

ORIGINAL ARTICLE

Circadian Modulation of Circumnutation Length, Period, and Shape in *Helianthus annuus*

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ABSTRACT

Modulation of a turgor-growth movement called circumnutation in sunflower (*Helianthus annuus* L.) was investigated using a picture analysis system. Two photoperiod conditions were applied: light–darkness conditions (LD) 8:8 and LD 20:10. After about 3 weeks of these regimes, the plants were placed under constant light to determine whether circadian regulation of circumnutation existed or not. The rhythms of movement activity with regard to the trajectory length, period, and shape of individual circumnutations were examined. Data were processed by Fourier spectral analysis. All the parameters, trajectory length, period, and shape, revealed the ability to entrain to the administered daily cycles (16 h or 30 h). We observed diurnal fluctuations of the circumnutation parameters with the phase of the highest trajectory length, the shortest period, and the highest shape coefficient

(the most circular form) during the dark period. After the LD–LL transition, the parameters revealed periodicity, which was close to 24 h. After several days of a clear circadian free running rhythm, a gradual decrease of the amplitude of the rhythm was observed. However, the rhythm did not disappear completely. The trajectory length manifested the strongest entrainment; the circumnutation period and the circumnutation shape were less modulated by photoperiod. These findings indicate for the first time that different parameters of circumnutation in sunflower are circadian-regulated rhythms, not solely ultradian as had been thought previously.

Key words: Circumnutation; Growth movement; Circadian rhythm; Plant clock; Sunflower; Fourier analysis.

INTRODUCTION

Circumnutation is a rotary movement of elongating plant organs, such as stems, roots, and tendrils. The

tip of a plant organ describes ellipses, circles, or pendulum-like movements that can alternate between clockwise and counterclockwise directions (Johnsson 1997; Hashimoto 2002). Circumnutation is a universal oscillation probably occurring in all plant species (Darwin and Darwin 1880).

Originally, circumnutation was thought to be the consequence of unequal, irreversible growth (Brown

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1993). However, it was shown that the growth mechanism is at least partially independent of circumnutation, because some substances (for example, aluminum) stop circumnutation but not elongation (Hayashi and others 2004). Moreover, it has been shown that the growth rate is too small to generate such intense oscillations, and reversible volume variations occurring in the cells of the bending zone were observed (Caré and others 1998). The areas with rhythmically changing cell volumes move around the stem (Millet and others 1988). The volume variations are caused by differences in water content between the convex and concave sides of the bending zone, associated with turgor and ion concentration differences (Lubkin 1994). It seems that the turgor wave rotating around the stem during circumnutation drives a helical acidic growth that results in stem bending. Such a wave causes tissue stresses, and tissue stress is required for the manifestation of acid-induced elongation (Hejnowicz and Sievers 1996). Turgor changes may be generated by endogenous, spontaneous oscillations. As a consequence, oscillatory growth and movement are generated (Vanden Driessche 2000). The helical growth is hypothesized to be the mechanism that increases the stability of the hypocotyl (Schuster and Engelmann 1997) during cell wall loosening (Cosgrove 2000) that accompanies growth.

Many different substances, for example, auxins (Jouve and others 1999), abscisic acid (ABA; Vanden Driessche 2000), ethylene (Engelmann and Johnsson 1998), potassium (Millet and Badot 1996), and calcium (Giboz and others 1995), among others, can form waves around the bending zone by rhythmically varying their concentration. Ultradian ion flux oscillations (Ca^+ , H^+ , and K^+) have been found to be associated with root circumnutation (Shabala 2003). The cells of the bending zone communicate during circumnutation via plasmodesmata (Brown 1993), ion channels (Badot and others 1990), and aquaporins (Comparot and others 2000).

Although the processes by which circumnutation occurs are well understood, the controlling mechanism of circumnutation is still unknown. There are two main models for circumnutation. One is an "internal oscillator" model proposed by Darwin and Darwin (1880), which assumes the existence of an inner oscillator driving circumnutation independently of external stimuli. The second is the "gravitropic overshoot model," which in its original form explained circumnutation as a continuous gravitropic response (Johnsson 1979). However, it has been shown that gravitropism is not essential for circumnutations, because the movements have

been observed to continue under microgravity (Brown and Chapman 1984).

