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Phosphorus nutrition of oats genotypes in acidic soils: Exploiting responsive plant-microbe partnership

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ABSTRACT

Genotype-microbes interactions in rhizosphere can be a promising approach to improve P nutrition of crop plants in acidic soils. This study explored the response of contrasting oat genotypes to the conjunctive application of microbial consortia and differently soluble phosphatic fertilizers. Effect of microbial consortia [vesicular arbuscular mycorrhiza (VAM), *Azotobacter chroococum*, *Aspergillus niger*, and *Pseudomonas* sp.] with tri-calcium phosphate or potassium di-hydrogen phosphate on the P nutrition of oat genotypes (Kent and JHO-851) was evaluated in controlled condition. Microbial consortia alone or in conjunction with 50% recommended dose of P fertilizers significantly increased the forage yield and P uptake. Kent was more responsive compared with JHO-851 to consortia and P fertilization. Plant P content in Kent genotypes showed strong correlation with microbial biomass carbon (MBC), nitrogen (MBN), acid and alkaline phosphatases activities, Bray's P and actinobacteria population in soils. Forage yield and P uptake response was similar with tri-calcium phosphate and potassium di-hydrogen phosphate. Root biomass, MBN and Bray's P contributed for 90% variability in P uptake. Results advocated that responsive oat genotype and microbial consortia with 50% recommended P fertilizers dose or tri-calcium phosphate can be a low-cost option for efficient P nutrition in acidic soils.

1. Introduction

Oats (*Avena sativa* L.) are the sixth most important crop of the world after wheat, maize, rice, barley and sorghum (Pandey and Roy, 2011). It is well adapted to marginal ecologies (Holland et al., 2019; Zwer, 2016) and mainly cultivated in countries of the northern hemisphere including the Himalaya-Hindukush region. The annual world production of oat is nearly 22.2 million Mt (USDA, 2020). In Asia, the crop was introduced from Canada, Europe and New Zealand (Stevens et al., 2004). Oat is a multi-purpose crop grown for human and livestock consumption (Boczkowska et al., 2016). Its green biomass is used for fodder or making hay and silage for feeding livestock (Pandey and Roy, 2011).

Oat is the most important cereal fodder crop of the winter season in north-western, central and eastern India. Although, oat is cultivated on marginal land characterized by low nutrient supply, its productivity is further limited in acidic soils, predominant in the eastern, north-eastern and Himalayan regions of India, because of nutrient deficiency and/or Al and Fe toxicity. Among the deficient nutrients, low phosphorus (P) availability is the major cause of concern for soil productivity in these regions (Badole et al., 2015). Acidic soils usually have high total P but its concentration in soil solution is often less than 1.0 μM which is inadequate for the plants and soil organisms (Tomar, 2000). Efficiency of P fertilizers in acidic soils is low because of its adsorption and precipitation as Al—P and Fe—P (de Oliveira et al., 2020; Kaleem Abbasi and Manzoor, 2018; Mitran et al., 2016). Frequent application of high dose of phosphatic fertilizers results in an increase in cost of cultivation and build-up of phosphates with a potential threat of soil and water pollution (Andersen et al., 2017; Liu et al., 2020). The P management in acidic soils using fertilizers alone is also unsustainable because of high cost of phosphatic fertilizers, its low use efficiency and a finite natural reserve

Abbreviations: VAM, vesicular arbuscular mycorrhiza; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; AcP, acid phosphatase; AlK, alkaline phosphatase; $Ca_3(PO_4)_2$, tri-calcium phosphate; KH_2PO_4, potassium di-hydrogen phosphate; PCA, principal component analysis; CFU, Colony Forming Units.

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of apatite (Dodd and Sharpley, 2015). Limited availability of P fertilizers in many parts of the world also raises concern of P nutrition (Cordell et al., 2009).

It is essential to devise an alternate strategy of nutrient management for producing good yield using minimum quantity of chemical fertilizers (Bindraban et al., 2020; Macintosh et al., 2019; Wu et al., 2020). Key to successful cultivation in acidic soils lies with exploiting beneficial rhizosphere interactions of crop and helpful soil microbes, such as vesicular arbuscular mycorrhizal (VAM) fungi, other P solubilizing and nitrogen fixing microorganisms with different P sources (Briat et al., 2020; Cobb et al., 2016; Estrada-Bonilla et al., 2020; Martínez-Hidalgo and Hirsch, 2017). Mycorrhizal plants have a higher capacity for acquisition of P and other nutrients under water stress and soils of high P fixation capacity (Arihara and Karasawa, 2000; Ranoarisoa et al., 2020). Once grown successfully, VAM fungal hypha associated with plant roots facilitate an extension of rhizospheric effect and thus cause an increased access to growth-limiting resources (Smith et al., 2018). Phosphate solubilizers and N fixers gain the benefit of proto-cooperation by promoting the availability of the growth limiting nutrients by solubilization of native phosphate minerals and N fixation, respectively (Wu et al., 2005; Yu et al., 2012).

It has long been recognized that roots of different species of plant have different capacities to absorb nutrients from soil in which they grow (Briat et al., 2020). Low P tolerant genotypes of different crops have capacity to utilize low soluble phosphate fractions of soil for P nutrition (Cong et al., 2020; Marschner et al., 2007). The high P acquisition capacity in some genotypes from low P soils was due to vigorous rooting, excretion of phosphatases, organic acids, or other compounds for releasing P locked with native insoluble P compounds and forging mutualistic partnership with soil biota (Campos et al., 2018; Cobb et al., 2016; Lyu et al., 2016). In fact, relationship between P uptake by plants and their phosphatase activities in rhizosphere is common (Asmar et al., 1995; Lyu et al., 2016; Tarafdar and Claassen, 1988). Thus, selecting crop genotypes with capacity for acquiring insoluble P compounds and manipulating rhizosphere communities with beneficial microbial consortium can be a promising approach to improve P nutrition of crop plants in acidic soils. The relative profusion of C, N and P under such mutualistic association can substantially influence the nutrient cycling and also C:N:P stoichiometry of plant and microbes growing in acidic soils (Yuan et al., 2019). Examining the crop genotypes for difference in benefits gained from rhizosphere interaction will help in understanding the nature of the association for increased P use efficiency (Cobb et al., 2016).

Oat cultivars responded differently to Al—P, Fe—P and Ca—P in acidic soils (Rai et al., 2009). Therefore, we hypothesized that integrated application of P fertilizers, microbial consortia with responsive genotype is more efficient than individual component for improving P nutrition in acidic soils. With this view point, the present study was carried out using two oat genotypes having contrasting growth habit, breeding background, and response to native P. The primary objectives of this study were: (1) to assess the response of two oat genotypes to microbial consortia in low P soils amended with water soluble and insoluble P sources; and (2) to assess the effect of plant-microbial consortia interaction under different P levels on forage yield and soil biological properties of acidic soil where the crop was grown.

2. Materials and methods

2.1. Microbial inoculants

An efficient nitrogen fixer, *Azotobacter chroococcum* (MTCC 25045), isolated from the rhizosphere of wheat, a widely available phosphate solubilizing fungi, *Aspergillus niger* (ITCC 6719) isolated from the rhizosphere of soybean, and a phosphatic nodules solubilizing bacterial strain, *Pseudomonas sp.* (NCIM 2847) isolated from the fields of ICAR-Indian Agriculture Research Institute (IARI), New Delhi were used in the present study. The vesicular-arbuscular mycorrhizal (VAM) fungus, *Glomus* sps. isolated from the rhizosphere of maize grown in the fields of IARI was also used to increase soil phosphate mobilization to the host plant. *Pseudomonas* sps. was grown at 30 ± 2 °C for 48 h on nutrient agar plates consisting of (g L^{-1}) peptone, 5.0; yeast extract, 2.0; sodium chloride, 5.0; agar, 15.0; dH_2O 1 L adjusted to pH 7.0 ± 0.2. While *A. chroococcum* were grown at 28 ± 2 °C for 4 days on Ashby's Mannitol Agar consisting of (g L^{-1}) mannitol, 20.0; di-potassium phosphate, 0.2; magnesium sulphate, 0.2; sodium chloride, 0.2; potassium sulphate, 0.1; calcium carbonate, 5.0; agar, 15.0; dH_2O 1 L adjusted to pH 7.4 ± 0.2. Similarly, *A. niger* was grown at 28 ± 2°C for 2 days on Potato dextrose broth (39.0 g L^{-1} dH_2O; pH: 5.6 ± 0.2). These microbial inoculums were maintained in their respective growth medium slants and were stored for short term at 4 °C; on the other hand, for the medium term, the glycerol stocks of bacterial and fungal spore suspensions (in 10%, *v*/v glycerol) were stored at −20°C. The soil-based VAM inoculum containing spores (20 spores g^{-1} soil), fragments of mycorrhizal fungal filaments and infected roots bits were stored in polythene bags at 4°C. Spore populations were counted using wet sieving method (Al-Raddad, 1995).

