Applied Soil Ecology 95 (2015) 73–85

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Review

Elevated CO_2: Plant associated microorganisms and carbon sequestration

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ARTICLE INFO

Article history:
Received 23 September 2014
Received in revised form 20 April 2015
Accepted 20 May 2015
Available online 30 June 2015

Keywords:
Elevated CO_2
Climate change
Rhizodeposition
Plant associated microorganisms
C-sequestration

ABSTRACT

Alterations in plant rhizodeposition under elevated CO_2 (eCO_2) are likely to influence below-ground plant–microbe interactions and soil C dynamics. There are studies on influence of elevated CO_2 on soil microorganisms and below-ground microbial processes. However there is general lack of information on how altered plant–microbe interactions under eCO_2 will influence belowground C-sequestration. In the present review we focus on the greenhouse gas CO_2 with relevance to its effect on plant associated beneficial and pathogenic microorganisms in terrestrial ecosystems. Role of these microorganisms in belowground nutrient cycling and soil aggregation is discussed with reference to soil C-sequestration. This review demonstrates that eCO_2 influence the richness, composition and structure of soil microbial community and the influence is more on active microbial communities and in the vicinity of roots. High C:N ratio under eCO_2 favors fungi with wider C:N ratio and nutrient acquisition ability and biological nitrogen fixers. The ecosystems with fungal-dominated soil communities may have higher C retention than bacterial dominated soil communities. However, soil C-sequestration through plant growth, is strongly controlled by availability of nitrogen and nutrients required for biological nitrogen fixation. Nitrogenous and other chemical fertilizers show positive effect on C-sequestration but carry a carbon cost. Promotion of biological nitrogen fixers, and nutrient solubilizers and mobilizers may help in maintaining soil nutrient balance for higher C-sequestration. However more data need to be generated on the response of various plant beneficial as well as pathogenic microbial communities to eCO_2. We suggest that plant associated communities and related processes to be researched in long term studies for alteration under eCO_2 so as to assess their C-sequestration potential and identify management strategies for enhanced sequestration.

Contents

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http://dx.doi.org/10.1016/j.apsoil.2015.05.006
0929-1393/

1. Introduction

Increasing concentrations of greenhouse gas carbon dioxide (CO_2) in the earth's atmosphere are of major concern worldwide. Starting at around 280 parts per million (ppm) in pre-industrial times, CO_2 concentrations have now exceeded 400 ppm (http://www.esrl.noaa.gov/gmd/ccgg/trends),[1] and are expected to reach 600–800 ppm by the end of the century (Knohl and Veldkamp, 2011). For sustaining human life on the earth, it is very important to control the rapidly increasing CO_2 levels in the atmosphere through controlling the emission of greenhouse gases or through sequestration of atmospheric CO_2 in recalcitrant forms.

Biological systems through C-sequestration play potential role in mitigating effects of rising atmospheric CO_2 levels. Plants allocate approximately 40% of photo-synthetically fixed C to soil through rhizodeposition (van Veen et al., 1991; Bais et al., 2005; Jones et al., 2009). The organic compounds exuded through roots serve as nutrients for the soil biota thus attracting high microbial activity in the rhizosphere (Singh et al., 2004). Composition of rhizodeposits can selectively regulate the soil microbial communities in the rhizosphere, thereby encouraging beneficial and protective associations ensuring supply of vital nutrients and influencing the chemical and physical properties of the soil (Bais et al., 2004). The assimilation of C in the root and microbial biomass adds to soil C pool (C sink) whereas root and microbial respiration and decomposition of soil organic matter by soil biota results in C efflux (C source) (Fig. 1). The changes in soil-borne C pools, acting as C sink or source have direct influence on CO_2 concentration in the atmosphere and therefore have implications for global climate.

In general, rhizodeposition is expected to be altered under elevated CO_2 (eCO_2) due to changes in physiology and C status of the plant (Darrah, 1996; Barron-Gafford et al., 2005; Drigo et al., 2009). The alteration might be in the composition/availability of chemo-attractants or signal compounds, C:N ratio or nutrient availability in the rhizosphere (Kandeler et al., 2006; Haase et al., 2007) that may influence the colonization and functional behavior of the soil microorganisms in the rhizosphere (Singh et al., 2004; Phillips, 2007; Drigo et al., 2009). As soil micriobial communities play important role in C dynamics, any alteration in structure or function of microbial communities is likely to influence soil C-storage. Further, altered plant–pathogen interactions under eCO_2, which may influence soil C-sequestration potential directly or indirectly need to be understood (Yáñez-López et al., 2012). According to O'Neill (1994) the global fate and effects of the additional C under eCO_2 in the ecosystem is likely to be determined by soil biota. As the microbial communities form important component of soil biota, hence have key role in C dynamics under eCO_2. Elevated CO_2 may stimulate symbiotic associations to some degree, however more information need to be generated on microbial responses including those of plant pathogens to eCO_2 (O'Neill, 1994). Another review by Freeman et al. (2004) reported contradictory results on responses of soil microbial community structure and soil microbial processes to eCO_2 and emphasized the need to use advanced tools and techniques to understand microbial responses to eCO_2.

Moreover, to understand the role of altered plant–microbe interactions in soil C-sequestration under eCO_2, it is important to know how microbial communities influence below-ground processes like nutrient cycling and maintenance of soil structure under eCO_2. Effect of eCO_2 on below-ground processes has been reported in many studies (Cheng and Johnson, 1998; Jin and Evans, 2007 Singh et al., 2010; Drigo et al., 2013). However, there is need to link the alteration in below-ground processes with structural and functional changes in microbial communities under eCO_2. Further, agriculturally beneficial plant associated microbial communities like mycorrhizae and plant growth promoting micro-organisms that can influence the belowground processes and hence C-sequestration under eCO_2 need to be understood, so as to develop strategies for enhanced C-sequestration.

Study of plant–microbe interaction under eCO_2 is particularly important in the terrestrial agroecosystems, because C storage in these ecosystems could be very sensitive to management practices (tillage and cropping systems) (Torbert et al., 2000). Soil is the major organic C pool in the terrestrial ecosystems and the potential to manage terrestrial systems to conserve and sequester C appears promising (Wisniewskil et al., 1993). The present review is an attempt to present current stage of knowledge on impacts of eCO_2 on soil microorganisms with major emphasis on plant associated microorganisms and their role in soil structure formation, nutrient dynamics and ultimately soil C-sequestration under eCO_2. Altered plant–pathogen interactions under eCO_2 also have implications on C assimilation and hence their influence on C-sequestration needs to be understood. The present paper is an attempt to address these issues in the terrestrial ecosystem at global scale.

2. Effect of elevated CO_2 on plant associated microorganisms

The effects of the eCO_2 on soil microorganisms may be direct or indirect. The concentrations of CO_2 in the pore space of soil are generally much higher (2000–38,000 ppm) than those in the atmosphere even under ambient CO_2 condition. Therefore the direct effect of eCO_2 on soil microbial communities may be negligible as compared to potential indirect effects, such as increased plant C inputs to soil and changes in soil properties (He et al., 2012). Bacteria, archaea and fungi in soil respond differently

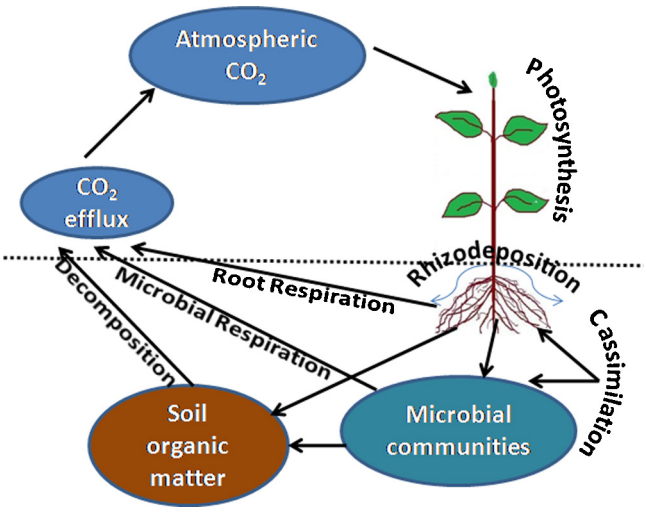

Fig. 1. Carbon flow in the plant–soil system.

