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Autor: Jouve, Laurent / Greppin, Hubert / Degli Agosti, Robert
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FLORAL STEM GROWTH OF *ARABIDOPSIS* ECOTYPES. II. SHORT TIME SCALE EVENTS AND EVIDENCE FOR ULTRADIAN RHYTHMS

BY

Laurent JOUVE*, Hubert GREPPIN* & Robert DEGLI AGOSTI*

ABSTRACT

Floral stem growth of *Arabidopsis* ecotypes. II. Short time scale events and evidence for ultradian rhythms - The extension rate of the first inflorescence node of four *Arabidopsis* ecotypes was measured during light/dark or continuous light exposure and was found to exhibit oscillations that showed various ultradian rhythms. During the processes *Arabidopsis* ecotypes growth rate displays ultradian rhythms with periods in the range of 18 to 72 min. The rate oscillations were not in relation with mechanical noise or environmental oscillatory conditions. Indeed, our studies suggest that the oscillations in growth rate are endogenous in their origin. Moreover than ultradian oscillations, each ecotype displayed special growth rate variations, after the transition from light to dark or reciprocally. This could be assimilated as individual growth rate signature for the four different ecotypes.

Key-words: Floral stem, elongation, light-on, light-off, ultradian rhythms, ecotypes, *Arabidopsis thaliana*.

Abbreviations: Ler = Landsberg *erecta*; Col = Columbia. Ws = Wassilewskija. LVDT = linear voltage differential transformer.

INTRODUCTION

Plant growth exhibits many rhythms and pseudo-rhythms with very different periods, such as annual (GWINNER, 1986), seasonal (COLLIN *et al.*, 1994) and circadian rhythms (LECHARNY & WAGNER, 1984; JOUVE *et al.*, 1998, 2000). Some rhythms with short periods have been also studied. Indeed, variations of plant growth with short periods of few minutes have been shown (KRISTIE & JOLLIFFE, 1986; PRAT & PARÉSYS, 1995, DEGLI AGOSTI *et al.*, 1997). Nevertheless, the significance of these oscillations is still poorly understood.

The analysis of rhythms with short periods requires accurate measurement apparatus. Furthermore, experiment based on auxanometry must be very reproducible for study of the spontaneous changes in the dynamic of growth in order to discriminate the physical or biological origin of these variations. Using linear voltage differential transformers

* Plant Biochemistry and Physiology Laboratory, University of Geneva, 3 place de l'Université, CH-1211 Geneva 4, Switzerland. *Corresponding author: Fax 41-22 329 77 95, E-mail Laurent.Jouve@bota.unige.ch

(LVDT) PRAT & PARÉSY (1989, 1995) have been able to observe periodical changes in the growth velocity of mung bean hypocotyl excised segments of about 4 to 10 min. Their results showed that these oscillations were related to the biological activity of the sample.

Moreover than these short time scale oscillations, alternative light and dark induces short events directly due to the transition from light to dark and reciprocally. These responses result in the modification of the stem elongation rate in a particular shape and these changes could be in relation with phytochrome (KERCKHOFFS *et al.* 1997) or blue light receptor (ZEIGER, 1994).

Our aim of this study was to investigate the extension growth kinetics of four different *Arabidopsis* ecotypes. This, in order to see if, depending on the origin, the short time scale events measured during the floral stem growth could be a good marker for studying the growth processes. Indeed, we will review here the rapid growth rate variation and discuss their differences in function of the considered ecotype.

MATERIAL AND METHODS

Plant material and growth conditions

Four *Arabidopsis thaliana* (L.) ecotypes (Ler, Col, C24 and Ws) seedlings were grown in potting compost for 3 weeks after sowing. Afterwards they were transplanted in a new pot (7 x 7 x 6 cm), as single plants, and cultured for 3 weeks waiting for inflorescence primordia initiation. All four ecotypes were cultivated at the same time. During growth, light (L:D 12:12) was provided by Sylvania (OSRAM GmbH, Munich, Germany) 36 W Luxline-Plus fluorescent lamps ($75 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR). Temperature was $20 \pm 5^\circ\text{C}$ and humidity $70 \pm 15\%$.