Therefore, in its newer version, the gravitropic model hypothesizes that a mechanism internal to the plant drives the circumnutation movements and is affected and amplified by gravitropic stimuli (Johnsson and others 1999). Hatakeda and others (2003), using genetic evidence, showed that gravitropism and circumnutation are related, although recently Yoshihara and Iino (2005) have shown that gravitropism is not a cause of circumnutation. Thus, the relationship between these two phenomena is still controversial.

The second matter of argument is the role of the circadian clock in circumnutation. The circadian clock controls many processes in plants, including gene expression (McClung 2000), Ca^{2+} oscillations (Webb 2003), stem elongation (Jouve and others 1998), leaf movement (Engelmann and Johnsson 1998), and leaf hydraulic conductance (Nardini and others 2005). Several genes (*LHY*, *CCA1*, *TOC1*) that encode components of the plant clock have been identified in *Arabidopsis* (Salomé and McClung 2005). In the past, circumnutations were believed to be based only on an ultradian rhythm, because of their 2–3-h period. The circadian occurrence of circumnutations in *Arabidopsis* was shown by Schuster and Engelmann in 1997, but the first molecular report that circumnutation could be circadian was reported recently by Niinuma and others (2005). They showed that *Arabidopsis* clock mutants (*toc1* and *elf3*) had disrupted circumnutation. We found that circumnutation in *Helianthus* reveals diurnal fluctuations (Buda and others 2003).

The purpose of the present study was to determine whether the fluctuations are only diurnal (externally regulated) or possibly circadian (internally regulated). Therefore, we tried to determine if circumnutation in sunflower can be circadian modulated in its intensity and shape, that is, if the movements could be influenced by the biological clock.

MATERIALS AND METHODS

Plant Material, Growth, and Experimental Conditions

All experiments were undertaken on 0- to 6-week-old plants of *Helianthus annuus* L. (seeds were provided by PNOS, Ożarów Maz., Poland). They were planted in pots filled with garden soil. Seed husks were removed prior to planting to make germination uniform. The plants were well irrigated

with tap water, and no other treatment was applied. Plants were grown in an air-conditioned room: the temperature was $25 \pm 1^\circ\text{C}$ and relative humidity $50\% \pm 10\%$. Light was provided by Power Star HQT-T400 Osram lamps (OSRAM GmbH, Munich, Germany) that were mounted above the plants to provide a fluence rate of $65 \times 10^{-6} \pm 5 \times 10^{-6} \text{ mol m}^{-2} \text{ s}^{-1}$ PAR at leaf level. The lamps were mounted in such a way that the plants could be assumed to experience more or less parallel light from above. Light, temperature, and humidity were kept constant and monitored with a system equipped with a PAR LITE sensor (Kipp&Zonen, Delft, Netherlands) and thermo-hygrometer LB-710 (LAB-EL, Warsaw, Poland). To make recording possible in darkness, dim green light of a fluence rate lower than $1 \times 10^{-7} \text{ mol m}^{-2} \text{ s}^{-1}$ was used. The plants were grown essentially as described by Buda and others (2003), where we showed how photoperiod conditions (light–darkness period [LD] 16:8, constant white light conditions [LL], and LD 16:8 followed by LL) affected circumnutation. In the experiments presented in the present article two additional measurement conditions (LD 8:8 and LD 20:10) were tested. On the 16-h day as well as the 30-h day, the light was turned on and off at different times of day to give LD regimes of 8:8 and 20:10, respectively. In both groups, the light was turned on permanently about 3 weeks after seedling emergence to allow observation of the plants' behavior after LD–LL transition. The dark periods are illustrated as dark-gray panels in Figure 1. The dark periods that would appear if the LD persisted are illustrated as light-gray panels and denoted as “subjective nights.”

Circumnutation Measurement and Data Collection

Measurements were carried out from the onset of seedling emergence. The pictures of the plants were taken from above with three video cameras. Data were collected at one frame every 5 min. Plant recording allowed a reconstruction of the stem apex movement in a horizontal plane. Monochromatic analog cameras (Mintron MTV-1368CD, Mintron Enterprise Co. Ltd., Taipei, Taiwan) were used in conjunction with a PC computer. The frame grabber video surveillance software GOTCHA! Multicam (Prescient Systems Inc., West Chester, PA, USA) with a motion detection algorithm was used. To make plants visible in the frame even at significant deviations from the plumb line, a calibrated zoom change protocol was carried out.