[1] http://www.esrl.noaa.gov/gmd/ccgg/trends/. Trends in Atmospheric Carbon Dioxide. Visited on 3rd August, 2014.

Table 1
Effect of elevated CO_2 on plant associated microorganisms below-ground.

Target organisms	Test plant	Ecosystem represented (setup of experiment)	Observed effect of eCO_2	Elevated/ ambient CO_2 level	Duration of exposure to eCO_2	Reference
Rhizobium leguminosarum bv. *trifolii*	White clover (*Trifolium repens*)	Field-scale grassland (FACE facility)	Two-fold increase in the populations of *R. leguminosarum* bv. *trifolii* in the rhizospheres under eCO_2	600/ 350 ppm	~18 Months	Schortemeyer et al., 1996
Rhizobium leguminosarum	White clover (*Trifolium repens*)	Field-scale grassland (FACE facility), microcosm (growth chambers)	Genetic difference in the rhizobial strains isolated from plots exposed to ambient and eCO_2 indicating a shift in composition. In microcosm studies, strains isolated from plots exposed to eCO_2 showed higher (17%) nodule occupancy under eCO_2, indicating the effect of eCO_2 on the competitive ability of root nodule symbionts	600/ 350 ppm	~3 Years, 49 days	Montealegre et al., 2000
Rhizobium leguminosarum bv. *trifolii*	Perennial ryegrass (*Lolium perenne*)	Field-scale grassland (FACE facility)	No effect of the CO_2 concentration on the rhizobial populations	600/ 350 ppm	~18 Months	Schortemeyer et al., 1996
Rhizobium spp.	Common bean (*Phaseolus vulgaris* L.)	Microcosm scale agro-ecosystem (growth chamber)	Nodule number, biomass and the proportion of leghaemoglobin-producing nodules enhanced. The release of nod-gene-inducing flavonoids stimulated. Total N content of the plants decreased in response to eCO_2 treatments, whereas no significant effect on plant biomass observed	800/ 400 ppm	21 Days	Haase et al., 2007
R. leguminosarum and *Pseudomonas* spp.	White clover (*Trifolium repens*)	Field-scale grassland (FACE facility)	Increased abundance of *R. leguminosarum* and decreased dominance of *Pseudomonas* spp. in the rhizosphere (soil and root) under eCO_2. No effect of eCO_2 on bacterial population in bulk soil	60/35 Pa	Entire growing seasons	Marilley et al., 1999
Pseudomonas spp.	Perennial ryegrass (*Lolium perenne*)	Field-scale grassland (FACE facility)	Increased dominance in the rhizosphere (soil and root). No effect of eCO2 on bacterial population in bulk soil	60/35 Pa	Entire growing season	Marilley et al., 1999
Pseudomonas spp.	Perennial ryegrass (*Lolium perenne*), soil	Field-scale grassland (FACE facility)	Stimulation of siderophore-producing and nitrate dissimilating strains, decreased abundance of HCN producing strains	60/36 Pa	Entire growing seasons	Tarnawski et al., 2006
Actinobacteria, δ-proteobacteria	Perennial ryegrass (*Lolium perenne*), purple moor grass (*Molinia coerulea*), Root and soil	Field-scale grassland (FACE facility)	Active and root-associated component of the bacterial community influenced by eCO_2. Actinobacteria in soil and δ-Proteobacteria in root stimulated under eCO_2	60/36 Pa	2 Growing seasons	Jossi et al., 2006
Soil microbial communities	Eastern cottonwood (*Populus deltoides*) soil	Artificial ecosystem	Increased dominance of β-Proteobacteria, and higher fungal biomass under eCO_2 as compared to that of α-Proteobacteria and Acidobacteria under optimum conditions	800 and 1200/ 400 ppm	–	Lipson et al., 2006
Soil microbial communities, nitrate reducers	Trembling aspen (*Populus tremuloides*), soil	Field-scale forest (FACE facility)	No effect of eCO_2 on total bacterial and eukaryotic abundance, however, increase in heterotrophic decomposers and decrease in nitrate reducers	560/ 360 ppm	4 Years	Lesaulnier et al., 2008
Soil microbial communities, genes involved in C fixation, and N cycling	16 native species (4C4 grasses, 4C3 grasses, 4 N-fixing legumes and 4 non-N-fixing herbaceous species)	Field scale grassland ecosystem (FACE facility)	Increased abundance of genes involved in C fixation (Rubisco, CODH, PCC/ACC) and N cycling (*nifH, nirS*) under eCO_2, indicating alteration in soil microbial community structure and their ecosystem functioning for C and N cycling	560/ 368 ppm	10 Years	Xu et al., 2013
Fast growing (r-strategist) and slow growing (k-strategist) microorganisms	Spring wheat (*Triticum aestivum* cv. Triso) followed by oilseed rape (*Brassica napus*), soil	Agro-ecosystem (FACE facility)	Stimulation of microbial community and increased the contribution of r-strategists especially in soil micro-aggregates under eCO_2, indicating acceleration of available C mineralization in soil. No significant response of microbial biomass to eCO_2	540/ 380 ppm	5 Years	Dorodnikov et al., 2009
Purple phototrophic (α and β proteobacteria)	flooded paddy (*Oryza sativa*) soil under rice wheat cropping system	agro-ecosystem (FACE facility)	Significant increase in the number of sulfate-reducing bacteria and nitrogen-fixing bacteria in the rhizosphere. Soil organic carbon increased significantly under eCO_2	550/ 350 ppm	100 Days	Feng et al., 2009
AMF (*Glomus* sp.)	Self-heal (*Prunella vulgaris*), a semi-evergreen perennial herb	Microcosm scale grassland (climate chambers)	Increased allocation of AMF biomass to external hyphae (5 times increase in length). Significant increase (double) in plant biomass	600/ 350 ppm	18 Weeks	Sanders et al., 1998
AMF (*Glomus caledonium*)	Pea (*Pisum sativum* cv. Solara)	Microcosm scale agro-ecosystem (growth room)	No significant effect of eCO_2 on colonization. Stimulating and additive effect of eCO_2 and mycorrhiza on shoot and total plant weight	700/ 360 ppm	60 Days	Gavito et al., 2000
AMF (*Glomus caledonium* and *G. mosseae*)	*Plantago lanceolata* (narrowleaf plantain)	Microcosm-scale agro-ecosystem (environmental chambers)	Increase in extraradical mycorrhizal hyphal under eCO_2	700/ 360 ppm	84 Days	Staddon et al., 2004
AMF (*Glomus intraradices*)	Sour orange (*Citrus aurantium*)	Microcosm-scale agro-ecosystem (glasshouse)	No significant effect of CO_2 concentrations on colonization. Net photosynthesis and plant biomass increased under eCO_2	70/36 Pa	14 Weeks	Jifon et al., 2002

Table 1 (*Continued*)