Experimental conditions

Experiments were done in thermo- and hygro-regulated culture chambers: temperature was $22.5 \pm 0.5^\circ\text{C}$ and relative humidity $80 \pm 6\%$. During growth measurements, the photon flux was decreased to $42 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR using Sylvania 36 W Gro-Lux fluorescent lamps in order to increase inflorescence growth.

Two measurement conditions were tested: L:D (12:12) and continuous light. The duration of the experiment was 10 days. The four ecotype batches were used for experiment in parallel.

Data acquisition and treatment

The measurement of the first inflorescence internode elongation was carried out with a custom designed plant growth measuring apparatus (DEGLI AGOSTI *et al.*, 1997; JOUVE *et al.*, 1998). Data were collected each 60 seconds. In order to reduce mechanical and electronic noise, a first basic treatment is performed as following: 3 successive points are averaged. From the resulting time series a moving mean over 3 points is calculated on it. Sampling is reduced to 1 point per 3 min. The resulting time series represents the elongation of the plant, and to obtain the stem extension rate, measurements are differenced (DEGLI AGOSTI *et al.*, 1997; JOUVE *et al.*, 1998).

Statistical analysis

ANOVA and Student-Newman-Keuls multiple comparison tests (NEWMAN, 1939; KEULS, 1952) were used for data treatment using Instat for Macintosh 2.01 software.

RESULTS

Light-on and light-off

The sudden transition from dark to light or from light to dark induced changes in the growth rate of the first internode of the *Arabidopsis* floral stem (Fig. 1). Looking to our results, major differences are observable between the four ecotypes, but also inside the same ecotype depending on the light-on or the light-off transition. Firstly, the main character observable was that these perturbations in the growth rate have been going on for about one to two hours after the transition. Ler ecotype displayed a major peak and a small valley after light (Fig. 1A). The same transition induce the same result with Ws (Fig. 1D) but displayed only a major transitory valley with Col (Fig. 1B) or C24 (Fig. 1C). The light off response was generally more complex than the light-on one. A first peak followed by a deep valley and a second peak in growth rate composed the growth answer to the light to dark transition with Ler (Fig. 1E) and Col (Fig. 1F) ecotypes. Columbia ecotype displayed a stronger variation in amplitude than Ler and the phenomenon span on a higher time period. C24 and Ws displayed also a similar reaction shape. After a first valley in the growth rate curve, a secondary peak was observable (Fig. 1GH).

Ultradian rhythms

All along the whole growth span of the growth of the first internode of the *Arabidopsis* floral stem it has been possible to observe repetitive variations in the growth rate with different periods between 15 to 90 min. These kind of variations have been detected as well during the light or the dark periods of the L:D (12:12) photoperiod (Fig. 2; Fig. 3; Fig. 4) than during continuous light exposure (Fig. 5). Ultradian growth rate rhythms have been shown in the four ecotypes, as well during light than dark period, with an oscillatory median period of 22.6 ± 1.5 min (Fig. 2). Excepting with C24 ecotype, it was possible to observe an ultradian growth rate oscillation, as well during light than dark period, of 30.6 ± 2.2 min mean period with Ler, Col and Ws ecotypes (Fig. 3). A third ultradian rhythm could be also encountered during *Arabidopsis thaliana* growth under L:D (12:12) photoperiodic condition. Indeed, regarding to the C24 or Ws ecotypes, we have been able to see some successive oscillations of the growth rate with a mean period of 63.5 ± 9.6 min (Fig. 4). These oscillations, lower in frequency, were present only during dark periods of culture.

Measuring the growth during continuous light exposure had shown that two different ultradian oscillations could be seen as well with Ler than Col, C24 or Ws ecotype. One with the smallest mean period (17.5 ± 0.6 min) and one with a greater (27.3 ± 4.3 min) (Fig. 5).

