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Review Article

Structural and Functional Relationships Between Plant and Soil Microbial Communities for the Management of Grasslands

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Abstract

Plant and soil microbial communities were dependent on each other being producer and decomposer, respectively, in the terrestrial ecosystems. Any change between these two communities was likely to alter the structure and function of the ecosystems. Grasslands were complex ecosystems where interactions occurred among plants, soil microbes, grazing animals and the human interventions. However, it remained unclear whether there was any pattern of relationship between plant and soil microbial communities in the grasslands. This study was aimed to study the structural and functional relationships between plant and soil microbial communities at both spatial and temporal scales. Data revealed significant effects of vegetation on the structure of soil microbial communities. Results also showed differences in microbial biomass and community composition between unimproved and improved grasslands indicating the influence of management activities. Although some studies showed significant effect of plant diversity on microbial diversity and community composition relatively less evidence were found in favor of a positive relationship between these two communities. Data also revealed the difference in soil microbial functions between grasslands with different disturbance regimes: soil microbes of the unimproved grasslands were more efficient in carbon and nitrogen mineralization than those in the improved grasslands. This review was relevant for the management and conservation of the grassland ecosystems as well as for enhanced knowledge about the ecological mechanisms by which diversity and composition of plant and soil microbial communities were regulated and maintained.

Key words: Grasslands, microbial communities, nitrogen mineralization, plant diversity, soil microbes, ecological mechanisms, microbial diversity

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INTRODUCTION

Plant and soil microbes were dependent on each other as producer and decomposer, respectively in the terrestrial ecosystems. Plants provided soil microbes with carbon substrates through litter and root exudates and soil microbes, on the other hand, supplied plants with nutrients by breaking down the organic matter¹⁻³. Any change in the relationship between these two biotic communities was likely to alter the structure and functions of the ecosystems. Understanding the mechanisms that might control microbial community structure and function had important implications for conservation and management of biodiversity as well as for the improvement of soil fertility⁴.

Grasslands, one of the most complex ecosystems on Earth, showed interactions among plants, soil microbes, grazing animals and human interventions and experience various disturbances including grazing, trampling, sowing, mowing and fertilization^{5,6}. One of the human interventions, commonly practiced in the grasslands was the conversion of unimproved to improved grassland in order to increase its productivity⁷. A number of management activities like sowing of pasture species and application of chemical fertilizers were done while such conversions were made in grasslands⁸. This modification in plant community composition and soil fertility altered the microbial communities in soil through the changes in plant growth, biomass allocation, photosynthetic rate, litter quality and water use efficiency⁹. Changes in microbial communities, in turn, might influence decomposition processes and hence the aboveground plant community⁵ via changes in nutrient availability. Therefore, the importance of studying soil microbial communities in grasslands were realized over the decades as such changes were likely to interfere with the soil functions including organic matter decomposition and nutrient mineralization processes and hence, plant productivity and soil fertility⁶.

Study on the links between plant and soil microbial communities remained limited in the past since these two communities were studied by plant and microbial ecologists separately as well as due to the nature of tremendous diversity of the microbes in soil and methodological limitation to study them^{1,10}. Although culture dependent methods provided limited data on the diversity of soil microbes, culture-independent methods like fatty acids profiling and PCR-based molecular approaches had paved the way to investigate whole microbial communities in soil¹⁰.

Grasslands played the important role in agriculture by providing food, forage and livestock and by serving aesthetic values and by maintaining biodiversity and atmospheric carbon balance through sequestering organic carbon from the atmosphere^{7,11}. However, grasslands became one of the most imperiled ecosystems in the world and were facing increasing threats by multiple anthropogenic activities causing loss of biodiversity and degradation of habitats¹². Moreover, it is not yet exhaustively explored whether plant diversity could drive soil microbial diversity in the grassland ecosystems¹³. Integrated approach to study the ecological association between plant and soil microbial communities were not substantially available^{8,14,15}. This study, therefore, reviewed the studies on the structural and functional relationships between plant and soil microbial communities in order to enhance the understanding for better management and conservation of the grassland ecosystems.

