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Characterization of Diurnal Movements of Primary Pulvinus in *Mimosa pudica* L. and their Relation to Day-Night Cycles

By

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With 6 Figures

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Summary

MORIMOTO N., SHICHIJO C., WATANABE S. & SUDA S. 1994. Characterization of diurnal movemnts of primary pulvinus in *Mimosa pudica* L. and their relation to day-night cycles. – Phyton (Horn, Austria), 34 (1): 57–66, 6 figures. – English with German summary.

The diurnal movements of the primary pulvini of *Mimosa pudica* were recorded every day throughout a year, and the daynight cycles analyzed. The rhythm exhibited on long days was determined by the light-on signal (sunrise), characterized by a rapid downward movement, and by an evening downward movement about 12 hr after sunrise. The rhythm on short days was determined by the light-off signal (sunset), characterized by a transient upward movement which preceded a downward movement around sunset, and by the highest position about 12 hr after the transition from day to night. In the day-night rhythm about 12 hr/12 hr both the light-on and the light-off signals are equally effective.

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Zusammenfassung

MORIMOTO N., SHICHIJO C., WATANABE S. & SUDA S. 1994. Die diurnalen Bewegungen an den primären Blattkissen von *Mimosa pudica* L. und ihre Beziehung zu Tag-Nacht Rhytmen. – Phyton (Horn, Austria) 34 (1): 57–66, 6 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Die diurnalen Bewegungen an den primären Blattkissen von *Mimosa pudica* wurden täglich während eines Jahres protokolliert und der Tag-Nacht Rhythmus analysiert. Der Rhythmus wird an Langtagen durch ein Licht-An-Signal (Sonnenaufgang) bestimmt, charakterisiert durch eine schnelle Abwärtsbewegung während des Sonnenaufgangs und eine abendliche, gleichgerichtete Bewegung ca. 12 Stunden danach. Der Rhythmus an Kurztagen wird von einem Licht-Aus-Signal (Sonnenuntergang) bestimmt. Charakterisiert ist er durch eine vorübergehende Aufwärtsbewegung, die einer Abwärtsbewegung während des Sonnenuntergangs vorangeht; die höchste Position wird ca. 12 Stunden nach dem Tag/Nacht/Übergang erreicht. Bei einem Tag-Nacht Rhytmus von 12/12 Stunden sind sowohl das Licht-An–Signal als auch das Licht-Aus-Signal gleich wirksam.

Introduction

It has been considered that the diurnal leaf movement is basically controlled by one circadian rhythm which is triggered by a light-on and a light-off signal (BÜNNING 1967). However, in the leaf movement of *Xanthium strumarium,* HOSHIZAKI & al. 1969, 1974 suggested the presence of two distinct rhythms, a light-on and a light-off rhythm. FONDEVILLE 1964 interpreted the diurnal movement of the primary pulvinus of *Mimosa pudica* as a simple up and down movement in which the upward movement was initiated by a light-off signal and the downward movement by a light-on signal. WATANABE 1971 observed a downward movement at the beginning of the night period followed by a nocturnal upward movement in *Mimosa.* However, the rhythm of the diurnal movement of the *Mimosa* leaf has not yet been well characterized, since its extreme seismonastic sensitivity has made it a difficult subject for experimental work.

This report presents significant features of the diurnal movements of the primary pulvinus of *Mimosa pudica,* and their analysis related to the day-night cycles that suggest the probability that the rhythm is influenced by two signals (clocks).

Material and Methods

The plants of *Mimosa pudica* L. used were grown as reported previously (MORIMOTO & al. 1986). The diurnal movements of their primary pulvini were recorded as up and down movements of the petioles everyday throughout one year (September, 1982 to August, 1983) in the greenhouse in Kobe (N 34° 41′ E 135° 11′). Sets of 4 plants each were used in the experiments. When the plant had 3 fully expanded leaves with 4 pinnae, its 2nd youngest leaf without cutting as done in our previous report (MORIMOTO & al. 1986) was employed. The movement was recorded until the leaf became the 4th. All curves on the cahrt were converted to the curves of the angle (θ, degrees) between the stem and the petiole. The data from the 4th day after the beginning of the experiments were used to obtain normal curves eliminating irregular movements which occur on the first 3 days as a result of manipulating the petiols in preparation for the experiments. The margin of error in measurements was always about ±1° (degree). In this study "long day" and "short day" stand for, respectively, more than and fewer than 12 daylight hours.