Table I precises the period of each ultradian growth rate rhythm encountered with each ecotype. Moreover, Table I display the relative presence of each oscillation during

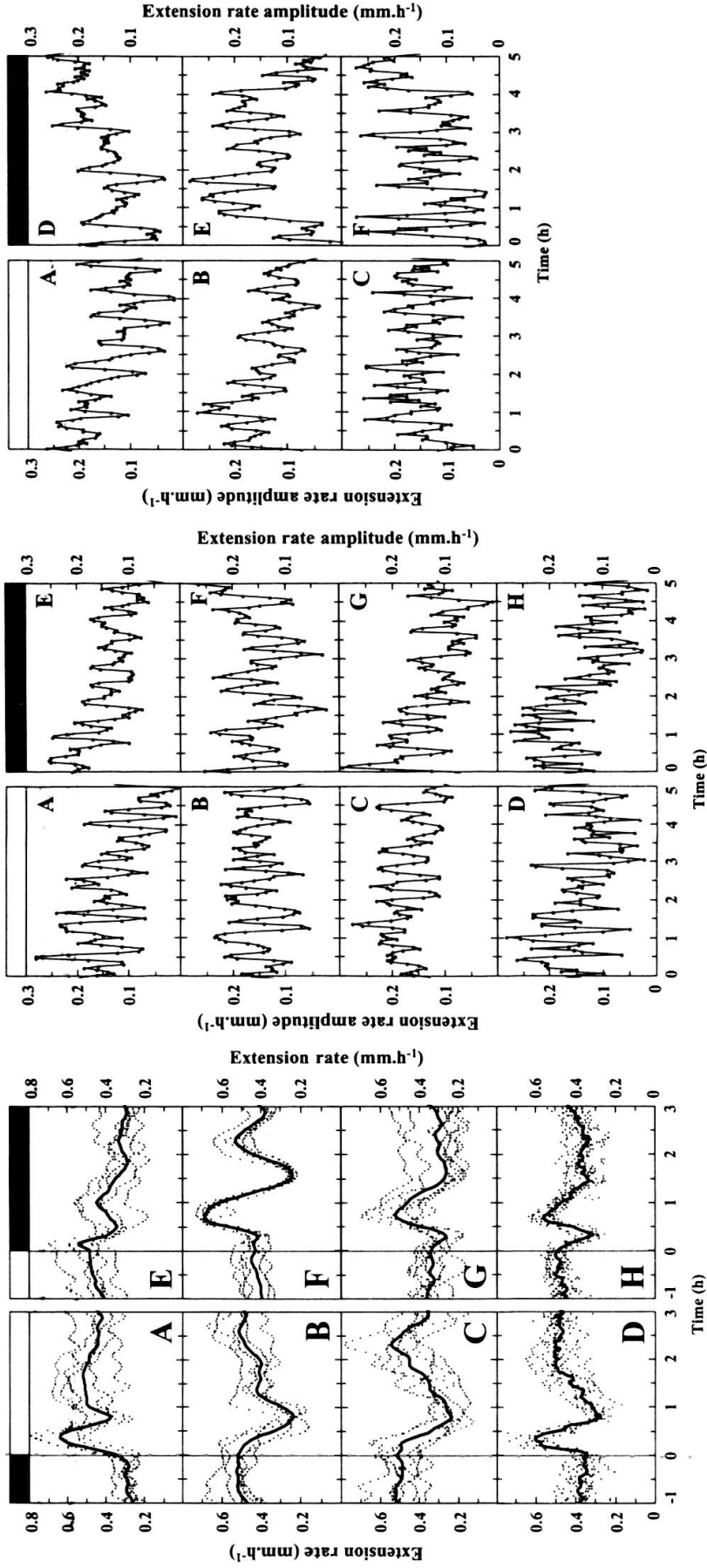


FIG. 1.

Arabidopsis thaliana first inflorescence internode extension rate, focused onto light-on (A, B, C, D) or light-off (E, F, G, H), of four ecotypes as a function of time. A and E: Ler = Landsberg *erecta*. B and F: Col = Columbia. C and G: C24. D and H: Ws = Wassilewskija. Time 0 was considered as the transition from light to dark or reciprocally. Points represent data from at least 5 measured plants and the bold curve is the averaged resulting growth rate curve. Extension rate is expressed in mm.h⁻¹.

