Chapter 14
Circadian Rhythms in Plant-Microbe Interaction: For Better Performance of Bioinoculants in the Agricultural Fields

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Abstract Circadian rhythm (CR) is an important regulator of numerous basic functions of the living organisms such as carbon metabolism, gene expression and regulation, growth and reproduction. It is widely accepted, and several research activities prove its implication on health and disease especially in humans and plants including microbes associated with it. CR is reported to regulate circadian clock which is subjected to extensive natural variation during day and night, light intensity, availability of nutrients, stress and other factors. CR varies within and between species; this underlies the importance of understanding the phenomenon at the individual level to develop disease management strategies or production of microbial formulations used for growth promotion. In plants, rhizosphere microorganisms extensively depend on the root exudates, and its composition is reported to alter with CR in response to external stimuli including global warming and pollution. These microbes play an important role in plant growth and its environmental fitness and hence the concept of plant growth-promoting rhizobacteria (PGPR) came to existence. However, even today circadian clock regulating interaction of PGPR with plants is not extensively studied, and hence most of the time, microbes developed in the laboratory fail to perform in the field level. The world is awaiting another green revolution to feed the growing population with bitter experience of the previous revolution. It is the right time to understand the circadian clock at the species level and to develop suitable formulations to exploit the beneficial aspect of plant-microbe interaction to achieve high yield in the agricultural fields as a part of the sustainable agriculture. Understanding the CR in plant-pathogen interaction will also help to develop suitable treatment strategies to overcome the yield loss due to infection.

Keywords Plant growth-promoting rhizobacteria · Sustainable agriculture · Rhizosphere microflora · Circadian clock

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14.1 Introduction

Genes not only inherit the capacity of the organisms to clone but also the capacity of the generations to endure environmental changes referred to as chronon, which means the cyclical, irreversible, recursive and chronological expression of genes as a function of biological time. The stimulation of these constitutive biological rhythms of the living organisms defines its fitness to the environmental variations. Halberg et al. (1959) referred this rhythm as circadian (daily clock phenomenon) derived from the Latin word circa for "about" and dies for "day". It is defined as the biological activities with a frequency of one activity cycle every 24 h (Halberg et al. 1977).

Linnaeus (1770) is the pioneer in studying the plant behaviour in response to time. He observed the periodical movement of flowers in response to external conditions such as temperature and change in light. His observations on timely response of different varieties of flowers recorded using garden clock helped in developing a concept of unique rhythms in many species. He named it as sleep of plant analogous to that of animals. Even though these observations are connected with plant response to external stimuli in time scale, detailed research on this concept was taken up later to prove it.

Animals also respond to this clock and select the feed accordingly based on the variation in the plant metabolites. Related to this, an interesting study on feeding habit of olive baboon was reported by Adeola et al. (2014). These animals showed different choices of feeding during wet and dry season. Among the plants used for consumption, 7 plants, viz. *Andropogon gayanus*, *Strychnos spinosa*, *Nuclear larifiora*, *Vitellaria paradoxa*, *Ficus sycomorus*, *Annona senegalensis* and *Tamarindus indica*, were consumed in wet season with 303 feeding events, while other 10 plants *Detarium macrocarpum*, *Gardenia sotoemsis*, *Parkia biglobosa*, *Piliostigma thonningii*, *Pterocarpus erinaceus*, *Prosopis africana*, *Ficus sycomorus*, *Ximenia americana*, *Annona senegalensis* and *Vitex doniana* were consumed with 315 feeding events during dry season. It is a clear indication that the plant with higher nutritional quality was consumed by the animals. The change in feeding habit also indicates that the plants are subjected to seasonal variation due to which the nutritional composition also alters. It is a best example for how animals choose their feeding to satisfy the nutritional balance. This change in feeding habit also indicates change in plant metabolism in response to seasonal variation and provides clear evidence that plant physiology is altered with season and time.

Present-day advanced research is providing more insights into this concept, the broader understanding of this phenomenon and its widespread application in several aspects of plant growth and adaptability. The study on this behaviour needs accurate observations and mathematical interpretation of numerous experimental data recorded in different intervals of day and night. Recording the biological fluctuations or variability in measurements of hormone and pigment concentrations, membrane transport rates, growth, ion fluxes, protein production, etc. underlies the basic understanding of rhythms.