Results

The highest position

Fig. 1 shows representative curves for every month. The highest position of the leaf in diurnal movements reached peaks between 130–160 degrees in each curve.

On long days, from April to August, the highest position was reached at or immediately after sunrise. This shows that on long days, there may be relationship between the time of the highest position and sunrise.

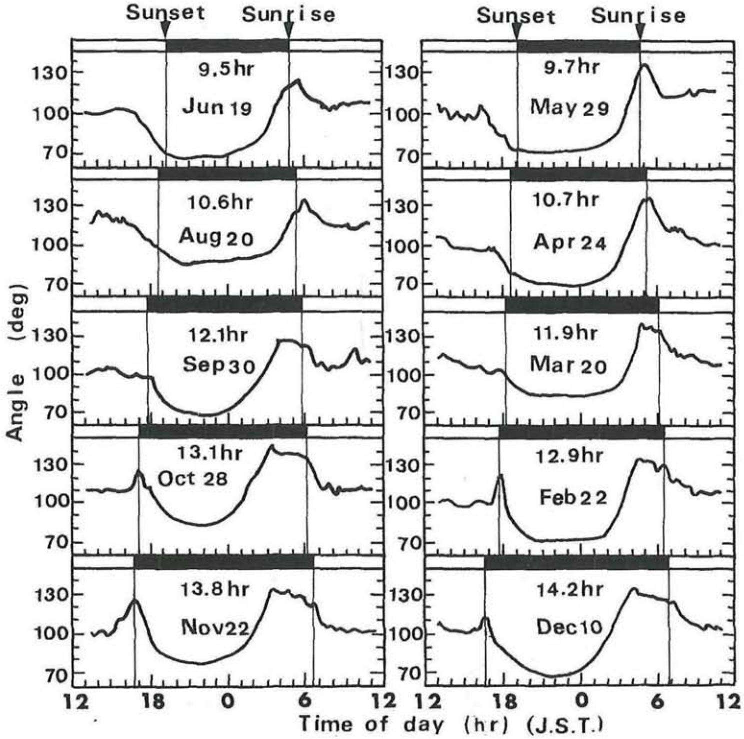

Fig. 1. Seasonal variation of diurnal movements of *Mimosa* primary pulvini. The hours of night period are indicated in each figure. The curve of July, which was almost the same as that of June, and the curve of January, the same as that of December, are omitted. Abscissa shows Japan standard time (J. S. T.).

On short days, the highest position was reached 1–1.5 hr before sunrise in March and September, 2–2.5 hr in February and October, and 3–3.5 hr in November, December and January. The time difference to the earlier sunset was the same as that of the earlier attainment of the highest position. This shows that on short days, there may be a relationship between the highest position and sunset.

Rapid downward movement

The rapid downward movements of the leaf in the morning always commenced within 30 min after sunrise throughout the year (Figs. 1, 2). On long days, the rapid downward movement occurred directly after the highest position. On short days, however, it occurred after a gradual downward movement from the highest position. These results indicate that in every season sunrise induces the rapid downward movement of the leaf.

Day position

The day position followed the downward movement after the highest position in the morning (Fig. 1). The petiole remained in the day position of 100–120 with a number of small oscillations. The day position terminated before sunset on long days, but persisted throughout the day on short days.

End of day position and evening downward movement

On long days, the day position was followed by the evening downward movement. The day position terminated about 2.5 hr before sunset in May, June and July, about 1.5 hr before sunset in April and August, and at or just before sunset in March and September (Fig. 1). On long days, time difference to the earlier sunrise was the same as that of the terminating time of the day position (Fig. 1). This indicates that there may be some relationship between the terminating time of the day position and sunrise.

On short days, from October to February, the day position always terminated 0.5–1 hr before sunset, and was followed by a transient and rapid upward movement. The evening downward movement at the beginning of the night period occurred immediately after the transient upward movement. This shows that on short days the day-to-night transition before sunset may induce a transient upward movement before the beginning of the evening downward movement.

The lowest position and nocturnal upward movement

After the evening downward movement, the lowest position at 60–90 held for several hours (Fig. 2). On longer days, in May, June and July, the lowest position was reached at or immediately after sunset, but always after sunset in the other seasons. A nocturnal upward movement followed the lowest position, began at different times, and fluctuated from day to day throughout the year, indicating that it may be affected by some environmental variable such as night temperature.