Target organisms	Test plant	Ecosystem represented (setup of experiment)	Observed effect of eCO_2	Elevated/ ambient CO_2 level	Duration of exposure to eCO_2	Reference
AMF (*Glomus mosseae*, *Glomus versiforme*, *Glomus geosporum*, and *Scutellospora* spp.)	C4 barnyard grass (*Echinochloa crusgalli* L.)	Microcosm-scale agro-ecosystem (growth chamber)	Increased mycorrhizal colonization in monoculture (16.8%) and mixed culture (36.9%), enhanced N and P uptake and higher shoot biomass of barnyard grass	700/ 400 ppm	~4 Months	Tang et al., 2009
	C3 upland rice (*oryza sativa* L.)		No effect			
AMF (general)	C3 western wheat grass (*Pascopyrum smithii*), C4 blue gamma (*Bouteloua gracilis*)	Microcosm-scale grassland (environmental chambers)	Increased mycorrhization (46%) of *B. gracilis* under eCO_2. No effect on *P. smithii*	700/ 350 ppm	4 Annual growth cycles	Monz et al., 1994
	C3 wild oat (*Avena fatua*),	Microcosm-scale agro-ecosystem	Elevated CO_2 had no impact on total soil C in the absence of AMF, but significantly reduced it by 9% in the presence of AMF. CO_2 stimulation of AMF resulted in considerable soil carbon losses	580/ 380 ppm	10 Weeks	Cheng et al., 2012
	Wheat (Triticum spp.) - soybean (*Glycin max*) system	Field-scale agro-ecosystem	Increased colonization of fine roots and external AMF biomass. Soil C loss rate induced by the hyphae-ingrowth effect was high (upto 80%) under eCO_2	560/ 380 ppm	~3 Years	Cheng et al., 2012
ECM (*Pisolithus tinctorius*)	Loblolly pine (*Pinus teada* L.)	Microcosm-scale forest (greenhouse)	Increased root carbohydrates, but no significant effect on mycorrhizal colonization	71/ 35.5 Pa	120 Days	Lewis et al., 1994
	Pine (*Pinus ponderosa* Dougl. ex Laws.)	Field-scale forest (open top chambers)	Extensive ectomycorrhizal formation. Decreased shoot/root ratios under eCO_2	700/ 525 ppm/ ambient	1 Year	Walker et al., 1995
	Pine (*Pinus silvestris* L.)	Microcosm-scale forest (growth chamber)	Higher root biomass (57%) at eCO_2. More (3 times) mycorrhizal root clusters and biomass (double) of the extraradical mycelium. High water use efficiency	600/ 350 ppm	3 Months	Ineichen et al., 1995
ECM (*Laccaria bicolor* and *Suillus bovinus*)	Scots pine (*Pinus sylvestris* L.)	Microcosm-scale forest (ESPAS phytotrons)	Elevated CO_2 increased the total net C uptake (64%) and total number of root tips (26%) irrespective of fungal species. *S. bovinus* acquired or transferred nitrogen better than *L. bicolor* and enabled the seedlings to perform better under eCO_2. Decreased shoot-to-root ratio in the *Suillus*-inoculated seedlings. Whereas, *Laccaria*-inoculated seedlings increased below-ground respiration	700/ 350 ppm	140 Days	Gorissen and Kuyper, 2000
ECM (*Hebeloma crustuliniforme, Paxillus involutus)*	Scots pine (*Pinus sylvestris* L. Karst)	Microcosm-scale forest (growth chambers)	Three-fold increase in mycelial biomass. Significantly lower concentrations and total amounts of N in plants exposed to eCO_2 due to sequestration of N in the fungal mycelium	700/ 350 ppm	6 Weeks	Fransson et al., 2005
ECM communities	Paper birch *(Betula papyrifera* Marsh.), Eastern white pine (*Pinus strobus* L.) and Eastern hemlock (*Tsuga canadensis* L. Carr.)	Microcosm-scale forest (glass house CO_2 chambers)	Increased ECM colonization in *B. papyrifera* and *P. strobes*. However, in *T. canadensis* the degree of colonization with arbuscular mycorrhizas increased significantly. Distinct changes in the ectomycorrhizal morphotype assemblage of *B. papyrifera* observed under eCO_2 with increased frequency of ectomycorrhizas with a higher incidence of emanating hyphae and rhizomorphs	700/ 375 ppm	27–35 Weeks	Godbold et al., 1997
	Longleaf pine (*Pinus palustris* L.)	Microcosm-scale forest (OTC)	Increased fine-root length and ECM colonization under eCO_2 resulted in higher (double) numbers of ectomycorrhizas	720/ 365 ppm	20 Months	Runion et al., 1997
	Paper birch (*Betula papyrifera*)	Microcosm- scale forest (green house CO_2 chambers)	Significant changes in the composition of the ECM assemblage toward morphotypes with a high production of hyphae and rhizomorphs, beneficial for nutrients and water acquisition	700/ 375 ppm	24 Weeks	Godlbold and Berntson, 1997
	Trembling aspen (*Populus tremuloides*), soil	Field-scale forest (FACE facility)	Increased abundance	560/ 360 ppm	4 Yrs	Lesaulnier et al., 2008
	Pine (*Pinus taeda* L.)	Forest (FACE facility)	14% Increase in colonization under CO_2	200 ppm above normal	Long term	Garcia et al., 2008

Abbreviations: FACE: free-air-carbon-dioxide-enrichment; ESPAS: experimental soil plant atmosphere system; OTC: open top chambers.

to eCO_2 causing a shift in richness, composition and structure of soil microbial communities (Compant et al., 2010; Hayden et al., 2012; He et al., 2012). Table 1 summarizes the effect of eCO_2 on plant associated microorganisms.

2.1. Elevated CO_2 and plant–mycorrhizae interactions

Mycorrhizae are associated with majority of the land plants (approximately 90%), and 60% of these plants establish symbiosis with obligate symbionts such as arbuscular mycorrhizal fungi (AMF) belonging to the group of plant growth promoting fungi (PGPF) (Compant et al., 2010). AMF are known to promote plant growth by nutrient mobilization and help in soil aggregation through extended hyphae (Harris and Paul, 1987; Wright et al., 1998; Syvertsen and Graham, 1999). In general, it is observed that improved AMF colonization under eCO_2 will have positive effect on plant growth (Tylianakis et al., 2008). Elevated CO_2 levels have been reported to affect hyphal growth and root colonization of mycorrhizal fungi. For example, increased growth of external as well as internal hyphae of AMF has been reported in the rhizosphere of perennial herb self-heal (*Prunella vulgaris*) under eCO_2 (600 ppm), possibly due to increased root biomass and higher allocation of fixed C to the external hyphae (Sanders et al., 1998; Rillig and Allen, 1999). A meta-analysis by Alberton et al. (2005) revealed a significant positive response of AM fungi (an increase of 21%) to eCO_2. However, some workers observed no significant effect of eCO_2 on plant–AMF association. For example, Gavito et al. (2000) observed no effect of eCO_2 (700 ppm) on mycorrhizal development in pea (*Pisum sativum* L.). It has been observed that response of AMF colonization under eCO_2 varies in C_3 and C_4 plants, with C_4 plant showing improved AMF colonization under eCO_2, whereas C_3 plants showing no such effect (Monz et al., 1994; Tang et al., 2009). A meta-analysis by Poorter and Navas (2003) revealed higher increase in biomass production in C_3 plants (45%) than in C4 plants (12%) under eCO_2. This may be explained on the basis of physiological difference in two plants. C_4 plants have more efficient C concentrating mechanism or probably, C allocation of C_4 plants is more towards mycorrhizal growth while C_3 plants assimilate additional C for biomass production (Poorter and Navas, 2003).

