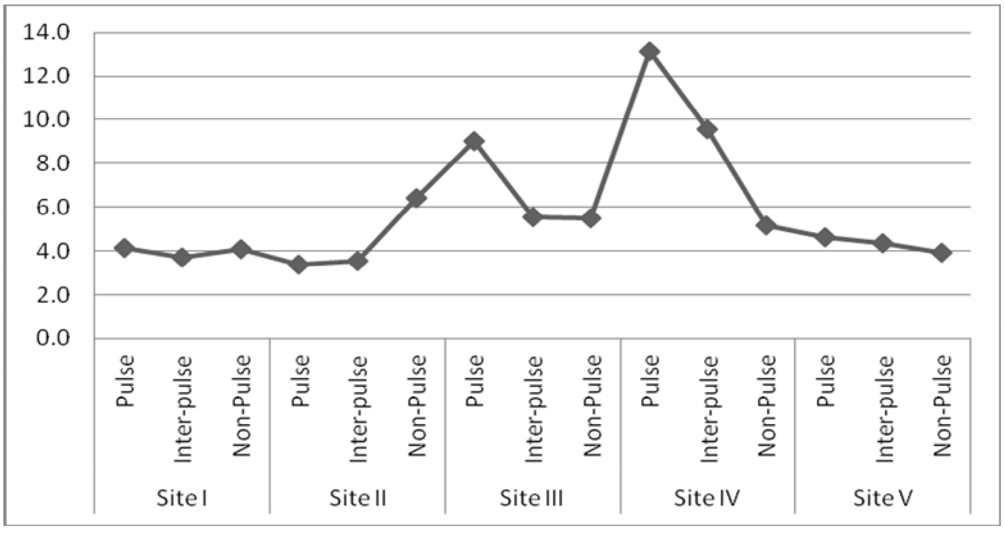


***Figure 1**. Coefficient of variance of biomass during various spatial and temporal events*

***Table 3**. Range of Phosphorus (mg g-1) in various modules of C. depressus*

Modules	Range	Modules with higher
Root	1.12-9.86	Seed/I/Pulse Event
Stem	4.72-15.04	
Leaves	6.53-19.41	
Seed	8.09-38.37	
ANOVA results/Source of	Mean squares	Computed F Value
Sites	3789	40.19**
Season	139E+07	2017.89**
Sites x Season	960	164.52**
Plant Part	131E+07	225**
Sites x Plant Part	3300	56.59**
Season x Plant Part	216.11	370.60**
Sites x Season x Plant Part	2180	37.39**

**P < 0.01

QUTIL, ratio of seed biomass and the P content in seed, exhibits higher spatial and temporal variability's. At site 1, 3 and 5 it was recorded higher during non-pulse events while at other sites it was recorded maximum during inter-pulse event (*Table 4*). Thus moderate to low resources supports the seed biomass. Phosphorus Harvest Index (PHI), ratio of seed P to plant P recorded maximum during pulse events at most of the sites.

Analysis of variance revealed that all the factors taken in the present study (i.e., sites, events, and the interactions between them) caused PAE, PUTIL, PUE and QUTIL to vary at the 99% probability level (*Table 5*). However, for PHI sites and events individually brought significant variation, but their interaction was non- significant.

Results indicate that with the set of different temporal and spatial impacts, for phosphorus use efficiency, PAE was 10-37 fold more important than PUTIL, 3-9 time fold at low P environment (non-pulse events) and 2-10 fold more during moderate (inter-pulse) and high P environment (pulse event), respectively. Similarly, the related importance of QUTIL and PHI in PUTIL indicates that QUTIL was 17-56 folds more important than PHI at low P environment and 1-6 fold higher during high P condition. Greater importance of PAE to the tune of 94-100 % in P use efficiency at low or high P level in soil has also been reported in wheat (Manske *et al.,* 2001).

Multivariate Analysis

Result of Kaiser-Meyer-Olkin (KMO) and Bartlett's test of sphericity are presented in *table 6*. The Kaiser-Meyer-Olkin (KMO) is an index used to examine the appropriateness of factor analysis. A high value (between 0.5 and 1.0) indicates that the factor analysis is appropriate, value below 0.5 imply that factor analysis may not be appropriate. In this study KMO was 0.597, which indicates appropriate use of factor analysis. For Bartlett's test of sphericity there are two levels to interpret this test (a) H0: There is no correlation significantly different from 0 between the variables and Ha: at least one of the correlations between the variables is significantly different from 0. As the computed p-value is lower than the significance level = 0.05, one should reject the null hypothesis H0 and accept the alternate. In other words it can be conclude that there are significant relationships between studied variables (*Table 6*).

The PCA analysis was performed with the use of Pearson correlation coefficient, and the results are presented in *Figure 2*. The interpretation of the correlation circle was carried out using the following criteria, when two variables are far from the centre.