BASIS FOR RELATIONSHIPS BETWEEN PLANT AND SOIL MICROBES

Plants can influence soil microbial communities through several ways including root exudates, litter, belowground root biomass and root systems creating microhabitats¹⁴. The quality, quantity and heterogeneity of plant derived resources were the important drivers for microbial community structure in soil since these carbon sources were used as substrates by the soil microbes (Fig. 1). Plants released carbon as rhizodeposits, in the rhizosphere and the entire pool of these rhizodeposits could reach up to 40% of the photoassimilates allocated to the roots¹⁶. Plant litter was another important factor that influenced soil microbial communities¹⁷. In addition to aboveground plant litter, belowground plant parts which might be larger than that of the aboveground in primary productivity¹⁸ after death could be a potential driver of the soil microbes. Plants also influenced soil microbial diversity through creating heterogeneity of rhizodeposits and microhabitats⁸. High plant diversity was likely to supported high microbial diversity through diverse rhizodeposits and microenvironment⁸.

The variation in quality and quantity of the plant-derived resources acted as the key factors in influencing the abundance, composition, diversity and functions of the soil micro-organisms^{9,12,19,20}. While high quality litter (N-rich) enhanced the bacterial community, on the other hand, poor quality litter (phenolics-rich) enhanced fungal community in soil²⁰. The quality of litter inputs also determined both the genetic structure of the soil microbial communities and their substrate use patterns, which might have effects on soil microbial structure^{21,22}.

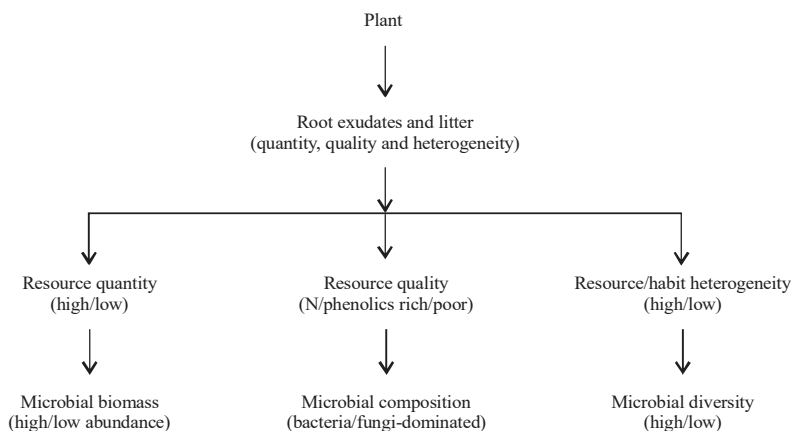


Fig. 1: Schematic diagram showing the basis for relationships between plant and soil microbial communities

Soil microbes, in turn, could drive the above ground plant communities since microbes played the key role in making nutrients (e.g., carbon, nitrogen, phosphorus and other mineral elements) available for plants²³. Soil microbes also influenced the growth and distribution of plants by competing for nutrients, antagonistic and beneficial effects as pathogen and growth promoting factor, respectively^{24,25}. The linkage between plant and soil microbial communities operated at a wide range of spatial and temporal scales^{20,26}. Spatial variability in soil microbial community might occur at scales from millimeters to hundreds of meters²⁷. Temporal linkages between plant and soil microbes might operate over a hierarchy of timescales ranging from short terms of diurnal and seasonal, through intermediate timescales of tens of thousands of years to long timescales of thousands of years to millennia²⁶. Spatial and temporal variation in plant-derived resources such as root exudates and litter might be responsible for the changes of soil microbial community structure²⁸.

LIMITATIONS IN STUDYING MICROBIAL COMMUNITIES

Study on the relationships between plant and soil microbial communities was hampered in the past due to the approach of studying soil microbes and plant communities by plant and microbial ecologists separately, tremendous diversity of microbes in soil and the lack of an appropriate technique to study them^{9,11,29}. Culture-dependent methods like colony counting in plate culture and community level physiological profiling provided limited information on microbial composition and diversity in soil since the methods were selective^{10,30}. On the contrary, culture-independent methods such as phospholipid fatty acid (PLFA) profiling and molecular techniques paved the way to better understanding about the soil microbial community composition and diversity, although these methods had their own merits and demerits¹⁰.

For instances, biochemical methods were useful for the estimation of microbial biomass, but not for studying microbial diversity. Molecular fingerprinting method, on the other hand was useful for studying genetic diversity, but not for estimating microbial biomass. Although analysis of rRNA gene in studying microbial diversity was popularly being used it had some limitation in linking community with ecosystem function, for example, until now, most of the studies of microbial diversity focused on the diversity of ribosomal gene sequences¹⁰. However, microbes with the same ribosomal gene sequences were often functionally diverse. Thus, to link microbial diversity with the ecosystem function it was necessary to focus on functional traits and functional genes that were important for biogeochemical processes³¹. Therefore, methodological improvement was important for better understanding about the linkage between plant and microbial communities in soil.