2.2. Compatibility test of different microbial strains

Compatibility among the *A. chroococcum, Pseudomonas* sp. and *A. niger* were verified by the plate cross streak method (Fitriatin and Nurmala, 2019). Criss-cross streaking was carried out on freshly prepared nutrient agar medium. Firstly, *A. niger* was seeded on the nutrient agar plate and allowed to grow for 24 h at 28 ± 2 °C; thereafter, *A. chroococcum* and *Pseudomonas* sp. were streaked perpendicularly to make a square with *A. niger* colonies in the centre. Plates were examined every 24 h interval for the appearance of inhibition zones at the intersection of the paired strains (Plate 1).

2.3. Development of microbial consortia

Bacterial cultures grown for forty-eight hours were suspended in 20 mM sodium phosphate and 150 mM NaCl buffered at pH 7.0. These cultures were pelleted by centrifugation (10,000 ×*g* for 10 min) and re-suspended in phosphate buffer to a final count of 1×10^9 CFU mL^{-1}. Spore suspension inoculum of *A. niger* (1×10^9 spores mL^{-1}) was prepared by washing the 5-day old fungal culture grown on potato dextrose agar. Spores of *A. niger* were counted using a haemocytometer under a microscope and suspension of 1×10^9 spores mL^{-1} was prepared (Wang et al., 2015). Finely ground sterilized charcoal and soil passed through 150 and 200 meshes sieve, respectively, and then mixed in 1:1 ratio was used as a carrier. The 10 mL of cell suspension of each microbe was thoroughly mixed with 100 g carrier. The moisture content was maintained at 40% and incubated at 28 ± 2 °C for one week. A microbial consortium was prepared by mixing the equal proportion of charcoal-soil based inoculum and VAM culture before coating the seed.

2.4. Oat genotypes

Two oat genotypes, Kent and JHO-851 were selected to study their responsiveness to the consortia inoculation for a low phosphorus acidic soil amended with different phosphate sources. The selected genotypes were of contrasting growth habits and breeding background (Pandey and Roy, 2011). Kent is an erect type, single cut cultivar with long droopy leaves. It was introduced from the USA and released in 1975 for cultivation across India. While, JHO-851 is a multi-cut cultivar with a prostrate growth habit but becomes erect after tillering. It was released through selection from exotic Japanese germplasm "Hiugo Karyokuro" in 1998. In our earlier study, both the cultivars showed a wide range of responses to native soil P (Rai et al., 2009).

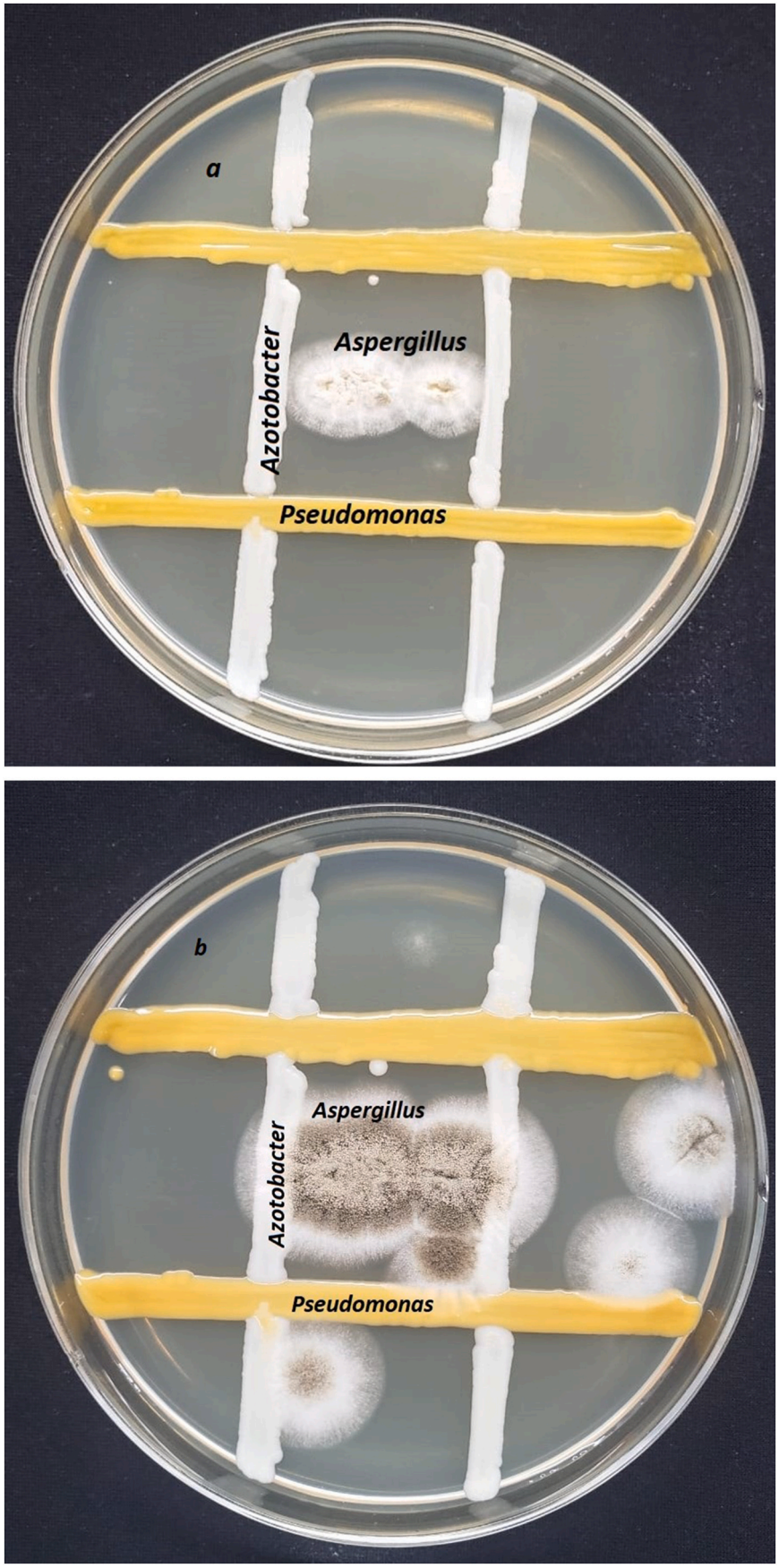

Plate 1. Compatibility test of microbial inoculums; photograph at 48 h (a) and 72 h (b) after the inoculation; without any inhibition.

2.5. Pot experiment

A pot experiment was conducted in the net house of ICAR-Indian Grassland and Fodder Research Institute (ICAR-IGFRI), Jhansi, India. The experimental site is located in the semi-arid, continental and monsoonic climate (25°27′ N, 78°35′ E, at 271 m mean sea level). The meteorological data for the experimental site during the cropping season (October to April) is presented in Fig. 1. The soil used for the study was collected from 0 to 15 cm soil depth of a terraced field of Regional Research Station, ICAR-IGFRI, Palampur, Himachal Pradesh (32°07′ - 32.12° N, 76°32′ - 76.53° E, 1220 m mean sea level). The site was uncultivated fallow, but vegetated with *Chrysopogon echinolatus, Heteropogon contortus* and *Cynodon dactylon*. The collected soil samples were analyzed for physico-chemical properties at the start of the experiment (Jackson, 1973, Table 1). Ten kg portion of the air dried and pulverized soil samples was placed in thirty six numbers of plastic pots and laid out in a randomized block design with three replications for the experiment. The details of the treatments imposed including combinations of the consortia, sources of phosphorus, doses of P and lime were given in Table 2. Urea and potassium sulfate were used as the sources of N and K at the rates of 100 and 50 mg kg^{-1} soil, respectively; wherever required the dose of K through K_2SO_4 was adjusted because of the use of KH_2PO_4 as a source of P. Oats seed were surface sterilized for 5 min with 1% sodium hypochlorite solution and washed 5 times with sterilized distilled water. Surface sterilized seeds were then coated with a slurry of microbial consortium and carboxymethyl cellulose [CMC, 1% (*w/v*)] as binding agent (Hameeda et al., 2008). Briefly, 100 g seeds were coated with slurry of the microbial consortium prepared by mixing 20 g each of charcoal-soil based inoculum, and VAM culture with 40 mL CMC. The non-treated seeds were used as control. About 6–7 seeds were sown in each pot; after germination, keeping three, the excess plants were uprooted. Deionized water was used for irrigating the pots as and when needed. Crop was free from disease and insect pests and phytosanitary measures were not required.

