Stable diurnal growth rhythms modulate root elongation of *Arabidopsis thaliana*

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Abstract: Arabidopsis root growth kinetics were investigated with high temporal and spatial resolution in combination with detailed statistical analysis to resolve presence of diurnal modulation of root tip displacement. In particular, high resolution video imaging was used to monitor root-tip displacement of *Arabidopsis thaliana* seedlings over several days. Root growth kinetics were sampled and statistically analyzed in two different photoperiods: long day LD (16 h-8 h) and equal LD (12 h-12 h) light. Diurnal root elongation kinetics exhibited five highly reproducible phases, one of these being a maximum of root growth rate displayed 1-2 h after the light on phase. Then, during the later part of the light period, root growth rate decreased. Several hours before darkening root elongation rates started to increase, with a profound decrease immediately after darkness. Subsequent to this dark-induced reduction in root growth rate the remaining part of the night was characterized by increasing growth activity. Together, tip elongation, in Arabidopsis roots is modulated by strong diurnal rhythms that are maintained in both photoperiods used and also in continuous illumination.

Keywords: *Arabidopsis thaliana*, digital image processing, diurnal cycle, root growth kinetics

Introduction

Due to the daily rotation of the earth around its axis diurnal rhythms evolved within the majority of living organisms (Buijs and Escobar 2007). Existence of these rhythms in plants has been described for a long time and have been found to modulate many physiological and biochemical parameters (Bünning and Tazawa 1957, Acevedo et al. 1979, Geiger and Servaites 1994, Seneweera et al. 1995, Zeemann 2007,

Walter et al. 2009). Photosynthesis is a product of light and starch accumulates. In darkness, the plant degrades the starch reserves (Geiger and Servaites 1994). This switch in energy metabolism ultimately affects major primary and secondary metabolic pathways as well as the growth process. In connection with the alternating daily light-dark periods, diurnal movements of leaves and hypocotyls have been detected in *Arabidopsis thaliana* (Nozue and Maloof 2006, Nozue et al. 2007, McClung 2008). Early studies by time lapse recordings with cherry root tips demonstrated significant increase in the averaged rate of root growth in the night compared to the day (Head 1965). In a previous study, the root elongation rate of rice seemed to show a rhythmic pattern, the timing of the maxima and minima deviated day by day indicating that this pattern did not have a daily rhythm (Iijima et al. 1998). These authors concluded that detailed mathematical analyses of root elongation rates are necessary to clarify the presence of endogenous rhythmicity in root elongation growth (Iijima et al. 1998).

Although the mathematical basis for root growth modelling has been developed in great detail (Evans 1972, Silk and Erickson 1979, Silk 1984), tools to monitor root elongation with sufficient sensitivity have emerged only slowly. The most recent platforms for non-invasive analysis of root growth provide accurate and reliable results with high temporal and spatial resolution (van der Weele et al. 2003, Roberts et al. 2006, Rahman et al. 2007, Walter et al. 2009). However, these methods are time-consuming, often targeted and have a low throughput. This means that available data for root elongation is often based on only a small number of replicates, making it difficult to detect small changes and separate them from background noise inherent to the growth measurement procedure. We developed a novel root growth monitoring platform (PlaRoM) for non-invasively quantifying the root growth rates of large numbers of young Arabidopsis seedlings by digital imaging

sequence processing (DISP) analysis (Yazdanbakhsh and Fisahn 2009). Applying this technology we addressed the question whether root growth exhibits diurnal rhythms, as has been observed in elongating hypocotyls and leaf movements. In a second set of experiments we asked if the growth patterns observed in one photoperiod could be observed in shorter photoperiods, or even when there was no photoperiod but only constant light.

Materials and Methods

Plant material and cultivation procedure

Seeds of *Arabidopsis thaliana* wild-type were surface-sterilised for 20 minutes with 10% sodium hypochlorite solution containing 0.1% surfactant (Triton X-100). After sterilisation seeds were rinsed several times with sterile water and plated on the surface of solid nutrient agar (7.0% m/v) supplemented with half-strength Murashige–Skoog medium (Murashige and Skoog 1962, M02 555, pH 5.6, Duchefa, Haarlem, Netherlands). After 4 days stratification at 4°C in a refrigerator, Petri dishes were placed vertically in the phytotron (21°C constant day and night temperature, 100 μmol m^{-2} s^{-1} photon flux density). Photoperiod was set to 16 h-8 h light-dark. At day 9, seedlings that had developed roots of 1-2 cm length were selected and distributed equally in a row 3 cm from the top edge of the surface of solid medium filled in 120 × 120 mm rectangular Petri dishes. After 2 further days in the phytotron, Petri dishes were transferred to the root measuring unit (PlaRoM, Yazdanbakhsh and Fisahn 2009). In all cases, roots were vertically oriented, with the root tips pointing down.