14.2 Rhizosphere Microflora and Root Exudates

Soil being a natural media supports plant-microbe interaction. Beneficial microorganisms such as asymbiotic and symbiotic nitrogen-fixing microorganisms, ecto- and endomycorrhizal fungi and plant growth-promoting rhizobacteria including K and P solubilizers play a vital role in plant growth. Soil microbes also exhibit antifungal activity, produce volatile organic compounds and induce systemic resistance in plants. To maintain these microorganisms in the vicinity of the root, plants release 5–10% of net photosynthate by roots, and this percentage increases when it is grown in nonsterile system (Barber and Martin 1976). This indicates that the structure and diversity of the rhizosphere microflora vary among plant species and over time (Baudoin et al. 2002). It is also interesting to note that different root zones of the same plant choose colonization of specific microbial communities by releasing specific substrates which varies from simple sugar to complex aromatic compounds (Kamilova et al. 2006). Composition of the root exudates hence is an important selection force for beneficial plant-microbe interaction. It comprises phenolics, sugars, amino acids and secondary metabolites of low molecular weight and polysaccharides, proteins and other biomolecules of high molecular weight (Abbot and Murphy 2003; Walker et al. 2003). These biomolecules are often less diverse but available in larger proportion in the exudates, and polysaccharides in general decide the association of heterotrophic rhizobacteria with rhizosphere and rhizoplane. Glycosides and hydrocyanic acid are considered as toxic metabolites of root origin which is known to inhibit the growth of pathogens (Rangaswami 1988).

Recent studies proved that rhizosphere microbiome associated with plant growth is also influenced by the type of soil, climate change and anthropogenic activities (Igiehon and Babalola 2018). Even plant cultivar which is having variations in single gene is reported to alter the microbiome. Bressan et al. (2009) observed change in rhizosphere microflora between wild-type and transgenic *Arabidopsis*, due to release of glucosinolates. They revealed that the presence of a single metabolite significantly affected alphaproteobacteria and fungi population in the rhizosphere.

Abiotic factors such as pH, type of soil, availability of oxygen, intensity of light, soil temperature, availability of proper nutrients and even presence of specific microorganisms govern the qualitative and quantitative composition of root exudates. It varies among the plant species, for example, differential exudation pattern was observed in pines and variation in the amount of amino acids in pea and oat root exudates. Diverse carbohydrates are released by young maples compared to mature trees, which exude more and diverse amino acids.

Even the organic acids released in root exudates vary. Study conducted by Schilling et al. (1998) revealed that root exudates of *Zea mays* found to contain citric acid, where as in *Triticum turgidum* var. *durum* L. it was oxalic acid and acetic acid and acetate is a dominant acid released by roots of *Linum usitatissimum* L. (Cieslinski et al. 1997). This shows composition of root exudates varies with several factors and it is specific to plant species.

Ultimately it is the quantity and quality and type of carbon sources released in root exudates that decide the composition of microbial communities in the rhizosphere (Merbach et al. 1999). It is not only beneficial organisms; even pathogenic fungi such as *Rhizoctonia*, *Fusarium*, *Sclerotium*, *Aphanomyces*, *Pythium*, *Colletotrichum*, *Verticillium* and *Phytophthora* are allowed to germinate in response to specific metabolites released by the roots (Vancura 1964). Plants can maintain high number of antagonists by providing specific nutrients required for the growth of these organisms to develop resistance against specific pathogens.

Raja et al. (2006) reported another interesting observation that even rhizosphere microflora influence composition of root exudates. They observed that the composition varies after application of bioinoculants, viz. *Azospirillum lipoferum*-A2 204, *Bacillus megaterium* var. *phosphaticum* and *Pseudomonas fluorescens* pf-1, into the soil. It was also supported by rRNA gene profiling and community-level physiological profiles conducted by Miethling et al. (2000). Gomes et al. (2001) reported the alterations in rhizosphere microflora even during senescence.

