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Development of Maize Internode under Drought Stress

B. Bennouna, A. Lahrouni, [1]O. Bethenod, [1]C. Fournier, [1]B. Andrieu and S. Khabba
Faculté des Sciences Semlalia, Laboratoire d'Hydraulique et d'Aérodynamique Expérimentale,
Département de physique, BP 2390 Marrakech Maroc
[1]Institut National de la Recherche Agronomique, Centre de Versailles-Grignon, Unité
Environnement et Grandes Cultures, 78850, Thiverval-Grignon, France

Abstract: The dynamics of elongation of individual internodes of maize were studied under drought stress in field experiment in Marrakech (Morocco), for three irrigations treatments. T_1 is a control treatment, which was irrigated once a week. T_2 was irrigated until the appearance of collar of the 6th leaf. The irrigation was stopped for three weeks and then initiated again when the collar of the 10th leaf appears on plants. T_3 was irrigated until the appearance of the collar of 10th leaf. The irrigation was stopped for three weeks and started when silks emerge. After these three weeks, the irrigation retook place once a week for all treatments. Internode extension in maize was described in four phases. Phase (I), during which elongation was exponential, phase (II), which was short during which the extension rate increases rapidly. A constant elongation rate defined phase (III), followed by phase (IV) in which elongation rate decreased. The co-ordination between collar emergence and the end of the exponential phase stay valid in each treatment. This confirms the contention that the kinetics of internode elongation is constantly controlled by the emergence of leaf collars. The final length of internodes was correlated to the linear elongation rate in each treatment (up to 90%).

Keys words: *Zea mays*, internode, elongation, drought stress, model

INTRODUCTION

Internode extension has two primary functions: elevation of the photosynthetic organs for optimum interception of photosynthetically active radiation (PAR) and elevation of reproductive organs so that successful pollination is assured[1]. Crop models use semi-empirical approaches, drawing on the fact that much of what is known relates to elongation of the whole internode and the correlation of this elongation with reproductive development. In most cases, a sigmoidal model is used to calculate plant height, coupled with empirical modelling of the vertical leaf area distribution[2-4]. In maize, internodes elongation patterns were studied by Sach[5], Martin[6], Morrison *et al.*[1], Robertson[7], Fournier and Andrieu[8,9]. They identified four phases during the elongation of an individual internode, based on the spatial distribution of the component cell lengths and/or the segmental elongation rates within the internode. In the first phase, the distribution of cell lengths was unchanged over the entire internode. The extension is exponential. In the second phase, a gradient of cell length developed at the distal end of internode and the rate of internode elongation increased. As most of the internode length is formed during the third phase, during which the elongation rate is appreciably constant, corresponding to a linear phase. The most distal cells matured, so that the region with a gradient of cell lengths moves to the upper end of the internode. Finally, in the fourth phase, the region of non-elongated cells at the base of the internode decreases in length, resulting finally in the cession of elongation. This pattern of elongation is also examined by Birch *et al.*[10] for two cultivars of maize that were adapted to the sub-tropics of grown at Gatton (Australia). The duration and analysis of each phase of elongation was examined: Morrison *et al.*[1] observed coordination between the start of elongation at node *n* and the end of elongation at node *n-4*. Robertson[7] measured the average growth rates for individual internodes varying between 2 and 5 cm per phyllochron. Kirby *et al.*[11] have shown in the wheat and barley, that the start of fast elongation phase was synchronised with the end of elongation of the sheath of the same phytomer. Fournier and Andrieu[8] specified that the beginning of phase II occurred close to the emergence of the collar and confirmed that the linear phase corresponds to the time that sheath elongation ended.

Under the climatic conditions in southern Morocco (semi-arid zone), growth rate was very limited by water supply due to rain irregularity. However in maize, two

Corresponding Author: Dr. B. Bennouna, Faculté des Sciences Semlalia, Laboratoire d'Hydraulique et d'Aérodynamique Expérimentale, Département de physique, BP 2390 Marrakech Maroc E-mail: b.bennonna@ucam.ac.ma

stages of plant development were noticed to be sensitive to water stress: at the vegetative stage[12,13] (stage 5-6 leaves) and at the seedling stage[14,15]. Maize is apparently more droughts resistant in the early stages of growth than when fully developed. This is well known by traditional Moroccan maize farmers. Extreme water stress at different stages of crop development has been reported to reduce leaf area, photosynthesis, leaf chlorophyll contents, plant height, stem diameter, tiller number and consequently grain yield (up to 50%)[16-18].