Acquisition of root growth kinetics

Root growth kinetics were established as described previously (Yazdanbakhsh and Fisahn 2009). In brief, a custom designed phytochamber housed the central measuring head of the plant root monitor (PlaRoM). This central unit comprised a XY motion robot that moved two vertically oriented rectangular Petri dishes (12 cm × 12 cm) that contained the experimental seedlings. During the measurement, seedlings started to develop their first two rosette leaves. The actinic light intensity in the chamber at the surface of the leaves of the seedlings amounted to 90 μmol m^{-2} s^{-1}. Temperature was controlled by a cooling device offering 0.5°C accuracy. Temperature was set to 21°C.

The PlaRoM imaging platform screened the surface of the two sample containing Petri dishes and captured time lapse records of the seedlings growing

therein (Yazdanbakhsh and Fisahn 2009). Screening of the Petri dishes was enabled by the PlaRoM imaging software application (Yazdanbakhsh and Fisahn 2010) which controlled the stepwise movement of the robot arm. As a result, each 4.58 × 3.33 mm area over the surface of the Petri dish was imaged every half hour. With the presently used magnification set by the microscopes (detailed description of the setup is provided in Yazdanbakhsh and Fisahn 2009), each pixel in the captured images covered an area of 5.96 × 5.78 μm^2.

The root extension profiling software application analysed the time lapse records and provided the growth velocity profiles and custom specified visualisation of root extension profiles (Yazdanbahksh and Fisahn 2010). A statistical package was included in the PlaRoM imaging software application that provided user-defined averaging and normalization of various combinations of data, together with the standard error (Yazdanbakhsh and Fisahn 2010). This package normalizes each elongation rate value to the daily mean value of the same individual on the same solar day period.