Crop was harvested for biomass production at 95 and 110 days after sowing coincided with 50% flowering stage of Kent and JHO-851 genotypes, respectively. After harvesting of the above-ground biomass, roots were collected on a sieve for washing off the adhered soil using water jet. Both the roots and shoot of the three plants per pot, after washing through deionized water, were oven dried at 60 °C, and their dry-weight was recorded. For determining P concentration and its uptake by plants, the oven-dried samples were ground to pass through a one mm sieve and digested with di-acid digestion ($HClO_4$ and H_2SO_4 in 10:4 ratio). Phosphorus in the digest was estimated following ascorbic acid blue colour method (Jackson, 1973). The response of the consortia

Table 1
Initial physicochemical properties of the soil used for pot experiment.

Soil properties	Mean ± standard errors (n = 3)
$pH_{1:2}$	5.5 ± 0.2
$EC_{1:2}$ (dS m^{-1})	0.09 ± 0.01
Walkley and Black organic carbon (g kg^{-1})	11.4 ± 0.1
$KMnO_4$ oxidizable N (kg ha^{-1})	421.2 ± 7.9
Bray's P (kg ha^{-1})	10.1 ± 1.5
NH_4OAc extractable K (kg ha^{-1})	128.5 ± 10.6
Lime requirement (Mg ha^{-1})	7.2 ± 0.3
Sand (%)	50 ± 2.8
Silt (%)	29.5 ± 1.2
Clay (%)	20.5 ± 1.6
Texture	Sandy loam
Classification (U.S. Soil Taxonomy)	*Typic Haplustepts*

Table 2
Microbial consortium and P fertilizer treatments.

Treatments code	Treatments detail
Control	Without P fertilizer, liming and consortium application[a]
IP0	Consortium inoculation without application of fertilizer phosphorus[b]
IP1	Consortium application, with application of fertilizer phosphorus in the soluble form (KH_2PO_4) at a rate of 10 mg kg^{-1})
IP2	Consortium application, with application of fertilizer phosphorus in the soluble form (KH_2PO_4) at a rate of 20 mg kg^{-1})
IPCa	Consortium application, with application of fertilizer phosphorus in the slightly soluble form [$Ca_3(PO_4)_2$] at a rate of 20 mg kg^{-1})
LP2	Consortium application fertilizing with the recommended dose in this type of soil [soluble form (KH_2PO_4) at a rate of 20 mg kg^{-1}] and liming at the rate of 10% of lime requirement[c]

[a] Absolute control representing natural condition in the soil.

[b] Representing potential of microbial consortium interacting with natural P reserves.

[c] Positive control representing ideal management practices for P fertilization and to ameliorate the soil acidity associated problem.

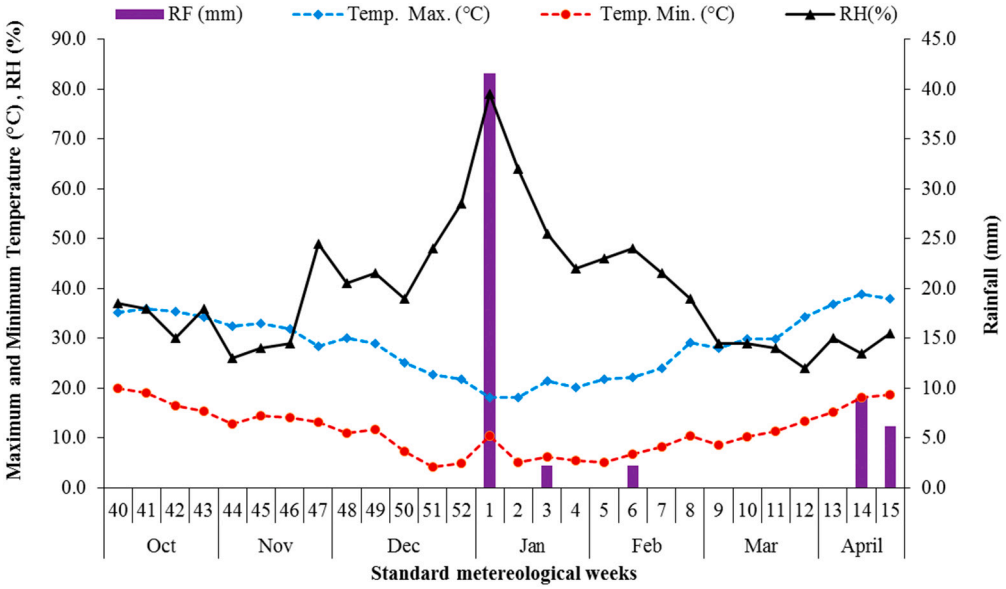

Fig. 1. Mmeteorological data of the experimental site during the cropping season (October to April).

alone (Consortia response %) or in conjunction with P fertilizers (Conjunctive P fertilizer response %) was calculated separately for oats genotypes (Kent and JHO-851) using P-uptake data (Cobb et al., 2016).

$$Conjunctive\ P\ fertilizer\ response\ (\%) = \left[\frac{P\ uptake\ in\ the\ consortia\ with\ P\ fertilized\ plant - P\ uptake\ in\ uninoculated\ and\ unfertilized\ plant}{P\ uptake\ in\ the\ consortia\ with\ P\ fertilized\ plant}\right] \times 100$$

$$Consotia\ response\ (\%) = \left[\frac{P\ uptake\ in\ the\ consortia\ inoculated\ plant - P\ uptake\ in\ uninoculated\ plant}{P\ uptake\ in\ the\ consortia\ inoculated\ plant}\right] \times 100$$

2.6. Soil analysis

After harvesting, the rhizosphere soils, adhering to the roots, were removed aseptically with sterilized brush and stored at <4°C for analysis of microbiological parameters. Another set of bulk soil was also collected removing visible roots, air dried and passed through a two mm sieve for analysis of pH, organic carbon and Bray's phosphorus (Jackson, 1973). Soil samples stored at <4°C were analyzed for dehydrogenase activity (Dick et al., 1997), mineralizable C (Anderson, 1982), acid (AcP, pH 6.5) and alkaline (AlP, pH 11.0) phosphatases activities (Dick et al., 1997)' and microbial biomass C and N (MBC, MBN) (Vance et al. (1987). C-flush was converted to MBC by using the relationship: MBC $= \left[\frac{1}{0.41}\right] \times$ C flush (Voroney and Paul, 1984), while N-flush was converted to MBN by dividing with a calibration factor of 0.38 (Brookes et al., 1985).