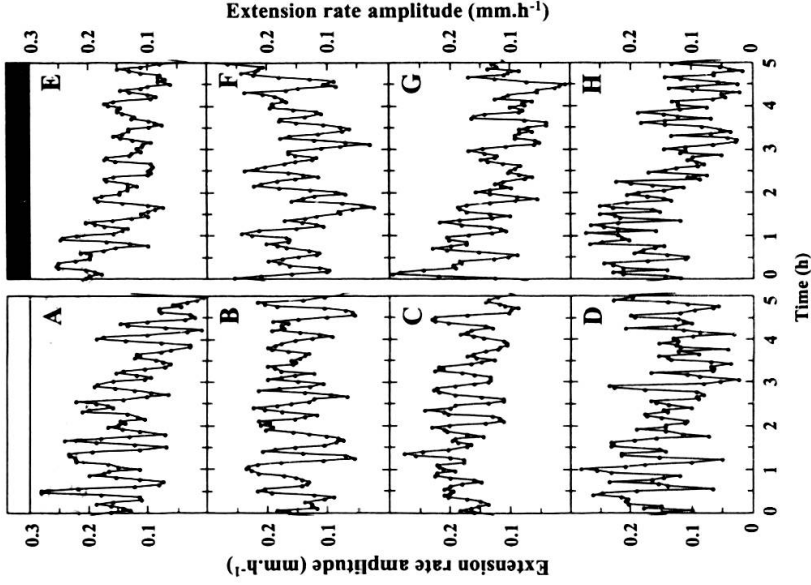


FIG. 2.

Arabidopsis thaliana first inflorescence internode extension rate of four ecotypes under L:D (12:12) photoperiod condition, as a function of time. Expression of a high frequency (± 22.6 min) ultradian rhythm during light (A, B, C, D) and dark (E, F, G, H) periods. A and E: Ler = Landsberg *erecta*. B and F: Col = Columbia. C and G: C24. D and H: Ws = Wassilewskija. Results are the data displayed by a representative measured plant, extension rate is expressed in mm.h⁻¹.

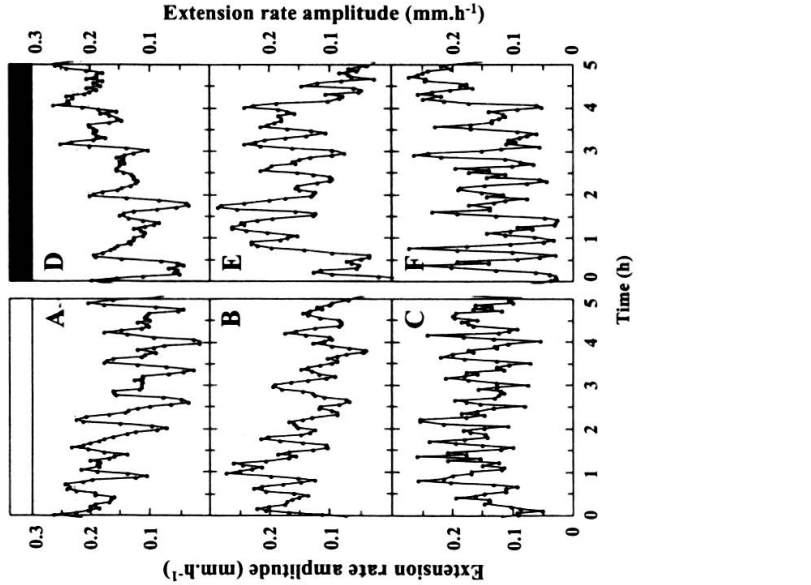


FIG. 3.

Arabidopsis thaliana first inflorescence internode extension rate of three ecotypes under L:D (12:12) photoperiod condition, as a function of time. Expression of a median frequency (± 30.6 min) ultradian rhythm during light (A, B, C) and dark (D, E, F) periods. A and D: Ler = Landsberg *erecta*. B and E: Col = Columbia. C and F: Ws = Wassilewskija. Results are the data displayed by a representative measured plant, extension rate is expressed in mm.h⁻¹.

TABLE I.

Calculated periods and presence of floral stem elongation rate ultradian rhythms of four *Arabidopsis* ecotypes during L:D (12:12) or continuous light exposure. sd = standard deviation. The different letters indicate significantly different values (n = 50; P < 0.01).

