

# Leaf elongation rate in tomato: evidence of an inversion of the day-night rhythm

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**LEAF ELONGATION RATE IN TOMATO : EVIDENCE OF AN  
INVERSION OF THE DAY-NIGHT RHYTHM.  
ELONGATION FOLIAIRE CHEZ LA TOMATE : INVERSION DU  
RYTHME JOUR-NUIT DU TAUX D'ÉLONGATION AU COURS DU  
DEVELOPPEMENT FOLIAIRE.**

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**RESUME**

Le taux d'élongation foliaire (LER) varie généralement au cours du nyctémère. Dans cet article, nous proposons une étude du rythme jour-nuit de l'élongation foliaire chez la tomate en relation avec le stade de développement de la feuille. Les plants de tomates sont cultivés en serre sur solution nutritive. Au stade végétatif, la longueur des feuilles est mesurée en début et en fin de photopériode (à 8h et à 20h). Les courbes d'élongation foliaire en fonction du temps sont du type sigmoïdal. L'élongation foliaire est caractérisée lors de la croissance exponentielle, en représentation semi-logarithmique, par des droites parallèles et équidistantes pour les niveaux de feuilles successifs. Le taux d'élongation foliaire (LER) présente des oscillations jour-nuit, avec un taux plus élevé le jour que la nuit au début de l'élongation, puis un taux plus élevé la nuit que le jour en fin d'élongation. Le rythme jour-nuit du taux d'élongation foliaire ainsi que l'inversion du rythme sont statistiquement significatifs. L'inversion du rythme est observée lorsque les feuilles ont une longueur de 9 à 12 cm. L'interprétation du phénomène d'inversion est discutée en relation avec l'utilisation du plastochrone index. Les phases successives du développement foliaire ont été caractérisées par d'autres auteurs, chez la tomate, en fonction de l'index plastochrone foliaire (LPI) et en particulier la transition entre les phases de division et d'élongation cellulaires pour laquelle LPI=1. Dans notre expérimentation, cette dernière phase semble correspondre à l'inversion du rythme d'élongation. Le taux d'élongation foliaire pourrait être influencé par des variations jour-nuit de température dans la serre (17/30°C J/N) avant le point d'inversion et ensuite par des variations de potentiel hydrique.

**ABSTRACT**

Leaf elongation rate (LER) generally vary over a day-night cycle. In the present study, we investigate the day-night rhythm of the LER of tomato plants in relation with the leaf development stage. Tomato plants were grown in a nutrient solution in a glasshouse. At the vegetative stage, the leaf lengths of 12 plants were measured with a ruler at the beginning and at the end of the photoperiod (8.00 a.m. and 8.00 p.m.). The leaf elongation curves showed typical sigmoid feature. The exponential growth phase at early leaf elongation was characterized as linear, parallel and

equidistant curves for each successive leaves (logarithm plot). Then, LER showed day-night oscillations, pointing out a daily rhythm. Moreover, LER appeared higher during the light period at early leaf development, and then, higher during the night period. The daily rhythm and the inversion phenomenon were statistically significant. The inversion phase occurred when leaves were between 9 and 12 cm in length. The significance of this inversion phenomenon was discussed in relation with the use of the plastochron index. Different successive phases in leaf development have been characterized by the leaf plastochron index (LPI), and in particular the transition between cell division and cell expansion (LPI=1). In our experiment, this latter phase seemed to correspond to the inversion phase. The LER rhythm could be influenced by the day-night temperatures (17/30°C N/D) before the inversion point, and after then, by the daily variations of leaf water potential.

## 1 - INTRODUCTION

Plants exhibit growth rhythms during their development. Some plants present low frequency rhythms such as *Quercus* or *Hevea*, with alternations of growth and dormancy periods of about 25 and 42 days respectively (Payan, 1982; Hallé and Martin, 1968). Circadian fluctuations in growth of plant parts are more common, in particular for stem and leaf elongations. Oscillations have been reported for a long time in soybean leaf expansion rate during the light/dark cycle, with a maximum at the middle of the dark period (Bunning, 1956). The elongation rate of tall fescue leaf blades is higher during the night period by 60 to 65% than during the light period (Schnyder and Nelson, 1988), and stem elongation rate in *Chenopodium rubrum* exhibits circadian rhythm too (Lecharny, Schwall and Wagner, 1985).