2.7. Culturable microbial population

Culturable microbial communities in the rhizosphere soils were evaluated by examining microbial populations and *r/K* bacterial strategists by serial dilution method (Chandra et al., 2020). For bacterial growth strategists and total population count, tryptone soy agar (tryptone, 15.0 g; soya peptone, 5.0 g; sodium chloride, 5.0 g; agar, 15.0 g in 1 L deionized water adjusted at pH 7.3 ± 0.2) was used (Zuberer, 1994). Czapek-Dox (sucrose, 30 g; sodium nitrate, 2.0 g; di-potassium phosphate, 1.0 g; magnesium sulphate, 0.5 g; potassium chloride, 0.5 g; ferrous sulphate, 0.01 g; agar,: 15.0 g in 1 L deionized water at pH 7.3 ± 0.2) and actinobacterial isolation agar (sodium caseinate, 2.0 g; L-asparagine, 0.1 g; sodium propionate, 4.0 g; di-potassium phosphate, 0.5 g; magnesium sulphate, 0.1 g; ferrous sulphate, 0.001 g; agar, 15.0 g in 1 L deionized water at pH 8.1 ± 0.2) of Himedia® was used for enumeration of culturable fungal and actinobacterial populations, respectively. The collected soils of each treatment were serially diluted and one mL of soil suspension each from 10^{-5} to 10^{-8} dilutions were poured on respective media filled plate in triplicate. Petri plates were then incubated at 28 ± 2 °C. Bacterial colonies appearing within 24 h were labelled as *r*-strategists, and the remaining as *K*-strategists (De Leiij et al., 1993). Fungal and actinobacterial colonies were counted after 3–4 and 6–7 days, respectively. Results were expressed in Colony Forming Units (CFUs) per gram of soil sample.

2.8. Statistical analysis

Statistical analysis of the data was performed using SAS 9.3. Shapiro Wilk and Bartlett tests were used to check the normality and heterogeneity of the database, respectively. Microbial counts data were log transformed before the analysis of variance. Analysis of variance (ANOVA) was carried out to determine the statistical significance of treatment effects. Tukey's test was used for pairwise comparison of response variables ($P < 0.05$). Further, separate principal component analysis (PCA) was performed for JHO-851 and Kent genotypes using soil properties and plant growth parameters. Pearson correlation coefficients and stepwise regression equations were computed to evaluate

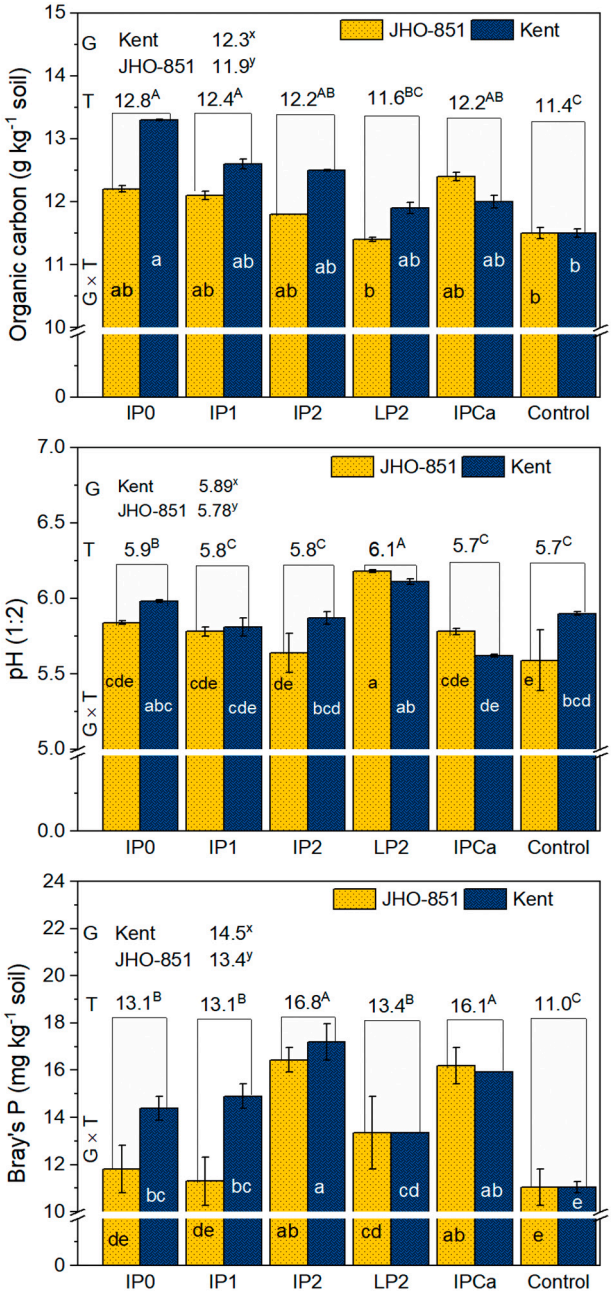

Fig. 2. Effects of genotype (G), phosphorus and microbial consortium treatments (T) and their interaction on soil pH, Bray's P and organic C; capped lines on bars are standard deviation; $n = 3$, 6 and 18 for G × T, T and G, respectively; numbers and bars followed by different letters (A-C; a-e and x-y) are significantly different ($P < 0.05$).

the relationships among the response variables.

3. Results

3.1. Soil chemical properties

Of the two genotypes, pH, and contents of organic C and Bray's P were higher in soils under Kent than those under JHO-851 (Fig. 2). On average, all the treatments recorded a higher pH value than the control. Bray's P content was highest in soils under IP2 (16.8 mg kg^{-1}) followed by that under IPCa (16.1 mg kg^{-1}) and LP2 (13.4 mg kg^{-1}). Its content, in general, was higher in soils with Kent than with JHO-851 genotypes, and the differences were greater with lower P and in consortia alone (IP0). Organic C content of soils was higher with the treatments, excepting LP2, than the control (Fig. 2).

3.2. Microbial biomass C and N, mineralizable C and soil enzymes

Microbial biomass C, N (MBC, MBN) and dehydrogenase (DHA), acid phosphatase (AcP) and alkaline phosphatase (AlP) activities in soils differed significantly, and on average, their values were higher with Kent than those with JHO-851 ($P < 0.05$) genotypes. However, such values for mineralizable C hardly varied between the genotypes (Fig. 3). Among the treatments, LP2, IP2, and IP1 had higher values for MBC indicating that its values were higher with supply of water-soluble P compared to water insoluble tri-calcium phosphate (IPCa), and with conjunctive P fertilizer than the consortia alone (IP0). The IP2 and LP2

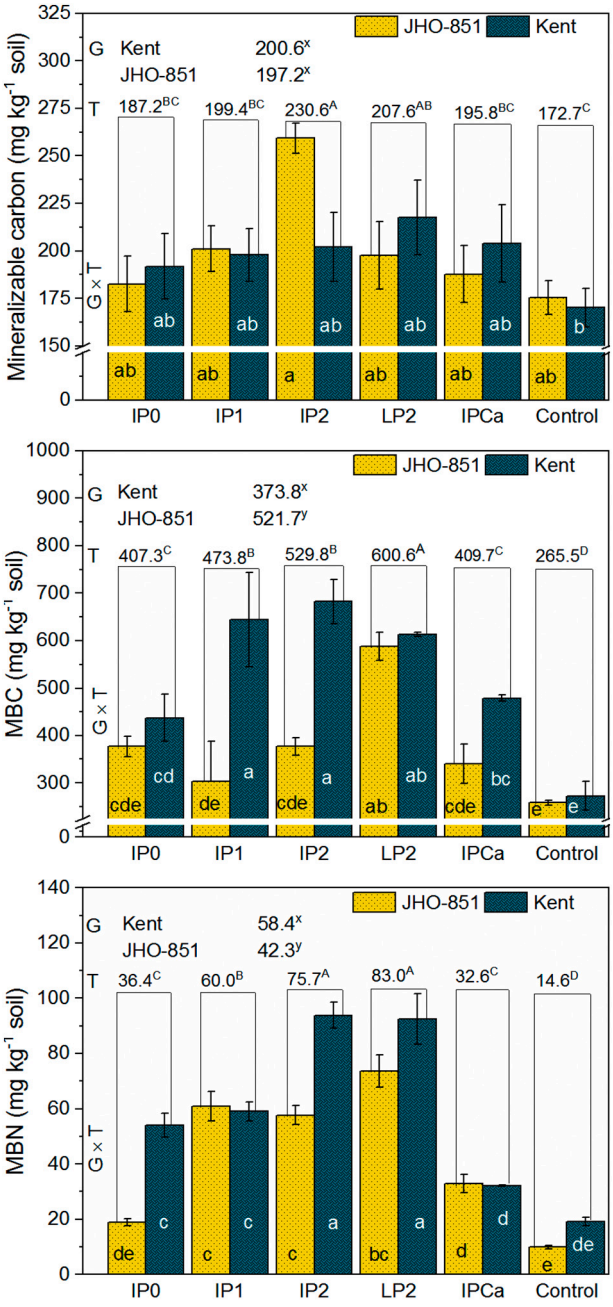

Fig. 3. Effects of genotype (G), phosphorus and microbial consortium treatments (T) and their interaction on mineralizable carbon, microbial biomass C and N in soils; capped lines on bars are standard deviation; n = 3, 6 and 18 for G × T, T and G, respectively; numbers and bars followed by different letters (A-D; a-e and x-y) are significantly different ($P < 0.05$).