Table 4*. Different Phosphorus variables at various pulse events and spatial levels.*

Variables	Site 1			Site 2			Site 3			Site 4			Site 5		
	Pulse Event	Inter-pulse Event	Non-pulse Event	Pulse Event	Inter-pulse Event	Non-pulse Event	Pulse Event	Inter-pulse Event	Non-pulse Event	Pulse Event	Inter-pulse Event	Non-pulse Event	Pulse Event	Inter-pulse Event	Non-pulse Event
PAE	51.28	39.16	109	26.75	50.32	117.22	68.97	17.132	51.65	37.4	23.92	279.6	37.5	29.993	136.82
PUTIL	7.406	12.01	10.01	10.68	9.272	4.8793	3.324	18.946	16.603	2.23	34.7	11.88	2.15	17.951	17.163
PUE	228.2	157.2	491.9	598.9	294	649.1	288.3	616.6	872.9	332.6	893.2	709.2	304.95	864.65	816.7
QUTIL	6.74	12.65	17.8	14.2	16.26	10.823	5.851	22.165	53.646	2.09	61	25.32	2.44	28.903	31.047
PHI	1.099	0.95	0.57	0.752	0.57	0.4508	0.568	0.8548	0.3095	1.07	0.569	0.469	0.88	0.6211	0.5528

Table 5*.Analysis of Variance of Phosphorus Variables*

Variables	Sites			Events			Sites x Events		
	Sum of Square	Mean Square	Computed F Value	Sum of Square	Mean Square	Computed F Value	Sum of Square	Mean Square	Computed F Value
PHI	21998.7	5499.69	8854.84**	102159.8	51079.9	189513.9**	69032.96	8629.11	26455.74**
PUTIL	309.99	77.49	569.38**	1349.19	674.59	1183.59**	1309.43	163.67	2700**
PUE	815488	203861	81544**	969761	48488.5	19395**	10193	12741	33978.6**
QUTIL	221.50	552.87	3924.74**	4618.86	2309.43	7166.2**	6003.3	750.42	4813.99**
PHI	0.702	0.1754	9.3**	1.44	0.72	43.89**	0.7235	0.009	5.15^{NS}

Table 6*. Bartlett's sphericity and Kaiser-Meyer-Olkin sampling adequacy tests*

Chi-square (Critical value)	202.51
DF	171
p-value	0.09
Alpha	0.05
KMO	0.597

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); if they are on opposite sides of the centre, then they are significantly negatively correlated (r close to 2). Squared cosines were used to link the variable with the corresponding axis; the greater the squared cosine, the greater the link with the corresponding axis. PCA were considered (*Table 7* and *Fig. 2*) useful if their cumulative percentage of variance approached 80% (Wei-Giang *et al.,* 2008).

In the present investigation cumulative percentage indicates that the first four axes together accounted for 80.98% variability in the data set (*Table 7*) with their individual contribution being 49.82%, 15.53%, 8.94%, and 6.68%, respectively. From present study correlation circle (*Fig. 2*) as well as *Table 8*, revealed that PUTIL related with

PUE (r = 0.69**) and with QUTIL (r = 0.88**). Similarly PUE related with QUTIL (r = 0.80**) and with PHI (-0.65**).

Table 7. *Eigen value analysis and other attributes obtained from Principal Component Analysis*

	F1	F2	F3	F4
Eigenvalue	9.467	2.951	1.699	1.271
Variability (%)	49.828	15.530	8.943	6.687
Cumulative %	49.828	65.358	74.301	80.988