These studies indicate that the interaction between rhizosphere microflora and plant is not simple and it is the interface which is gaining importance nowadays as a hot spot of plant-microbe interactions, whether it is beneficial or pathogenic. As discussed earlier, this interaction is very specific and influenced by several abiotic and biotic factors including light and temperature, which directly alters the composition of the root exudates and through which metabolic exchange between rhizosphere community and roots is also altered (Berg and Smalla 2009; Harmer 2009). Hence it is the right time to study the alterations in the composition of the root exudates in general and rhizosphere microbial population in particular. If it is not done, the beneficial interaction of specific microbes with specific plant root through metabolites is not going to be established, and it may remain as a major setback in developing microbial formulations for generalized field applications. Sustainable agriculture hence may be achievable only through overall information on plant and its response to various environmental signals in the era of drastic climate change.

14.3 Climate Change and Plant Response

Significant statistical change in distribution of weather patterns over an extension period of time, ranging from decades to millions of years, refers to climate change. It is caused by oceanic circulation, variation in solar radiation, plate tectonics, volcanic eruptions and even human interferences. These changes lead to loss of sea ice, increased in sea level, intense heat waves, extended drought periods and increase in tropical storms. Another important drastic change is the increase in global surface temperature in range of 1.8–3.6 °C by 2100 as a result of increased CO_2 levels derived from both anthropogenic and natural sources (IPCC 2007).

The world is witnessing drastic environmental fluctuations such as local cooling, increased global temperature, shifting of vegetation and extreme weather due to climate change. Is it not influencing the CR, plant physiology and root exudation?
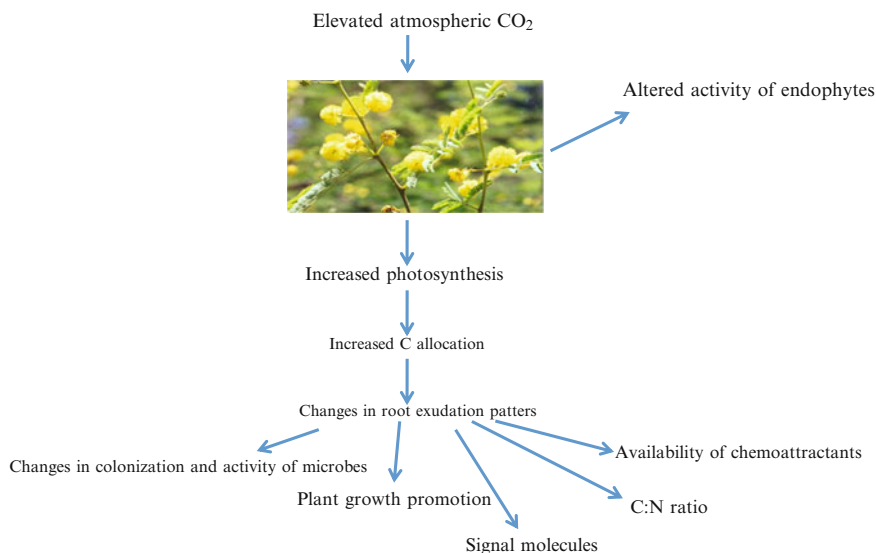
Fig. 14.1 Influence of elevated CO_2 on plant physiology

Scientific reports support the influence of altered environmental conditions on all these plant processes. Especially elevated CO_2 increases carbon allocation to root zone and also alters the composition of the root exudates (Fig. 14.1). It is also influenced by C/N ratio, nutrient availability, elevated temperature and drought (Kandeler et al. 2006; Haase et al. 2008). Hence Drigo et al. (2008) opine that the climate change substantially impacts the diversity and activities of microorganisms leading to impaired beneficial effects of these organisms on plant growth and health. It is the right time to develop a strategy to develop holistic approach involving all the factors influencing the composition of root exudates to favour the growth of the beneficial rhizosphere microflora and antagonists to confer resistance to plant pathogens.