These circadian growth rhythms are endogenous in some cases, since they persist for several cycles in continuous darkness and under constant conditions (Lecharny and Wagner, 1984; Verbelen *et al.*, 1981). In tomato plants, a circadian endogenous rhythm in stem elongation has been observed (Assaad-Ibrahim, Lecharny and Millet, 1981), and a diurnal variation in fruit growth rate (measured as a change in diameter) has been reported with a maximum during the day (Erhet and Ho, 1986).

Growth of tomato has been studied in relation to light, CO<sub>2</sub> concentration or nutrient conditions, indicating that leaf area ratio can be five times larger in low light than in high light conditions (Hurd and Thornley, 1974). The development of tomato leaf is quite sensitive to thermoperiodic and photoperiodic changes (Hussey, 1963, 1965; Aung and Austin, 1971). Then, a description of the growth of tomato leaf using the plastochron index has been developed (Coleman and Greyson, 1976 a, b). These studies indicate that the mean duration of one plastochron (the time between initiation of successive leaves) vary from 2 days in summer to 2.5 days in winter. Moreover, leaves can be characterized by the plastochron index (LPI), which is a description of the developmental age of all leaves, based on a common scale of plastochrons (Lamoreaux *et al.* 1978). Thus, each stage of leaf development has been associated with a precise LPI value in tomato (Coleman and Greyson, 1976).

However, none of these studies has reported a day-night analysis of the leaf growth during the entire development of the leaves, so in this paper, we tended to investigate the day-night rhythm of the leaf elongation rate in tomato in relation with the development stage.

## 2 - MATERIAL AND METHODS

Seeds of tomato (*Lycopersicon esculentum* cv. Prisca) were sown in 3 x 8 cm rock-wool cylinders, then placed in the darkness at 25°C in a growth chamber. Four days after sowing, they were germinated and put into a glasshouse, where they were pricked out into a nutrient solution. Each plant was in a 140 x 10 x 8 cm grey polypropylene trough with a slope of 4°, which allowed the nutrient solution to flow and to be recycled continuously from a 200 l container pooled for 12 plants. The mineral composition of the nutrient solution was as follows : 13.2 mM NO<sub>3</sub>, 1.5 mM H<sub>2</sub>PO<sub>4</sub>, 1.5 mM SO<sub>4</sub>, 7 mM K, 3.85 mM Ca, 1.4 mM Mg. Micronutrients were supplied from a commercial solution, "Kanieltra", and pH was adjusted to 5.8 with HNO<sub>3</sub>.

Leaf growth was followed on each 12 plants at the vegetative stage (from the 6 to 9 th leaf appearance). Leaf lengths were measured with a ruler, twice a day for 10 days from the base of the petiole to the tip of the limb. During the experiment, photoperiod was 14 h (the end of April) and growth measures were done at the beginning and at the end of the light period (8:00 am and 8:00 pm) in the purpose of a comparison between day and night elongation rates. Data were statistically analysed by variance analysis (Statview-Macintosh).