Grassland ecosystems: Grasslands were one of the complex terrestrial ecosystems with the components of plants (as producers), soil microbes (as decomposers), grazing animals (as consumers) and human interventions interacting with each other (Fig. 2). A semi-natural grassland was characterized as relatively less disturbed system without application of fertilizers, but encountered by disturbances such as grazing, trampling and burning⁵. An improved grassland, on the other hand was manipulated by human management activities like sowing, mowing and fertilization. Intensity of grazing might influence the vegetation structure of the grasslands: high grazing intensity resulted into the formation of short-grass vegetation and relatively less or no grazing resulted into the formation of tall-type vegetation⁸. Overgrazing might caused the removal of perennial grasses and led to shrub invasion and sometimes might result in the widespread replacement of perennial grasses by forbs and annual grasses^{12,32}.

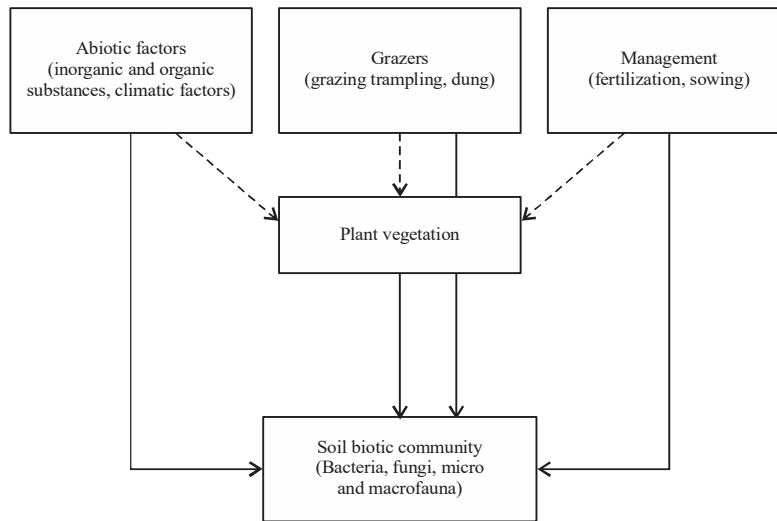


Fig. 2: Schematic diagram showing the major components of an improved grassland ecosystem. Unbroken and broken lines indicate the direct and indirect effects of the components, respectively

Grasslands are the largest land-use system on Earth occupying 30% of the world's ice-free surface and contributing 40% of global agricultural gross domestic product³³. Grasslands were distinct in structure and function compared to other ecosystems and they supported uniquely large and active soil microbial community⁶. Microbial communities in grassland soil were influenced directly or indirectly by a number of factors including plant vegetation, grazing animals and management activities such as; fertilization and sowing of pasture species (Fig. 2).

Grazers influenced soil microbial community through producing dung, trampling and reducing organic matter³⁴. Readily available nutrients in dung stimulated microbial growth and functions. Trampling stimulated root exudation and microbial growth in soil³⁴. Invertebrate herbivores often feed preferentially on dicotyledonous herbaceous plants that produce superior litter quality than grasses indicating their potentials in influencing the belowground microbial communities³⁵.

Fertilization altered microbial community structure and functions directly or indirectly through changed in vegetation. Increased fertilization with nitrogen and phosphorus stimulated growth of plants as well as enhanced production of high quality litter and hence favored bacterial growth²⁰. Sowing legume species such as *Trifolium repens* stimulated fertility of soil through increased biological nitrogen fixation from the atmosphere into the soil¹⁸.

Grassland ecosystems often experienced modifications to maximize the efficiency of conversion of solar energy or plant mass into animal product³⁶. Management activities that were commonly practiced in grasslands included fertilization,

sowing and mowing. Grasslands experienced disturbance with various intensity as well as with the variation in number and size of grazing animal, period and intensity of grazing and frequency and quantity of fertilization. These management activities interacted with the components of the grassland ecosystems resulting characteristic features including changes in plant community composition^{8,37-39}. Grazing, therefore, had the potential to influence decomposer community directly through excreta and indirectly through increased root exudation as well as plant litter^{19,40}.