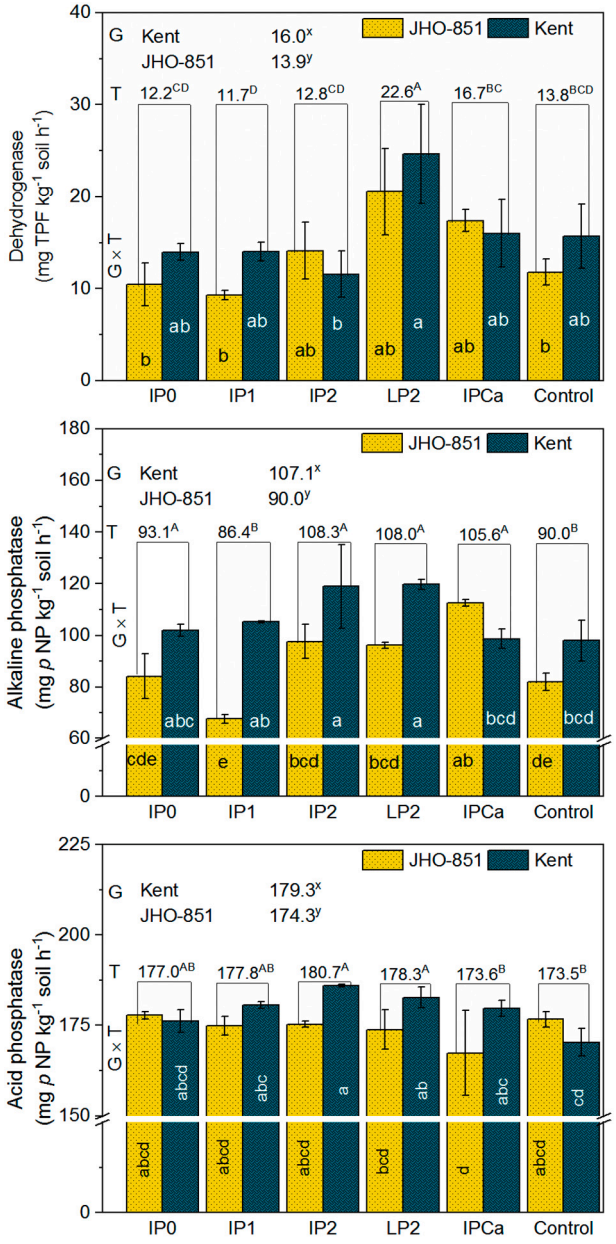

Fig. 4. Effects of genotype (G), phosphorus and microbial consortium treatments (T) and their interaction on soil enzymes; capped lines on bars are standard deviation; n = 3, 6 and 18 for G × T, T and G, respectively; numbers and bars followed by different letters (A-D; a-e and x-y) are significantly different ($P < 0.05$).

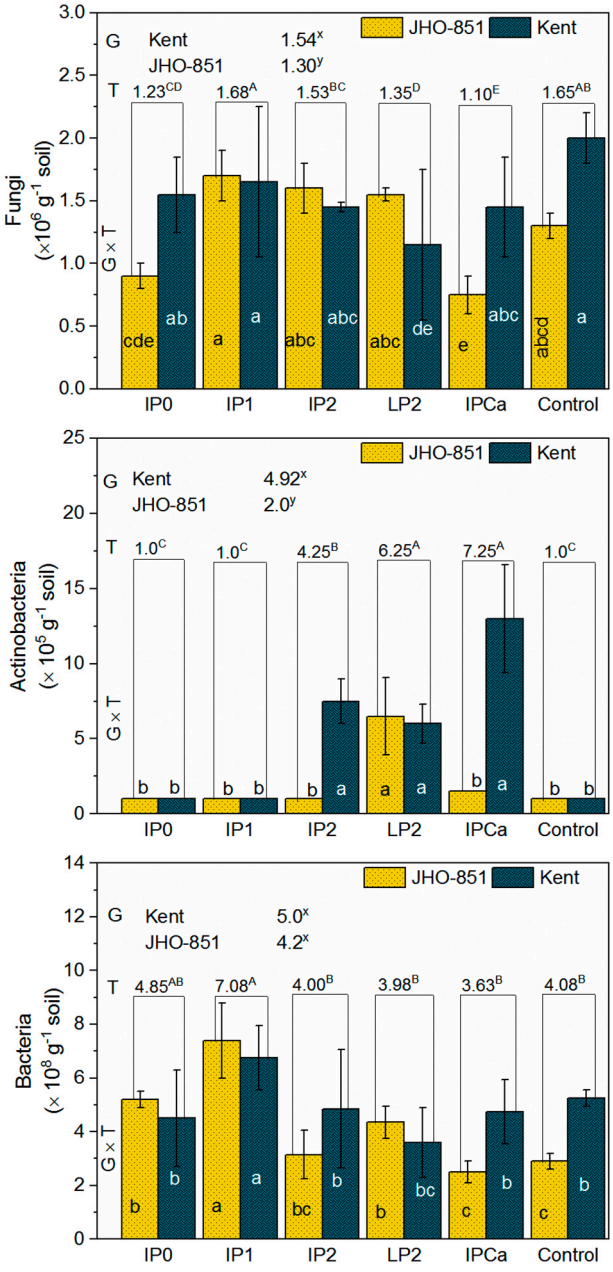

Fig. 5. Effects of genotype (G), phosphorus and microbial consortium treatments (T) and their interaction on culturable microbial populations; capped lines on bars are standard deviation; n = 3, 6 and 18 for G × T, T and G, respectively; numbers and bars followed by different letters (A-E; a-e and x-y) are significantly different ($P < 0.05$).

fertilized soil under Kent had greater MBN compared to the same under JHO-851. Similarly, mineralizable carbon in soils with LP2 was also higher under Kent. Again, liming caused a significant increase in DHA (Fig. 4); while phosphatase activity (except IP1 for AlP and IPCa for AcP) were higher with all the treatments over the control.

3.3. Microbial population

There was a higher population of fungi, actinobacteria and *r*-strategist bacteria in soils under Kent compared to those in soils under JHO-851 ($P \leq 0.05$; Figs. 5 and 6). Out of the studied organisms, *K*-strategists were dominant over others and constituted about 86–90% of bacterial population in soils under both the genotypes. Of the treatments, LP2 and IPCa favored the growth of *r*-strategist bacteria and

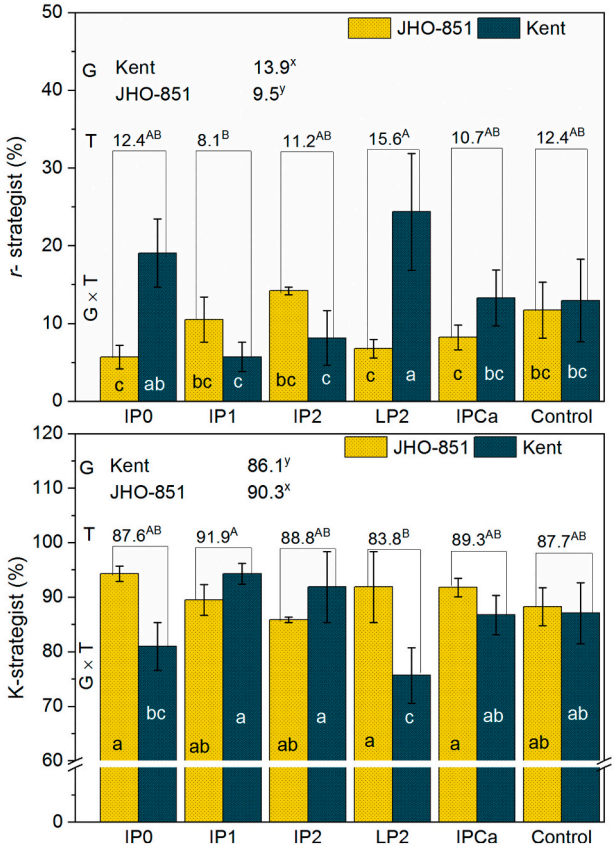

Fig. 6. Effects of genotype (G), phosphorus and microbial consortium treatments (T) and their interaction on *r*- and *K*-strategists population; capped lines on bars are standard deviation; n = 3, 6 and 18 for G × T, T and G, respectively; numbers and bars followed by different letters (A-B; a-c and x-y) are significantly different ($P < 0.05$).

actinobacteria, respectively.