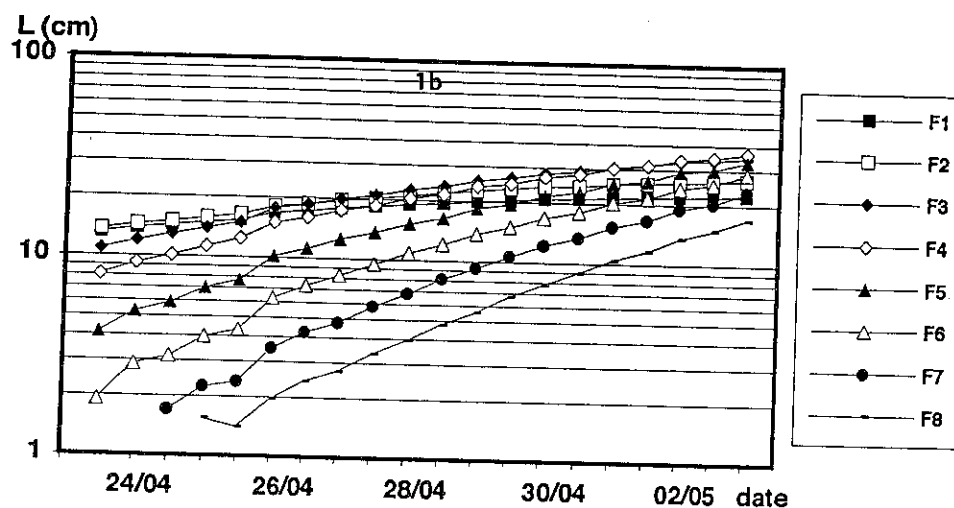
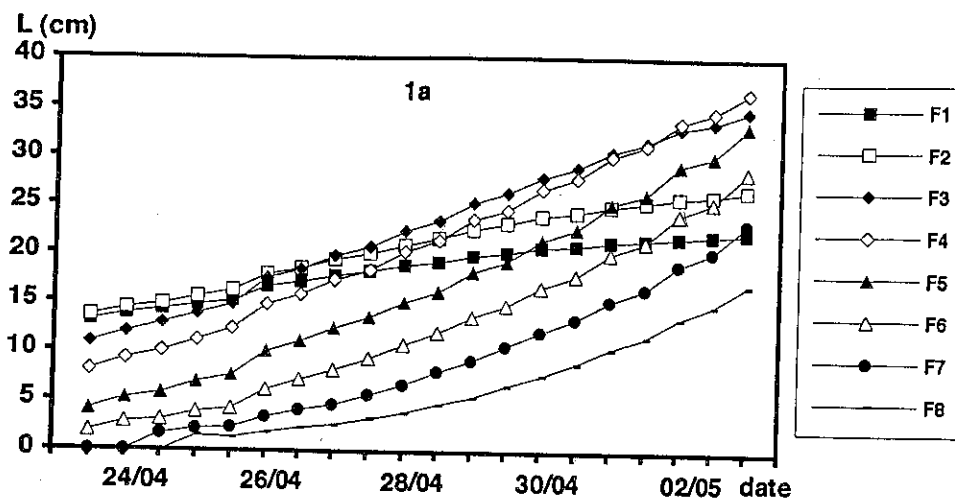
## 3 - RESULTS

### 3.1 - Leaf elongation

Leaf lengths plotted versus time (Fig. 1a) indicated that during the experiment period some leaves reached their maximal size (F1 and F2), while others expanded (F3 to F5) or just lengthened (F6 to F8). Although not really full plotted for all leaves, these curves showed a typical sigmoid feature, with an exponential first phase followed by a second slowing down growth phase. When the logarithm of leaf lengths was plotted versus time, the exponential growth phase at early leaf elongation was characterized as linear, parallel and equidistant curves (Fig. 1b). This exponential phase ended when the leaves were between 10 and 20 cm in length.

**Figures 1a and 1b** : Elongation des feuilles de tomate en fonction du temps (de F1 pour la plus âgée à F8 pour la plus jeune) (1a), et en représentation semi-logarithmique (1b). Chaque longueur de feuille est mesurée deux fois par jour, à 8 h (N-night) et à 20 h (D-day).

Elongation of tomato leaves (F1 for the oldest leaf to F8 for the youngest one) plotted versus time (1a) and its semi-logarithm representation (1b). Each leaf length was measured with a ruler twice a day, at 8.00 am. (N-night) and 8.00 pm. (D-day).