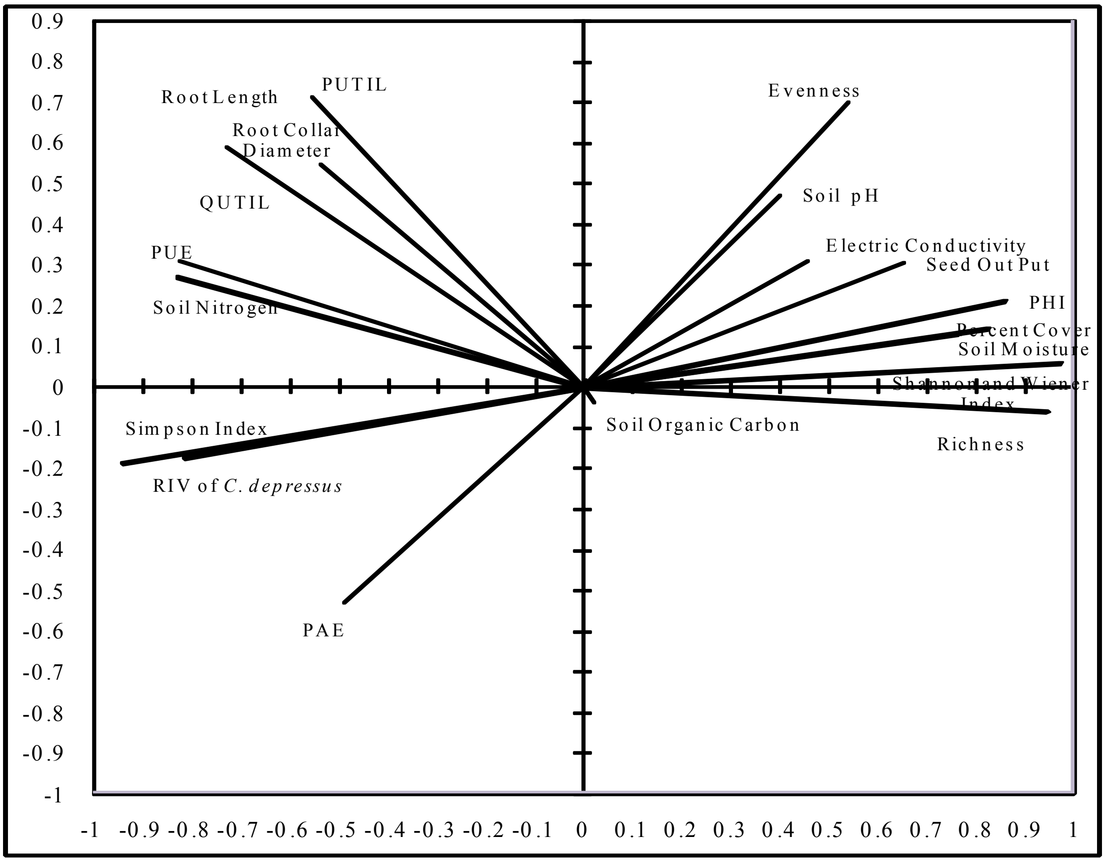


Figure 2. *Bi-Plot Analysis of Principal Component Analysis*

QUTIL was also negatively related with PHI (r = -0.58**). These significant correlations were observed at 0.01% (**) and 0.05% (*) levels. Correlation was not found between PAE and PUTIL, indicating that these variables are independent. Correlation between nitrogen acquisition and nitrogen internal utilization efficiency has also been not found in wheat, triticale and maize (Anderson, 1985 and Parentoni & Junior-Souza, 2008).

Table8. *Correlation Matrix Emerged from Principal Component Analysis*

	Variables	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	PAE																		
2	PUTIL	-0.122																	
3	PUE	0.212	**0.696**																
4	QUTIL	0.019	**0.889**	**0.805**															
5	PHI	-0.442	-0.311	**-0.656**	**-0.589**														
6	Percent Cover	-0.404	-0.418	**-0.677**	**-0.532**	**0.787**													
7	Seed out put	**-0.643**	-0.032	-0.283	-0.213	**0.566**	0.497												
8	Root length	0.098	**0.517**	0.419	**0.569**	-0.273	-0.229	-0.428											
9	Root Collar Diameter	0.101	**0.521**	0.421	**0.572**	-0.275	-0.234	-0.430	**1.000**										
10	RIV of *C. depressus*	**0.667**	0.271	0.515	0.434	**-0.667**	**-0.544**	**-0.739**	0.419	0.424									
11	Richness	-0.327	**-0.601**	**-0.767**	**-0.715**	**0.792**	**0.833**	**0.539**	-0.445	-0.449	**-0.771**								
12	Simpson Index	**0.539**	0.337	**0.703**	**0.565**	**-0.824**	**-0.827**	**-0.618**	0.418	0.421	**0.786**	**-0.895**							
13	Shannon and Wiener Index	-0.467	-0.462	**-0.775**	**-0.666**	**0.853**	**0.826**	**0.586**	-0.471	-0.474	**-0.801**	**0.951**	**-0.980**						
14	Evenness	**-0.529**	0.199	-0.253	0.013	**0.583**	**0.660**	0.500	0.085	0.085	-0.445	0.447	**-0.696**	**0.571**					
15	Electric conductivity	-0.431	-0.142	-0.243	-0.127	0.476	0.246	0.212	-0.181	-0.176	-0.430	0.363	-0.405	0.432	0.316				
16	Soil Organic Carbon	-0.065	-0.110	-0.104	-0.194	-0.070	-0.223	0.014	0.036	0.040	-0.034	-0.115	0.044	-0.090	0.091	-0.075			
17	Soil Moisture	-0.300	-0.389	-0.507	-0.450	**0.537**	**0.555**	**0.647**	-0.294	-0.294	**-0.723**	**0.806**	**-0.709**	**0.726**	0.481	0.264	0.220		
18	Soil Nitrogen	0.222	**0.674**	**0.996**	**0.786**	**-0.674**	**-0.672**	-0.294	0.408	0.408	0.506	**-0.765**	**0.706**	**-0.776**	-0.275	-0.288	-0.116	**-0.520**	
19	Soil pH	-0.171	0.047	-0.257	-0.068	**0.515**	0.288	0.223	0.068	0.077	-0.125	0.319	-0.406	0.388	**0.531**	**0.606**	0.172	0.436	-0.330

Values in bold are different from 0 with a significance level alpha=0.05

In the present study, the lack of correlation between P acquisition and P utilization efficiency indicates that the selection of one of these should not affect the other, which would facilitate simultaneous selection of these traits, in the set of environmental studies. The main selection criteria for P internal utilization efficiency should be toward reducing the seed P concentration (inverse of the quotient of utilization) and in this case a negative weight should be used in the selection of species for ecosystem stability. Since this species is largely consumed along-with seed for its aphrodisiac properties, hence reduction in seed P concentration would have a positive impact on nutrition. Since seed P is stored as the anti-nutritional factor phytate; and it would also reduce environmental pollution from higher P manures produced by large animal feeding lots. However the strategy of reducing seed P concentration should have a limit, since seed P is needed for its germination and initial establishment (Philip & Veneklaas, (2012).

