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Mathematical models of the plant circadian clock: impact of phase regulation by sugar on
plant growth

（植物概日時計の数理モデル:糖による位相応答が成長に及ぼす影響）

Plants need to avoid carbon starvation and resultant growth inhibition under environmental fluctuations for optimal growth and reproduction. To this end, plants have to coordinate the timing of metabolism and physiology with periodic environmental cycles and also flexibly regulate them in response to sudden changes of environmental conditions. The endogenous pacemaker called circadian clock plays a crucial role in the temporal control of diverse biological processes. In the model plant *Arabidopsis thaliana*, diurnal oscillation pattern of starch turnover is an important output of the circadian system. The coordination of the endogenous rhythm of starch turnover with external environments is essential for appropriate usage of carbon resources. The regulation of the internal timing of the clock or the phase by external stimuli such as temperature or light is fundamental for synchronizing biological processes with environments. In addition to signals from external environments, endogenous signals such as photosynthetic sugars have been also shown to shift the circadian phase in *A. thaliana*; the sugar signals advance the circadian phase in the morning and delay in the night. However, whereas the effect of environmental signals on the plant circadian system has been well studied, the significance of the sugar-induced phase regulation (sugar entrainment) has been largely unknown. In addition, how the above-mentioned phase response to sugar signals is realized has been poorly understood at mechanistic levels.

In the present thesis, in order to theoretically investigate the effect of sugar entrainment on plant metabolism and growth, the applicant models the interaction between carbon metabolism and the circadian clock in photosynthetic leaves. The model is then extended to a whole plant scale by incorporating growth dynamics of sink tissues dependent

on phloem transportation of sucrose from source tissues. The carbon metabolism model suggests that the phase advance in the morning and delay in the night in response to sugar signals are optimal for carbon homeostasis. The applicant simulates sugar profiles and growth patterns of the sugar-sensitive wild type and sugar-insensitive mutant that cannot adjust the circadian phase in response to sugar signals. The model predicts that sugar entrainment is necessary for plants to flexibly regulate starch turnover under environmental fluctuations and that the wild type grows faster than the sugar-insensitive mutant by stabilizing sucrose supply to sink tissues. These results highlight the importance of clock entrainment by endogenous signals for optimizing plant carbon metabolism and growth. Furthermore, by using the clock-gene regulatory network model with explicit formalization of sugar effects, the applicant theoretically investigates the conditions under which the circadian phase is advanced in the morning and delayed in the night in response to sugar signals. The applicant simulates the phase response to sugar pulses using various combinations of a target clock gene for sugar signals and their property (activation or repression effect). The model suggests that sugar-induced repression of a morning-phased clock component that acts as a repressor is essential for optimal phase shifts for carbon homeostasis. The biological significance of this specific combination is explained in terms of the efficient usage of carbon resources for growth.

The examination committee recognized that this thesis developed and analyzed models for the feedback between circadian clocks and carbon metabolism, providing theoretical insights into the complex relationship between starch and sucrose profiles in different photoperiod conditions. The committee evaluated enthusiasm of the applicant in developing and analyzing models, and for collaboration with international researchers during the course of graduate school, thereby concluded that the applicant is eligible for the degree of Doctor of Philosophy (Environmental Science).