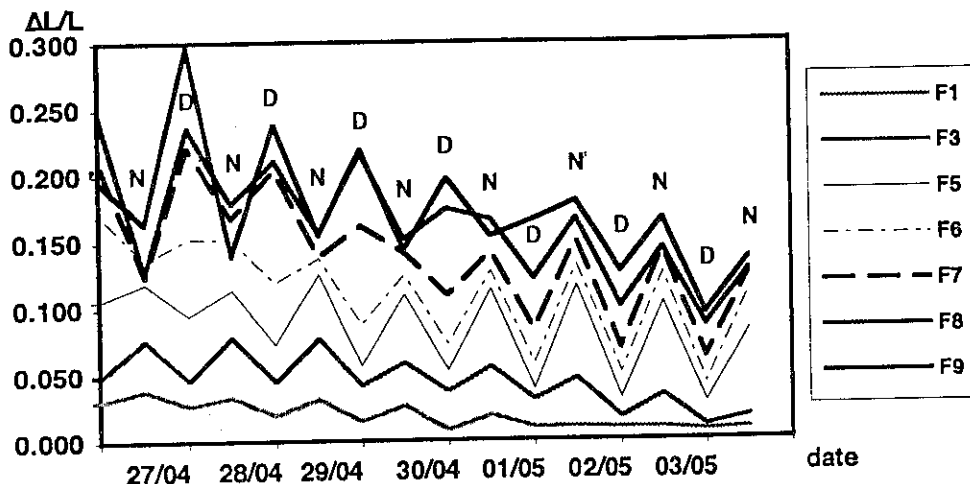


### 3.2 - Daily rhythm of leaf elongation rate

Relative leaf elongations were plotted versus time for each successive day and night periods and for each leaf (Fig. 2). A statistical analysis of data (by variance analysis) pointed out significant effects of the leaf level, the hour of measure (day or night) and the date (Table 1).  $\Delta L/L$  increased as the leaves were younger (leaf level increased) and decreased as the leaves lengthened. Differences between day and night elongation rates were pointed out, enlightened by the oscillations of each curve. Besides, the day-night differences of elongation rates depended on the leaf level, being higher for young leaves than for old leaves (F8 and F1 for instance). Then, the day-night differences depended on the date as a lessening, and an inversion of the oscillations were observed along the time axis. This inversion was enlightened by higher elongation rates during the day period at the early leaf development, followed by higher elongation rates during the night period till the end of leaf growth. This inversion phase occurred with a lag time for each leaf, and so it was observed from F6 to F8 only. Since leaf appearance was lagged too, the

elongation rates was plotted versus the leaf lengths (Fig. 3). This presentation pointed out that the inversion phase occurred when leaves were between 9 and 12 cm in length.

**Figure 2 :** Taux d'élongation foliaire ( $\Delta L/L$ ) en fonction du temps pour les feuilles F1, F3, F5, F6, F7, F8, F9. Le taux d'élongation foliaire pendant le jour (D) est estimé par le rapport de l'élongation entre 20 h et 8 h sur la longueur de feuille à 20 h. Le taux d'élongation foliaire pendant la nuit (N) est estimé par le rapport de l'élongation entre 8 h à 20 h sur la longueur de feuille à 8 h. Relative leaf elongation ( $\Delta L/L$ ) plotted versus time for leaves F1, F3, F5, F6, F7, F8, F9. Leaf elongation rate during the day (D) was calculated as the ratio of leaf length elongation (from 8.00 am. to 8.00 pm.) to leaf length at 8.00 pm. Leaf elongation rate during the night (N) was calculated as the ratio of leaf length elongation (from 8.00 pm. to 8.00 am.) to leaf length at 8.00 am.



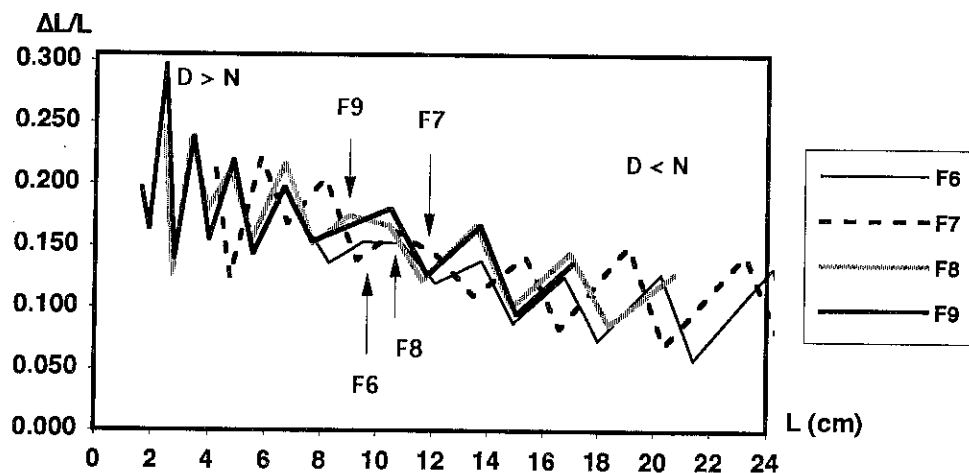
**Table 1 :** Tableau des moyennes  $\pm$  écart-types pour les variations de  $\Delta L/L$  entre le jour et la nuit pour les feuilles 6, 7, 8 et 9, pendant 8 jours consécutifs. Means  $\pm$  standard deviations of  $\Delta L/L$  variations between day and night periods, for the leaves 6, 7, 8, and 9, for 8 days.