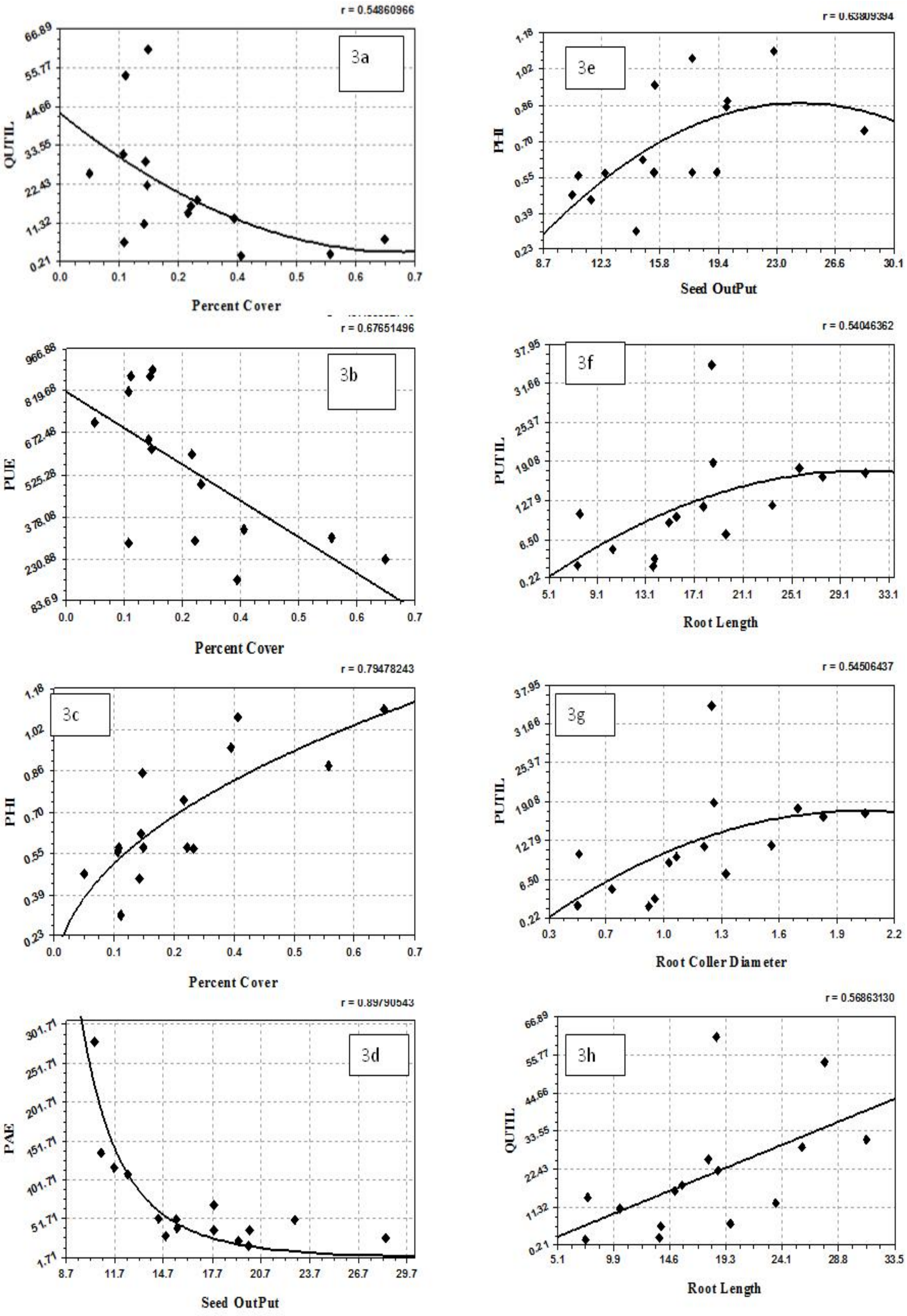
Path Analysis

P Variables and Plant Parameters

Polynomial negative relation was observed between percent cover and QUTIL (QUTIL = 43.05+-117.74 Percent Cover +86.38 Percent Cover$^{\wedge 2}$, R^2 = 0.548*, *Fig. 3a*). Percent cover also shows negative linear relation with PUE (PUE = 819.08+-1087.95Percent Cover, R^2 = 0.67**, *Fig.3b*). On the other hand, percent cover support Phosphorus Harvest Index in power fashion (PHI = 1.319Percent Cover ^0.448, R^2 = 0.79**, *Fig.3c*). Percent cover calculated through the two dimension of the plant that do not positively reflect in seed biomass, but this parameter certainly favour the P content in seed and this ultimately reflects with its initial establishment and subsequent growth (Nadeem *et al.,* 2011a).