The first aim of this study is to compare the parameters values that describe internode extension from the growth analysis established by Fournier and Andrieu[8,9] and Birch *et al.*[10] to determine the extension length of the internode in each phase under drought stress at the vegetative stage and at the seedling stage; to verify the relationship between the linear elongation rate of each internode and its final length and the coordination between the appearance of the collar of the leaf and the end of the exponential phase under drought stress.

MATERIALS AND METHODS

A field study experiment was carried out at the domain of Regional Center of the National Institute of Agronomic Research of Haouz, Marrakech, Morocco (31°37'N, 7°52'W). Maize, (*Zea mays* L., cv RAISSA) was sown by hand on a deep silt loam soil on April 24th 1999, row spacing was 70 cm and plant population density was 7 plants m^{-2}. We use the variety RAISSA, which is well adapted to climatic data of Marrakech and its region (Morocco). The soil was treated with 200 kg N ha^{-1}, 160 kg P ha^{-1} and 200 kg K ha^{-1}There were no leaf diseases and weeds were controlled by hand.

Three irrigation treatments T_1, T_2 and T_3 were used. T_1 acted as a control treatment in which the maize was irrigated once a week. In T_2, the irrigation was stopped when the 6th leaf was fully expanded (leaf 6 emerged from node 7 and encircles internode 7)[12]. The irrigation was stopped during three weeks. For the T_3 treatment, irrigation was stopped for three weeks, when the 10th collar of leaf appeared.

The date of rising was determined visually by the daily numbering on a line of the number of visible plants (30 plants). The raised stage is defined as the date when leaf 1 of 50% of the sown seed population had emerged from the soil. In our experiment it was in May 5th (i.e. 150.25°Cd). 10 plants were selected in the middle row of each treatment. At each sampling, the number of visible and fully expanded leaves and the length of the most recently fully expanded leaf (LL) and the width (LW) was measured (from the collar to tip and from the point of emergence from the whorl to tip). Leaf area index (A) has been calculated while using the formula of Montgomery[19], A=KxLLxLW, with the coefficient K=0.75 for the expanded leaves and, K=0.5 for leaves of the cone (leaf that doesn't have his visible collar again).

When plants had six fully expanded leaves (coincide with May 24th), six plants were harvested for every treatment. They were dissected in order, internode length was measured from the lower side of one node to the lower side of the node above it, with the internode below the attachment of the leaf given the same number as the leaf. Also, once present, the lengths of the stem and panicle were measured (the measure of panicle is made from the superior limit of the internode until the tip of panicle). This operation was repeated every day, until the final stage of stem elongation.

Temperature measurements: The primary factor affecting leaf and internode phenological events is temperature. Temperature effects are modulated by other factors such as day length, vernalization, heat and cold stress and water stress. Modelers have attempted to quantitatively assess the effects of temperature by calculating accumulated growing degree-days, i.e., the total effective temperature to which a plant has been exposed[20]. The following method is widely used to calculate growing degree-days:

For a given day = I, let DDi = degree days, T_{base} = base temperature, $T_{max}(I)$ = maximum temperature of the i'th day, $T_{min}(I)$ = minimum temperature of the i'th day.

If

$$T_{min}(i) > T_{base} \Rightarrow DD_i = \frac{T_{max}(i) + T_{min}(i)}{2} - T_{base}$$

Else, if

$$T_{min}(i) < T_{base} < T_{max}(i) \Rightarrow DD_i = \frac{T_{base} + T_{max}(i)}{2} - T_{base}$$

Else, if

$$T_{max}(I) < T_{base} \Rightarrow DD_i = 0$$

So, accumulated growing degree days:

$$GDD = \sum_{i=0}^{k} (DD_i)$$

The ambient daily maximal and minimal temperature were measured, in the maize field, since the seedling, with a thermometer ' Nutrisoil-Nutrifer ' placed to the test of cornfield. The base temperature used is 10°C.

Construction of the model and kinetic analysis

Internode growth model: The maize internode extension is represented by a sigmoidal curve (Fig. 1), which it divided in four phases. The principal's phases were:

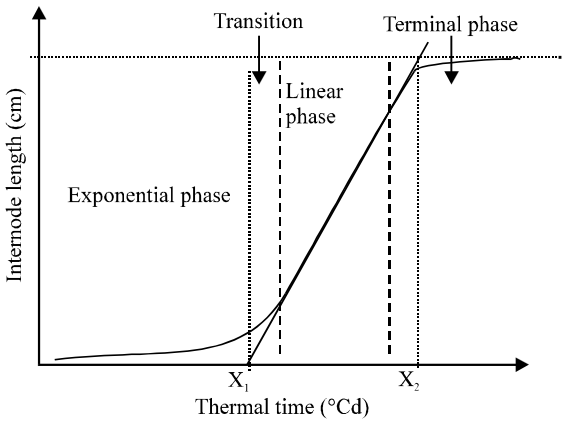

Fig. 1: Schematic thermal time course of internode elongation and the associated parameters used for the analysis of phases. The regression line that fits the linear phase of elongation defines two thermal time parameters: x_1 is the intersection between the regression line and the x-axis and x_2 is the intersection between the regression line and the upper asymptote of the sigmoidale curve