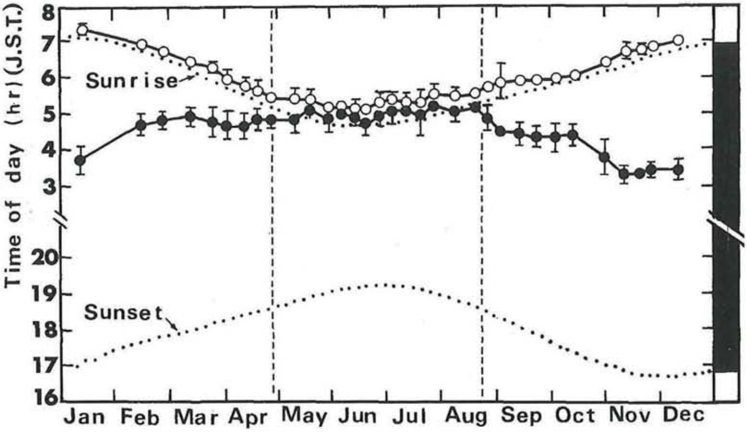

Fig. 2. Time of the highest position (●), and beginning time of rapid downward movement in the morning (○).

Each value is the mean ±SD of 5–20 experiments during 3–10 days. Sunrise and sunset were dotted every 5 days. Two vertical broken lines indicate the days of 10.5 hr night. Ordinate shows Japan standard time (J. S. T.).

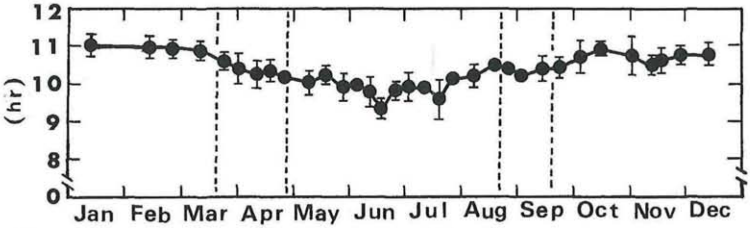

Fig. 3. Time interval between sunset and time of the highest position. Each value indicates the mean ±SD of 5–20 experiments. Two inner and two outer vertical broken lines show day-night 10.5 : 13.5 and 12 : 12, respectively.

Time of the highest position

Fig. 2 shows the time of the highest position throughout the year. Outside the two vertical broken lines (Sept.–April), the curve of the highest position separated from the sunrise curve during the days when night periods were 10.5–11 hr, and almost paralleled the sunset curve throughout the period of short days. However, from May to August, when night periods were shorter than 10.5 hr, every highest position occurred at sunrise. The time interval between sunset and the highest position is shown in Fig. 3.

On short days, the highest position appeared about 11 hr after sunset. On the other hand, on long days, when the night period was shorter than 10.5 hr, the time interval between sunset and the highest position was 9.5–10.5 hr, which clearly coincided with the night period for these seasons (Figs. 2, 3). When the night period was about 11 hr, the highest position occurred 10–11 hr after sunset. These results clearly indicate that the time of the highest position was determined by sunset in periods over 12 hr of night, whereas it was determined by sunrise in periods of under about 11 hr of night.

Terminating time of day position

On long days (May–Sept.), in the area between the two vertical broken lines in Fig. 4, the terminating time of the day position was earlier than at sunset, and the curve of the terminating time almost paralleled the sunrise curve. The time interval between sunrise and the terminating time of the day position was 11–12 hr (Fig. 5). However, on short days (Sept.–May) the day position terminated at sunset (Fig. 4). The time interval between sunrise and the terminating time was 9.5–11.5 hr and coincided with the