Plant-microbe relationships at spatial scales

Microbial biomass and community composition in relation

to plants: Structural relationships between plant and soil microbial communities might operate at both spatial and temporal scales^{1,27}. Study showed significant effect of vegetation on structuring soil microbial communities⁴¹. Microbial biomass was compared among different land-use types and the lowest microbial biomass was found in the bare ground compared to other land uses like agricultural lands, forests and grasslands and such difference was attributed to the effects of vegetation. When soil microbial biomass was compared between grazed and ungrazed sites of a tropical grassland of Queensland in Australia, high microbial biomass was reported in the ungrazed control sites than the grazed sites⁴². The reason for higher microbial biomass in the ungrazed grassland was attributed to the high plant-derived resources and it was postulated that heavy grazing might have reduced the organic materials and carbon into the soil that limited resources available for the microbial growth. By using community level physiological profiles, it was found that

floristic composition and carbon substrate utilization patterns of rhizobacterial communities were more diversified in unfertilized than fertilized plots⁴³. This result was explained in the way that the development of *Convolvulus arvensis* and legumes (*Trifolium pratense* and *Trifolium repens*) might maintain observed floristic diversity in the unfertilized plots. Another study reported higher cultivable bacteria and total bacterial biomass evaluated by PLFA profiles in the improved grasslands than that in the unimproved grasslands indicating the stimulation of bacterial growth by the enhanced nutrients in the fertile soil⁴⁴.

In experimentally modified grassland, a significant positive correlation was observed between plant diversity and soil microbial biomass as measured by substrate induced respiration⁴⁵ as well as with microbial composition⁴⁶. Result was explained in the way that relationships of microbial biomass largely resulted from higher level of plant productivity associated with greater diversity, rather than from plant diversity *per se*. Although synergistic effects of the diversity of grassland plant species on microbial biomass was reported by previous research⁴⁷, it was explained in the way that the effect was dependent on what species and how many species were present. It was also observed that soil microbial biomass and functions were influenced, in part, by changes in litter diversity associated with the management activities⁴⁸.

Plant species richness influenced the soil microbial biomass in an experimentally modified grassland⁴⁹. This experiment also revealed that the positive effect of plant diversity was mainly mediated by higher leaf area index resulting in higher soil moisture in the top soil layer. Their study also showed that the fungal-to-bacterial biomass ratio was positively affected by plant functional group richness and negatively by the presence of legume indicating the influence of litter quality on microbial community composition.

Analysis of PCR-based DNA fingerprint patterns did not show any relationship of bacterial community composition with plant species, however, it showed relationship with plant community composition and data also revealed more influence of topography and other environmental factors in driving bacterial community composition in grassland soils⁵⁰.

Effect of cutting on arbuscular mycorrhizal fungal colonization in roots was compared among different plant species by using molecular approach and it was found that cutting caused much more change in arbuscular mycorrhizal fungal flora in *Miscanthus sinensis* roots than in *Zoysia japonica*¹⁴ indicated that effects of cutting on mycorrhizal association in soil depended on the identity of plant species perhaps due to interspecies variation in the root exudates.

Coverage by the tall grass *Miscanthus sinensis* decreased with the increase of grazing intensity, however, that by *Pleioblastus chino* did not change over the period of 4 years in a semi-natural grassland in Japan³⁹. Results also demonstrated that the degrees of AM fungal colonization and spore population in the rhizosphere did not show remarkable change during the period of 4 years. These results implied that the AM fungal community in the semi-natural grassland might remain stable despite changes in the coverage of some dominant plant species over time. Since mycorrhizae played important role in plant community organization and nutrient availability in soil²⁵ knowledge about plant-mycorrhizae interactions might be of great importance for the management of grassland ecosystems.

RELATIONSHIPS BETWEEN PLANT AND SOIL MICROBIAL DIVERSITY

Considerable interest grew on studying the relationship between plant and soil microbial diversity from the aspects of biodiversity conservation. A significant positive correlation between plant species richness and microbial functional diversity was observed in temperate grassland of China⁵¹. This relationship between plant and soil microbes was explained in the way that aboveground plant biomass increased with the increase of plant species richness enhancing nutrient flow to the soil which might had contributed to the positive effects on the soil microbial community. Increased plant productivity increased soil carbon input through enhanced turnover of plant biomass and root exudation which might had influenced carbon limited microbial communities in the soil^{45,51}. However, functional diversity of soil microbes did not necessarily indicate species richness. At local scale, field data collected from the Shiriyazaki grasslands in Japan, by using DNA band counting on PCR-DGGE analysis revealed that diversity of soil fungi was positively correlated with the plant species richness⁸. This study suggested that herbivores influenced soil biological community through their indirect effects on productivity and composition of plant community in the semi-natural grasslands. However, richness of all fungi and functional groups were causally unrelated to plant diversity, with the exception of ectomycorrhizal root symbionts at the global scale⁵². All these results suggested that effects of plant diversity on the fungal diversity could be related with the range of spatial scale of the study area, functional groups and methodological approaches such as: the kind of markers, universal or species specific used to study fungal diversity in soil.