Exponential phase of elongation (phase I): In the first phase, which appears to begin immediately after initiation of the internode and extends until the internode reaches approximately 10% of its final length, the elongation is exponential. A model for the first phase is:

$$ln = l_{0,n}\exp[R_n(t-t_{0,n})] \quad (1)$$

Where l_n is the length of the internode n, R_n is the relative elongation rate of internode 'n' ($°C^{-1}d^{-1}$), t is the thermal time and $l_{0,n}$ is the length of the internode at time $t_{0,n}$.

The natural logarithm of individual internode, stem and panicle length permitted us to calculate the relative elongation rate R_n in each treatment. The upper limit was chosen from graphical analyses of internode length plotted against thermal time since the seedling, to ensure that the internodes were in phase I.

Linear phase of elongation (phase III): After the exponential phase, elongation goes into a transition phase, which is short, the relative rate of elongation of internode (R_n) increased rapidly after about 50 °Cd. After this, internode elongation is a linear function of thermal time. The linear rate of elongation (cm $(°Cd)^{-1}$) was calculated for each internode, stem and the panicle during each treatment by regressing internode length on thermal time from the seedling.

Elongation period

Thermal time of initiation of the internode: Measures of elongation of the internodes began after their initiation, whereas they already had some millimeters of length. However, the exponential function (equation 1) permitted us to estimate the date of initiation of every internode. The parameter $t_{0,n}$ defined the thermal time at which the internode was a single layer of cells, (i.e., when l_0 = 20 µm[6]. Using (equation 1), $t_{0,n}$ is then defined by:

$$t_{0,n} = \frac{1}{R_n}\ln\left(\frac{0,002}{l_{0,n}}\right) \quad (2)$$

Duration of the linear phase: The beginning and the end of the linear phase were identified graphically according to the method suggested by Fournier and Andrieu[8]. The regression equation was then used to determine the intercept X_1 on the thermal time axis by setting internode and panicle length = 0. Similarly, X_2 was determined as the intersection of the fitted value of linear regression and the final internode and panicle length (Fig. 1). The duration of linear elongation phase can be calculated by the difference between X_2 and X_1.

RESULTS

Plant level kinetics

Appearance of leaf tips and collars: The temporal appearance of leaf tips and collars in each treatment is shown in Fig. 2. The average rate appearance calculated from seedling until all tips were 0.027, tips $(°Cd)^{-1}$ in T_1 and T_3 and 0.0226 tips $(°Cd)^{-1}$ in T_2. In the same way, the average rate appearance of the first eight collars is the same in the three treatments with 0.0155 collars $(°Cd)^{-1}$, but change in the following collars and becomes 0.0341, 0.0396 and 0.0294 collars $(°Cd)^{-1}$ in T_1, T_2 and T_3, respectively.

Initiation of the internode: The initiation of the various internodes for the control T_1, T_2 and T_3 treatments, using equation (2) showed one internode, on every 18.77°Cd (Fig. 2). The dates of initiation of the internodes were not can be positioned, but can also be estimated starting from the rate of initiation for leaf primordia. These two rhythms are strongly synchronised at the graminaceous ones[4,21-23]. Lejeune and Bernier[24] established the following relation: $N_p = 1.95 + 1.84 \times L_s$ (N_p is the number of primordia initiated and L_s the number of visible leaves). For the Raissa variety, the relation verified this synchronization in T_1 and T_3 is:

$$N_p = 1.929 + 1.43 \times L_s \quad (3)$$

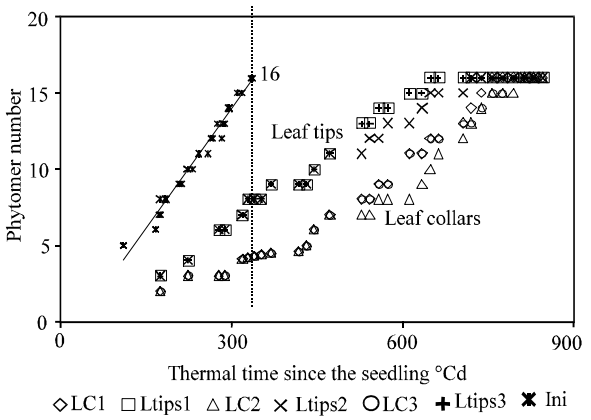

Fig. 2: Number of visible leaf tips (Ltips) and collars (LC) in each treatment from seedling. Estimation of the timing of initiation of internodes in all treatments (initiation was considered as the time and internode was 20 µm long). The line represent the linear regression between the phytomer number and thermal time