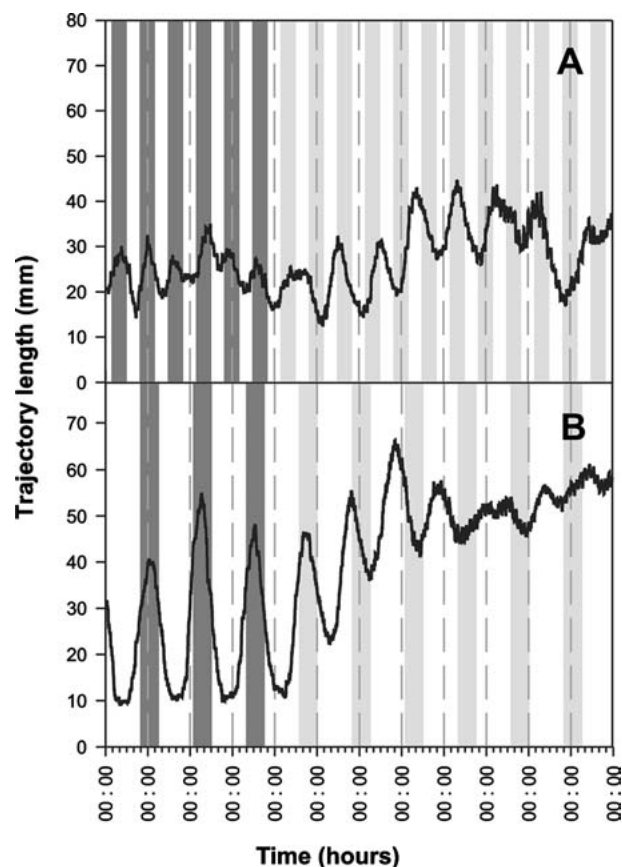


Figure 1. The changes of circumnutation trajectory length in *Helianthus annuus*. (A) light–darkness conditions (LD) 8:8 transferred to constant white light conditions (LL), running average from 5 plants; (B) LD 20:10 transferred to LL, running average from 10 plants. White areas, light; dark gray panels, dark; light gray panels, “subjective night”.

Data Analysis

The video pictures were digitized using the Tracer (custom-made) program. Experimental points (coordinates of the stem apex) were determined at 5-min intervals in a coordinate system with axes directed along N-S and W-E lines. Subsequent moments of maximal northward stem deflection were adopted as the beginning and end of one rotational trajectory. We applied the custom-made program enabling calculation of the parameters of the ellipses inscribed (by the least squares method) into the points taken by the cameras. The trajectory length (Figures 1 and 2) and the period (the duration of one single circumnutation; Figure 3), as well as the shape coefficient (the ratio between the short and long half-axis of circumnutation; Figure 4) will be discussed later in this article. The shape coefficient resembles eccentricity, which is used in