3.4. Crop yield and P uptake

Of the two genotypes, Kent had higher shoot and root biomass compared to JHO-851, and responded more to the consortia and conjunctive P fertilization. Among the treatments, conjunctive P fertilization (IP1, IP2 and IPCa) was more effective than IP0 and control ($P < 0.05$) (Table 3), particularly for Kent; however, such responses both for shoot and root were at par among IP1, IPCa, IP2 and LP2 treatments, excepting a few. The genotype × treatment interaction was significant for root biomass of Kent. The P uptake was higher by Kent than JHO-851 ($P < 0.05$) (Table 4). Among the treatments, P uptake was highest in LP2 followed by IPCa, IP2 and IP1, and the effect was more pronounced for Kent than JHO-851 (Table 5).

Principal component analysis (PCA) was performed to find out the effects of consortia inoculation and P fertilization on soil properties and plant P content (Fig. 7; Supplementary Table 1). For Kent, the first two PC axes accounted 55.9% variability and the treatments IP1, IP2 and LP2 were clustered closely in one quadrant, while control and IP0 clustered in opposite quadrants. While for JHO-851, the first two PC axes accounted for 48.7% of the variability, and soil properties and plant P content under different treatments were clearly separated and only IP2 and IPCa were clustered together in fourth quadrant. The *r*-strategist population was separated from the *K*-strategist population for both the genotypes. Besides, both MBC and AlP showed a unique separation as it laid on those quadrants which gave a strong response to soil biological activities and soil P availability. In both genotypes, organic C and Bray's P showed different spatial distribution along the coordinate axes.

Table 3
Effects of genotype (G), phosphorus and microbial consortium treatments (T) and their interactions on biomass yield (g pot^{-1}) of oat genotypes in acidic soils.

Treatments	Green biomass of aerial parts			Dry biomass of aerial part			Root dry weight		
	G × T		T	G × T		T	G × T		T
	Kent	JHO-851		Kent	JHO-851		Kent	JHO-851	
Control	82.6 ± 8.7^{D}	47.5 ± 2.7^{F}	65.1 ± 20.1^{d}	18.9 ± 2.0^{C}	11.2 ± 0.6^{D}	15.1 ± 4.4^{d}	9.2 ± 1.2^{CD}	6.4 ± 0.5^{E}	7.8 ± 1.8^{c}
IP0	113.9 ± 3.4^{C}	50.3 ± 5.0^{EF}	82.1 ± 35.0^{c}	25.5 ± 0.8^{B}	12.3 ± 1.2^{D}	18.9 ± 7.2^{c}	11.2 ± 0.2^{BC}	6.3 ± 0.7^{E}	8.8 ± 2.7^{bc}
IP1	161.6 ± 9.7^{B}	62.5 ± 9.4^{DEF}	112.05 ± 54.9^{b}	35.2 ± 2.1^{A}	15.0 ± 2.3^{CD}	25.1 ± 11.2^{b}	11.9 ± 0.2^{AB}	5.8 ± 0.9^{DE}	8.9 ± 3.2^{b}
IP2	148.9 ± 11.1^{AB}	68.1 ± 8.3^{DE}	108.5 ± 46.5^{b}	33.5 ± 4.7^{A}	14.0 ± 2.4^{CD}	23.8 ± 11.1^{b}	13.4 ± 2.1^{BC}	7.3 ± 0.6^{D}	10.4 ± 3.3^{a}
LP2	176.3 ± 6.2^{A}	84.1 ± 7.8^{D}	130.2 ± 51.2^{a}	36.6 ± 0.4^{A}	19.9 ± 1.8^{BC}	28.3 ± 9.9^{a}	11.6 ± 0.2^{AB}	5.8 ± 0.9^{DE}	8.7 ± 3.2^{bc}
IPCa	173.8 ± 1.9^{AB}	77.1 ± 14.5^{DEF}	125.5 ± 53.4^{a}	37.7 ± 1.3^{A}	15.8 ± 3.0^{CD}	26.8 ± 11.5^{b}	13.2 ± 0.8^{A}	7.3 ± 0.6^{D}	10.3 ± 5.5^{ab}
G	143.0 ± 36.1^{x}	65.0 ± 15.5^{y}		31.3 ± 7.3^{x}	14.7 ± 3.3^{y}		12.42 ± 2.3^{x}	6.40 ± 0.9^{y}	
CV (%)			8.9			9.0			9.5

±standard deviation; n = 3, 6 and 18 for G × T, T and G, respectively; numbers followed by different letters in the columns (A-F; a-d) and row (x-y) are significantly different ($P < 0.05$).

Table 4
Effects of genotype (G), phosphorus and microbial consortium treatments (T) and their interactions on P content and uptake by oat genotypes in acidic soils.

Treatments	P content (mg g^{-1})			P uptake (mg pot^{-1})		
	G × T		T	G × T		T
	Kent	JHO-851		Kent	JHO-851	Mean
Control	0.20 ± 0.02^{C}	0.19 ± 0.01^{D}	0.19 ± 0.02c	37.9 ± 6.7^{DE}	21.7 ± 0.8^{F}	29.8 ± 9.8^{d}
IP0	0.21 ± 0.01^{BCD}	0.23 ± 0.03^{AB}	0.22 ± 0.02^{bc}	53.2 ± 3.4^{C}	27.9 ± 2.3^{FE}	40.6 ± 14.0^{c}
IP1	0.22 ± 0.02^{AB}	0.24 ± 0.03^{A}	0.23 ± 0.02^{b}	79.6 ± 12.3^{AB}	36.2 ± 7.2^{DE}	57.9 ± 25.4^{b}
IP2	0.23 ± 0.02^{A}	0.24 ± 0.01 ^{A}	0.24 ± 0.04^{a}	76.8 ± 12.4^{B}	33.8 ± 5.0^{DE}	55.3 ± 25.1^{b}
LP2	0.24 ± 0.01^{A}	0.24 ± 0.02 ^{A}	0.24 ± 0.03^{a}	91.8 ± 15.3^{A}	49.1 ± 1.6^{CD}	70.5 ± 25.3^{a}
IPCa	0.24 ± 0.04^{A}	0.25 ± 0.02^{A}	0.24 ± 0.03^{a}	88.9 ± 18.7^{AB}	38.0 ± 3.5^{DE}	63.5 ± 30 3^{ab}
G	0.22 ± 0.03^{y}	0.23 ± 0.03^{x}		71.3 ± 22.6^{x}	34.5 ± 9.4^{y}	
CV (%)			7.5			14.5

±standard deviation; n = 3, 6 and 18 for G × T, T and G, respectively; numbers followed by different letters in the columns (A-F; a-d) and row (x-y) are significantly different ($P < 0.05$).

Table 5
Effects of genotype (G), phosphorus and microbial consortium treatments (T) and their interactions on response (%) for P uptake in oat genotypes in acidic soils.

Genotypes	Consortia response	Conjunctive P fertilization response				
	G × T					G
	IP0	IP1	IP2	IPCa	LP2	
Kent	28.8 ± 11.1^{DE}	52.4 ± 2.0^{AB}	50.6 ± 4.2^{AB}	57.3 ± 4.3^{A}	58.7 ± 6.8^{A}	49.5 ± 12.4^{x}
JHO-851	21.9 ± 5.8^{E}	40.5 ± 11.0^{C}	35.6 ± 5.6^{CD}	42.8 ± 1.0^{BC}	55.7 ± 12.9^{A}	39.3 ± 14.5^{y}
T	25.3 ± 8.8^{c}	46.5 ± 11.5^{b}	43.1 ± 9.1^{b}	50.1 ± 3.2^{ab}	57.2 ± 11.9^{a}	
CV (%)						15.5

±standard deviation; n = 3, 5 and 15 for G × T, T and G, respectively; numbers followed by different letters in the columns (A-E; x-y) and row (a-c) are significantly different ($P < 0.05$).