	Light		Dark		Continuous light	
	Period \pm sd (min)	Presence (%)	Period \pm sd (min)	Presence (%)	Period \pm sd (min)	Presence (%)
Ler	22.6 \pm 1.8 b	71.4	25.0 \pm 2.1 b	73.3	17.0 \pm 1.2 a	37.5
	29.6 \pm 2.9 c	28.6	33.6 \pm 3.1 c	26.7	22.5 \pm 1.3 b	62.5
Col	23.3 \pm 2.7 b	92.3	23.6 \pm 2.1 b	44.5	17.5 \pm 0.8 a	86.4
	32.4 \pm 0.5 c	7.7	28.6 \pm 1.8 c	33.3	28.5 \pm 2.1 c	13.6
			71.3 \pm 3.6 d	22.2		
C24	23.3 \pm 2.4 b	100	23.7 \pm 2.0 b	88.0	18.1 \pm 1.6 a	66.7
			56.3 \pm 4.4 c	12.0	25.4 \pm 2.8 b	33.3
Ws	21.2 \pm 2.4 b	57.1	19.9 \pm 2.6 ab	73.4	18.2 \pm 2.3 a	72.7
	29.1 \pm 3.2 c	42.9	29.9 \pm 3.0 c	31.6	33.2 \pm 0.7 c	27.3

the whole growth time of the first internode. So, we can remark that generally the most represented oscillations, as well during L:D (12:12) than during continuous light measurement, were those which has the smallest periods. This has just two exceptions with Ler and C24 measured under continuous light condition.

Observed oscillations along the growth span do not stay at the same frequency. For instance, figure 6 presents growth rate variations during a dark-light-dark period succession. Thus, low frequency oscillations measured during the first night could be followed by a higher frequent one during day and be restored the next night. Moreover, the oscillations could change their period in the same photoperiod time as we can observe during the second presented night (Fig. 6).

Some other important remarks regarding the ultradian growth rhythms of *Arabidopsis* floral stem have to be done in light of figure 7. Comparison of the growth rhythm oscillations (Fig. 7C) with light or temperatures oscillations (Fig. 7AB) showed that there was no incidence of such kind of environment variations onto the growth ultradian oscillations. Moreover, measurement of three different plants in the same time (Fig. 7C) showed that expressed oscillations could have the same period in different phases (○ and ●; Fig. 7C) but also have a different period (□; Fig. 7C).

DISCUSSION

As we have already presented in JOUVE *et al.* (2000), some studies focused onto the physiological differences (floral stem growth) between *Arabidopsis thaliana* ecotypes. Chemical composition (RASHOTTE *et al.*, 1997), developmental activities (NORDBORG & BERGELSON, 1999; KISS *et al.*, 2000) or genetical (SWARUP *et al.*, 1999) comparisons have