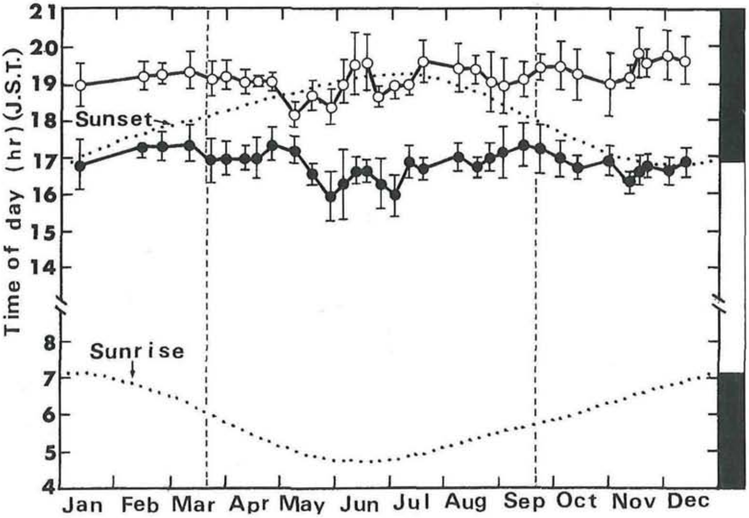

Fig. 4. Terminating time of day position (●), and beginning time of the lowest position (○).

Beginning time of the lowest position was decided as the time when the tangent of the curve of evening downward movement crossed horizontal line from the lowest position. Each value is the mean ±SD of 5–20 experiments during 3–10 days. Sunrise and sunset were dotted every 5 days. Two vertical broken lines indicate day-night 12 : 12. Ordinate shows Japan standard time (J. S. T.).

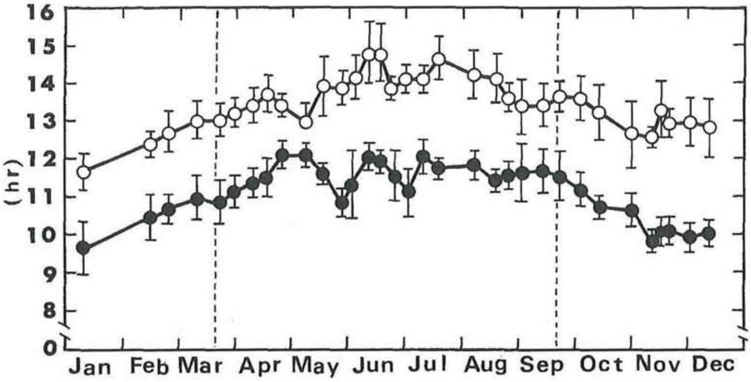

Fig. 5. Time interval between sunrise and terminating time of day position (●), and between sunrise and beginning time of the lowest position (○).
Each value indicates the mean ±SD of 5–20 experiments. Two vertical broken lines shows day-night 12 : 12.

length of the daytime period (Figs. 4, 5). These results indicate that the terminating time is determined by sunrise on long days, but by sunset on short days.

Starting time of the lowest position

Fig. 4 shows the starting time of the lowest positions. On short days (Sept.–Mar.) sunset determined the terminating time of the day position, and the curve of the starting time of the lowest position paralleled the curve of the terminating time of the day position (Fig. 5). The time interval between the lowest position and the day position was 2–3 hr. These results indicate that sunset may determine the lowest position on short days. However, on long days (Mar.–Sept.) the time interval between the terminating time and the lowest position was 0.5 hr at least and 4 hr at most (Fig. 5). This fluctuation may be due to some influence of sunset on the downward movement between the terminating time of the day position and the starting time of the lowest position (Figs. 1, 4).

Discussion

Based on the observations of the diurnal movements of the primary pulvini in *Mimosa,* in LD = 14.5 : 9.5, Fondeville 1964 proposed that the downward movement was initiated by a light-on signal, and the lowest position of the petiole appeared at the end of the light period, and that the upward movement was induced by a light-off signal and reached the highest position at the end of the dark period. His curves were similar to ours obtained when LD cycles were about 14.5 : 9.5 in May and June, but all of our curves observed throughout the year could not be explained by his model. We found that the curve of the diurnal movement in *Mimosa* pulvinus was modulated by the day-length, and furthermore, the petiole did not exhibit a simple up and down movement induced by a light-on or a light-off singnal.

In the diurnal movements of *Mimosa,* it should be noted that there are significant differences between the curves of long days and short days (Fig. 1). Our results are summarized in the curves of long days (Fig. 6A) and of short days (Fig. 6B). On long days, sunrise initiated the leaf movement rhythm. This rhythm started with the rapid downward movement which lead to the commencement of the day position. The day position terminated 11–22 hr after the beginning of the light period, and was followed by the evening downward movement and then the lowest position. The lowest position persisting for several hours was followed by the nocturnal upward movement. This rhythm was completed by the highest position which occured at sunrise of the following morning. In the rhythm of long days, the duration of the evening downward movement between the terminating time of the day position and the starting time of the lowest position fluctuated (Fig. 5). During the evening downward movement (Fig. 1) sunset may have some influence on this phase. In *Xanthium strumarium,* HOSHIZAKI & al. 1969 reported that a light-off signal induced an immediate upward movement. In our experiments of short days, sunset induced a transient upward movement (Fig. 1). If sunset basically has the common action of inducing an upward movement, it is possible that the duration of the evening downward movement fluctuates because of the antagonistic effect exerted by sunset. However, it should be realized that the basic oscillations of long days are rephased not by sunset but by sunrise. Thus, the light-on signal (sunrise) appears to be a dominant factor in the rhythm of long days.