Soil bacterial activity and number of substrates used and catabolic diversity were measured in different plant communities using BIOLOG GN and GP microplates and the results showed that culturable soil bacterial activity and diversity was higher in the four-species plant community than in any of the plant monocultures⁵³. Catabolic activity and catabolic diversity of culturable soil bacteria were studied as their abundance and functional diversity, respectively in experimental grassland ecosystems, where plots were planted with different level of species richness and functional type and results showed that both these parameters increased linearly with the logarithm of plant species number and with the number of plant functional groups⁵⁴. This result was explained in the way that the effects might have been caused by an increased diversity and quantity of material and energy flows to the soil as well as by increased diversity of soil microhabitats via stimulation of the soil fauna.

Other study reported that bacteria was more closely related to abiotic differences caused by plant diversity, while fungi was more affected by plant-derived organic matter inputs⁴⁹. Bacterial diversity as evaluated by rDNA fragment analysis showed a negative correlation with the soil fertility (soil P) indicating a productivity-diversity relationship⁴³. These results suggested that fungi and bacteria perhaps maintained different mechanisms for their diversity in the grassland ecosystems; nevertheless, further data is needed to predict such relationships between these two communities in soil.

PLANT-MICROBE RELATIONSHIPS AT TEMPORAL SCALE

Relationships between plant and soil microbial community might occur at varied timescales ranging from short term of diurnal to long timescales of thousands of years to millennia²⁶. Seasonal variation of soil microbial communities in grasslands were reported by a number of studies, although no consistent patterns appeared. Some studies reported higher microbial biomass in spring than other seasons of the year⁵⁵. The reason behind such a high active microbial biomass in spring was attributed to the mobilization of the soil organic matter accumulated over the winter resulting from higher amount of litter fall during autumn compared to other seasons of the year. Soil microbial community composition studied by molecular marker also showed significant seasonality and it was reported that microbial biomass grew to its highest levels during the winter and early spring, when soils were frozen¹⁵ and the reason was attributed to the fact that shortly after the snow melted in the spring, biomass began to rapidly turn over when nutrients were available and biomass levels were

dynamic throughout the summer. On the contrary to these results, some studies reported higher soil microbial biomass in summer associated with the seasonal variation of temperature and soil moisture⁵⁶. The highest biomass of fungi was found in spring while that of bacteria was found in summer in the Shiriyazaki grasslands, Japan⁵⁷.

Experimental data showed that functional diversity of soil microbial communities varied significantly with time of sampling and plant community composition and phenology⁵⁵. This study reported that diversity of soil bacteria increased with the increase of plant diversity. They explained their results in the way that differences in the composition of rhizodeposits existed between different plant species but also, for the same plant species between developmental stages. Variation in the C and N distribution between aboveground and root biomass during the vegetation cycle probably induced a variation of rhizodeposition which might influence the microbial communities in soil⁵⁵.

Soil microbial communities in grasslands showed seasonal variation which could be related with the seasonal fluctuation of the temperature and other environmental conditions^{57,58}. Microbial communities evaluated by PLFA profiles showed seasonal variability⁵⁷. Data of this study showed significant differences in total microbial, total bacterial, Gram-positive bacteria and mycorrhizal biomass among the seasons in the semi-natural short-type grasslands. Bacterial biomass in the short-type grassland was significantly and negatively correlated with soil moisture content. In the improved grasslands, total bacterial biomass was affected by seasons, but it did not correlate with soil physico-chemical properties. Fungal biomass, on the other hand, showed a large seasonal effect only in the semi-natural tall-type grasslands and it was correlated with soil C:N ratio⁵⁸. These results suggested that linkage between plant and soil microbe at temporal scale might be related to site under study and history of the vegetation establishment.

FUNCTIONAL LINKAGES BETWEEN PLANT AND SOIL MICROBES

Since microbial communities played the key role in decomposition of organic matter and mineralization of nutrients in soil study on their relationships with plant composition was of interests for the management of grassland ecosystems. Microbial functions in the grassland soils were influenced by a number of factors such as; species identity, vegetation composition and disturbance regimes^{17,57}.