Seed output depletes the PAE in power fashion (PAE = 2646787 Seed Out Put^-4.0, R^2 0.89**, *Fig.3d*). Seed output exhibits polynomial relation with PHI (PHI = -0.528+0.115 Seed Out Put+-0.002 Seed out Put$^{\wedge 2}$, R^2 0.63*, *Fig.3e*). This result revealed that the highest level of PHI was recorded at intermediated seed output level. Since PAE is the ration of P in plant to P in soil, and on the other hand this plant is under the category of R selection species (produce high number of seed) that ultimately pumps the more P in seed compare to other plant part. Thus this parameter negatively related with PAE but positive for PHI.

PUTIL exhibits positive polynomial relation with both root length (PUTIL = -7.007+1.586 Root Length +-0.0255 Root Length$^{\wedge 2}$, R^2 = 0.54*, *Fig. 3f*) and with root collar diameter (PUTIL = -7.725+24.328Root Collar Diameter+-5.956 Root Collar Diameter$^{\wedge 2}$, R^2 = 0.54*, *Fig. 3g*). Similarly QUTIL shows linear positive relation with root length (QUTIL = -4.424+o1.414 Root Length, R^2 = 0.56*, *Fig. 3h*) and with root collar diameter in polynomial positive fashion (QUTIL = -8.21+28.228 Root Collar Diameter+-2.729 Root Collar Diameter$^{\wedge 2}$, R^2 = 0.57*, *Fig. 3i*). PUTIL and QUTIL are the ratio of seed biomass to P in plant and seed biomass to P in seed, respectively, root morphological parameters like root length and root collar diameter supports seed biomass.



***Figures 3a to 3h**. Relationships between various P variables and plant parameters*

It is often observed that phosphate uptake by roots is regulated systemically by plant P status (White, 2012). It has been suggested that sucrose transported in the phloem from the shoot to the root acts as a systemic signal to regulate phosphate uptake by roots (Hammond & White, 2008).