Changes in the atmospheric CO_2 levels can also induce a shift in the abundance as well as composition and structure of ECM (ectomycorrhizal) communities (Tingey et al., 1997; Alberton et al., 2005; Courty et al., 2010), potentially leading to altered plant–microbe interactions and affecting plant growth. A meta-analysis by Cudlin et al. (2007) showed increased colonization of ECM on root tips under eCO_2. Number of species forming extensive extra mycorrhizal mycelia and rhizomorphs increased under eCO_2 (Rouhier and Read, 1998; Parrent et al., 2006; Courty et al., 2010). Positive effect of eCO_2 on ECM can be highly relevant for water and nutrient supply to plants (Loewe et al., 2000). However some reports suggest temporary or no effect of eCO_2 on ECM. Gorissen and Kuyper (2000) reported fungal genotype-specific responses of ECM colonizing plants under eCO_2. Ectomycorrhizal seedlings of scots pine (*Pinus sylvestris*) inoculated with *Laccaria bicolor* and *Suillus bovinus* were exposed to ambient (350 ppm) and eCO_2 (700 ppm). Total net percent C uptake increased under eCO_2, however, the extra carbon in the *Suillus*-inoculated seedlings was translocated to the roots and resulted in a decreased shoot-to-root ratio, whereas *Laccaria*-inoculated seedlings did not incorporate the additional carbon in root or fungal tissue but only increased below-ground respiration. *S. bovinus* acquired or transferred nitrogen better than *L. bicolor* and enabled the seedlings to perform better with regard to net carbon uptake under eCO_2. The results suggested that the ability of ectomycorrhizal scot pine seedlings to respond positively to elevated atmospheric eCO_2 was fungal-species specific. Plant species also influence the effect of eCO_2 on associated mycorrhizal assemblages (Godbold and Berntson, 1997; Godbold et al., 1997; Fransson et al., 2001) which can potentially affect plant growth promotion.

Majority of the studies have shown positive effect of eCO_2 on plant–mycorrhizae interactions. However the extent of response varied with plant species and the mycorrhizal strains.

2.2. Elevated CO_2 and Plant–PGPB (plant growth promoting bacteria) interactions

Numerous plant growth promoting bacteria (PGPR) have been identified to date, each possessing one or more mechanisms for supporting plant growth. Soil bacteria, including free-living as well as associative and symbiotic bacteria belonging to the genera like *Acinetobacter, Alcaligenes, Arthrobacter, Azospirillum, Azotobacter, Bacillus, Burkholderia, Enterobacter, Erwinia, Flavobacterium, Proteus, Pseudomonas, Rhizobium, Serratia, Xanthomonas* in particular, are the integral parts of rhizosphere biota (Glick, 1995; Kaymak, 2011). Beneficial effects of PGPB have been attributed to biological nitrogen fixation (BNF), production of phytohormones that promote root growth, solubilisation and mobilization of soil nutrients, stimulation of plant resistance to pathogens and parasites, modifying rhizospheric soil environment by exo-polysaccharides production and providing tolerance to host plant against abiotic stress/es (Grover et al., 2010; Bhattacharyya and Jha, 2012).

Plant associated bacterial communities including rhizosphere colonizers as well as endophytes are prone to be influenced by increased atmospheric CO_2 levels due to their high dependence on plants for nutrients. Most of the studies on plant-bacterial interaction under eCO_2 have been performed in long term 'Free Air CO_2 Enrichment (FACE)'. These experiments reported improved legume–rhizobia symbiosis under eCO_2 (Compant et al., 2010). Studies on white clover (*Trifolium repens*) revealed increased population of *Rhizobium* sp. under eCO_2 (60 Pa) (Marilley et al., 1999). Montealegre et al. (2000) selected 120 strains of *Rhizobium leguminosarum* which were favored either by ambient (350 ppm) or eCO_2 (600 ppm) and tested a mixture of these strains with white clover under eCO_2. Elevated CO_2 favored strains formed 17% more nodules than the strains favored by ambient CO_2 indicating that the bacterial strains favored by eCO_2 were more competitive in forming symbiotic relationships with plant roots. Thus eCO_2 can influence competitive ability of rhizobial strains.

Schortemeyer et al. (1996) studied the response of NH_4^+-oxidizing bacteria, and *Rhizobium leguminosarum* bv. *trifolii* to eCO_2 (600 ppm) with white clover and perennial ryegrass (*Lolium perenne*) in a model field-scale grassland ecosystem. No significant effect of eCO_2 was observed on the total number of cultivable heterotrophic bacteria and autotrophic NH_4^+-oxidizing bacteria with both the plant species. However, the population of *R. leguminosarum* bv. *trifolii* increased two-fold in the rhizosphere of white clover exposed to eCO_2, whereas no such effect was observed in the rhizosphere of perennial ryegrass. The result indicated that the response of rhizobial population to eCO_2 was host specific.

The effect of eCO_2 has been studied on some non-symbiotic plant-associated bacteria. Under eCO_2 (60 Pa) the dominance of *Pseudomonas* spp. increased with perennial ryegrass and decreased with white clover indicating the plant species specific response (Marilley et al., 1999). However the proportion of HCN-producing *Pseudomonas* strains was reduced under eCO_2 (60 Pa) conditions and the proportion of siderophore producers and nitrate-dissimilating strains increased with perennial ryegrass, whereas no effect on auxin producing *Pseudomonas* sp. was observed (Tarnawski et al., 2006). The genera *Burkholderia* and *Pseudomonas* known as highly rhizo-competent genera (Vancanneyt et al., 1996;

Lugtenberg et al., 2001; Treonis et al., 2004; Berg et al., 2005) were significantly influenced by eCO_2 (700 ppm), whereas other antibiotic producers like *Actinomycetes* and *Bacillus* spp. known as bulk-soil inhabitants (Smalla et al., 2001) were not affected under eCO_2 (Drigo et al., 2009). An increase in abundance of fast growing bacteria (r-strategic) as compared to slow growers (k-strategic) under eCO_2 (540 ppm) was also reported (Dorodnikov et al., 2009). The rhizosphere competent and fast growing bacteria are more responsive to any changes in quality or quanitity of rhizodeposition as compared to bulk soil inhabitants and slow growers.

Further, the effect of eCO_2 is more pronounced on metabolically active than on total bacterial communities as reported by Jossi et al. (2006). They assessed the response of total and active bacterial communities to eCO_2 (60 Pa) under field conditions by using two perennial grasses: the nitrophilic perennial ryegrass and the oligonitrophilic purple moor-grass. It was observed that eCO_2 (60 Pa) stimulated *Actinobacteria* which use soil organic matter as main C source, in soil and *Deltaproteobacteria* known to be cellulolytic organisms, in the root, indicating nutrient specific response of microbial communities. In another study, Lesaulnier et al. (2008) studied microbial diversity associated with trembling aspen (*Populus tremuloides*) and observed significant decrease in nitrate reducers of the domain bacteria and archaea, potentially implicated in ammonium oxidation, under eCO_2 (560 ppm). No change in total bacterial and eukaryotic abundance was observed, however, an increase in heterotrophic decomposers and ectomycorrhizal fungi was observed. However, Deiglmayr et al. (2004) did not observe any effect of eCO_2 (600 ppm) on the community structure of nitrate reducers in the rhizosphere soil of white clover and perennial ryegrass.

In the climate change scenario, the application of microorganisms in agriculture will depend on the performance based selection under eCO_2 concentration. Many studies have reported plant growth promotion by microorganisms under different abiotic stress conditions like drought, high and low temperature, salinity, flooding, nutrient deficiency (Yang et al., 2009; Grover et al., 2010; Selvakumar et al., 2012). These abiotic stresses are related to or influenced by eCO_2. Alguacil et al. (2009) inoculated seedlings of lettuce (*Lactuca sativa*) with *Pseudomonas mendocina* and subjected to two levels of watering and two levels of atmospheric CO_2. Inoculation with PGPR improved plant growth, foliar potassium concentration and leaf relative water content under eCO_2 (760 ppm) and drought. Similar, studies need to be conducted under eCO_2 and multiple stress conditions to understand the dynamics of plant microbe interactions and to develop coping strategies.

2.3. Elevated CO_2 and host–pathogen interactions

Under eCO_2 levels, the morpho-physiology of the crop plants is significantly influenced. Elevated CO_2 has the potential to accelerate plant pathogen evolution, which may, in turn, affect virulence. However, lack of experimental data and the subsequent ability to predict future outcomes constitute a fundamental knowledge gap. Furthermore, mechanistic bases of increasing pathogen aggressiveness are not known (Lake and Wade, 2009).