Results and Discussion

Root extension pattern of Arabidopsis thaliana in 16 h light periods

Root growth kinetics of Col0 seedlings were studied under a 16 h-8 h photoperiod (long day, LD). Seedlings in two Petri dishes (*n*=10, *n*=16) were monitored simultaneously by taking images every half hour over a period of 72 hours. The mean and SE is shown for each plate separately (Fig. 1, blue and red distinguish data from the separate plates). The position of each individual root tip plotted over the monitoring period is near to linear (Fig. 1a). Growth rates per half hour time interval were calculated from the displacement of each root tip, in both *x* and *y* directions, at successive measuring points. These quantities were then averaged among individuals within each plate (Fig. 1b) (i.e. root elongation is approximately rectilinear). Root elongation exhibited a diurnal course with the highest extension rate occurring 1.5–2 hours after the beginning of the light period. In these light conditions, extension rates then decreased to a minimum 9-10 hours into the light period. The growth rate started to increase during the last part of the light period. This recovery continued during the night. Closer examination reveals a transient stimulation of growth immediately after illumination, and a transient inhibition after darkening (see below for more data), which is superimposed on the more gradual changes during the 24 hours cycle. The rate of growth varied between a maximum of 145.52 ± 11.87 μm h^{-1} and a
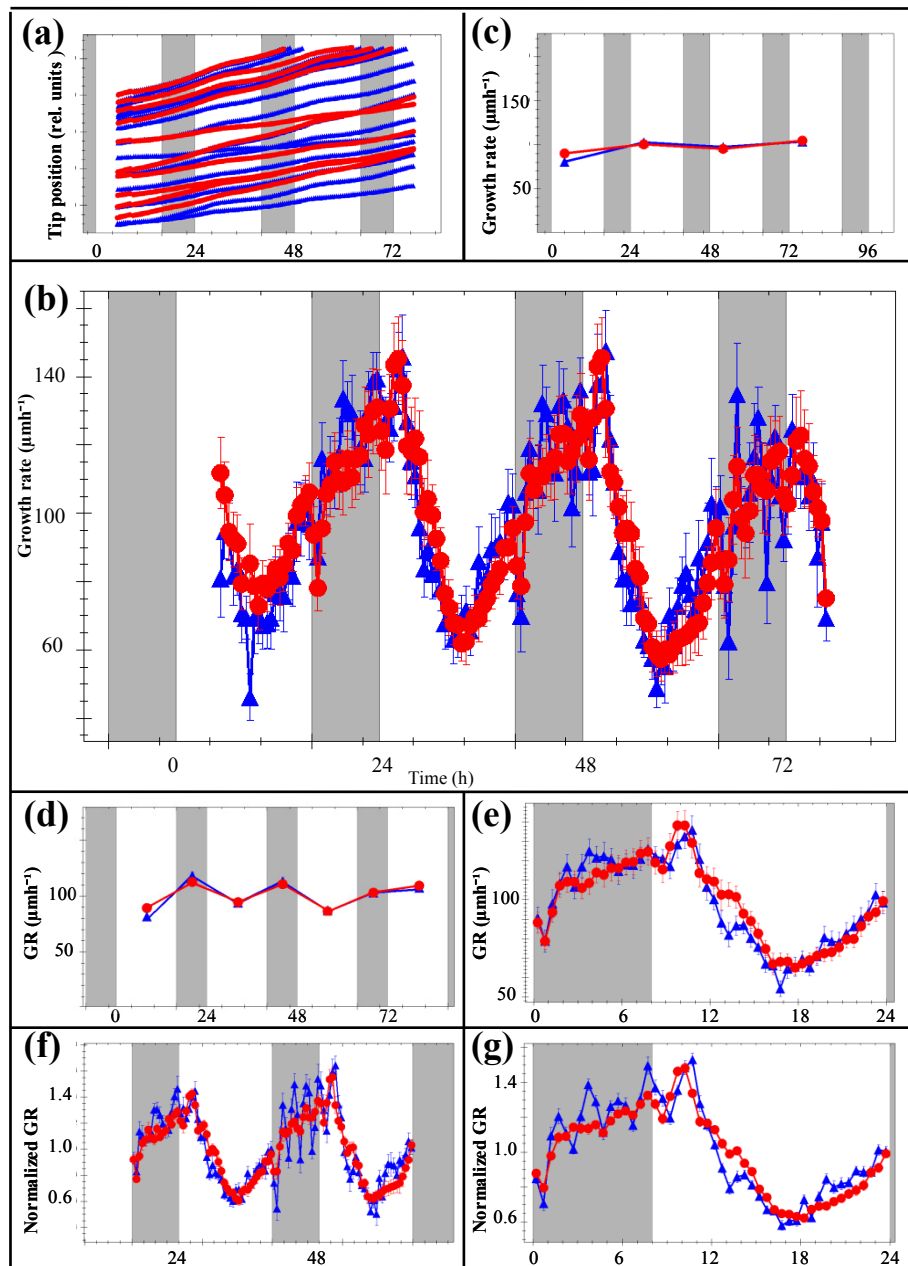
Fig. 1. Root growth profile of Col0 seedlings growing in 16 h photoperiod. 13-d-old seedlings growing in 21°C in two Petri dishes (*n*=10, red dots; *n*=16, blue dots) were monitored simultaneously for 72 hours. (a): Positions of the root tips plotted over the time present almost straight lines. (b): Averaged growth rate of seedlings growing on the same Petri dish grouped together during the measuring time period. (c): Average of the extension rate of all individuals of a group, each averaged over consecutive days. It should be noted that as the measurement had not been started or finished at midnight (solar time), the changed values for first and last day should not be considered. (d): Timecourse of average extension rate. Average of the extension rate of all individuals of a group, each averaged over consecutive light or dark periods, plotted over time. This curve reveals that the extension rate of the seedlings averaged in light period present slightly lower values than the average at night. (e): Average of extension rates of all individuals of a group, each averaged over a 24 h period. This plot presents a 24 h rhythm of the extension rate. (f): Average of normalized extension rates of each individual of a group over time. This curve presents a similar pattern to (b) but due to the normalization algorithm, it starts from midnight and ends at midnight (solar time). (g): Average of normalized extension rates of all individuals of a group, each averaged over a 24 h period. Normalized curves present similar patterns as (b) and (e) but with smaller error bars. Values are the average extension rate of all 10 seedlings and error bars present the SE. GR: growth rate.

minimum of 57.41 ± 10.23 μm h^{-1} , resulting in a >2-fold daily change in the rate of growth.