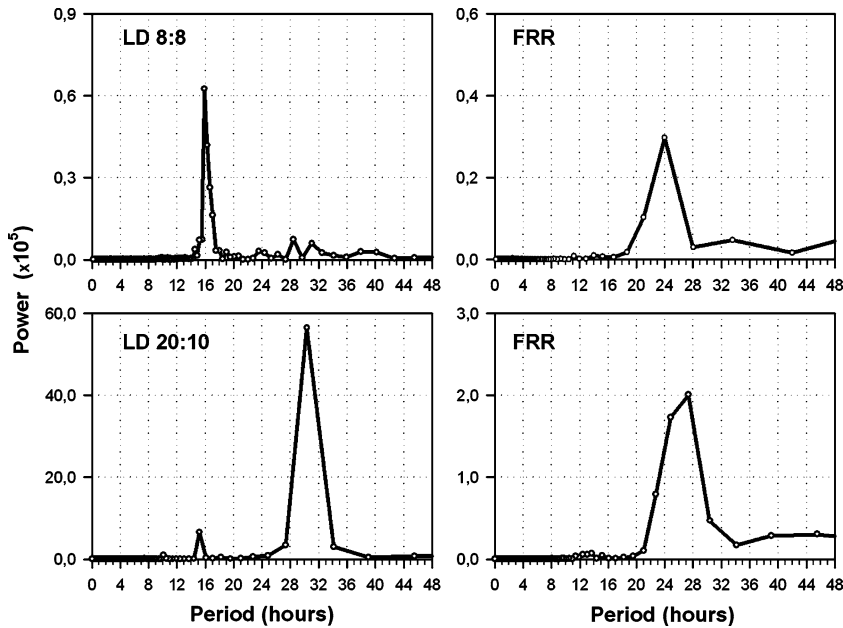


Figure 2. The spectral analysis of circumnutation trajectory length in *Helianthus annuus*. Left-hand column; LD 8:8 (top) and LD 20:10 (bottom). Right-hand column; corresponding spectra of free running rhythm (FRR) after LD–LL transition. The power is a parameter of Fourier transform indicating the amplitude of the sinusoidal component of a given period.

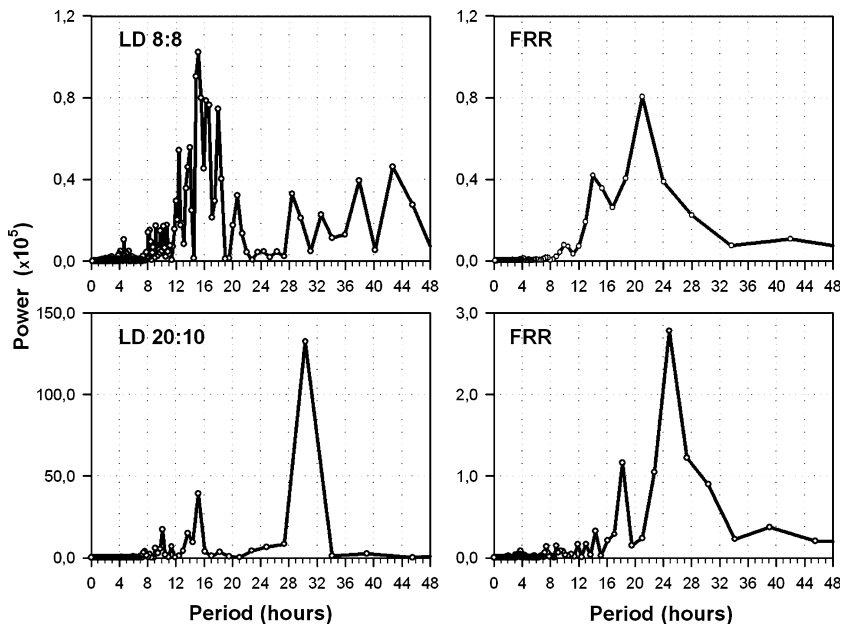


Figure 3. The spectral analysis of circumnutation period in *Helianthus annuus*. Left-hand column; LD 8:8 (top) and LD 20:10 (bottom). Right-hand column; corresponding spectra of FRR after LD–LL transition. The power is a parameter of Fourier transform indicating the amplitude of the sinusoidal component of a given period.

astronomy and mathematics to describe the shape of an elliptic trajectory. The coefficient was assumed to be in the range of 0.0–1.0. Small values indicated an elliptical shape of nutations, whereas the higher the value, the more circular the nutation was. To distinguish the period of single circumnutation from the period of the modulation of that parameter, the former is denoted as the “circumnutation period” and the latter as the “modulation period.” The values of the parameters obtained from the programs mentioned above were ordered and illustrated by Sigma Plot 9.01 software (Systat Software

Inc., Richmond, CA, USA). A 5-h window was to calculate the running average of the parameters.