Table 1: Features of semi-natural and improved grasslands

Semi-natural grassland	Improved grassland
Disturbance intensity	
Low grazing intensity	High grazing intensity
No chemical fertilization	Chemical fertilization
No sowing and mowing	Sowing and mowing
Vegetation	
Slow growing plant species	Fast growing plant species
Low quality litters (Phenolics-rich)	High quality litter (N-rich)
Dominated by tall grass	Dominated by short grass
Soil chemical properties	
Low N and P contents	High N and P contents
High C content	Low C content
High C/N ratio	Low C/N ratio
Soil microbial community	
Fungi-dominated	Bacteria-dominated
K-strategists	R-strategists
Less nutrient-use by microbes	High nutrient-use by microbes
Low soil respiration rate	High soil respiration rate

Source: Sugiyama *et al.*⁸, Wardle²⁰, Pasternak⁵⁸, Grime⁶¹

Analysis of community level physiological profiles showed that functional diversity of the soil bacterial community was linearly correlated with the number of plant species and functional groups in an experimental grassland ecosystem⁵⁴. The reason of such relationship was attributed to the diversity and quantity of the energy flows to the soil as well as to the increased diversity of the soil microhabitats. Data from experimentally modified microcosms also demonstrated the greater importance of plant functional type on microbial functions rather than diversity *per se*¹⁷. A number of studies revealed that unfertilized grasslands had larger and more active soil microbial communities than the fertilized grasslands^{6,55,59}. The reason of higher microbial biomass in the unfertilized grasslands was explained in the way that unfertilized grasslands tended to be more botanically diverse than fertilized sites which could lead to a supply of more diverse plant litter to the soil system.

Grasslands under different management regimes showed difference in microbial functions in soils^{39,44,55,60}. Unimproved grasslands dominated by slow-growing plant species were fungi-based microbial community while improved grasslands, dominated by fast-growing plant species were bacteria-based microbial community²⁰. Microbial communities of these two different grasslands differed in their respiration rate and carbon utilization patterns too; improved grassland showed higher rates of respiration and utilization of sugars and citric acid and unimproved grassland showed a lower respiration rate, but greater utilization rate of carboxylic acids, phenolics and neutral amino acids⁴⁴. These results, thus, indicated the influence of grazing intensity on structuring soil microbial community structure and function via changes in plant communities (Table 1). It is also postulated that fast-growing plant species selected bacteria-based decomposer community

for rapid nutrient cycling and the slow-growing plant species in the low-nutrient sites selected fungi-dominated microbial community for slow nutrient cycling²⁰. The fast-growing plant species adapted to fertile soils in the improved pastures had high nutrient content in the litter that was more easily decomposable⁶¹. Litter of these plant species allowed bacteria-based energy channel which promoted fast decomposition resulting higher supply of mineralized nutrients to soils⁶². On the other hand, plant community dominated by slow-growing species in the semi-natural grasslands provided hardly decomposable litter which led to the fungi-dominated decomposer community²⁰. However, semi-natural grasslands had low soil respiration and low rate of nitrogen absorption by microbes⁴⁴. The low respiration rate of the semi-natural grasslands showed that microbial communities of this soil was of low metabolic quotient indicating that they were more efficient in N mineralization and decomposition than those of the improved grasslands²⁰. Thus, soil microbial communities of the semi-natural grasslands were of R-strategists while those of the improved grasslands were of K-strategists⁶³. Microbial communities of a long-term semi-natural grasslands were resistant to periodical application to litter while that of improved grasslands are responsive to that indicating the selection of r-strategists by the plant communities of the semi-natural tall-type grasslands over 300 years and the K-strategists by the improved grasslands of Shiryazaki, Japan. The implications of these results were significant for the better understanding about the function of the terrestrial ecosystems and management of grasslands.

CONCLUSION

Data revealed that changes in vegetation via management interventions like sowing, grazing and fertilization played role in structuring microbial communities in grasslands. Results also demonstrated that unimproved and improved grasslands differed in microbial biomass, community composition and functions. Although data indicated that plant diversity influenced microbial diversity, community composition and function relatively less evidence appeared in favor of a positive relationship between these two communities.

SIGNIFICANCE STATEMENT

The present study uncovered the complex interactions among plant, soil microbes, grazing animals and human interventions in the grassland. Interactions among the biotic components of the grasslands, therefore, influenced carbon

and nutrient cycling in the grassland ecosystem. The findings of the study were important for the management and conservation of the grassland ecosystems. This review was also relevant for enhanced knowledge about the ecological mechanisms by which diversity and composition of plant and soil microbial communities were regulated and maintained.

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