Contrasting results on influence of eCO_2 on plant pathogens have been reported (Table 1). Among the reports showing negative effect of eCO_2 on plant pathogens, Malmstrom and Field (1997) reported that CO_2 enrichment (700 ppm) in oat (*Avena sativa*) plants infected with barley yellow dwarf virus (BYDV) increased the persistence of the plants by altering the epidemiology of BYDV. Chakraborty and Datta (2003) reported loss of aggressiveness of *Colletotrichum gloeosporioides* on shrubby stylo (*Stylosanthes scabra*) over 25 infection cycles under eCO_2 (700 ppm) conditions. On the contrary, pathogen fecundity increased due to altered canopy environment. McElrone et al. (2005) found that exponential growth rates of leaf spot causing fungus *Phyllosticta minima* were 17% greater under eCO_2 (200 ppm above ambient). However, eCO_2 reduced leaf N by 20% and increased the C:N ratio by 20%, total phenolics by 15%, and tannins by 14% in the host red maple (*Acer rubrum*). Stomatal conductance was reduced by 21–36% under eCO_2 thereby leading to smaller openings for infecting germ tubes and resulting in reduced disease incidence and severity in infected plants. Reduced incidence of Potato virus Y on tobacco (*Nicotiana tabacum*) was reported under eCO_2 (1000 ppm) (Matros et al., 2006). Similarly, Braga et al., (2006) observed reduction in stem canker disease caused by fungus *Diaporthe phaseolorum* f. sp. *meridionalis* in soybeans (*Glycine max*) due to enhanced glyocellin (phytoalexins) accumulation at eCO_2 (720 ppm). Reduced leaf spot in stiff goldenrod (*Solidago rigida*) was reported under eCO_2 (560 ppm) due to reduced leaf nitrogen content that imparted resistance against disease (Strengbom and Reich, 2006). Potato (*Solanum tuberosum*) cultivar Indira, developed resistance against *Phytophthora infestans* after exposure to eCO_2 (700 ppm) (Plessl et al., 2007). Thus, under eCO_2, plants undergo changes in physiology, anatomy and morphology that increase their resistance to pathogens (Yáñez-López et al., 2012).

In contrast, Lake and Wade (2009) reported increased aggressiveness of *Erysiphe cichoracearum* (causal agent of powdery mildew in cucurbits) under eCO_2 (800 ppm), together with changes in the leaf epidermal characteristics of the model plant *Arabidopsis thaliana*. Stomatal density, guard cell length, and trichome number on leaves developing post-infection increased under eCO_2 in contrast to non-infected responses. These changes in epidermal features may facilitate an enhanced susceptibility of newly developed leaves to further pathogen attack. *Alternaria alternata* (causal agent of leaf spots and blights) has been reported to sporulate three times more on timothy grass (*Phleum pretense*) plants cultivated under eCO_2 (600 ppm) conditions (Wolf et al., 2010). As the fungus has wide host range, the increased spore density can be devastating. Elevated CO_2 (200 to 280 ppm above ambient) also increased the susceptibility of rice (*Oryza sativa*) plants to *Magnaporthe oryzae* (causal agent of leaf blast) and *Rhizoctonia solani* (causal agent of sheath blight) as opposed to ambient CO_2 concentrations. Higher number of tillers observed under eCO_2 concentrations may increase the chance for sclerotia of *Rhizoctonia solani* to adhere to the leaf sheath at the water surface. Consequently, the potential risks for infection of leaf blast and epidemics of sheath blight may increase in rice grown under eCO_2 concentration (Kobayashi et al., 2006).

Elevated CO_2 is also likely to influence the interactions between pathogens and biocontrol agents. Gamper et al. (2004) noted that colonization levels of arbuscular mycorrhizae tended to be high on perennial ryegrass and white clover grown under eCO_2 (60 Pa) which may help in increased protection against stresses. Rezácová et al. (2005) observed that *Chlonostachys rosea*, a biological control agent of *Botrytis*, and *Metarrhizium anisopliae*, an important entomopathogen were strongly associated with the cover crop under eCO_2 (60 Pa) environment. The abundance of these biocontrol agents has been related to increased suppressiveness (ability to suppress) of the soil to phytopathogenic fungi. Under the Indian Council of Agricultural Research, initial work was initiated under national network project 'Impacts, Adaptation and Vulnerability of Indian Agriculture to Climate Change' to understand impacts of climate change on plant pathogens and beneficial microorganisms. Further the work was strengthened and scaled up under National Initiative on Climate Resilient Agriculture'. Under this project, at Central Research Institute for Dryland Agriculture, studies are being conducted to understand the impacts of eCO_2 and temperatures on major soil-borne plant pathogens viz. *Sclerotium*

rolfsii, *Macrophomina phaseolina*, *Fusarium oxysporum* f. sp. *ricini*, *Botrytis ricini* and *Rhizoctonia solani* as well as biocontrol agents, viz. *Pseudomonas* and *Trichoderma*. So far, it has been observed that after exposure for 30 generations to eCO_2 (700 ppm) sporulation increased in *Trichoderma* considerably. Similarly, enhanced chitinase production was observed in *Trichoderma* under eCO_2 (unpublished data). Efforts are being made to build probable scenarios for major pathogens and biocontrol agents under modified eCO_2 conditions.

Under eCO_2, plants develop different mechanisms to enhance their resistance to pathogen. However, increased biomass and changes in leaf epidermal features under eCO_2 may increase the incidents and/or intensity of pathogenic infections. On the other hand, eCO_2 may increase the aggressiveness and growth rate of some pathogens and increase the fecundity of other pathogens. Further the effect of eCO_2 on biocontrol agents will also influence pathogen-biocontrol agent interactions. Thus, generating scenario of major plant pathogens and biocontrol agents under eCO_2 conditions will be very helpful in assessing their impacts on primary production in agricultural systems which has a direct influence on soil C dynamics.

The changes in soil biota are evidence for altered interactions between host plant and the microorganisms in its surrounding soil, and support the theory that greater plant detritus production under eCO_2 significantly alters soil microbial community composition. However, the rhizosphere competent and metabolically active microorganisms are more responsive to any changes in quality or quanitity of rhizodeposition due to increased CO_2 concentrations, as compared to bulk soil inhabitants and slow growers. In general, biological nitrogen fixing legume–rhizobia symbiosis is favored under eCO_2. Majority of the studies have shown positive effect of eCO_2 on plant–mycorrhizae interactions due to increased root biomass and higher allocation of fixed C for mycorrhizal growth. However the extent of response varies with plant species and the mycorrhizal strains. Further, considering the significance of plant diseases on primary production in agricultural systems, comprehensive analysis of how eCO_2 will influence plant–pathogen interactions is needed.

3. Plant associated microorganisms and soil structure

Soil structure controls the habitat of soil microorganisms as well as the accessibility of soil organic matter to microbial decomposition. Different microorganisms play important roles in the formation and maintenance of soil structure (Lynch and Bragg, 1985). Fungi generally occupy macroaggregates (>50 mm diameter) because hyphae cannot penetrate small pores whereas bacteria are found in small pores of <10 mm diameter (Dorodnikov et al., 2009).

Mycorrhizal fungi are one of the most important biotic factors influencing soil aggregation (Jastrow et al., 1998). Mycorrhizal hyphae form channels between plant roots and soil for the acquisition of nutrients. These extended hyphae along with plant roots and root hairs help in the formation of micro- and macroaggregates. The recalcitrant glycoprotein glomalin, produced by AMF, plays an important role in stabilizing aggregates (Wright and Upadhyaya, 1996; Rillig et al., 2002), as does extracellular polysaccharide secreted by microorganisms (Sandhya et al., 2009). The clay particles get deposited on the polysaccharide layer by drying and shrinkage to form soil aggregates. The size of the soil aggregates increase as more layers of polysaccharide and clay are deposited on the surface. As the layers are built concentrically, the younger C (C added to the soil freshly) is deposited in the outer layers. The clay shell thus formed inhibits the decomposition of SOC (soil organic carbon) in the inner layers and also protects microbial biomass and soil organic matter from predators (protozoa and nematodes) hence increases the residence time of SOC (Six et al., 2006). Organic matter bound in aggregates decomposes more slowly, leading to accumulation of soil C. Rillig et al. (2001) reported increased water stable aggregates, glomalin and AMF hyphal lengths with sorghum under eCO_2. The direct effect of glomalin on water stable aggregation was much stronger than the direct effect of AMF hyphae themselves, suggesting the involvement of glomalin in soil aggregate stabilization (Rillig et al., 2002).