In T_2 treatment the synchronization has been modified because of the delay of the appearance of upper leaf tips and becomes:

$$N_p = 2.305 - 1.1 \times L_s \quad (4)$$

Stem and panicle elongation: The progressive increase in total height of the stem is shown for T_1, T_2 and T_3 in Fig. 3a. This shows that the elongation of the stem in T_3 remain similarly in T_1 until 757°Cd when it attains 77% of final height, then decreases to reach final height. In T_2, the elongation of stem has been affected since the beginning of stress (611°Cd) that decreased the growth rate until it reaches its final size. Similarly, the elongation of the panicle was not affected in T_3 but was affected in T_2 (Fig. 3b). The effect of stress reduced the final length of the panicle and the stem of 20% each in T_2. On the other hand, in T_3 the reduction is only 5% for the panicle and 12% for the stem.

Temporal internode extension: The progressive increase in length of the internodes for three treatments of the thermal time followed the curve shown in Fig. 1. Fig. 4 presents the thermal time courses of the length of the 8th (lower) and 14th (upper) internodes during each treatment. In treatment T_2 internode 8 is more affected by the water stress than internode 14. The partition to four phases was applied to each internode. To determine the impact of the drought stress on each phase we must delimiting each phase.

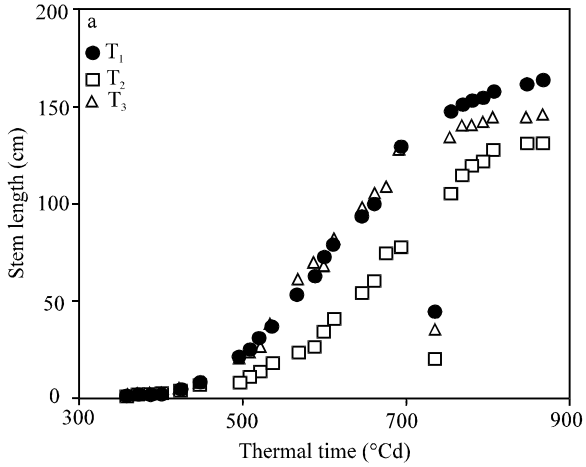

Fig. 3a: Length of stem plotted against thermal time from seedling

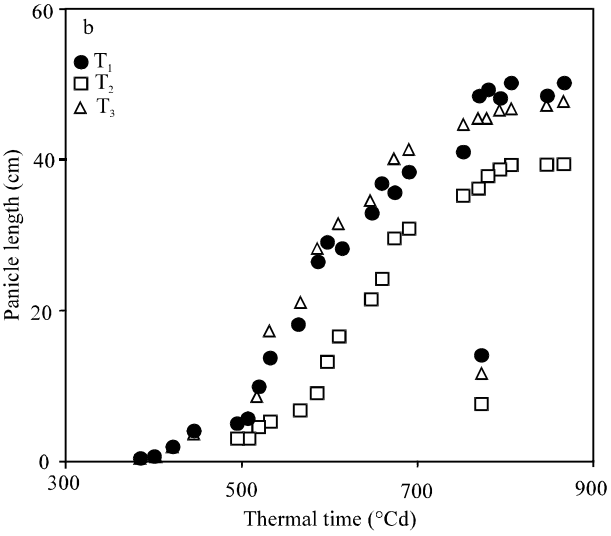

Fig. 3b: Length of panicle plotted against thermal time from seedling

Internode final length: The final size of each internode depends on its position. In Raissa, which had 15 to 16 vegetative internodes (no peduncle data), the first internode to extend significantly was internode 5, but only to approximately 1.8 cm. Subsequent internodes progressively increased in length until internode 10 which had 18.5 cm of length. Above the longest internode, internode lengths initially declined, then increased slightly for the three last internodes. Under drought stress the final length of each internode was modified according to which phase of elongation, stress has been applied (Fig. 5). In the treatment T_2, internodes 6 to 14 had a final length lower than that of the control (Table 1). The final

Table 1: Internode length in several time: at May 26th in control T_1 and T_2 (begiuning of water stress in T_2), at June 7th in control T_1 and T_3 (beginning of water stress in T_3), at June 14th in control T_1 and T_2 (end of water stress in T_2) and at June 20th in control T_1 and T_3 (end of water Stress in T_3)