However, the population of total bacteria and soil pH resided at the second and fourth quadrant, respectively. Multiple regression equations were computed for varying screened variables' contributions to the variability of P-uptake and found root dry weight (RDW), microbial biomass N (MBN) and Bray's P to predict the uptake significantly (adjusted $R^2 = 0.90$) with beta coefficients (β) varying from 0.75–0.85 under different soil management practices (Table 6).

4. Discussion

Phosphorus is a major nutrient essential for synthesis of nucleic acids and energy storage (Theodorou and Plaxton, 1993). Plants growing in acidic soils often encounter multiple stresses such as Al and Fe toxicities and P, Ca and Mg deficiencies particularly in tropical and subtropical regions (Kunhikrishnan et al., 2016). To alleviate P deficiency and improve P nutrition of oat in such soils, we studied the effectiveness of an integrated strategy using P fertilizers, microbial consortia and responsive genotypes of the crop, since oat genotypes showed large variations in their capacity to utilize P from Al—P, Fe—P and Ca—P compounds (Rai et al., 2009). Two oat genotypes (Kent and JHO-851), co-inoculated with a microbial consortium, alone or in combination with phosphate fertilizers had a positive impact on soil pH compared to control. This pH change was more in soils under Kent compared to JHO-851. This is consistent with the results of Żebrowska et al. (2017), who reported differential alkalization of the rhizosphere by different oat genotypes. Plant-mediated increase in soil pH is controlled by the release of charges carried by OH^- ions because of greater anion uptake, accumulation of HCO_3^-, excretion of organic acids, redox coupled processes and crop genotypes (Hinsinger et al., 2003; Riley and Barber, 1969). Besides the accumulation of OH^- and HCO_3^-, protonation of the conjugate base of organic acids in soils having pH lower than the cytosolic pH (Jones and Darrah, 1995) or decomposition of these anions (Yan et al., 1996) also might have resulted in an increase in soil pH.

Effect of genotype and microbial consortium with phosphate fertilization was also evident from the increase in soil organic carbon and Bray's P content. A significant proportion of photosynthates allocated to growing media through root exudation, sloughed off biomass and necromass was responsible for the observed increase in soil organic carbon (Poffenbarger et al., 2020). The Bray's P represents the moderately labile inorganic P associated with sparingly soluble Al—P, Ca—P and Fe—P, and also a part of the inorganic P associated with positively charged oxide and hydrous oxide surfaces such as gibbsite, haematite, and goethite (Tiwari, 2012). The increased Bray's P in consortium inoculated soil compared to control can be explained by the ability of the phosphate solubilizers to solubilize those insoluble phosphate minerals through secretion of organic acids (Magallon-Servín et al., 2020). The conjugate bases of organic acids secreted in the rhizosphere also compete with phosphate ions for positively charged sorption sites resulting in an increase in phosphate concentration in soil solution (Hinsinger et al., 2003; Jones and Darrah, 1995). Notably, consortium inoculation itself (IP0) was able to replace the conventional P management in acidic soil (LP2). The largest impact of consortium inoculation on P availability was observed with the application of water soluble and insoluble P fertilizers (Fig. 2). In contrast, reduced Bray's P in LP2 was

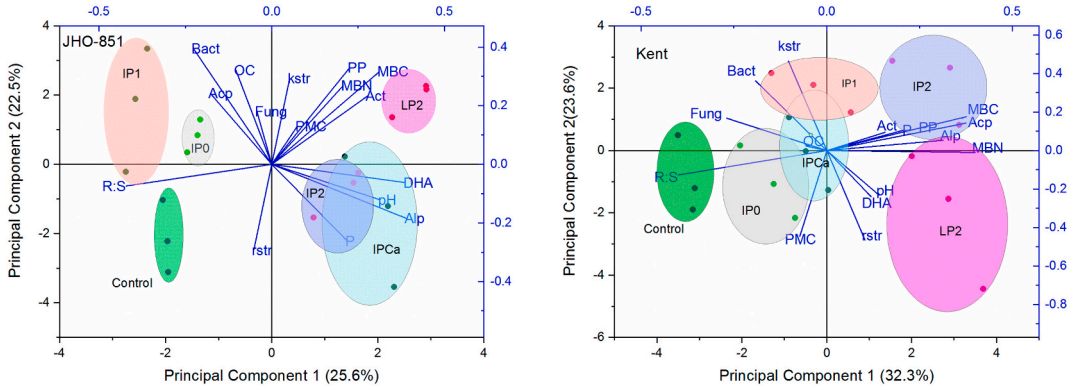

Fig. 7. Principal component analysis of soil chemical and biological properties with plant P content of oat genotypes; [DHA: dehydrogenase activity; PMC: mineralizable C; AcP: acid phosphatase; AlK: alkaline phosphatase; MBC; microbial biomass C; MBN: microbial biomass N; pH: $pH_{1:2}$; OC: organic C; P: Bray' P; PP: Plant P content; *r*-str: *r*- strategist population; *K*-str: *K*-strategists population: Fung: fungi; Act: actinobacteria; Bact: bacteria; R:S: root: shoot ratio].

Table 6
Stepwise regression analysis of P uptake.

Model	Constant	Root dry weight	Microbial biomass N	Bray's P	R^2	Adj. R^2	Significance
1	-5.17^{ns} ± 6.55	6.16*** ± 0.65 (0.85)[a]			0.72	0.72	$P < 0.001$
2	−14.49** ± 4.75	5.23*** ± 0.47 (0.72)	3.23*** ± 0.52 (0.41)		0.87	0.87	$P < 0.001$
3	−45.54*** ± 10.0	5.44*** ± 0.42 (0.75)	3.28*** ± 0.45 (0.41)	2.07** ± 0.61 (0.19)	0.91	0.90	$P < 0.001$

[a] Figures in parenthesis denotes standardized coefficients beta (β) of each dependent variable; ns-non significant.

** $P < 0.01$.

*** $P < 0.001$.

attributed to the formation of insoluble Ca—P compounds (Tiwari, 2012). Consortia and conjunctive P fertilization supported greater values of MBC, MBN, fungal and actinobacteria population and enzymes activities in the Kent rhizosphere. Greater availability of water soluble P with active microorganisms in the form of consortia provided favorable conditions for increased MBC, MBN and mineralizable carbon content in soils (Basak et al., 2017; Chu et al., 2007). Soil pH up to 5.5 is considered beneficial to soil microbial biomass and function (Aciego Pietri and Brookes, 2009). The positive response of MBC and MBN in LP2 was mainly related to change in soil pH because of liming. The neutralization of soil acidity by liming maintained an increased amount of labile carbon and nitrogen substrate by mineralization of recalcitrant organic matter (Grover et al., 2017). Liming also regulate N cycling by affecting microbial activity and community composition (Aciego Pietri and Brookes, 2009; Garbuio et al., 2011). Similar response of liming on improving MBC and MBN content were also reported in different acidic soils (Garbuio et al., 2011; Grover et al., 2017). Effect of water-soluble P source (IP1, IP2) on MBC and MBN emphasized the role of phosphate availability in regulating microbial activity in acidic soil (Zheng et al., 2020). Our results also showed a declined soil biomass for a low P availability in this soil (10.1 kg ha^{-1}). A greater quantity of organic carbon (11.4 g kg^{-1} soil) and $KMnO_4$ oxidizable N (421.4 kg ha^{-1}) in this soil was sufficient to meet the C and N requirements of the microbes (Table 1). Further, the co-inoculation of *Azotobacter* also contributed some amount of ammonium to the rhizosphere in presence of root exudates (Narula and Gupta, 1986). However, low P in IPCa might cause a reduction in microbial activity. Although, P sources vary in their response to MBC and MBN but similar Bray's P content after harvest of the crop, suggest that further work is required to identify the mechanisms involved.