From the above studies it is indicated that promotion of fungal growth under eCO_2 could increase soil OM as well as protect OM from predators by improving soil structure and thus help in C sequestration. However, soil structure improvement is a function of several factors including physical forces present in soils, amount of organic C present and the composition of the organic matter (Dormaar, 1983; Martens, 2000). Altered biochemistry and decomposition of plant residues also influences soil aggregation and C cycling. The compounds which are quickly decomposed exert a rapid stabilization effect on soil structure, but the effect is transient. On the other hand, the compounds which decompose slowly require a longer time for soil aggregation, but aggregation is effective for longer time (Martens, 2000). Humus formation, which is reported to promote long term soil aggregation, also increases with more resistant compounds (Chaney and Swift, 1986). Thus influence of different plant species on soil aggregation may vary due to difference in biochemical composition of residue.

Stimulation of mycorrhizal fungi under eCO_2 can directly increase input of OC into soil through increased biomass and glomalin content. Increased mycorrhizal biomass under eCO_2 helps in protecting SOC from decomposition through improved soil aggregation. Further, mycorrhizal fungal propagules persist longer in soil due to slow turnover of fungal carbon thus increasing the residence time of SOC and contributing to soil carbon sequestration.

4. Plant associated microorganisms and nutrient availability under eCO_2

Under eCO_2 conditions, as the photosynthesis rate increases the plant accumulates more N into its biomass and litter resulting in higher C:N ratio in the soil. The simple organic compounds exuded by roots may be preferred by the rhizosphere microorganisms over recalcitrant soil organic matter thus helping in C storage (Cheng, 1999). However the imbalance in nutrient availability increases the competition between microbe-microbe and/or plant–microbe. For example, Haase et al. (2007) reported nitrogen deficiency in common bean under eCO_2 conditions, probably due to increased root exudation and a related stimulation of rhizosphere–microbial growth causing enhanced plant–microbial N competition. Alternately, the nutrient imbalance may cause priming effect thus stimulating microbial degradation of recalcitrant soil organic matter for nutrients and converting soil C-sink into C-source. Due to the priming effect, eCO_2 significantly increases plant biomass even in unfertilized experiments. Priming simultaneously increases soil N availability but reduces the soil C reservoir (van Groenigen et al., 2006), however the whole plant–soil system resulted in a net C gain at the end, because of C input in the forms of rhizodeposits and root biomass (Cheng, 2009). However the priming effect is controlled by N availability (Chen et al., 2014). Low-N availability in pools accessible for micro-organisms facilitates the decomposition of recalcitrant soil organic matter (SOM) by k-strategic (slow growers) microorganisms to acquire N, whereas the presence of N (C:N ratio matching the microbial demand) facilitate the decomposition of labile C by r-strategic (fast growers). For example, with grain sorghum, the high C:N ratio led to slow microbial decomposition resulting in increased new soil C.

With soybeans, the low C:N ratio promoted microbial decomposition of new C inputs and apparently reduced the decomposition of old C, resulting in a trend for increased soil storage of C (Torbert et al., 1997).

Effect of added N on soil C has been studied under eCO_2. A direct linear relationship between long-term nitrogen addition and accumulation of organic C in some semi-arid soils in Oregon has been reported (Rasmussen and Rohde, 1988). A meta-analysis by de Graff et al. (2006) revealed that soil C contents and above- and below-ground plant growth increased under eCO_2 in experiments receiving high N treatments. In another study, eCO_2 increased soil organic matter decomposition in nitrogen-added treatments (22%) as compared to only 18% decomposition without nitrogen (Cheng and Johnson, 1998). Probably high C:N ratio under eCO_2 suppressed the microbial activity r-strategic microorganisms thus decreasing rate of decomposition, while addition of nitrogen lowered the C:N ratio thus promoting microbial growth and subsequently decomposition by fast growers. In a short-term experiment (64 days), Paterson et al. (2008) studied the effect of eCO_2 (570 ppm) and nutrient amendments in soil-grown perennial ryegrass and quantified the relative use of plant- and SOM-carbon by microbial communities using phospholipid fatty acids (PLFAs) analysis. Elevated CO_2 and nutrient amendment resulted in increased root growth and rhizosphere volume along with increased rates of SOM-mineralisation. However, the treatments did not affect the balance of microbial-C use and hence the soil C-balance. The study demonstrated that plant-induced priming of SOM-mineralisation can be driven by increased root growth. However, it is important to consider that although changes in root C-deposition quality may not occur during the initial response phase to elevated CO_2, effects may become apparent when plant growth has acclimated and a new equilibrium is established coupling plant and soil processes. For example, progressive nutrient limitation under elevated CO_2 may result in decreased nutrient content and increased recalcitrance of leaf and root litter (Paterson et al., 2008). As the recalcitrant inputs require specific microbial communities for their decomposition, impacts of elevated CO_2 on microbial communities may take a considerable time to develop as indicated in a study by Grayston et al. (1998), on *Danthonia richardsonii* (Australian grass). The microbial communities from the rhizosphere of *D. richardsonii* grown for four years at twice ambient CO_2 had significantly greater utilisation of carbon sources with a high C:N ratio indicating a change in microbial community composition suggesting that under elevated CO_2 compounds with a higher C:N ratio were exuded. Nitrogen was an additional rate-limiting factor for microbial growth in soil and had a significant impact on the microbial response to elevated CO_2. Microbial populations were higher in the rhizosphere of plants receiving the highest N application, but the communities receiving the lowest N application were most active metabolically (Grayston et al., 1998). However, eCO_2 only caused accumulation of soil C when N was added at rates well above typical atmospheric N inputs (30 kg $ha^{-1}\,yr^{-1}$), as revealed by a meta-analysis performed by van Groenigen et al. (2006).

Biological nitrogen fixation is suggested to be another source of soil nitrogen. Symbiotic nitrogen fixation across several types of plant–microbe associations is positively influenced by eCO_2 (Aronone and Gordon, 1990; Thomas et al., 1991; Tissue et al., 1997). Xu et al. (2013) reported increased abundance of *nif*H gene (involved in N fixation) at eCO_2. At eCO_2, the increased *nif*H abundance indicate potential increase of soil microbial N_2 fixation and such increase could supplement N for the plant growth. However availability of nutrients required for N_2 fixation (e.g., phosphorus, molybdenum, and potassium) is a constraint (van Groenigen et al., 2006). Mycorrhizae, due to extended hyphae, can mobilize nutrients in nutrient rich soils thus maintaining nutrient balance in the rhizosphere and promoting the associated bacterial communities. Inoculation of white clover with *Glomus claroideum* or *Glomus intraradices* species complex stimulated biological nitrogen fixation resulting in improved N concentration in leaves