The data was further processed to display additional features of the growth response characteristics. Fig. 1c displays the average daily growth rate (Yazdanbakhsh and Fisahn 2010). This remained almost constant during the three day measurement period. Fig. 1d provides the average rates of growth during each light and dark period. Average extension rates detected in the dark were higher compared to the light period. To substantiate the detected time constants of the root elongation characteristics, we calculated the averaged 24 h growth pattern of seedlings. Fig. 1e shows the average growth rate values at each time during the 24 h cycle. These were calculated by combining measurements from the three consecutive days (Yazdanbakhsh and Fisahn 2010). These averages unequivocally substantiate diurnal features already detectable in the responses of the individual days.

Notably, the blue and the red trace exhibited identical growth pattern (Fig. 1). The average growth rate observed during this period amounted to 97.63±0.98 μm h^{-1} in Petri dish 1 (1293 time points) and 97.36±0.94 μm h^{-1} in Petri dish 2 (2044 time points). In detail, graphs of the average growth rate over time (Fig. 1b), in each 24 hour cycle days (Fig. 1c), in each light and dark periods (Fig. 1d) as well as the 24 hour growth kinetics (Fig. 1e) exhibited identical results in both Petri dishes. Thus no plate artifacts emerged from the parallel recording of two individual Petri dishes in the dual recording unit.

Individual seedlings exhibited slight differences in the mean absolute growth rate. All growth rate values in Fig. 1b-e show averaged absolute elongation rates of roots. As indicated by the standard error, these averages are affected by the different mean elongation rates of the individual roots. Normalizing growth rates of each individual seedling to the median of each day (starting from the midnight) removes this source of noise. Normalized growth rates averaged in time and 24h growth profiles are depicted in Fig. 1f and 1g, respectively. In comparison to the non standardized quantities the standard errors are significantly reduced. These graphs clearly display the existence of highly

reproducible diurnal rhythms in *Arabidopsis thaliana* root growth rates. In conclusion, these results demonstrate that Arabidopsis root elongation, under constant temperature condition, is regulated on a diurnal basis. Furthermore, constant growth conditions in the phytochamber provide identical results in simultaneous recordings of two individual Petri dishes.

Root extension pattern of Arabidopsis thaliana in 12/12-h light-dark cycles

Preliminary results of a small number of root growth kinetics in neutral photoperiods have been reported earlier (Yazdanbakhsh and Fisahn 2010). These diurnal root extension profiles in equal 12/12 h L/D photoperiods (Fig. 6 in Yazdanbakhsh and Fisahn 2010) resembled those described in the present study for LD photoperiods. To confirm the existence of diurnal rhythms in root growth kinetics of Arabidopsis in 12/12 h photoperiods with sufficient statistical support we continued our previous investigation by performing additional recordings in this photoperiod. Results are summarized in Table 1. Together, existence of stable maxima and minima in 12 h photoperiods documents the modulation of Arabidopsis root growth kinetics by diurnal rhythms.

Comparative analysis of root growth profiles obtained in two photoperiods

Comparing root elongation rates of Arabidopsis wild type (Col0) in 16 h-8 h (Fig. 1), and 12 h, (Table 1; Fig. 6 in Yazdanbakhsh and Fisahn 2010) photoperiods reveals the existence of at least 5 growth phases throughout the diurnal cycle in *Arabidopsis thaliana*. 1) General inhibition of root elongation during major part of the light period; shortly after illumination, Col0 seedlings exhibited decreasing extension rates which ended before the beginning night. 2) Increasing growth activity before darkness; several hours before the start of the dark period root extension rates started to increase (Fig. 1, Table 1; Fig.6 in Yazdanbakhsh and Fisahn 2010). 3) Increasing root extension rates during the major part

Table 1. Statistical analysis of root tip displacement of *Arabidopsis thaliana* in 12 h photoperiods

Maximal growth rate at 9.30 am (Average)	Minimal growth rate at 9.30 pm (Average)
122 ± 5 μ m h^{-1}	57 ± 2 μ m h^{-1}