Also, these alterations indirectly alter the nature of soil and hence are known to influence the rhizosphere microbiome. Increase in CO_2 levels, one of the causes of global warming, is known to alter the root exudation patterns which in turn decide the soil food web structure and functioning by increasing the rate of photosynthesis (Haase et al. 2008; Stevnback et al. 2012; Drigo et al. 2013). The world is also witnessing changing weather pattern, for example, change in precipitation level with time is also reported to have significant influence on soil microbial population (Sheik et al. 2011; Castro et al. 2010). Singh et al. (2010) also observed that climate change induced alterations in natural ecosystems and microbial population will have similar changes in the biogeochemical cycles mediated by these microbes. They also reported that there could be addition of new processes to ecosystem due to altered microbial activities which is beneficial or detrimental to plants.

Forchetti et al. (2007) reported the altered plant-associated communities as a result of drought stress. They observed the different subpopulations of endophytes colonizing sunflower grown under drought conditions. Interestingly they could isolate endophytic bacteria with more plant growth-promoting ability in sunflower cultivated under drought than the cultivar grown with sufficient irrigation. Different PGPRs, ecto- or endomycorrhizal taxa, however, are also reported to respond differently to droughts in terms of their patterns of abundance. Examples are from Mediterranean shrubs such as *Pinus muricata*, *Pinus oaxacana*, etc. where drought significantly decreased the microbial colonization process (Compant et al. 2010a, b).

In view of these, proper exploitation of agricultural land and associated beneficial microbes remains as a best choice for climate change resilience farming systems as it supports the proper management of soil, water, biodiversity and local resource usage (Sharma et al. 2014).

14.4   Rhythm in Plants and Its Influence on Plant Processes

Intestines of the animals resemble rhizosphere of the plants in many aspects. Several host functions are regulated by microbes inhabiting these zones. Recently, in animals, feeding and diet of the host were reported to alter intestinal microbiota of humans (Leone et al. 2015) and mice (Liang et al. 2015; Zarrinpar et al. 2014) due to diurnal oscillations. It is also proven to silence the host molecular clock genes leading to gut dysbiosis (Thaiss et al. 2014). Harmer (2009) reported the plant innate ability to estimate time within 24 h period to synchronize biological events via circadian clock. Photosynthetic pattern and other physiological activities of the plant may also alter the rhizosphere microbiome similar to animals.

CR in plants regulates central metabolic pathways of carbon (Kolling et al. 2015), expression of genes, stomatal function and photoperiodism associated with seasonal reproduction (Michael et al. 2003; Yanovsky and Kay 2001). This clock shows variation in response to natural variation both between and within species leading to individual plant performance and fitness (Sulpice et al. 2014; Konmonth-Schultz et al. 2013; Yerushalmi et al. 2011) (Fig. 14.2). It also enhances the adaptations of plant to different environments by regulating physiological and developmental states periodically (Graf et al. 2010; Harmer 2009). Even plant pathogens regulate life cycle in response to diurnally regulated host plant metabolism. On the other hand, plant innate immune response for its fitness is regulated by CR through cellular metabolism (Seo and Mas 2015; Roden and Ingle 2009). Hence it serves as a fascinating adaptive force of life on earth. Obviously, it is endogenous helping in keeping the time of day and night for all living organisms. Photosynthetic organisms record such activity in response to different wavelengths of light as they use light as a source of energy. It is compulsory for them to adapt to daily and seasonal fluctuations of light which serves as a selective force to determine time in a circadian manner (Jarillo et al. 2003).
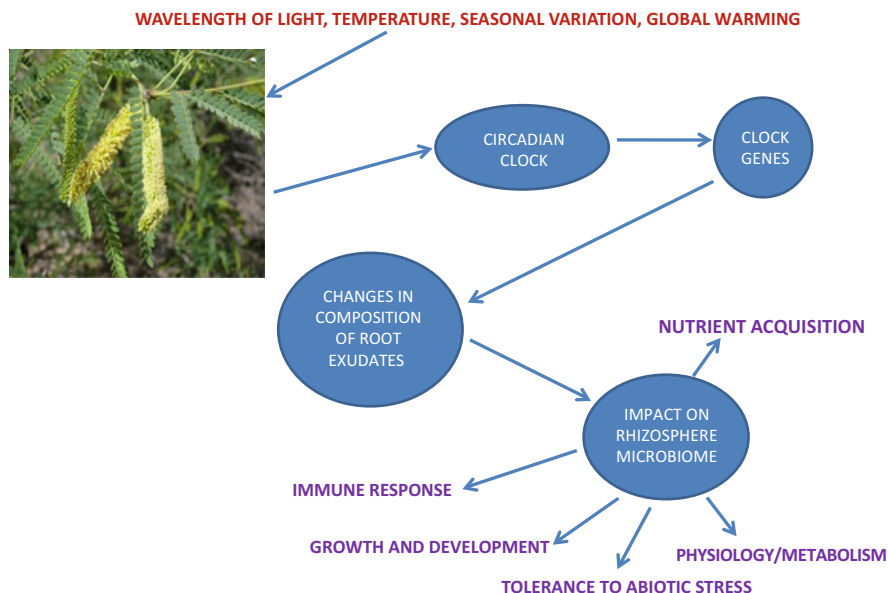
Fig. 14.2 Influence of climatic change on CR and rhizobiome

