Do plants have brains?

Many organisms have circadian clocks. These internal clocks play essential roles for predicting day-length or seasons, and they regulate behavior and hormonal secretion in animals, and also regulating flowering time and cell elongation in plants. In animals, it is well known that a strong master clock in the brain tunes peripheral clocks in peripheral organs. In contrast, since plants don't have an organ equivalent to the brain, and it has been difficult to excise specific tissues from plants, tissue-specific clock function has remained elusive (Fig. 1). However, there is evidence to suggest that plant circadian clocks may have tissue-specific roles similar to animals: (1) animal and plant clocks have similar underlying feedback-loop mechanisms, (2) plants should combine time-related information from individual cells into a unified signal to achieve coordinated physiological responses. Thus, there may be tissue-specific functions of the clock in plants that are similar to animals.

Fig. 1. Do plants have brains? Of course this question does not imply that there is a plant as shown in this figure. It just means that there might be a tissue that acts as a signaling command center of time keeping. In fact, we think the answer is No; instead, plants dedicate specific tissues to clock "hubs" that keep track of different types of time.

In our recent work, we have developed novel techniques to analyze tissue-specific functions of plant circadian clocks. Using these techniques, we tested if the circadian rhythms in the leaf veins and mesophyll cells of leaves are distinct. We found that the timing profiles of clock-regulated genes were drastically different in the leaf veins; the circadian rhythms in the leaf veins were more robust, and they affected the rhythms of neighboring mesophyll cells. We also demonstrated that when we perturbed leaf veins clock functions, plants could not sense the appropriate season (day-length) that normally triggers flowering.

Does this result mean that the leaf veins clock is a master clock, and the leaf veins itself is equivalent to the brain?

To answer this question, we then examined if the leaf veins clock also controls another clock-regulated response, cell elongation. If the leaf veins clock is a master clock, it should regulate both flowering and cell elongation. Interestingly, however, the circadian clock in the epidermis (the protective outer layer of the leaf) is crucial for the regulation of cell elongation, but it does not control the flowering time. On the other hand, the leaf veins clock does not control cell elongation at all.

In plants, both light and temperature are crucial circadian clock inputs, or external cues. We hypothesized that the distinct, tissue-specific circadian clock systems in plants can be controlled by changes in environmental signals. Compared to normal plants, transgenic plants with perturbed epidermal circadian clocks showed an increased cell elongation over a temperature range from 18-27^{o}C, a temperature range that is not stressful for the plants. However, the cell lengths at lower or higher temperatures were the same in normal plants and the transgenic plants.

Our results indicate that circadian clocks in different tissues process specific environmental cues and regulate physiological responses accordingly.

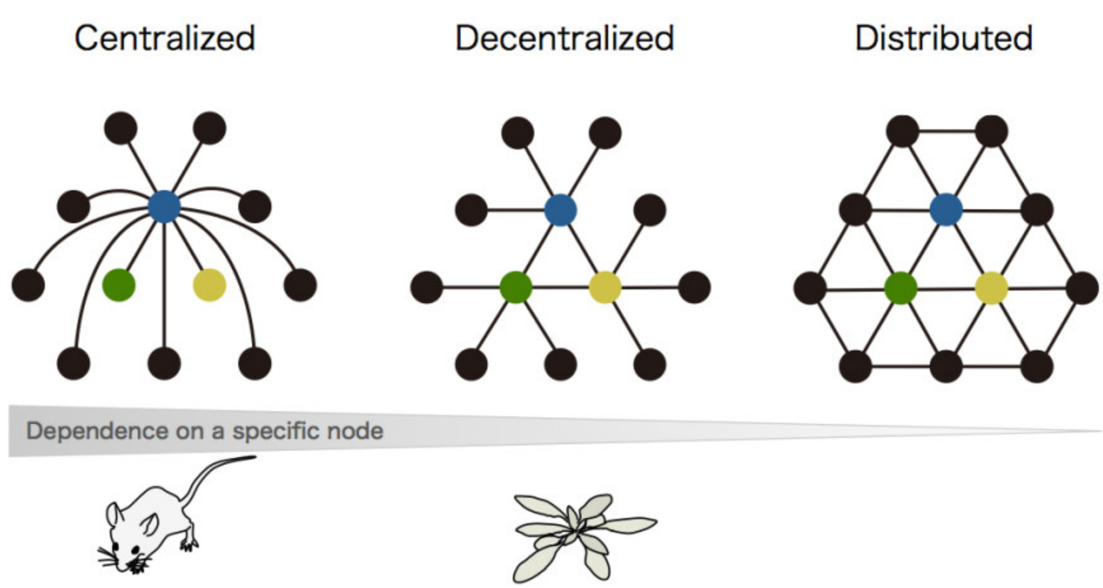

Fig. 2. An image of a centralized mammalian clock and a decentralized plant clock. Colonial

animals may have a distributed clock system.

In conclusion, we have revealed that plants have hub clocks in several tissues, and these clocks regulate different physiological processes, such as flowering or cell elongation, in response to different environmental cues. These observations are consistent with several studies that have shown that plants have unique clock-dependent patterns of gene expression in specific tissues/organs that have different sensitivities to light and temperature. These differences can now be explained in terms of tissue-specific circadian clock systems. In that sense, the circadian clock system in animals is more centralized, and that in plants is more decentralized (Fig. 2). Since plants are sessile and their structures (e.g., leaves) are always renewed, their decentralized circadian clock system provides more sensitivity to surrounding environmental changes, and it is more robust.

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Publications

Tissue-specific clocks in Arabidopsis show asymmetric coupling.
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