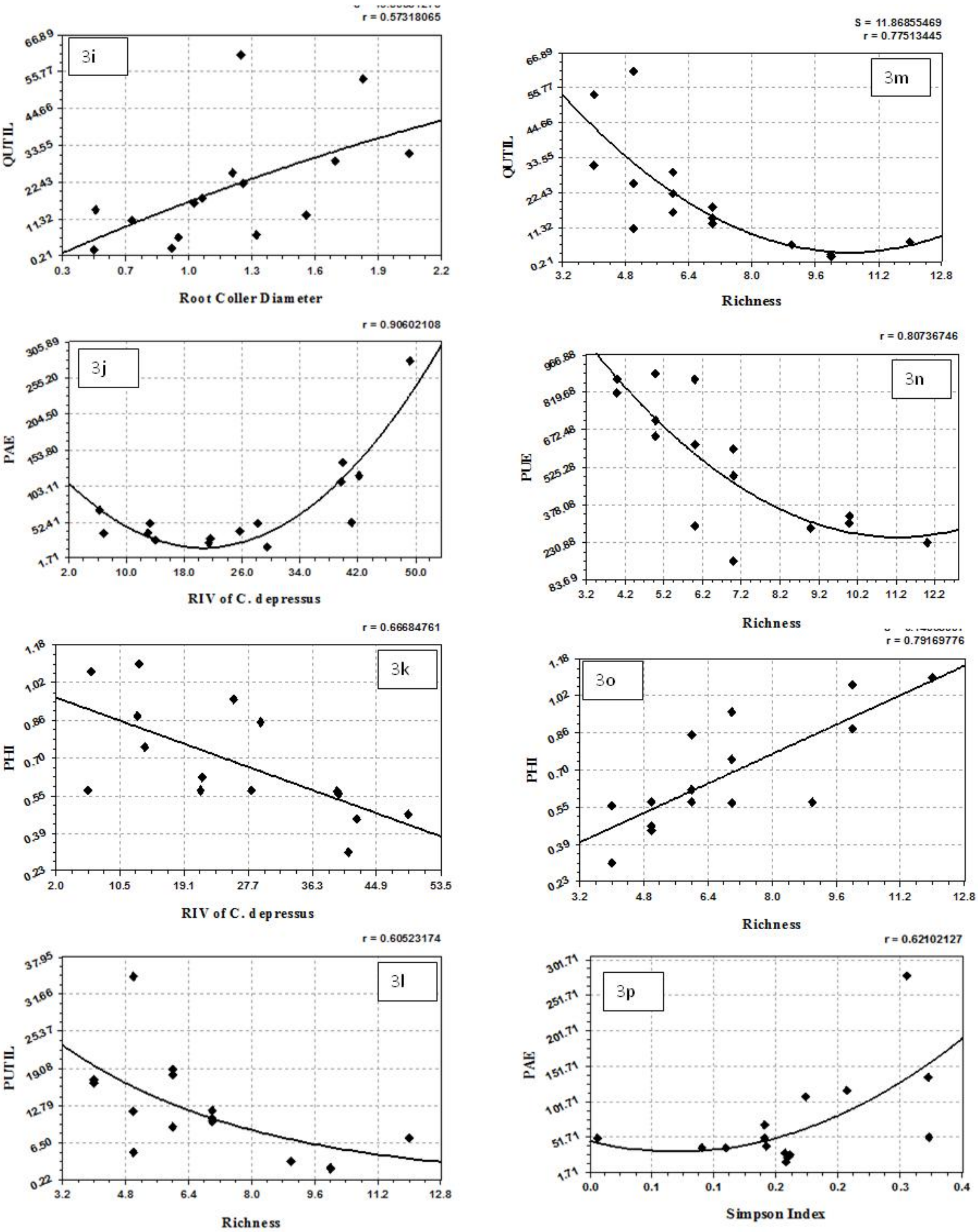
P Variables and Community Factors

Relative Importance Value (RIV) of *C. depressus* shows a positive polynomial relation with its phosphorus acquisition efficiency (PAE = 126.76+-10.749 RIV of *C. depressus*+0.262 RIV of *C. depressus*^^{2}, R^2 = 0.90**, *Fig.3j*) while on the other hand this ecological parameters held back the PHI of this plant in a linear fashion (PHI = 0.980+-0.011 RIV of *C. depressus*, R^2 = 0.66**, *Fig.3k*). Community richness inhibits PUTIL exponentially (PUTIL = 44.15e^ $^{(-0.203\ \mathrm{Richness})}$, R^2 = 0.60*, *Fig.3 l*) and polynomial to QUTIL (QUTIL = 107.796+-19.977 Richness + 0.955 Richness^^{2}, R^2 = 0.77**, *Fig.3m*) and to PUE (PUE = 1752.03+-267.130+11.890Richnes^2, R^2 = 0.80**, *Fig.3n*). But it supports seed production (PHI) in linear fashion (PHI = 0.148+0.0782 Richness, R^2 = 0.79**, *Fig.3o*).

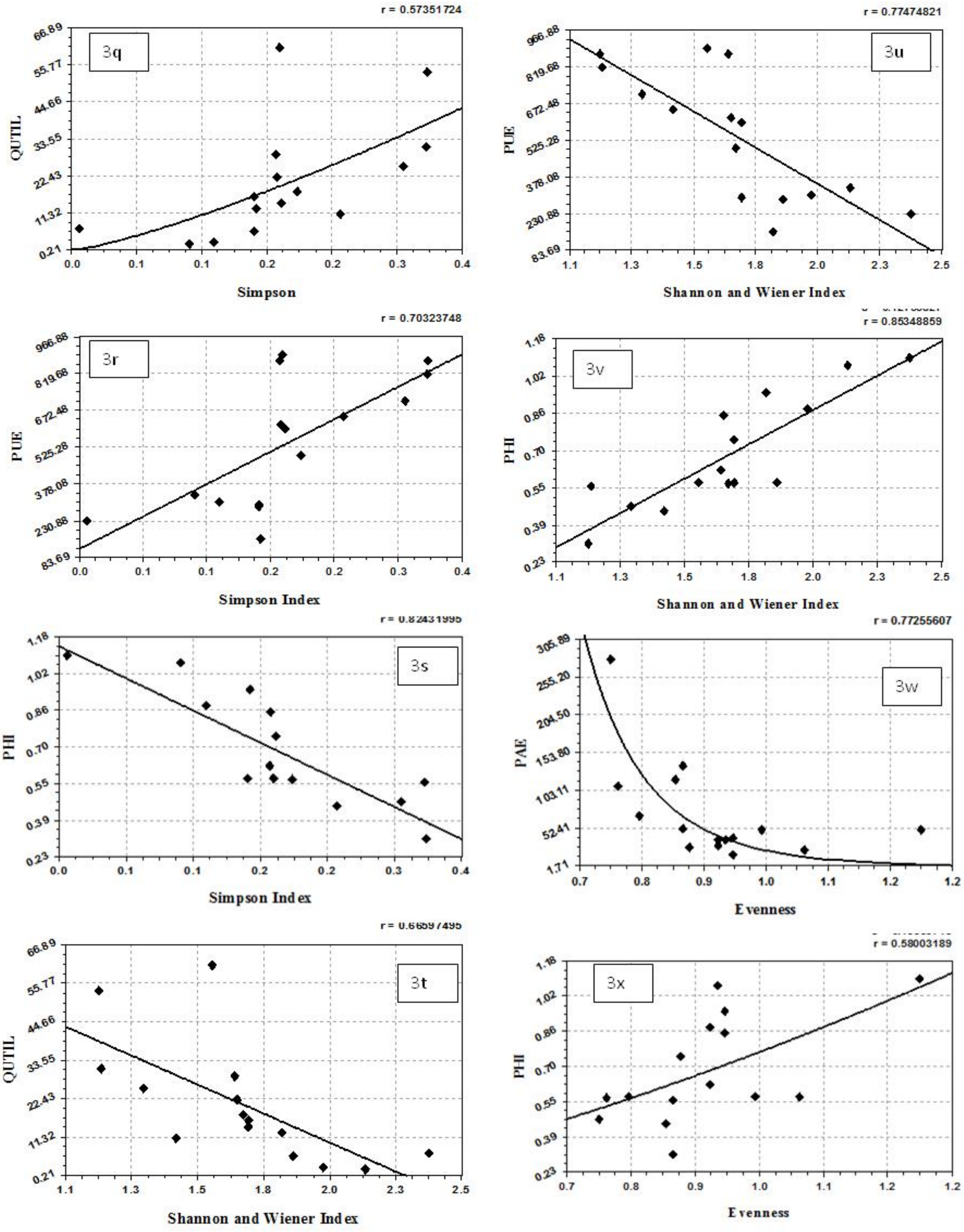
Different diversity indices gave the valuable information about community status. Simpson index measures the dominance of species and it ranges from 0 to 1. It measures the probability that two individuals selected at random from a sample will belong to the same species. Because Simpson index is actually an index of dominance, and then tend to be inversely to evenness and richness, but in some cases these two indices are independent from each other (Hill, 1973). Shannon-Weiner index (1949) is based on information theory.