Cultivated plants have varying adaptive capacity to low P acidic soils depending on their inherent root plasticity, C: N: P stoichiometry, and forging a mutualistic association with soil microbiota (Campos et al., 2018; Cobb et al., 2016; Rai et al., 2007). The positive effect of VAM, *Pseudomonas sps.*, *A. chroococcum*, and *A. niger* association on soil enzyme activities and the microbial population was observed in this study. The microbial consortium inoculation and P fertilization showed an increase in dehydrogenase, acid and alkaline phosphatase activities in Kent soil. The responsive genotypes develop mutualistic associations with beneficial microorganisms by increasing root exudates in the soil. These increased microbial activity (Emmerling et al., 2001; Schoebitz et al., 2016) and rising assay values of soil enzymes help the host through accelerated nutrients cycling (Asmar et al., 1995). These findings were corroborated with those of Turrini et al. (2016), Hetrick et al. (1993) and Cobb et al. (2016) who repoteded a positive responsiveness of VAM fungi with sunflower, wheat and sorghum genotypes, respectively.

A higher root biomass and easily decomposable rhizo-deposition support the fungi, actinobacteria (Dong et al., 2014) and *r*- strategists population in rhizosphere (Dilly, 2006). The P fertilization, liming and rhizo-deposition favored for fast-growing *r*- strategist population in Kent rhizosphere (Enwall et al., 2007). Contrarily, *K*-strategists were less sensitive and prevailed in biologically less active soil of JHO-851. Kent also f released more amounts of AcP and AlP because of the higher population of fungi, actinobacteria and *r*- strategist population in soil compared to JHO-851. Kent genotype under low P soil showed significantly higher values of AcP indicating adaptability of Kent to low P soil conditions. This was in agreement with the earlier report of higher AcP activity in P efficient genotypes under P starvation (Żebrowska et al., 2017).

Consortium inoculation and conjunctive P fertilization produced larger amount of aerial and root biomass and high root: shoot ratio for

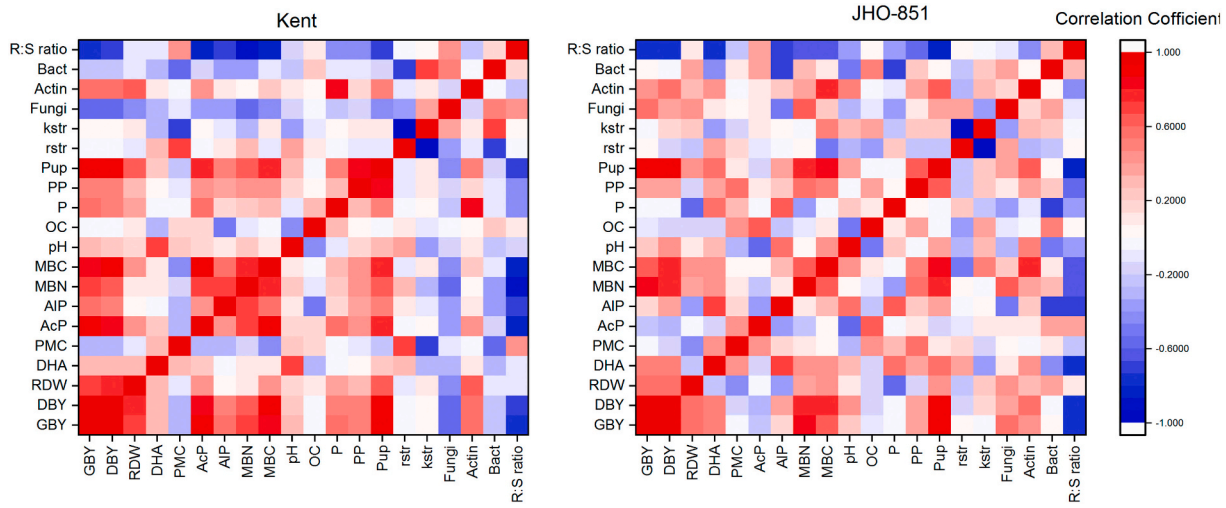

Fig. 8. Person's correlation matrix; [GBY: green biomass yield; DBY: dry biomass yield; RDW: root dry weight; Pup: P uptake; DHA: dehydrogenase activity; PMC: mineralizable C; AcP: acid phosphatase; AlK: alkaline phosphatase; MBC; microbial biomass C; MBN: microbial biomass N; pH: $pH_{1:2}$; OC: organic C; P: Bray' P; PP: Plant P content; *r*-str: *r*- strategist population; *K*-str: *K*-strategists population: Fung: fungi; Act: actinobacteria; Bact: bacteria; R:S: root: shoot ratio].

Kent compared to JHO-851, and supported greater values of MBC, MBN, Bray's P and organic C in soil under the former genotype. Higher P uptake response of Kent genotype to consortia inoculation and conjunctive P fertilization correlate well with significantly higher MBC, MBN, AlP, AcP, Bray's P and actinobacteria counts. These variables also showed a strong correlation with P uptake (Supplementary Table 2 and 3; Fig. 8). Plant P content in Kent genotypes was strongly correlated with MBC, MBN, AlP, AcP, Bray's P and actinobacteria population and lie on the same quadrant of PCA Biplot (Fig. 7). While in JHO-851, these variables were having weak correlation and AlP, AcP and Bray's P had different spatial distribution on the coordinate axis. The observed variation in genotypes for different P management strategies may be due to diverse genetic backgrounds. Although both genotypes were having similar biomass production potential under neutral soil pH conditions (Pandey and Roy, 2011); but under acidic soil condition, even alleviation of P deficiency through P fertilization could not improve the growth of JHO-851. This was because of the poor root growth of JHO-851 compared to Kent. Under different P fertilization strategies, Kent genotype showed 21–72% increase in root biomass. While in JHO-851, P fertilization and consortia inoculation did not increase root biomass except for LP2 (14% increase over control). These findings re-emphasize the importance of root morphology or architectural adaptation in enhancing P acquisition (Haling et al., 2011; Żebrowska et al., 2017). Aziz et al. (2014) and Żebrowska et al. (2017) also reported higher root biomass production by P efficient genotype of wheat and oats. Probably this was the reason for the selections of root dry weight as the most important cause, accounting for 72% variability in P uptake. Bray's P and MBN were the other variables selected in the prediction model. The observed beta coefficients for these variables (0.75–0.85) indicate a very strong influence of these variables on P uptake. Earlier studies also highlight the role of root biomass in increasing P uptake because of microbial inoculation (Kaleem Abbasi and Manzoor, 2018).

Our study indicates that the increased dry matter production and P nutrition of responsive genotypes was due to modified rhizosphere environment of the host plant by consortia partnership in low P acidic soils. This partnership can significantly improve the rhizosphere environment for enhanced forage yield and P uptake. However, at the establishment stage, increased availability of P in soil solution promoted the plant root growth and provided more root volume for colonization of consortia microorganisms. However, higher doses of fertilizer might reduce the effectiveness of the plant-consortia partnership because of the availability of readily available P sources to plant (Ehteshami et al., 2018). Our results also corroborate with this hypothesis, application of 50% recommended dose of P through KH_2PO_4 (IP1) or water insoluble tri-calcium phosphate caused 1.5–1.8 times increase in P uptake response (Table 2). The noted response was at par with lime amended soil with 100% recommended dose of P through KH_2PO_4. Further increase in P fertilizer through KH_2PO_4 was not effective in bringing any change in response. Therefore, the efficiency in the use of fertilizers should be reinforced through the concept of improving the rhizosphere effect and rhizophagy cycle (Arif et al., 2020).

5. Conclusion

Results of our study suggest that in low fertility soils, conjunctive P fertilization with suitable microbial consortia in responsive genotypes increased the biomass production and P uptake response. Phosphorus fertilization and microbial consortia application changed the composition of the culturable bacterial population as well as improved phosphatases activity and phosphorus availability to crops. Water insoluble P sources such as rock phosphate applied in conjunction with consortia and responsive genotypes were equally effective as KH_2PO_4 in acidic soils. These results have agronomic as well as economic importance for saving costly chemical fertilizers and also have associated environmental benefits. However, assessing the symbiotic potential of crop genotype is a critical factor in realizing the benefits of the plant-microbial partnership in acidic soils.

Declaration of competing interest

All authors agree with the no potential conflicts of interest on financially or non-financially, directly or indirectly related to the work, are relevant in all fields of science for publishing this manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2021.104094.

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