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A circadian and an ultradian rhythm are both evident in root growth of rice

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ABSTRACT

This paper presents evidence for the existence of both a circadian and an ultradian rhythm in the elongation growth of rice roots. Root elongation of rice (*Oryza sativa*) was recorded under dim green light by using a CCD camera connected to a computer. Four treatment conditions were set-up to investigate the existence of endogenous rhythms: 28 °C constant temperature and continuous dark (28 DD); 28 °C constant temperature and alternating light and dark (28 LD); 33 °C constant temperature and continuous dark (33 DD); and diurnal temperature change and alternating light and dark (DT-LD). The resulting spectral densities suggested the existence of periodicities of 20.4–25.2 h (circadian cycles) and 2.0–6.0 h (ultradian cycles) in each of the 4 treatments. The shorter ultradian cycles can be attributed to circumnutational growth of roots and/or to mucilage exudation. The average values across all the replicate data showed that the highest power spectral densities (PSDs) corresponded to root growth rhythms with periods of 22.9, 23.7, and 2.1 h for the 28 DD, 28 LD, and 33 DD treatments, respectively. Accumulation of PSD for each data set indicated that the periodicity was similar in both the 28 DD and 33 DD treatments. We conclude that a 23-h circadian and a 2-h ultradian rhythmicity exist in rice root elongation. Moreover, root elongation rates during the day were 1.08 and 1.44 times faster than those during the night for the 28 LD and DT-LD treatments, respectively.

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Introduction

Crop root growth is often determined by the increase in length per unit time, i.e., the root elongation rate (RER). Traditionally, RERs have been based on the total root elongation per day or week. However, only in a few studies, RERs were estimated by measuring root elongation every hour for the evaluations of root growth (Gordon et al., 1992), root tropisms (Ishikawa et al., 1991), and responses of roots to plant growth regulators (Tanimoto and Watanabe, 1986). Head (1965) was the first to demonstrate a diurnal fluctuation in RER of cherry trees grown in field soil; however, environmental factors, including the periodical illumination of roots by two reflector lamps, might have affected the estimated RERs. A previous study showed diurnal fluctuations in RERs calculated every hour under constant growth conditions for sorghum and upland rice (lijima et al., 1998). The maximum RERs were 1.4–4.4 times higher than the minimum RERs. However, details of the fluctuations could not be obtained in that study because of the limitation of the experimental

Abbreviations: RERs, root elongation rates; DD, continuous dark; LD, alternating light and dark; DT, diurnal temperature change; PSD, power spectral density.

* Corresponding author. Tel.: +81 742 43 7209; fax: +81 742 43 1155. *E-mail address:* iijimamorio@nara.kindai.ac.jp (M. lijima). set-up. In this study, we attempted to analyze the fluctuations in the RER in rice. Here there seems to be a basic circadian rhythm on which shorter rhythms were superimposed.

The circadian rhythm, an endogenous rhythm observed in plants, has been studied extensively in relation to plant shoot growth (Walter et al., 2009). Daily rhythmic patterns for plant root growth parameters have also been found with respect to various physiological phenomena such as nitrate uptake (Pearson and Steer, 1977), root respiration (Hansen, 1980), xylem sap exudation (Vaadia, 1960), hydraulic conductivity, root pressure (Henzler et al., 1999), water uptake (Nakanishi et al., 2001), and mucilage exudation (Iijima et al., 2003c). Recently, a diurnal growth pattern of root elongation was reported in Arabidopsis thaliana (Yazdanbakhsh and Fisahn, 2011; Yazdanbakhsh et al., 2011), although the endogenous rhythmicity itself was not analyzed. Root growth patterns of shorter duration, such as oscillation, were also analyzed in previous studies (Walter et al., 2003). The existence of an endogenous rhythm, such as a circadian and/or an ultradian rhythm, however, has never been analyzed as a parameter of root growth. A detailed mathematical analysis of the RER under continuous dark or light conditions is necessary to test predictions derived from the hypothesis that endogenous rhythms exist in root elongation. Therefore, this study aimed to analyze, for the first time, the endogenous rhythmicity of root elongation by using hourly growth measurements.