Mathematical and Statistical Analysis

Mathematical analysis was performed with Statistica 6.0 software (Statsoft Inc., Tulsa, OK, USA). To determine whether periodicity of circumnutation parameters existed or not, the data were processed by Fourier spectral analysis. To verify the correctness of the Fourier analysis, additional tests were used under the assumption that the series was a “white

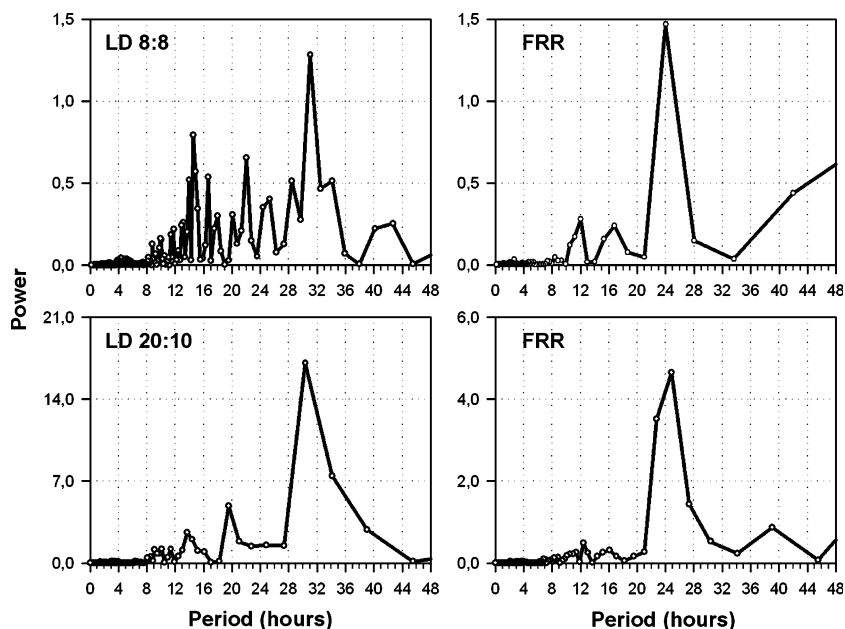


Figure 4. The spectral analysis of circumnutation shape in *Helianthus annuus*. Left-hand column; LD 8:8 (top) and LD 20:10 (bottom). Right-hand column; corresponding spectra of FRR after LD–LL transition. The power is a parameter of Fourier transform indicating the amplitude of the sinusoidal component of a given period.

noise" process (Box-Ljung's Q test and Bartlett's test). A more detailed description of the whole procedure is given in an earlier publication (Buda and others 2003).

RESULTS

The results shown in all the figures indicate the ability of circumnutation to be synchronized to the LD regime. Circumnutation trajectory length (Figure 1) rose rhythmically during dark periods and decreased during light periods in both LD 8:8 and LD 20:10 conditions. The rhythm showed acrophase drift, with a period slightly different from its environmental synchronizer. In LD 8:8 the trajectory length achieved values up to 40 mm (mean was 27.1 mm with a SE = 0.3, $n = 1102$), whereas LD 20:10 made sunflowers oscillate with a higher amplitude (values up to 65 mm; mean was 34.6 mm with a SE = 0.5, $n = 1499$). Nevertheless, under both entrainment conditions (LD 8:8, LD 20:10) the dark–light differences were clearly visible, and in both cases the period shifted to a circadian (close to 24-h) rhythm, when the plants were transferred to LL (Figure 1). Under the foreshortened LD 8:8, the dark/light differences were small during entrainment, but they increased noticeably after transfer to LL. Under the lengthened LD 20:10, the dark/light differences were quite large and decreased after transfer to LL. Although this circadian modulation of circumnutation trajectory length decreased in amplitude after several days of constant light, it

persisted with a period close to 24 h, even for a few weeks after the measurement (data not shown).

To investigate the rhythmic nature of circumnutation intensity changes, Fourier spectral analysis was applied. Running averages of circumnutation parameters taken from 5 plants (LD 8:8) and 10 plants (LD 20:10) were analyzed by the Fourier transform. Figure 2 illustrates spectral density curves of average circumnutation trajectory length in two photoperiods tested (left-hand column) and corresponding spectra of that parameter in the subsequent LL (free running rhythm [FRR], right-hand column). The trajectory length of circumnutation was almost perfectly fitted to the administered LD, with the most pronounced peaks at 15.9 h (LD 8:8) and 30.3 h (LD 20:10). The significant powers in the Fourier transform of the trajectory length in the FRR rhythm appeared at values about 4 h smaller than 24 h, and after the increase, they disappeared at 28 h. The most intense component (the maximum power) had a value of 24.0 h following LD 8:8 and 27.3 h following LD 20:10. In LD 20:10 the 8-h range of significant Fourier components was shifted by approximately 2 h toward the longer periods. In LD 20:10 we also found half-daily peaks of 15 h. This half period cycle (of 8 h) was absent in LD 8:8.