The list of plant processes regulated by CR is increasing; it is playing a vital role in expression of genes, cytosolic ion concentration, phosphorylation of proteins, movement of chloroplast, stomatal regulation, elongation of hypocotyl, movement of leaf and cotyledon, production of hormones, fitness and responsiveness. Its role in synchronizing developmental processes such as flowering time is well documented. Any change in the clock-associated genes was also reported to alter the photoperiodic control of flowering. Over the years even stem elongation, root pressure, cell membrane potential and CO_2 exchange are also included in the list (Hubbard et al. 2017). Activity of the plants regulated by CR is tabulated in Table 14.1, and it highlights the need of understanding the phenomenon in other plants too.

Johnsson (2007) observed that the rhythmic transpiration reflects rhythmic cellular control by guard and subsidiary cells which regulates assimilation of CO_2 and transpires water vapour by stomatal openings. In 1979, Raschke expressed the need of a model system to understand the regulation of water system in plant in association with photosynthesis and CO_2 transport through stomata. Even before this in 1729, French astronomer De Mairan reported his observation of persistent leaf movements of *Mimosa pudica* for several days even after the plants were placed in darkness. This laid a foundation for plants' accurate timing mechanism to synchronize their physiology with daily environmental fluctuations. It was Bunning (1931) who first identified the plant clock which monitor the duration of day and night. He proved its importance by inducing a mutation in a bean gene involved in clock regulation. Recent studies proved beyond doubt that CR increases ability of plants to anticipate and prepare for changes in the environment that occur during day and night.

Table 14.1 CR in plants and its associated activities

Plant	Activity	References
Mimosa pudica	Daily leaf movements	De Mairan (1729)
Phaseolus coccineus	Periodical movement of leaf	Bunning (1931)
Pea	Influence of light-harvesting chlorophyll a/b binding protein (CAB), small subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase and an early light-induced protein	Kloppstech (1985)
Wheat	Transcription rate for the Cab-1 gene	Nagy et al. (1988)
Tamarindus indica and *Mimosa pudica*	Rhythmic movement of leaf in legumes driven by turgor-induced expansion and contraction of the pulvinus	Kim et al. (1993)
Arabidopsis thaliana	Elongation rate of the abaxial and adaxial cells of the petiole	Engelmann and Johnsson (1998)
	Rate of hypocotyl elongation	Dowson-Day and Millar (1999)
	Elongation rate of inflorescence stem	Jouve et al. (1998)
	Transcription rate and transcript accumulation of *Arabidopsis* LHCB	Millar and Kay (1991)
	Other genes	McClung and Kay (1994)
	A short fragment of the *Arabidopsis* LHCB13(CAB2) promoter	Millar et al. (1992)
	Multiple metabolic pathways	Schaffer et al. (2001), Harmer et al. (2000)
	35% of the transcriptome	Michael and McClung (2003)
	Sugar metabolism	Blasing et al. (2005)
	Ability to respond to abiotic stresses such as cold	Fowler et al. (2005)
	Rates of chlorophyll production and carbon fixation	Dodd et al. (2005), Green et al. (2002)
	mRNA abundance of the CAT2 and CAT3 catalase genes	Zhong and McClung (1996)
	Glycine-rich RNA-binding protein (ATGRP7/CCR2) and a germin-like protein (AtGER3)	Strayer et al. (2000), Staiger and Apel (1999), Staiger et al. (1999)
	mRNA abundance of nitrate reductase	Pilgrim et al. (1993)
	RCA gene	Liu et al. (1996)
	Genes encoding phytochrome B (PHYB), cryptochrome 1 (CRY1), cryptochrome 2 (CRY2) and phototropin (NPH1)	Harmer et al. (2000)
	Genes CRY1 and CRY2 coding for homologs of the blue light photoreceptor	Dunlap (1999)
	SPA1 and RPT2 genes involved in downstream mediators of phototransduction pathways	Harmer et al. (2000)
	Desaturases involved in lipid modifications	Harmer et al. (2000)