The information content is a measure of the amount of uncertainty. It generally falls between 1.5 and 3.5, and rarely exceeds 4.5 (Margalef, 1972). Higher Shannon Weaver index values indicated that many species are represented by the same number and low value showed complete dominance of one species. In other words high value indicates high phytodiversity at particular stand. Evenness or equitability represents the distribution of individuals among the species. It is sometimes defined as the ratio of observed diversity to maximum diversity (Margalef, 1958). When all species are equally abundant, an evenness index would be at a maximum and decrease toward zero as the relative abundance of the species diverges away from evenness (Ludwig & Reynolds, 1999).

In the present investigation Simpson index supports PAE (PAE = 46.559+-351.419 Simpson Index+2074.70 Simpson Index^^{2}, R^2 = 0.62*, *Fig.3p*), QUTIL (QUTIL = 156.24 Simpson ^ 1.270, R^2 = 0.57*, *Fig.3q*), and PUE (PUE = 116.51+2154.85 Simpson Index, R^2 = 0.70**, *Fig.3r*) in polynomial, power and linear fashion, respectively. By contrast, this diversity parameters showed negative linear relation with PHI (PHI = 1.139+-2.300 Simpson Index, R^2 = 0.82**, *Fig.3s*). Shannon and Weiner Index (H') inhibits QUTIL (QUTIL = 80.97+-35.27 Shannon and Weiner Index, R^2 = 0.66**, *Fig.3t*) and PUE (PUE = 1585.09+-610.97 Shannon and Weiner Index, R^2 = 0.77**, *Fig.3u*) linearly but supports its PHI in a linear fashion (PHI = -0.361+0.613 Shannon and Weiner Index, R^2 = 0.85**, *Fig.3v*). Evenness shows two contrasting results with PAE and PHI of this species. It inhibits PAE (PAE = 20.100 Evenness^-8.802, R^2 = 0.77**, *Fig.3w*) but support PHI (PHI = 0.788Evenness^1.619, R^2 = 0.580*, *Fig.3x*), both in power fashion. Thus, from this study it can be concluded that at species level dominance (RIV of *C. depressus* and Simpson index) of this plant reflects its greater phosphorus acquisition efficiency, however, as the community diversity (richness, Shannon and Weiner index and evenness) increases the phosphorus internal utilization and phosphorus use efficiency inhibited.



***Figures 3i to 3p**. Relationships between various P variables and community parameters*



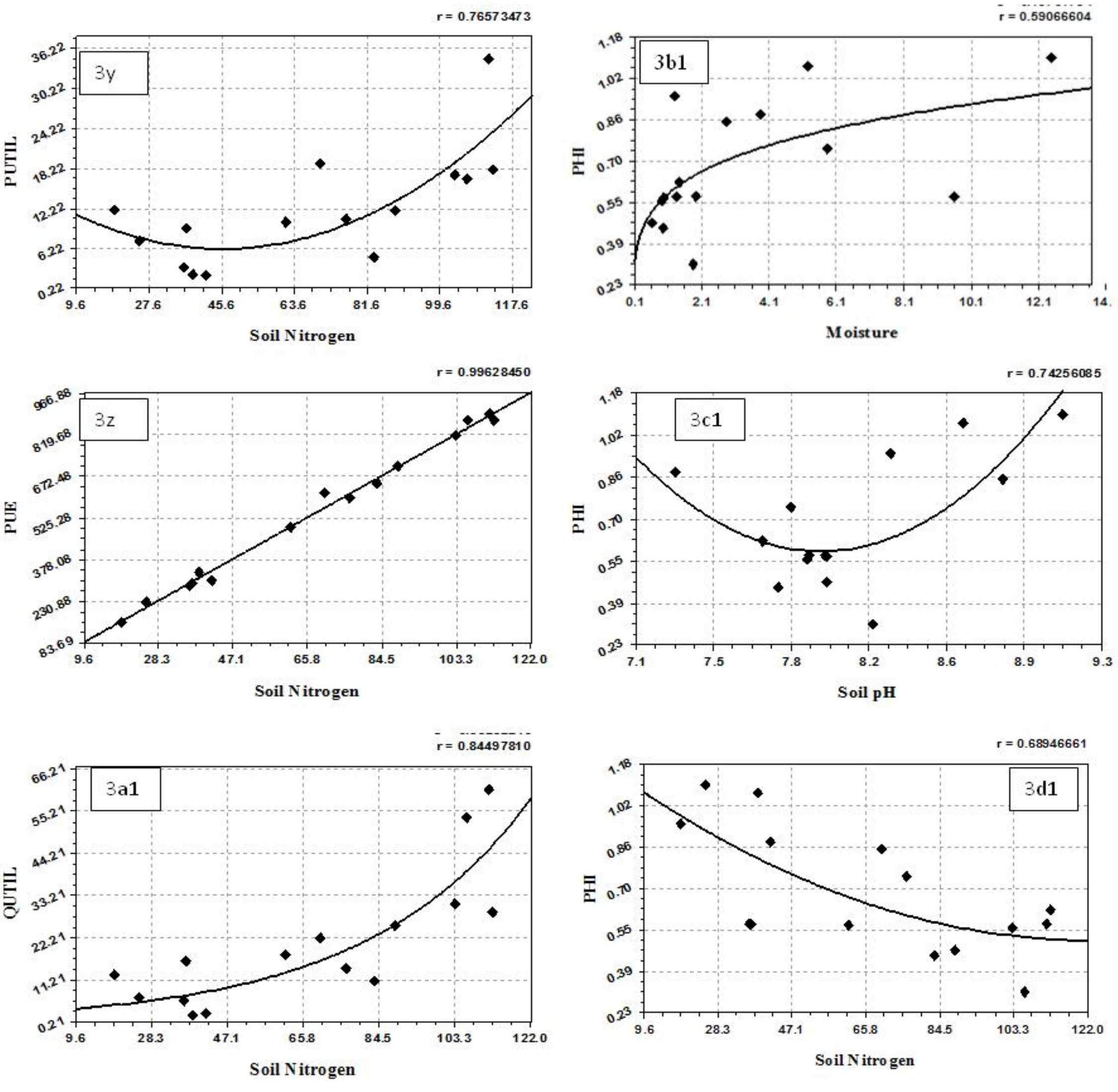
***Figures 3q to 3x**. Relationships between various P variables and community parameters*