Figure 3 illustrates a spectral analysis of an average circumnutation period shown in the same order as the trajectory length (Figure 2). The modulation period also entrained to daily photoperiods, with the most pronounced peaks

occurring at 15.2 h (LD 8:8), and 30.3 h (LD 20:10). The free running periods (FRPs) of the modulation were 21.0 h (LD 8:8) and 24.8 h (LD 20:10). On the other hand, the mean value of the period of one single circumnutation (circumnutation period) was 162 min (SE = 2.7, $n = 1102$) in LD 8:8 and 178 min (SE = 2.3, $n = 1499$) in LD 20:10 (data not shown).

Figure 4 illustrates a spectral analysis of the average shape of a circumnutation. Although circadian rhythms are present, the oscillations were less obvious than in the case of the other parameters, trajectory length (Figure 2) and period (Figure 3). Also note that the peaks of spectral density curves of the shape were much less pronounced (see the values of power in the spectral curves). The mean value of the shape coefficient was 0.45 for all groups tested, and the shape oscillated between values of 0.6 in the dark period of LD and 0.3 in the light period (data not shown). This fluctuation means that circumnutations were more circular at night and more elliptical during the day. In LD 8:8 we noted a small peak close to 16 h, but a much bigger peak close to 32 h. This implies that the rhythm of the circumnutation shape could not adjust to such an abnormally short (8 h) photoperiod and the plants were able to perceive only every other day, thus measuring the period of 32 h. After the LD–LL transition following LD 8:8, the rhythm revealed an oscillation of 24.0 h. In LD 20:10 we found the same scenario as was the case of the other parameters. The rhythm was almost perfectly synchronized (30.3 h) to the administered LD, and it then returned to the circadian FRP (24.8 h).

To verify the significance of the analyses, additional statistical tests were performed. Box-Ljung's Q test ($p < 0.05$) and Bartlett's Kolmogorov-Smirnov test ($d > 0.8$) confirmed the correctness of all the spectral analyses presented.

DISCUSSION

Both our previous data (Buda and others 2003) and the results shown in this article confirm the ability of circumnutation parameters to be synchronized to LD conditions. However, in the series of experiments that we show here, it is clear that after the synchronization to unnatural LD regimes, the transition to LL changed the conditions in such a way that the modulation close to 24 h of circumnutation parameters was able to occur. Thus, circumnutation rhythm revealed entrainment (adjustment of the rhythm phase to environmental signals), as well as persistence in the absence of

environmental cues with FRP close to 24 h. These are the rules the rhythm should obey to be acknowledged as circadian (Johnson and others 2004).

From Figure 1 it is possible to see that FRRs of circumnutation trajectory length are close to 24 h, but their phases are different. Free running rhythm after LD 8:8 achieves its maximum in the middle of a subjective day, and FRR after LD 20:10 achieves its maximum in the subjective evening. However, in our previous publication (Buda and others 2003), we demonstrated that FRR after LD 16:8 achieved its maximal phase close to subjective midnight. These findings exclude the possibility that the rhythms could emanate from unknown 24-h signal from the laboratory, because the ambient conditions were the same in all the presented experiments.

The values of FRPs differed among the parameters and the photoperiods. But it is important to recognize the Fourier spectra only as approximate results. This is so because the analysis gives averaging results, to say nothing about their temporal variability. Besides, the circumnutation signals also possess infradian frequencies (Buda and others 2003) that may be a cause of some irregularities in the circadian range. Moreover, entrainment conditions, as we showed here, can slightly affect FRP. After LD 8:8, circumnutation FRPs were a bit shorter than 24 h, whereas after LD 20:10 FRPs were slightly longer. On the other hand, circumnutation in LD 16:8 had a rhythm very close to 24 h when transferred to LL (Buda and others 2003). This feature of circadian rhythms has already been shown in animals, where FRP was dependent on previous entrainment (Farner and King 1975).