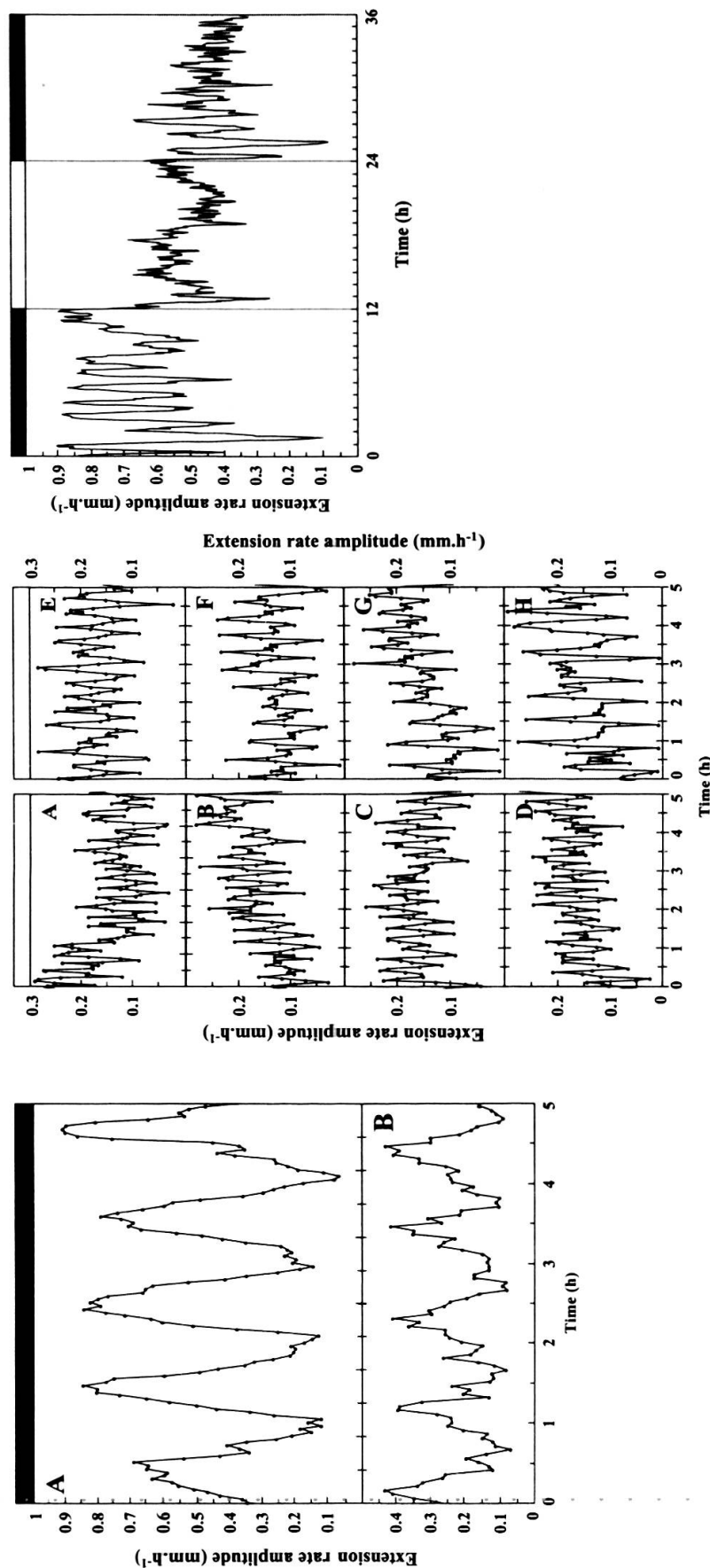


FIG. 4.

Arabidopsis thaliana first inflorescence internode extension rate of two ecotypes under L:D (12:12) photoperiod condition, as a function of time. Expression of a low frequency (± 63.5 min) ultradian rhythm during dark periods. A: Col = Columbia. B: C24. Results are the data displayed by a representative measured plant, extension rate is expressed in mm.h⁻¹.

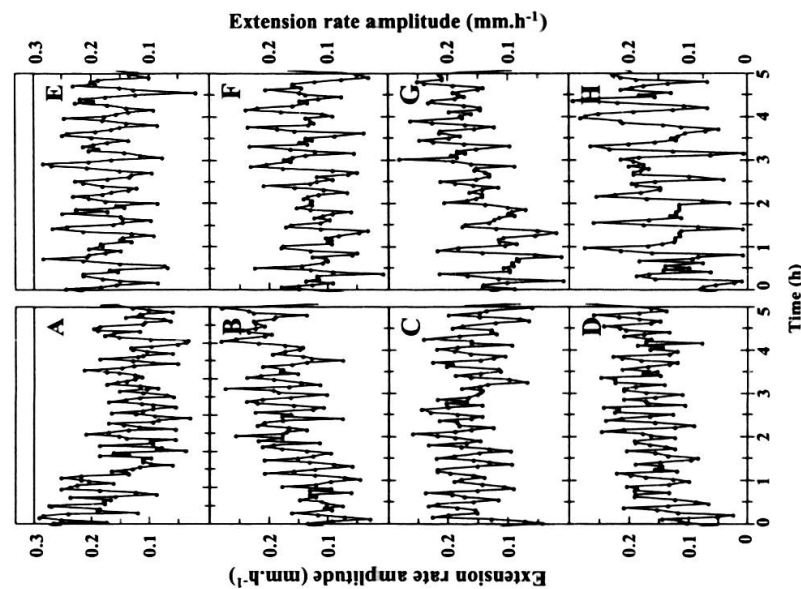


FIG. 5.