Leaf	26/04		27/04		28/04		29/04		30/04
	D	N	D	N	D	N	D	N	N
6	0,171 $\pm$ 0,034	0,136 $\pm$ 0,012	0,153 $\pm$ 0,041	0,152 $\pm$ 0,024	0,120 $\pm$ 0,039	0,138 $\pm$ 0,020	0,087 $\pm$ 0,020	0,125 $\pm$ 0,019	0,141 $\pm$ 0,020
7	0,211 $\pm$ 0,027	0,124 $\pm$ 0,024	0,221 $\pm$ 0,020	0,168 $\pm$ 0,016	0,204 $\pm$ 0,025	0,138 $\pm$ 0,023	0,162 $\pm$ 0,037	0,152 $\pm$ 0,029	0,152 $\pm$ 0,029
8	0,246 $\pm$ 0,057	0,126 $\pm$ 0,035	0,236 $\pm$ 0,039	0,179 $\pm$ 0,040	0,211 $\pm$ 0,040	0,156 $\pm$ 0,041	0,216 $\pm$ 0,030	0,152 $\pm$ 0,029	0,152 $\pm$ 0,029
9	0,196 $\pm$ 0,070	0,164 $\pm$ 0,005	0,297 $\pm$ 0,018	0,139 $\pm$ 0,033	0,238 $\pm$ 0,044	0,155 $\pm$ 0,034	0,218 $\pm$ 0,014	0,143 $\pm$ 0,024	0,143 $\pm$ 0,024

Leaf	30/04		01/05		02/05		03/05		04/05
	D	N	D	N	D	N	D	N	N
6	0,073 $\pm$ 0,013	0,127 $\pm$ 0,018	0,058 $\pm$ 0,010	0,132 $\pm$ 0,016	0,051 $\pm$ 0,009	0,126 $\pm$ 0,020	0,043 $\pm$ 0,012	0,112 $\pm$ 0,022	0,112 $\pm$ 0,022
7	0,109 $\pm$ 0,039	0,141 $\pm$ 0,022	0,083 $\pm$ 0,017	0,150 $\pm$ 0,020	0,069 $\pm$ 0,018	0,143 $\pm$ 0,017	0,062 $\pm$ 0,010	0,126 $\pm$ 0,015	0,126 $\pm$ 0,015
8	0,174 $\pm$ 0,043	0,166 $\pm$ 0,018	0,121 $\pm$ 0,036	0,167 $\pm$ 0,024	0,100 $\pm$ 0,033	0,144 $\pm$ 0,018	0,086 $\pm$ 0,018	0,128 $\pm$ 0,013	0,128 $\pm$ 0,013
9	0,197 $\pm$ 0,008	0,154 $\pm$ 0,024	0,165 $\pm$ 0,011	0,180 $\pm$ 0,039	0,126 $\pm$ 0,019	0,166 $\pm$ 0,051	0,095 $\pm$ 0,003	0,137 $\pm$ 0,013	0,137 $\pm$ 0,013

**Figure 3 :** Taux d'élongation foliaire ( $\Delta L/L$ ) en fonction de la longueur des feuilles pour les feuilles F6, F7, F8, F9. Le taux d'élongation foliaire pendant le jour (D) est estimé par le rapport de l'élongation entre 20 h et 8 h sur la longueur de feuille à 20 h. Le taux d'élongation foliaire pendant la nuit (N) est estimé par le rapport de l'élongation entre 8 h à 20 h sur la longueur de feuille à 8 h. Relative leaf elongation ( $\Delta L/L$ ) plotted versus leaf length for leaves F6, F7, F8, F9. Leaf elongation rate during the day (D) was calculated as the ratio of leaf length elongation (from 8.00 am. to 8.00 pm.) to leaf length at 8.00 pm. Leaf elongation rate during the night (N) was calculated as the ratio of leaf length elongation (from 8.00 pm. to 8.00 am.) to leaf length at 8.00 am.



#### 4 - DISCUSSION

Diurnal rate of leaf expansion is not constant as numerous studies have mentioned it for some decades. Most observations have shown higher rates during the night than during the day, but contrasting results have been reported too. Leaf elongation rate of young wheat seedlings has appeared lower during the dark period than the photoperiod (Christ, 1978), or even little difference between dark and light periods was observed in orchardgrass (Eagles, 1974). These contrasting results were attributed to differences in genotypes and sensitivity to plant culture conditions such as light intensity or day-night temperatures (Volenc and Nelson, 1982, Lecharny et al. 1985). However, an inversion of the day-night rhythm of leaf elongation rate has never been reported during the leaf development without modifying the external conditions. In this paper, the evidence of such a phenomenon clearly appeared, characterizing a tomato leaf between 9 and 12 cm in length. Then, we tended to find a physiological interpretation to this phenomenon.