The trajectory length of circumnutation achieves the highest values in LD 16:8, where the mean is on the level of about 60 mm (Buda and others 2003). In the experiments shown here, the mean values of trajectory length were considerably lower (about 27 mm in LD 8:8 and about 35 mm in LD 20:10). It seems possible that the closer the photoperiod is to natural conditions, the stronger synchronization it causes. Let us regard LD conditions as factors that modulate oscillations of a plant. In our previous publication (Buda and others 2003) we showed that FRR of circumnutation trajectory length had lower amplitudes than the rhythm upon LD 16:8 entrainment. This suggests the existence of oscillations, in which the condition of the resonance is fulfilled. The natural frequency of a plant was almost the same as the frequency of the driving force, so the resultant amplitude in LD was higher than the amplitude of free oscillations in LL. In contrast, in the experiments shown in the present work, the frequencies of

the driving factors (LD 8:8 and LD 20:10) were much different than the natural frequency of a plant. In consequence, the LD circumnutation trajectory length was around a lower mean level, lower even than the mean level of free running motion (Figure 1).

Thus, LD 8:8 made sunflowers oscillate with a very low amplitude. It was so far from natural conditions (the frequency of given light–dark transitions was very high) that plants “had difficulty” in tuning to them. It is especially obvious in the case of the shape where the 32-h peak was more pronounced than the 16-h peak. It seems that the plants lagged behind and could only identify every other night. Moreover, the half-daily peak of trajectory length connected with the plants’ “five o’clock” (Trębacz and others 1997) was absent in LD 8:8 (Figure 2). Again, the photoperiod administered could be too frequent for the plant to elicit the full response.

Circadian rhythm of the circumnutation period was far less pronounced in all the treatments tested than the rhythm of trajectory length. This confirms the high stability of the period mentioned in our previous publication (Buda and others 2003), which meant that the period is less manageable by photoperiod conditions than the trajectory length and has many fewer fluctuations. Considering the similar values of circumnutation period among the treatments and the highest values of trajectory length in LD 16:8, it is possible to conclude that circumnutation has the greatest intensity (reveals the highest speed) in natural conditions (that is, LD 16:8). Although the FRPs of the modulation period differed from one another, it is clear that the tendency was similar as in the case of the trajectory length; after LD–LL transition following LD 8:8, the modulation period lengthened, whereas after the transition following LD 20:10 the period shortened. Strong signals of FRPs were noted in each photoperiod in the same circadian range (see Figure 3). These results suggest it is a circadian phenomenon not merely physiological inertia (daily modulation) after the change of ambient conditions.

There is strict division of biological rhythms into ultradian and circadian categories in the chronobiological literature (Engelmann and Johnsson 1998). We show here that the rhythms can coexist where ultradian rhythms reveal circadian modulation. From a reading of our previous publication (Buda and others 2003) it might be concluded that the LD 16:8 plants “remembered” their night length and repeated that 24-h period in subsequent subjective nights. But this is most likely not the case, because LD 8:8 and LD 20:10 in the present work also

returned to a 24-h period during their subjective nights. This confirms the results obtained on *Arabidopsis* circumnutation that were also shown to be circadian regulated (Niinuma and others 2005). Based on our findings, it is worth emphasizing that the circadian modulation of circumnutation parameters in sunflower was revealed by the plants, which had never been exposed to a 24-h day.

The controlling mechanism of circumnutation is still unknown. It seems that circumnutation was internally regulated by a very complex oscillatory mechanism modulated by external stimuli (light, temperature, gravity, and so on). The processes that form such an oscillatory mechanism, especially rhythmic membrane-transport processes, reveal their own frequencies in the absence of environmental cues. The resultant periodicity of such processes is close to 24 h, and it has been speculated that it is the most beneficial value, giving the best adjustment to the environment and therefore the best evolutionary success. On the basis of the data presented here we can postulate that circumnutation is an ultradian rhythm that can be circadian modulated in its intensity and shape. The pathway by which circumnutation becomes a circadian output is still a mystery.

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