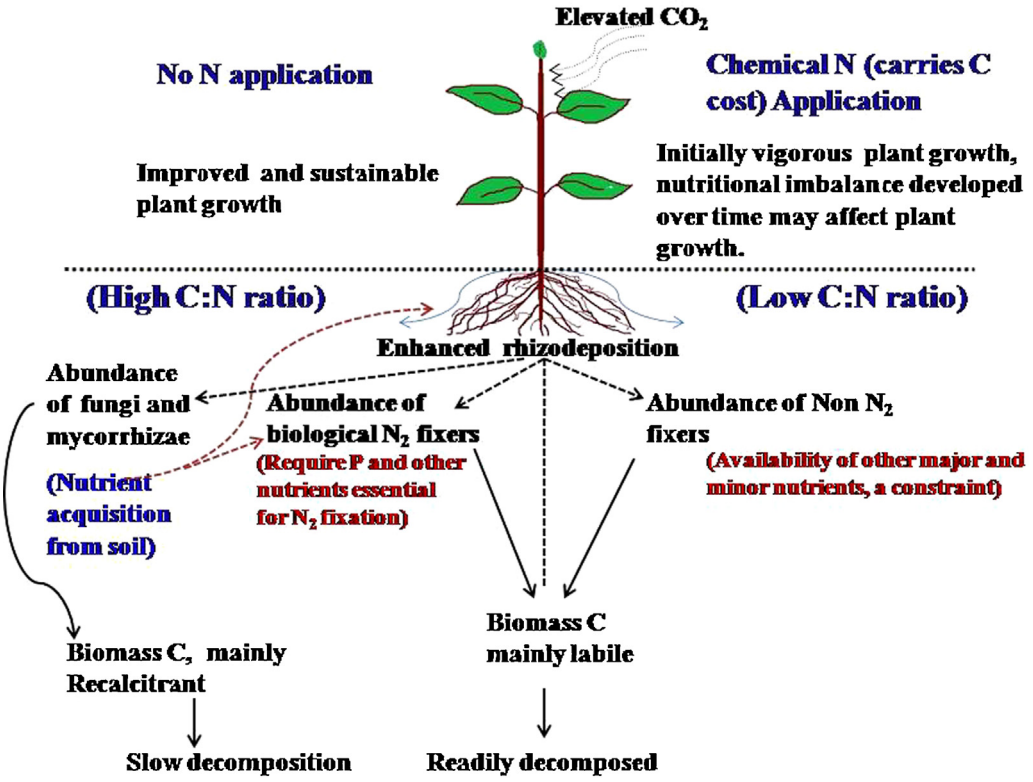

Fig. 2. A conceptual representation of how N availability can influence the effect of elevated CO_2 on N-fixing and non-N-fixing microbial communities.

(Gamper et al., 2005). Thus combinations of biological nitrogen fixer and nutrient mobilizers such as mycorrhizae in agriculture can be a strategy to improve C-sequestration potential. Cyanobacteria are also attractive candidates which besides N-fixing efficiency possess an essential C concentrating mechanism (CCM), which concentrates CO_2 at the site of photosynthetic carboxylation (Badger and Price, 2003).

These results suggest that the main driver of soil C-sequestration is soil C input through plant growth, which is strongly controlled directly by N availability and indirectly by nutrients needed to support N_2 fixation. Synthetic fertilizers provide no additional organic matter themselves but do carry a C cost and also affect soil health. Therefore promotion of combinations of biological N_2 fixers and nutrient solubilizers/mobilizers can be a sustainable and economic way for supporting soil C-sequestration in agricultural ecosystems. A conceptual representation of how N availability can influence the effect of elevated CO_2 on N-fixing and non-N-fixing microbial communities is depicted in Fig. 2. Increased exudation under eCO_2 causes increase in C:N ratio in the rhizosphere. Addition of chemical nitrogen lowers C:N ratio and also stimulates growth of non N_2-fixing bacterial communities with labile C. Low C:N ratio improves plant growth thus increasing C sequestration through plant biomass and rhizodeposition. However non-availability of nutrients other than N over time may become a constraint. Further chemical N does not add additional organic matter and its production carries a C cost. On the other hand, high C:N ratio under eCO_2 promotes biological N_2-fixer which can fulfill N requirement of plant. Promotion of fungi mainly the mycorrhizae under eCO_2 may improve nutrient availability for plants and N_2 fixers. Further, C assimilated in fungal biomass is more protected and add to recalcitrant C pool. We suggest that promotion of mycorrhizae and biological N_2 fixer can be the key to C sequestration under eCO_2 conditions, in a sustainable manner.

5. Plant associated microorganisms and C-sequestration under elevated CO_2

The balance between organic matter inputs (plant residues, roots and rhizodepositions) and organic matter losses (respiration, decomposition) determine soil C levels. Small changes in equilibrium between inputs and output can have a significant impact on the atmospheric CO_2 concentration, which may either exacerbate or reduce the consequences of increasing CO_2 concentration in atmosphere (Schimel, 1995). Organic C taken up by the microorganisms is partitioned between biomass production, and respiration. The microbial C input to the soil depend on the microbial growth efficiency (MGE) i.e. the amount of new biomass C produced per unit substrate C metabolized, degree of protection of microbial biomass in the soil and the rate at which microbial byproducts are decomposed by other microorganisms (Six et al., 2006). The lower the MGE and degree of protection of the microbial biomass the more microbial organic matter C is lost as CO_2. Bacterial-dominated microbial communities are associated with higher rates of CO_2 respiration (Six et al., 2006), thus have low C assimilation efficiency as compared to fungi-dominated microbial communities. Arbuscular mycorrhizal (AM) fungi are probably the most abundant component of the fungal community in most agricultural soils. In some systems, the

Table 2
Effect of elevated CO_2 on plant pathogens.

Target organisms and disease	Test plant	Observed effect of eCO_2	Elevated/ ambient CO_2 levels (ppm)	Reference
Erysiphe graminis (powdery mildew)	Barley (*Hordeum vulgare*)	Elevated CO_2 caused a reduction in the percentage of conidia that progressed to produce colonies in plants	700/350	Hibberd et al., 1996;
Colletotrichum gloeosporioides (anthracnose)	Pencilflower (*Stylosanthes scabra*)	Reduction in spore germination, extension of incubation period and reduction in anthracnose severity at eCO_2	700/350	Chakraborty et al., 2003
Phyllosticta minima (leaf spot)	Red maple (*Acer rubrum*)	Significant reduction in disease incidence under eCO_2	200 above ambient	McElrone et al., 2005
Leaf spot	Stiff goldenrod (*Solidago rigida*)	The incidence of disease was reduced by half under eCO_2 concentrations	560/368	Strengbom and Reich, 2006
Potato virus Y	Tobacco (*Nicotiana tobacum*)	Reduction in the titre of viral coat-protein under eCO_2 due to accumulation of phenylpropanoids	1000/350	Matros et al., 2006
Cronartium quercuum (rust) and *Fusarium circinatum* (pitch canker)	Loblolly pine (*Pinus taeda*)	Disease incidence was decreased by exposure to elevated CO_2	720/360	Runion et al., 2010
Cronartium quercuum (rust)	Red oak (*Quercus rubra*)	Increased in the latent period (time to sporulation) of Cronartium quercuum.	720/360	Runion et al., 2010
Colletotrichum gloeosporioides (anthracnose)	Shrubby stylo (*Stylosanthes scabra*)	Significant increase in number of lesions under eCO_2	700/350	Pangga et al., 2004
Pyricularia oryzae Cavara and *Rhizoctonia solani* (leaf blast)	Rice (*Oryza sativa*)	Elevated CO_2 increased the susceptibility of rice plants to leaf blast	200 to 280 above ambient	Kobayashi et al., 2006
Peronospora manshurica (downy mildew), *Septoria glycines* (septoria) and *Fusarium virguliforme* (sudden death syndrome)	Soybean (*Glycine max*)	Elevated CO_2 reduced downy mildew disease severity. But increased brown spot severity and without effect in sudden death syndrome	550/ambient	Eastburn et al., 2010
Erysiphe cichoracearum (powdery mildew)	Arabidopsis (*Arabidopsis thaliana*)	Significant increase in the number of established colonies (networks of mycelia) on mature leaves under eCO_2 together with increase in stomatal density, guard cell length, and trichome numbers on leaves under eCO_2	800/400	Lake and Wade, 2009
Alternaria alternata (leaf spots and blights)	Timothy grass (*Phleum pretense*)	Significant increase in sporulation under eCO_2	600/300	Wolf et al., 2010

predominant way in which carbon enters the SOM pool is via mycorrhizal networks, potentially exceeding the input via leaf litter, root leachate and fine root turnover (Godbold et al., 2006). Further, fungal cell walls contain polymers of melanin and chitin which are resistant to degradation whereas phospholipids, main components of bacterial cell wall membrane are energy rich, readily decomposable substrates available to a wide range of soil microorganisms. The storage of C is expected to be more persistent when mediated by fungal biomass and more labile when mediated by bacterial biomass (Bailey et al., 2002). Thus the ecosystems with fungal-dominated soil communities may have higher C retention than soil communities dominated by bacteria (Six et al., 2006; Clemmensen et al., 2013).