Higher elongation rates during the night have been interpreted in relation to water status of the leaf (Boyer, 1968; Volenc and Nelson, 1982; Parrish and Wolf, 1983). High water potentials are necessary to cell enlargement and occurs during the night, when transpiration is lower than during the day.

During leaf development, different stages follow one another. Firstly, lamina tissue is in a state of rapid and continuous cell division, then growth is characterized by cell expansion, and differentiation of veins, till the end of growth, when the leaf is anatomically and physiologically mature. Besides, relationships exist between growth and the translocation of assimilates. Growth of a young leaf is dependent on the import of assimilates from older expanded leaves, before being photosynthetically active, and then exporting (Moorby, 1981). Export usually begins when the leaf is about 15 to 25 % of its final area, with a transition from importing to exporting stage, which is a quite progressive and basipetal phenomenon in tomato leaf (Coleman and Greyson, 1976). Four growth stages of tomato leaf have been characterized in terms of LPI by Coleman and Greyson (1976) according to the formulae (Lamoreaux *et al.* 1978) as follows :

$$(1) \text{LPI}_n = \text{PI} - n$$

where  $n$  is the serial number of the  $n$ th leaf and

$$(2) \quad \text{PI} = n + \frac{\log L_n(t) - \log l}{\log L_n(t) - \log L_{n+1}(t)}$$

where  $L_n(t)$  is the length of the  $n$ th leaf at time  $t$ ,  $L_{n+1}(t)$  the length of the  $n+1$ th leaf at time  $t$ , and  $l$  the reference leaf length characterizing approximately the leaf length at the middle of the exponential growth phase. Then, from (1) and (2) it results :

$$(3) \quad \text{LPI}_n = \frac{\log L_n(t) - \log l}{\log L_n(t) - \log L_{n+1}(t)}$$

Since cell enlargement is sensitive to water status of the leaf, we hypothesized that the inversion of the leaf elongation rhythm observed in our experiment occurred at the transition stage between cell division and elongation. According to Coleman and Greyson (1976), when  $\text{LPI}_n = +1$ , mitotic activity ends in the lamina of the most basal leaflets, and thus, leaf growth is due to cell expansion only. From (3) we deduced that at this time  $L_{n+1} = l$ . That means that cell division stops in a leaf  $n$  when the leaf  $n+1$  is equal to  $l$ , and thus, is in the exponential growth phase. From our results, leaf length was about 10 cm when the inversion phenomenon occurred, while the  $n+1$  leaf length was about 5 cm as it appeared in Fig. 1b., which corresponded to the exponential growth phase of the  $n+1$  leaf (linear part of curves in Fig. 1b), so we assumed that  $l = 5$  cm in our experiment. Thus, these observations seemed to confirm our latter hypothesis that the inversion phenomenon corresponds to the transition phase between cell division and expansion in the leaf.

Other authors have observed a correlation between leaf elongation rhythm and import of assimilates from the source leaves in soybean (Huber, Kerr and Kalt-Torres, 1985). Moreover, they have noted synchronized changes in sink leaf Fru-2,6-P<sub>2</sub> concentration and diurnal fluctuations in sink leaf growth. Diurnal changes in sink leaf Fru-2,6-P<sub>2</sub> would play a role in the glycolytic use of imported assimilates. It would be interesting to investigate the import of assimilates and the Fru-2,6-P<sub>2</sub> concentration in young leaf of tomato, during the day-night cycle, in our experiment. Rhythm in partitioning of exported assimilates between different sinks could explain diurnal growth rhythm in the young leaf, before the fluctuations of water potential became a predominant factor at the cell enlargement stage. Finally, tomato LER rhythm could be influenced by the day-night temperatures (17/30°C Night/Day)



before the inversion point, and after then, by the daily variations of leaf water potential.