On the other hand, on short days, sunset initiated the leaf movement rhythm (Fig. 6B) which started with the evening downward movement. The lowest and highest positions appeared 2–3 hr and 10–11 hr, respectively, after sunset. This rhythm was completed by the termination of the day position. Another significant feature of the rhythm was that a transient upward movement preceded the evening downward movement. This upward movement commenced 0.5–1 hr before sunset. From this, it seems more likely that the leaf responded to day-to-night transition before sunset, so that the lowest and highest positions were determined 3–4 hr and 11–12 hr, respectively, after the day-to-night transition. Sunrise induced the rapid downward movement in the morning on short days (Figs. 1, 2). However, it seems untenable that sunrise could rephase the rhythm of short days, since the phase of the gradual downward movement had already commenced before the rapid downward movement. Therefore on short days, sunrise may only accelerate downward movement after the highest position is reached. Thus the light-off signal (sunset) appears to be a dominant factor in the rhythm of short days.

On the days of around LD = 12:12, in September and March, the highest position occurred 10–11 hr after sunset and the day position terminated 11–12 hr after sunrise without a transient upward movement (Fig. 1). This indicates that both sunrise and sunset have an equal effect on the rhythm of days of about LD = 12:12 hr.

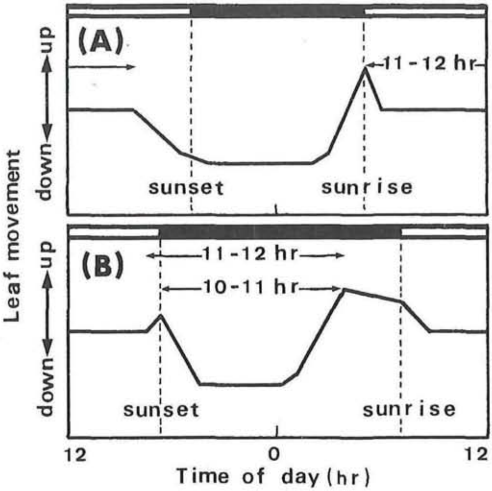

Fig. 6. Schematic curves of diurnal movement of primary pulvinus in *Mimosa pudica*. A: model of long days. B: model of short days.

It has been suggested that the circadian oscillations of the leaf movements are controlled by a time measuring process in response to light-dark transitions. In the leaf movement of *Phaseolus multiflorus,* the day maximum occurred 7–8 hr and the night maximum occurred 17–18 hr after the beginning of light (FLÜGEL 1949). The leaf opening of *Samanea saman* was induced by a light-on signal and its folding occurred about 12 hr after the opening, even though the leaf was still illuminated (PALMER & al. 1958). The leaf of *Coleus* showed that the time between the onset of darkness and the minimum leaf position was about 5 hr under 2 to 8 hr photoperiods and about 3 hr under 12 to 16 hr photoperiods (HALABAN 1968). The leaflets of *Albizzia julibrissin* alternately opened and closed with each phase persisting for about 12 hr in light of constant intensity (SATTER & al. 1971). A sudden and rapid downward movement of the leaf of *Xanthium strumarium* occurred about 16 hr after a light-on signal and an immediate and sudden upward movement of the leaf was induced by a light-off signal (HOSHIZAKI & al. 1974). The time measuring process of the circadian oscillation has been explained by one rhythm (BÜNNING 1967). However, in *Xanthium*, HOSHIZAKI & al. 1974 proposed the hypothesis of the participation of a light-on and a light-off rhythm which is controlled by two clocks. Our results clearly show that the rhythm of the diurnal movement of the *Mimosa pudica* primary pulvinus is dominantly controlled by the light-on signal on long days, and by the light-off signal on short days. Our results can be useful in further experiments to analyze the endogenous rhythm of *Mimosa* pulvinus.

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