Both P internal utilization and PUE of *C. depressus* are largely influenced by temporal factors (increase and decrease of community diversity during pulse and non-pulse events, respectively) and it also indicates the adjustments made by the species for their PUE and PUTIL according to their resources availability. Thus this species achieved its effective nutrient use through temporal partitioning, through which it full-fill its P requirements at low resource availability and that is ultimately reflected through its dominance (RIV) in community. Identification of such species are crucial for habitat stability, especially in rehabilitation programmes as supported by the findings of Aronson *et al.,* (1993) and Wortman *et al.,* (2012).

Regarding PHI, dominance of this species in community do not allow to allocate more P in seed, while as the community diversity increases plant switched on their P allocation in seed. This strategy could be the main approach to compete with their associates and this statement can be support by the findings of Nadeem *et al.,* (2011a, b) and White and Veneklaas, (2012) who reported that seed P is the only P source available to sustain the initial establishment and subsequent growth of seedling.

P Variables and Soil Factors

Soil nitrogen supports PUTIL (PUTIL = 14.341+-0.359 Soil Nitrogen+0.0039 Soil Nitrogen^^{2}, R^2 = 0.76**, *Fig.3y*), PUE (PUE = 13.05+7.844 Soil Nitrogen, R^2 = 0.996**, *Fig.3z*) and QUTIL (QUTIL = 2.897e^ (0.024 Soil Nitrogen), R^2 = 0.84**, *Fig.3a1*) in polynomial, linear and exponential fashion, respectively.



Figures 3y to 3d1. *Relationships between various P variables and soil parameters*

On the other hand both soil moisture and soil pH support PHI in power (PHI = 0.5729 Moisture^0.2062, R^2 = 0.59*, *Fig.3b1*) and polynomial (PHI = 32.656+-8.036 Soil pH+0.503 Soil pH$^{\wedge 2}$, R^2 = 0.74**, *Fig.3c1*) fashion, respectively. However, soil nitrogen inhibits PHI in polynomial pathway (PHI = 1.169+-0.0108+Soil Nitrogen+4.440 Soil Nitrogen$^{\wedge 2}$, R^2 = 0.68**, *Fig.3d1*).

Soil moisture and soil pH were recorded higher during the pulse event and that also related with bio-availability with soil P. During the high resource availability this species invests more P in seed compared to other plant modules. These results are in close agreement with those reported by George *et al.,* (2005). Due to increment in of plant growth, the P requirement is expected to increase. It may be a reason to get more PUTIL and PUE to meet the plant requirement when N availability and uptake enhances. Sanginga *et al.,* (2000) and Gao (2009) also reported higher relation of PUTIL and PUE with soil N in two different lines of cowpea.

Conclusion

Nutrient use efficiency at ecosystem level revealed that NUE increases with richness of species or life forms in a community. However this relation at species level has not been worked out, particularly in arid areas where resources are released in pulses. Present study shows that at species level dominance of *C. depressus* reflects with its higher P acquisition efficiency; however as the community diversity increases the P internal utilization and PUE are inhibited. Conclusively, dominance of this species inhibits the allocation of P in seed, in contrast as the community diversity increases this species switched on their P allocation in seed. This mechanism could be associated with its initial establishment and subsequent growth.

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