Arabidopsis thaliana first inflorescence internode extension rate of four ecotypes under continuous light condition, as a function of time. Expression of a high frequency (± 17.5 min; A, B, C, D) and a lower frequency (± 27.3 min; E, F, G, H) ultradian rhythms. A and E: Ler = Landsberg erecta. B and F: Col = Columbia. C and G: C24. D and H: Ws = Wassilewskija. Results are the data displayed by a representative measured plant, extension rate is expressed in mm.h⁻¹.

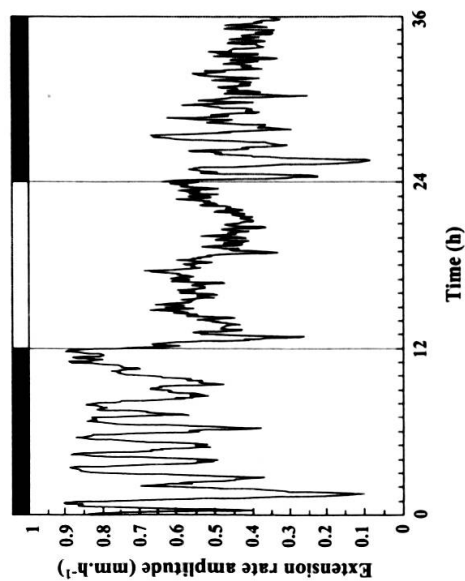


FIG. 6.

Arabidopsis thaliana, Columbia ecotype, first inflorescence internode extension rate under L:D (12:12) photoperiod condition, as a function of time. Expression of ultradian rhythms. Results are the data displayed by a representative measured plant, extension rate is expressed in mm.h⁻¹.

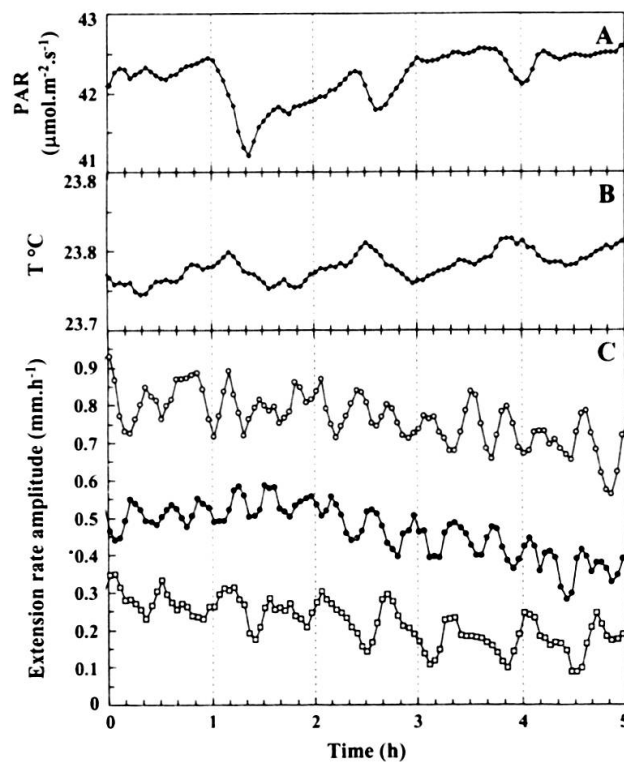


FIG. 7.

Arabidopsis thaliana, Landsberg *erecta* ecotype, first inflorescence internode extension rate as a function of time. Comparison of ultradian rhythms monitored with three different plants (C) and the measured light (A) and temperature (B) condition. Extension rate is expressed in mm.h^{-1} .

been done in some ecotypes, but this kind of study are not numerous and might be promoted. We have presented, in this issue, a first paper showing differences between four *Arabidopsis* ecotypes. Clear differences have been found in the primary inflorescence architecture and in the synchronization with light and dark alternation and circadian expressed endogenous rhythm (JOUVE *et al.*, 2000).

