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Circadian Clock: New Paradigm in Plant-Pathogen Interaction

Ratul Moni Ram[1] and Bharat Chandra Nath[2]
[1]Department of Plant Pathology, Faculty of Agricultural Sciences, SGT University, Gurugram, Haryana
[2]Department of Plant Pathology, Assam Agricultural University, Jorhat-785013, Assam

SUMMARY

Plant health is a significant aspect of food security, with pests, pathogens, and herbivores all adding to yield losses in crops. Plants' defense against microbes is intricate and uses a few metabolic pathways, including the circadian rhythm, to coordinate their response. Circadian rhythms play an important role in managing metabolic processes in an organism. It is functional in most organisms such as plants, microbes and insects. In plants, the circadian clock facilitates immune responses against any invader. Understanding the coordination between circadian rhythms and plants' innate immunity will empower the advancement of effective mitigating strategies against diseases of economically important crops.

INTRODUCTION

The term circadian has been derived from two Latin words, i.e., "circa" (about) and "dies" (day). So, its literal meaning is "about a day". These rhythms are the subclass of biological rhythms which comprises 24 hours (Dunlap *et. al.*, 2004). The circadian rhythms are the fluctuation of physiological, metabolic, and behavioural processes. This phenomenon was first observed by a French astronomer 'de Mairan' (1729). However, these rhythms are being governed by well-defined molecular machinery i.e., the circadian clock. The circadian clock usually coordinates all biological processes with diurnal environmental fluctuations, thus ensuring overall fitness. Most of the microorganisms (fungi and bacteria) as well as plants and animals possess a circadian clock in their daily life (Doherty and Kay, 2010). This phenomenon is observed in almost all species but predominantly studied in *Arabidopsis, Drosophila, Neurospora*, and *Oryza sativa*. In plants, circadian rhythms play a crucial role in carbon and water utilization, gas exchange and other important metabolic processes, along with response towards both various abiotic and biotic stresses (Muranaka and Oyama, 2017). Moreover, they also play a crucial role in plant's physiological functions such as flowering and photosynthesis and regulates many defensive pathways. The circadian clock allows plants to antedate dawn and dusk, ultimately facilitating growth optimization in a dynamic environment (Oakenfull and Davis, 2017). A study on *Arabidopsis* revealed that plants having a synchronized circadian clock with their environment were fast-growers having high carbon fixation rate, and enhanced chlorophyll than mutants with impaired clock functions. However, recent studies on circadian clock genes and genes involved in defence signalling have indicated a possible two-way interaction (Butt *et. al.*, 2020). Light and temperature are the two major inputs of a circadian system. The clock can be reset by altering these two variables. These input pathways carry environmental information, which primarily tunes the clock. The light is mediated through plant photoreceptors i.e., phytochromes (*PHY*) and cryptochromes (*CRY*). Phytochromes absorb red and far-red region of the spectrum while cryptochromes absorb the blue light (Devlin and Kay, 2001). Temperature is another factor affecting the circadian clock, although its role is less well understood (McClung, 2006).

Circadian system in plant pathogens

Circadian rhythms have been studied in plants, birds, mammals, fungi, cyanobacteria as well as insects. Bacteria being unicellular organisms having a reproduction cycle of less than a day; so initially, they were considered not to follow the circadian clock as per the "circadian-infradian rule". However, successive studies on cyanobacteria such as *Synechococcus* explicit the existence of a circadian system in photosynthetic bacteria. In comparison to bacteria, circadian rhythms have been found more operative in fungi. The two most important factors promoting pathogenicity is spore dispersal and sporulation (Brody, 2019). Few fungi produce and discharge their spores at dawn or dusk hours while some at night time. However, daily rhythms in asexual reproduction have also been reported viz., in *Pilobolus* spp., *Pellicularia filamentosa* and *Aspergillus nidulans*, spore dispersal and production are regulated by the circadian clock (Pedersen *et. al.*, 1996). Circadian rhythms in these plant pathogens influence their host-pathogen relationship during all infection stages. The model fungus *Neurospora crassa* has been widely studied to comprehend the fungal circadian clock. Moreover, the presence of the circadian clock has also been reported in *Caenorhabditis elegans* and *Drosophila melanogaster*, both of which are regarded as model organisms.

Role of the circadian clock in plant immune response

The major defence mechanism of plants against specific pathogens is the presence of their resistance (*R*) gene system, which is also known to get influenced by the circadian system. Impaired clock mutants of *Arabidopsis* show a deficit in basal resistance and the *R* gene. For example, Goodspeed *et. al.* (2012) reported that cabbage loopers almost always prefer to feed on *Arabidopsis* plants lacking rhythm which shows that the circadian clock enhances resistance towards herbivore attack mainly by affecting the SA and JA pathways. In case of infection by *Phytopthora infestans* and related oomycetes in the plant, germinating spores released arachidonate which is the prime inducer of systemic resistance against pathogens (Fidantsef *et. al.*, 1999) and it also found to regulate the genes *DEA1*. Similarly, in tomato plants, the *DEA1* gene got induced upon *P. infestans* infection and was found to be expressed readily under long days but constitutively expressed under short days (Tiwari *et. al.,* 2020).

The pathogen *Pseudomonas Syringae* pv. *Tomato* (Pst) DC3000 enters its host through the stomatal opening in leaf lamina. However, activation of pattern-triggered immunity (PTI) triggers rapid closure of the stomata to prevent the entry of the bacteria. The PTI-prompted stomatal closure involves machinery of both the salicylic acid (SA) and abscisic acid (ABA) signalling pathways, which shown to reveal circadian regulation. The stomatal opening usually takes place in the day and closes at night at regular intervals, a phenomenon which is also regulated by circadian rhythm according to light and humidity fluctuations (Greenham and McClung, 2015). Some pathogens can use open stomata as access gateways for space and nutrients, within the plant tissue. When the receptors at the cell surface identify an intruder, the plant automatically closes stomata at the site of invasion failing which lead to more intense disease.

CONCLUSION

The circadian rhythm regulates 24 hours and is helpful in the physiological, developmental and biochemical processes of living organisms. In plants, it imparts plant defence against various abiotic and biotic stresses. The circadian clock affects both the preformed and induced defence. Several mechanisms have been hypothesized on the contribution of circadian systems to plants' immunity and defence. However, unravelling the mechanisms underlying the relationship between the circadian system and plant immunity will greatly facilitate planning for a better plant health and disease management approach.

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