Data are calculated from measurements performed on 40 individual roots observed over three consecutive days according to Yazdanbakhsh and Fisahn 2010.
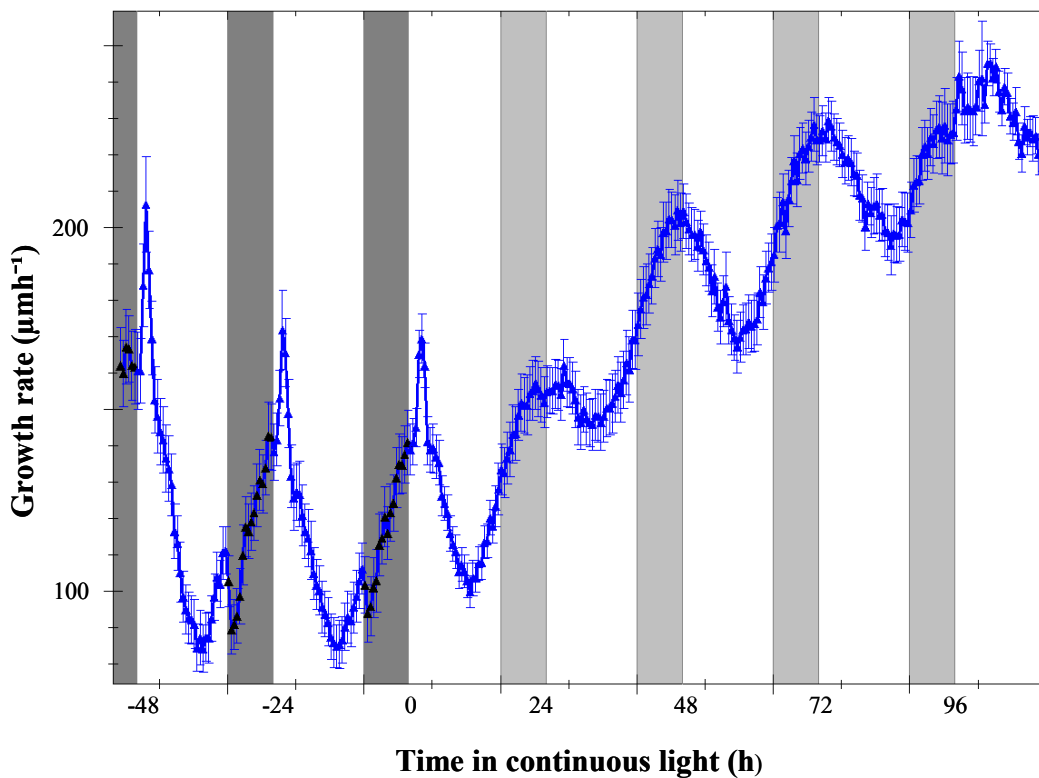
Fig. 2. Root elongation in continuous illumination. Averaged root elongating of 11 d old seedlings grown in 16 h photoperiod (n = 23). The 16 h light period started at 8 am and ended at midnight. Root elongation kinetics was measured for 2 d in a 16 h photoperiod. Consecutively, from time 0 (8 am solar time), the measurement was followed for 112 hours in continuous light. Dark grey shadings indicate the dark period whereas the light gray shadings indicate the subjective dark period. Error bars present the SE.

of the night; although carbon supply by photosynthesis is inactive at night roots continue to increase their growth rate throughout the entire night, fueled by the supply of carbon derived from degradation of starch. 4) Peak in growth rate shortly after the start of the light period (Fig. 1, Table 1; Fig.6 in Yazdanbakhsh and Fisahn 2010). These data suggest that light on induces a gradual increase of root elongation in 1.5-2 hours. 5) Transient inhibition of root elongation upon darkness; a transient period of growth inhibition was detected at the beginning of the night (Fig. 1, Table 1; Fig.6 in Yazdanbakhsh and Fisahn 2010). This inhibition of root elongation upon dark can be due to a change in energy metabolism from photosynthesis to starch degradation or due to a signaling pathway upon darkening. Characterizing this inhibition of growth requires more detailed studies of root extension profiles in different photoperiods. In a recent study that investigated the jasmonic acid response of *Arabidopsis thaliana* similar diurnal rhythms were described as reported here (Schmidt el al. 2010).

Growth dynamics of leaves, in comparison, had been followed for a long time and for all species investigated, clear diurnal rhythms have been observed (Walter and Schurr 2005). In general, leaves of dicotyledonous species exhibit maximal growth activity at the beginning of the light period (Schmundt et al. 1998, Walter and Schurr 2000) while in monocotyledonous species growth rate peaks in the middle of the day (Seneweera et al. 1995, Watts 1974, Acevedo et al. 1979). Diurnal leaf relative growth rates (RGRs) of *A. thaliana* ecotypes Ler and Columbia0 (Col0) growing in 12-12 h light-dark cycles display maxima in the morning soon after the onset of light with a subsequent decrease of growth during the day followed by a minimum early in dark (Wiese et al. 2007). Therefore, the diurnal growth kinetics of Arabidopsis roots is qualitatively in agreement with measurements performed on Arabidopsis leaves. However, the maximum growth is more pronounced in leaves compared to roots. Several reasons could account for the elevation of maximal growth in leaves. Leaves probably respond differently to environmental clues or processes which control leaf growth oscilla-