Here, we report differences in growth rate between ecotypes, with an emphasis onto shorter time scale events and ultradian rhythms. We observed important transients after the start of light or dark periods. These variations are possibly associated with water relations as a consequence of opening and closure of the stomata and likely sensed by a blue light photoreceptor (ZEIGER, 1994). Moreover than the putative role of a blue light receptor, results obtained by KERCKHOFFS *et al.* (1997) suggest that these short time scale events are linked to phytochromes. Indeed, an application of 10 min of far red could mimic a light to dark transition. The transient variations in growth have been observed for seedlings exposed to blue light and these were presumably a consequence of changes in cell elongation rate (COSGROVE, 1981; KRISTIE & JOLLIFFE, 1986). The described pattern; a direct decrease in stem extension rate when light was switched on, followed by an increase within minutes, and an opposite pattern immediately when light was switched off, have been observed in other species, e.g. for wheat leaves (CHRIST, 1978), lemon (BARTHOLOMEW, 1926) and potato (SCHNIEDERS *et al.*, 1988). Differences observed in

these light-on or light-off were repetitive, but they were not the same with each ecotypes. They were not necessarily the opposite after light-on and light-off. So the transient variations could be considered as growth rate signature for each *Arabidopsis* ecotype cultivated under L:D (12:12).

Concerning growth rate of the *Arabidopsis* floral stem, we have well characterized the expression of circadian oscillations in Ler (JOUVE *et al.*, 1998, 1999) and some other ecotypes (JOUVE *et al.*, 2000). Here, we have clearly shown the occurrence of superposed ultradian oscillations on circadian one (JOUVE *et al.*, 2000). This phenomenon has already been observed by, for example, KAYALI and GREPPIN (1993) and KAYALI *et al.* (1997). We demonstrate that the rate oscillations were not in relation with environmental conditions. Indeed, our studies suggest that the oscillations in growth rate are endogenous in their origin (see figure 7). Ultradian oscillations, often observed in plant growth and development (GUILLAUME and KOUKKARI, 1987; MILLET and KOUKKARI, 1990), have been related to basipetal movement of indoleacetic acid (SHEN-MILLER, 1973a, 1973b; ZAJACZKOWSKI *et al.*, 1984) or to nutation (HEATHCOTE, 1966; KOUKKARI, 1994; SCHUSTER and ENGELMANN, 1997; ADOLFSON *et al.*, 1998). The occurrence of those oscillations is rather complex, either in its presence or in its frequency. More studies are needed to better clarify this aspect.

This paper showed results monitored in a same species gender, but in several ecotypes. Differences between the four ecotypes were observed at the level of short time scale events such as light-on or light-off transitions and ultradian rhythms were observed. Some explanations at time are presented for such variations in growth rate, but they are not at all enough to clarify the individuality of each ecotype pattern. More investigations have to be done in order to elucidate the mechanisms of *Arabidopsis* floral stem growth and its components such as genetics dynamics ones. Indeed, ultradian rhythms, as well as circadian ones, might be studied including the species complexity such as for instance the different ecotypes.

RÉSUMÉ

CROISSANCE DE LA HAMPE FLORALE DE PLUSIEURS ÉCOTYPES D'*ARABIDOPSIS*.

II. VARIATIONS TRANSITOIRES ET RYTHMES ULTRADIENS.

La vitesse de croissance du premier entrenœud de l'inflorescence de quatre écotypes d'*Arabidopsis* a été mesurée en condition de lumière alternée jour/nuit ou en lumière continue. Celle-ci a montré de nombreuses oscillations correspondant à plusieurs rythmes ultradiens. Ainsi, pendant le processus de croissance des écotypes d'*Arabidopsis*, la vitesse de croissance montre la présence de rythmes ultradiens ayant des périodes de 18 à 72 min. Ces oscillations de la vitesse n'étaient pas liées au bruit mécanique ni aux variations rythmiques de l'environnement. Ainsi, notre étude suggère que les oscillations de la vitesse de croissance ont une origine endogène. En plus des oscillations ultradiennes, chaque écotype a montré des variations particulières dans la vitesse après les

transitions de la lumière à l'obscurité ou réciproquement. Celles-ci peuvent être interprétées comme des signatures individuelles à l'écotype considéré.

Mots-clés: Hampe florale, élongation, transition jour/nuit, transition nuit/jour, rythmes ultradiens, *Arabidopsis thaliana*.

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