(continued)

Table 14.1 (continued)

Plant	Activity	References
	Auxin efflux carriers PIN3 and PIN7	Taiz and Zeiger (1998)
	Flowering induction by photoperiodism	Samach and Coupland (2000)
	Twenty-three genes encoding enzymes in the phenylpropanoid biosynthetic pathway were coordinately regulated to peak before dawn at CT20	Landry et al. (1995), Li et al. (1993)
	Community structure of the rhizosphere during drought	Zolla et al. (2013)
	Increase the growth and fitness through stress signalling	Muller et al. (2014)
Tomato	Growth improvement	Hillman (1956)
	Sucrose phosphate synthase activity	Jones and Ort (1997)
	LHCA genes	Kellmann et al. (1999)
Beans	Regulation of stomatal opening and gas exchange along with Calvin cycle reactions	Hennessey and Field (1991)
Sorghum	Levels of gibberellic acid	Foster and Morgan (1995)
	ACC oxidase activity and increasing the availability of mRNA coding for 1-aminocyclopropane-1-carboxylic acid (ACC) transcribed by SbACO$_2$ gene	Finlayson et al. (1999)
Robinia pseudoacacia	Leaflet movement	Gomez and Simon (1995)
Angiosperms	LHCB mRNA abundance	Piechulla (1999), Fejes and Nagy (1998)
CAM plants	Phosphorylation and dephosphorylation of PEPc	Nimmo (2000)
Many plants	Regulates the composition of the root exudates	Hubbard et al. (2017), Greenham and McClung (2015)
	Plant stress response	Guadagno et al. (2018)

14.5   Mechanism of CR in Plants in Brief

Mechanism of CR regulated by circadian clock is well established in *Arabidopsis*; the clock was reported to consist of a series of transcriptionally and post-transcriptionally regulated intertwined feedback loops (Harmer 2009). Even though it is proved in this plant, its existence in other plant species needs to be evaluated (Song et al. 2010). The circadian clock has been found to influence a variety of metabolic functions in the plant including chlorophyll biosynthesis, transport photosystems, starch synthesis and degradation and nitrogen and sulphur assimilation. The clock timing was found to be altered to different concentrations of several metabolites such as glutamate, nitrate, glutamine and sucrose (Gutierrez et al. 2008; Knight et al. 2008). However, due to differences in methodology, these results

are sometimes inconsistent across studies, highlighting a need to consider photoperiod duration and the time of sample collection when describing results.

Advances in the identification and characterization of components of the plant circadian system have been made largely through genetic studies in *Arabidopsis*. The number of genes regulating *Arabidopsis* circadian clock is approximately 20, in contrast to smaller number of genes regulating the circadian clock of insects, mammals and fungi. As in the mammalian circadian clock, several clock-associated genes from *Arabidopsis* have overlapping functions. The complexity of phototransduction pathways in plants may contribute to the large number of genes implicated in clock function (Jarillo et al. 2003).

As in other organisms, the circadian system in plants consists of input pathways that provide temporal information from the environment to the clock, the central oscillator mechanism itself and a set of pathways through which the temporal information provided by the clock is used to generate overt rhythms in several processes. During the course of evolution, photoreceptors of plant have developed capability to detect light over a large range of wavelengths and transduce the signal-specific genes regulating the clock. There are three main classes: the phytochromes, having the ability to absorb the red and far-red region of electromagnetic spectrum, and the cryptochromes and phototropins which absorb blue and UV A region of spectrum (Jarillo et al. 2003).