tions compared to the roots. Alternatively, signals which may be transmitted from leaves due to light sensing might induce a reduced response in roots. In addition, the described leaf growth RGR had been measured on leaves of one month old plants whereas roots were 2-3 weeks old. The minimum growth in Arabidopsis leaves (Col0) growing in 12 h photoperiod has been detected in the beginning of the night (Wiese et al. 2007). In parallel, minimum root extension of Col0 seedlings growing in 12 h photoperiod was also detected after dark (Yazdanbakhsh and Fisahn 2010). However, comparison of root extension patterns in LD and 12 h photoperiods suggest a direct effect of light-dark transitions on root extension, the extent of inhibition being correlated with the photoperiod. A comparable characterization of leaf growth responses in different photoperiods has not been reported yet. However, similar patterns of leaf expansion and root elongation in 12 h photoperiod enable us to suggest existence of a similar effect of light-dark transitions on leaf growth. Furthermore, leaf expansion during the last hours of the light period exhibits an increased rate (Wiese et al. 2007). A similar increase in growth rate was recorded in Arabidopsis roots (Fig. 1).

Hypocotyl growth of *Arabidopsis thaliana* in diurnal conditions exhibits strong rhythmicity (Nozue et al. 2007). Similar to diurnal growth patterns of roots (Fig. 1), hypocotyl growth was inhibited by light in wild type Arabidopsis plants. Moreover, growth rates of hypocotyls reached a maximum at the end of the night (Nozue et al. 2007). Together, roots, leaves (Wiese et al. 2007) and hypocotyls (Nozue et al. 2007) of Arabidopsis display a unique diurnal growth pattern with increasing growth rates in the dark period.

Root extension pattern of Arabidopsis thaliana in continuous light

Roots grown in either continuous light or darkness exhibited significant modulation in their growth rates (Laxmi et al. 2008). As root elongation rates dramatically declined in continued darkness we measured root elongation of 11 d old *Arabidopsis thaliana* seedlings grown in a 16 h photoperiod. Measurements were performed for 2 days in the 16 h photoperiod followed by transfer to continuous light for 112 hours (Fig. 2, *n*=23). The root elongation pattern detected in the 16 h photoperiod resembled that of the previous experiment (Fig. 1). Transfer to continuous light induced a doubling of absolute elongation rate. However, the kinetics of root extension rate was superimposed by a clear oscillation with maxima detected at or after the expected day and minima several hours before expected darkness (Fig. 2). In contrast to the pattern detected in day-night cycles,

whether in the same experiment (Fig. 2), or the previous measurement (Fig. 1), the transient peaks occurring in the diurnal light conditions upon light on/off are absent in free running cycles. Existence of transient peaks of root elongation upon light transitions, which disappeared in continuous light, strongly supports our previous conclusion on their induction by changes in the illumination (see above).

Continuation of rhythmicity in continuous light has been also reported for elongating hypocotyls (Nozue et al. 2007). However, in contrast to elongation of hypocotyls, the maximum elongation rate of roots remained at the beginning of the anticipated light period in continuous light, whereas it shifted to the end of the light period in elongating hypocotyls (Nozue et al. 2007; Fig. 2).

Increasing growth rates of roots at the end of the night could combine several advantages related to the interaction between endogenous and environmental conditions. Starch reserves are not completely exhausted by the end of the night (Gibon et al. 2004), therefore increasing growth rate at the end of the dark period minimizes the risk to run into carbon starvation during the diurnal cycle. Water availability is not constant during the diurnal cycle. Therefore matching the timing of optimal water availability and growth rate increase allows to provide sufficient turgor pressure to drive expansion growth.

Conclusions

Arabidopsis root growth kinetics exhibit reproducible diurnal rhythms. These rhythms are maintained throughout all photoperiods and are characterized by 5 phases of growth rate. Root elongation increases towards the end of the night. Major parts of the light period are characterized by decreasing growth activity. Therefore, root growth kinetics resembles growth patterns of Arabidopsis leaves and hypocotyls.

Acknowledgments

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