However, Cheng et al. (2012) through microcosm and field experiments challenged the assumption that AMF protect against degradation of organic C in soil by demonstrating that CO_2 enhancement of AMF results in considerable soil C losses through increased decomposition of organic matter. Studies conducted in scrub-oak and chaparral ecosystems, revealed increased fungal to bacterial ratio and higher rate of soil organic matter decomposition in the soils exposed to eCO_2 (Lipson et al., 2005; Carney et al., 2007). The increase in rate of decomposition was related with increased levels of organic matter degrading enzymes indicating that altered microbial communities producing C degrading enzymes can cause a potential C sink to become a C source. Similar observations were made by Hungate et al. (1997) based on their experiment on carbon budgeting of two grassland ecosystems (serpentine and sandstone) exposed to eCO_2 for three years. Elevated CO_2 increased ecosystem carbon uptake, but greatly increased carbon partitioning to rapidly cycling carbon pools below ground. From this study it was concluded that elevated CO_2 concentration caused a greater increase in carbon cycling than in carbon storage in grasslands.

Xu et al. (2013) used high-throughput functional gene array (GeoChip 3.0) to examine the composition, structure, and metabolic potential of soil microbial communities from a grassland field experiment after ten-year field exposure to eCO_2 (560 ppm) and observed a shift in composition and structure of functional genes involved in C cycling with a general increase in abundance at eCO_2. Three key C fixation genes increased significantly at eCO_2, including Rubisco for the Calvin–Benson–Bassham (CBB) cycle, CODH (carbon monoxide dehydrogenase) for the reductive acetyl-CoA pathway and propionyl-CoA/acetyl-CoA carboxylase PCC/ACC for the 3-hydroxypropionate/malyl-CoA cycle. Further, significant increase in the abundance of genes involved in degradation of labile C substrates (such as starch, hemicellulose and cellulose) was observed, whereas no significant change was observed in the abundance of genes involved in recalcitrant C (e.g. lignin) degradation. These results indicated that eCO_2 significantly affected metabolic potentials for C fixation and degradation. However, such changes had little effect on soil C storage, probably due to accelerated degradation of labile C and not the recalcitrant C.

Further, high C:N ratio under eCO_2 may affect the quality of plant organic matter. The plant organic matter with high C:N ratio is not decomposed readily and that may slow the rate of degradation (Batjes and Sombroek, 1997). Denef et al. (2007) analyzed ^{13}C signatures in microbial biomarker phospholipid fatty acids (PLFA) from an *in situ* $^{13}CO_2$ pulse-labeling experiment in the Gießen free-air CO_2 enrichment grasslands (GiFACE, Germany) exposed to ambient and elevated (i.e. 50% above ambient) CO_2 concentrations. The study indicated a dominant role of fungi within 10 hrs of rhizodeposits assimilation and retention of significant amount of assimilated rhizosphere C in fungal biomass for 11 months as well as possible translocation of the rhizosphere-C from the fungal to bacterial biomass. Similarly, microbial community composition under eCO_2 studied by using extracellular enzyme activity assays, PCR-DGGE analyses, substrate-induced respiration measurements, and 16S rRNA clone libraries suggested stimulated fungal pathways. Drigo et al., (2013) studied the effects of prolonged eCO_2 on microbial C flow and microbial communities in the rhizosphere of a non-mycorrhizal plant sand sedge (*Carex arenaria*) and a mycorrhizal plant Red fescue (*Festuca rubra*) grown at ambient and eCO_2 concentration (350 and 700 ppm) for 3 years by assessing C flow by ^{13}C pulse-chase experiments. It was observed that the mycorrhizal plant exerted a greater influence on both bacterial and fungal communities under eCO_2. Rhizodeposited C first processed by AMF was subsequently transferred to bacterial and fungal communities in the rhizosphere soil. As the studies indicate that soil carbon may enter the soil organic matter pool predominantly via mycorrhizal networks. Thus increased dominance of mycorrhizal fungi under eCO_2 will increase the residence time of SOC thus helping in soil C sequestration.

6. Altered plant–pathogen interactions and C sequestration

Soil C-sequestration under eCO_2 will also be influenced by pathogenic microorganisms. Both positive and negative effects of eCO_2 have been reported on plant pathogens (Table 2). Though eCO_2 effects on the host may give beneficial effects, the impacts on pathogen cycles in terms of increased spore production capacity, faster multiplication rates and aggressiveness may nullify these positive effects. Further increased plant biomass and canopy size may become more conducive for rusts, mildews, leaf spots and blights development. Increased pathogenic potential or alien invasive species may cause extensive damage to crops and tree ecosystems. Foliage loss in plants will affect photosynthetic C assimilation and will also increase the plant litter. However high C:N ratio as a consequence of plant growth under elevated CO_2 may slow down the decomposition rate or the plant litter (Norby et al., 2001). However increased retention time of plant litter may extend survival of plant pathogen in the soil.

In contrast, delay in the establishmet of pathogens under eCO_2 due to modifications in pathogen aggressiveness and/or host susceptibility may increase C-sequestration potential due to increase in plant biomass. Altered plant physiology due to under eCO_2 may also affect source/sink relationship under pathogen attack. For example increase in stomatal density under eCO_2 would facilitate higher rates of C assimilation however an increase in stomatal numbers would also increase chances for pathogens for colonization (Ainsworth and Rogers, 2007). Accumulation of phenolic compounds under eCO_2 may cause down regulation of photosynthesis (Swarbrick et al., 2006). Intensive research and development of mathematical models on different host–pathogen interactions under eCO_2 can help in assessing their net effect on the source/sink relationships.

7. Conclusions and future prospects

Doubtlessly, eCO_2 will influence biological systems including rhizosphere microorganisms directly or indirectly and microbes will play important role in future climate scenarios. However the complexity of interaction between rhizosphere microbial communities and their surroundings make it difficult to pin point the responses of different soil microbes to eCO_2. It is clear from the present review that eCO_2 could lead to community shifts and altered metabolic activity in microorganisms involved in soil nutrient cycling. ECO_2 may also cause alterations in survival and virulence of plant pathogenic microorganisms. It is observed from different studies that, fungal communities due to wider C:N ratio, persistent C storage and ability to improve soil structure are likely to play important role in soil C-sequestration. However non-

availability of nitrogen and other nutrients could be a constraint in soil C-sequestration. Biological nitrogen fixers and nutrient solubilizers and mobilizers have scope to play important role in maintaining soil nutritional balance under eCO_2 conditions. However, complexity of interactions between physical, biological and chemical factors will require intensive interdisciplinary research efforts at local level with the option to scale up to global level, to understand the long-term responses of soil microbial communities to eCO_2 and assess the conditions required for efficient C-sequestration through plant–microbe interactions. Performance based selection of rhizosphere microorganisms under eCO_2 conditions may be the future key for their promotion/application in agriculture.

Acknowledgements

The authors of this manuscript are thankful to Indian Council of Agricultural Research for providing support under NICRA (National Initiative on Climate Resilient Agriculture) project. We also thank anonymous reviewers for their valuable comments on an earlier version of this manuscript.

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