14.6 Plant Rhythm and Its Influence on Rhizosphere Microflora

Waldon et al. proved that the rhizobacteria respond and adapt to increased temperature which in turn regulates the CR. They could isolate rhizobia from nodules of desert woody legume *Prosopis glandulosa* which is better adapted to 36 °C compared to other strains grown in normal conditions. This proves that the bacteria colonizing distinct soil sites respond differently to certain environmental conditions. Increase in temperature from 10 to 30 °C will decrease the ability of an endophyte *Burkholderia phytofirmans* to colonize tomato rhizosphere (Pillay and Nowak 1997). It is also reported that bacterial endophytic populations, which colonize plant internal tissues such as stems, roots, leaves, shoots as well as flowers, fruits and seeds, may be affected in a similar manner (Compant et al. 2005, 2008, 2010a, b; Hallmann 2001). Even mycorrhizal hypha reduces its growth in response to elevated CO_2 concentrations (Madhu and Hatfield 2013).

Composition and abundance of rhizosphere populations associated with strawberry, potato and oil seed was reported to change over the field season, and this alteration could be because of alternation in time.

Daniel et al. (2004) assessed cycling dynamics in *A. thaliana* diel cycle associated with exposure to dark and light periods, and they involved study associated with acyclic *Arabidopsis* line having cca1 gene ectopically overexpressed and also

another plant *Brachypodium distachyon* to prove any alterations in the rhizosphere community among species, wild types and mutants. The data obtained by them completely disproved the observations of Bulgarelli et al. (2012) and suggested that rhizosphere microflora is highly dynamic and are influenced by biotic and abiotic factors along with circadian clocks. This served as clear-cut evidence that CR plays a vital role in deciding both composition of root exudates and also the diversity of rhizosphere microbial community. Even recent reports involving next-generation sequencing of the 16S rRNA gene, soil organic matter composition in the rhizosphere characterized by high-resolution mass spectrometry and 21T Fourier transform ion cyclotron resonance mass spectrometry support this observation (Staley et al. 2017).

These reports suggest the possible role of circadian clock on the rhizosphere community. The timing of bacterial cycling in relation to that of *Arabidopsis* further suggests that diurnal dynamics influence microbial association with plant carbon metabolism and exchange. In view of this, Grayston et al. (2001), Staley et al. (2017) and Dunfield and Germida (2003) suggest that previous studies done without relevance to time of day may need to be reevaluated with regard to the impact of diurnal cycles on the rhizosphere microbial community. Along with this, they also suggest that caution should be taken when conclusions are drawn about root-associated microbial community structure based on the results of a single time point.

14.7 Conclusions and Outlook

Plant-rhizosphere microbiome interactions are highly relevant because rhizosphere microflora is reported to strongly influence plant fitness and biomass which in turn inform evolutionary studies of adaptation, agronomic practices and conservation much needed for sustainable agriculture. Climate change and global warming are the major threats to living organisms, resulting in alterations of normal process of evolution. It is a forced artificial evolution; inevitably all the organisms have to respond and adopt. Especially elevated CO_2 and pattern of light radiation are affecting several natural phenomena including plant-microbe interactions in rhizosphere. If this harmony is not understood and integrated with the bioinoculant performance in the field, the desired effect of bioinoculants on plant growth is naturally affected. It is the right time to evaluate the efficacy of all bioinoculants with special reference to individual plant CR responses.

Genes regulating CR are highly sensitive and regulated by several environmental parameters. Alterations in CR are reported to alter the rhizosphere community structure due to changing pattern of diurnal fluxes of carbon, water or nutrients from plant roots. Clock misfunction would bring in differences in this structure in general and alterations in rare taxa in particular leading to differences in community function required for plant performances. It is the right time to understand the clock genes associated with plants, after which rhizosphere engineering or suitable microbial consortia or bioinoculants can be developed to increase the plant processes associated with plant health, growth and yield.

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