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Materials and methods

Plant material and treatment

Upland rice (Orvza sativa L., cv. Norin 11) was used for RER measurements, because it has a single, positively gravitropic seminal root. To analyze the rhythmicity of root elongation, 4 treatments with different temperatures and light conditions were used: (1) 28 °C constant temperature and continuous dark (28 DD). (2) 28 °C constant temperature and alternating light and dark (28 LD), (3) 33°C constant temperature and continuous dark (33 DD), and (4) diurnal ambient temperature and alternating light and dark (DT-LD). The 28 DD treatment allowed observation of spontaneous rhythmicity in roots under constant darkness without any external rhythmic factors, and the 28 LD allowed observation of rhythms in a day-night environment (light:dark=12h:12h). By comparing the observations under these 2 treatment conditions, the rhythmicity can be judged as either endogenous or exogenous. Unfortunately, our experimental set-up did not allow testing under continuous light, but DD conditions can be used to assess rhythmicity. In the 33 DD treatment, the temperature was 5°C higher than that in the 28 DD treatment. By comparing the observations under these 2 treatment conditions, temperature compensation of the endogenous rhythmicity can be determined. The DT-LD treatment simulates a typical field environment for upland rice growth in summer in Nagoya, Japan, with an average temperature of 28 °C. The treatment enables estimation of the daily changes in RER under natural field environment. The day length was adjusted to 12 h to allow comparisons with other treatments. Phase shifting was not tested because of the limitation imposed by the experimental periods. The root elongation measurements were conducted for a maximum of 3 days, and this duration was insufficient for conducting phase shifttests.

Table 1

Pre-germination and pre-observation treatments that applied to plants of the four sets of experimental observations.

	Pre-germination	Pre-observation
28 DD	28 °C constant dark (0–48 h)	28 °C constant dark (48–72 h)
28 LD	28 °C constant dark (0–48 h)	28 °C LD = 12:12 (48–120 h)
33 LD	33 °C constant dark (0–48 h)	33 °C constant dark (48–72 h)
DT-LD	28 °C constant dark (0-48 h)	28 °C LD = 12:12 (48–120 h)

28 DD, 28 °C constant temperature and constant dark; 28 LD, 28 °C constant temperature and LD = 12 h:12 h; 28 DD, 33 °C constant temperature and constant dark; DT-LD, diurnal temperature change and LD = 12 h:12 h. In parentheses time since the start (0 h) of germination.

Seed germination and pre-treatment

Rice seeds were surface-sterilized by immersing them in 1% sodium hypochlorite solution for 10 min and washing them with deionized water for 60 min. Surface-sterilized caryopses were germinated at either 28 °C or 33 °C (depending on the subsequent experiment) in darkness for 48 h in deionized water, which was replaced twice daily. The duration of the germination and the temperature and light conditions before germination and before root observations are summarized in Table 1. From approximately 50 germinated seeds, 3-5 seedlings that had 5-10mm-long straight seminal roots were selected. The selected roots were grown in growth pouches moistened with deionized water for 24–72 h for pre-adjustment to the different temperatures and light conditions in each treatment. For the treatments that involved day-night cycles, i.e., the 28 LD and the DT-LD treatments, the pre-adjustment period was 3 days, because the shoots need to be exposed to light $(380 \,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1})$ for at least 24 h. The roots were not exposed to light during the pre-adjustment period.

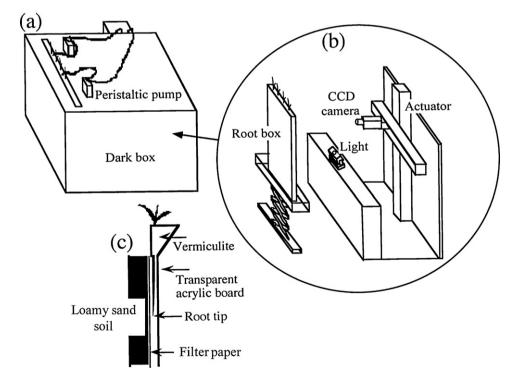


Fig. 1. Schematic diagram of the root observation chamber. (a) Root observation dark box (depth × width × height: $0.9 \text{ m} \times 0.6 \text{ m} \times 0.9 \text{ m}$). Light supplied from the top of the chamber did not penetrate into the dark box in which the roots grew. (b) The root box ($0.01 \text{ m} \times 0.25 \text{ m} \times 0.60 \text{ m}$) and camera system. The CCD camera position was controlled precisely by 2 industrial actuators. Roots were continuously illuminated with dim green light ($520 \pm 10 \text{ nm}$; $1.33 \times 10^{-3} \text{ W m}^{-2}$) which does not affect the root growth. (c) Side view of the root box. The roots were sandwiched between an acrylic plastic board and a loamy sand soil firmly. Contact between roots and soil was prevented by a sheet of filter paper. One-millimeter squares printed on the filter paper allowed comparative assessments of hourly increments in root growth.

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