## REFERENCES

- Assaad-Ibrahim C., Lecharny A. and Millet B., Circadian endogenous growth rhythm in tomato, *Plant Physiol.*, 1981, 67 (suppl) : 113.
- Aung L.H. and Austin M.E., Vegetative and reproductive responses of *Lycopersicon esculentum* Mill. to photoperiods, *J. Exp. Bot.*, 1971, 22: 906-914.
- Boyer J.S., Relationship of water potential to growth of leaves, *Plant Physiol.*, 1968, 43: 1056-1062.
- Bunning E., Leaf growth under constant conditions and as influenced by light-dark cycles. In *The growth of leaves*, ed. F.L. Milthorpe. 1956. pp. 119-126, Butterworths Sciences, London.
- Christ R.A., The elongation rate of wheat leaves. I - Elongation rates during day and night, *J. Exp. Bot.*, 1978, 29: 603-610.
- Coleman W.K. and Greyson R.I., The growth and development of the leaf in tomato (*Lycopersicon esculentum*). I - The plastochron index, a suitable basis for description, *Can. J. Bot.*, 1976a, 54: 2421-2428.
- Coleman W.K. and Greyson R.I., The growth and development of the leaf in tomato (*Lycopersicon esculentum*). II - Leaf ontogeny, *Can. J. Bot.*, 1976b, 54: 2704-2717.
- Eagles C.F., Diurnal fluctuations in growth and CO<sub>2</sub> exchange in *Dactylis glomerata*, *Ann. Bot.*, 1974, 38: 53-62.
- Erhet D.L. and Ho L.C., Effects of osmotic potential in nutrient solution on diurnal growth of tomato fruits, *J. Exp. Bot.*, 1986, 37 (182): 1294-1302.
- Halle F. and Martin R., Etude de la croissance rythmique chez l'Hévéa (*Hevea brasiliensis* Müll-Arg. Euphorbiacées- Crotonoïdées), *Adansonia* 1968, ser. 2, 8 (4): 475-503.
- Huber S.C., Kerr P.S. and Kalt-Torres W., Regulation of sucrose formation and movement. In *Regulation of carbon partitioning in photosynthetic tissue*. ed. R.L. Heath and J. Preiss. 1985, pp. 199-214. Proc. 8 th Ann. Symp. Plant Physiol.
- Hurd R.G. and Thornley J.H.M., An analysis of the growth of young tomato plants in water culture at different light integrals and CO<sub>2</sub> concentrations, *Ann. Bot.*, 1974, 38: 375-388.
- Hussey G., Growth and development in the young tomato. I - The effect of temperature and light intensity on growth of the shoot apex and leaf primordia, *J.*

*Exp. Bot.*, 1963, 14: 316-325.

Hussey G., Growth and development in the young tomato. III - The effect of night and day temperatures on vegetative growth, *J. Exp. Bot.*, 1965, 16: 373-385.

Lamoreaux R.J., Chaney W.R. and Brown K.M., The plastochron index : a review after two decades of use, *Am. J. Bot.*, 1978, 65 (5): 586-593.

Lechary A. and Wagner E., Stem extension rate in light-grown plants. Evidence for an endogenous circadian rhythm in *Chenopodium rubrum*, *Plant Physiol.*, 1984, 60: 437-443.

Lechary A., Schwall M. and Wagner E., Stem extension rate in light-grown plants. Effects of photo-and thermoperiodic treatments on the endogenous circadian rhythm in *Chenopodium rubrum*, *Plant Physiol.*, 1985, 79: 625-629.

Moorby J., Transport systems and growth. In *Transport systems in plants*. ed. Longman Inc., 1981, pp. 123-137. New York.

Parrish D.J. and Wolf D.D., Kinetics of tall fescue leaf elongation : responses to changes in illumination and vapor pressure, *Crop Sci.*, 1983, 23: 659-663.

Payan E., Contribution à l'étude de la croissance rythmique chez de jeunes Chênes pédonculés, *Quercus pedunculata* Ehrh - Thèse Doct. 3ème cycle, Morphogen. Ecophysiol. vég., Univ. Clermont II, 1982, 102p.

Schnyder H. and Nelson C.J., Diurnal growth of tall fescue leaf blades. I - Spatial distribution of growth, deposition of water, and assimilates import in the elongation zone, *Plant Physiol.*, 1988, 86: 1070-1076.

Verbelen J.P., Spruit E., Moreles E. and De Greef J.A., Endogenous rhythmicity in etiolated *Phaseolus* seedlings, *Biol. Jaarb.* 1981, 49: 190-199.

Volenc J.J. and Nelson C.J., Diurnal leaf elongation of contrasting tall fescue genotypes, *Crop Sci.*, 1982, 22: 531-535.