	At 443.25°Cd beginning water stress T_2 (26 May)		at 611°Cd begiuning water stress T_3 (7 June)		at 705.5°Cd end of water stress T_2 (14 June)		at 829°Cd end of water stress T_3 (20 June)	
IN	ILT_1	ILT_2	ILT_1	ILT_3	ILT_1	ILT_2	ILT_1	ILT_3
5	0.60	0.55	1.50	1.50	1.70	1.70	1.76	1.75
6	1.50	1.45	5.90	5.80	5.97	4.66	6.50	6.80
7	1.20	1.20	11.80	11.80	12.35	6.60	12.60	13.00
8	0.85	0.86	14.00	13.80	14.85	8.86	16.40	17.00
9	0.50	0.55	10.50	10.40	14.80	10.20	15.75	16.00
10	0.40	0.44	6.80	6.50	17.00	7.13	18.50	18.2
11	0.20	0.20	2.85	3.00	12.10	5.40	18.00	15.00
12	0.00	0.00	1.60	1.50	9.00	1.90	15.00	13.00
13	0.00	0.00	1.00	1.05	4.80	1.50	13.60	11.75
14	0.00	0.00	0.65	0.65	3.70	1.07	10.00	9.00
15	0.00	0.00	0.45	0.50	1.15	1.03	9.00	8.00
16	0.00	0.00	0.00	0.00	1.60	1.00	8.00	6.00

IN: internode number ILT_1: internode length in treatment T_1

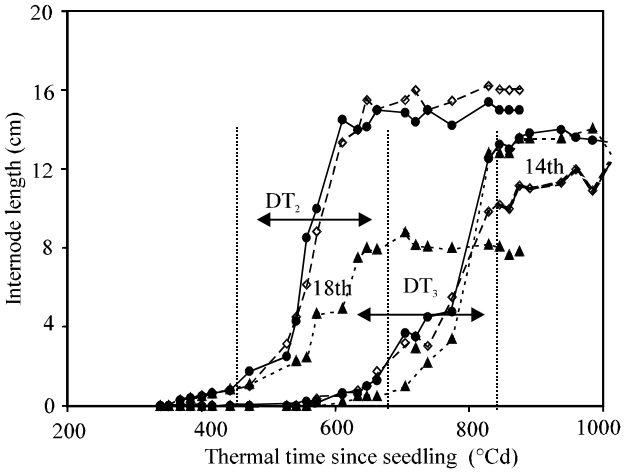

Fig. 4: Thermal time course of internode 8 and 14 in each treatment. (●) Control T_1, (◊) T_2 and (▲) T_3. DT_2 is the period of stop of irrigation in T_2 and DT_3 is the period of stop irrigation in T_3

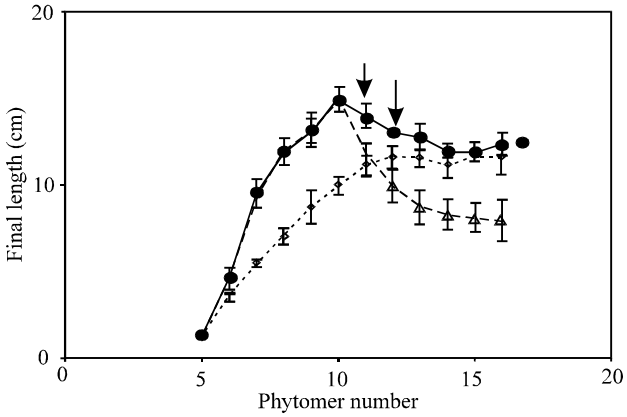

Fig. 5: Final internode length in each treatment plotted against phytomer number (●) Control T_1, (◊) T_2, (△) T_3. The arrow indicated the phytomer bearing the ear. Measurements are means of six plants and bars represent 95% confidence intervals

length has been reduced by 23% for internode 6 (Fig. 4), by 42 and 40% for internodes 7 and 8, by 33% for internodes 9 and 10 and by 20% for the 11th internode. Internodes 12 through 16 whose linear phase of extension started after the irrigation stopped have final lengths slightly lower than that of the control and underwent only a reduction of 11% for internode 12. The following internodes 13 to 16, for which the irrigation cutting off took place before the end of phase I showed a final length reduction of 9% (internode 13), 6% (internode 14 and 16) and 3% (internode 15). In the treatment T_3, final length of the ten first internodes has not been affected. The final lengths of the 11th and 12th internodes has been reduced with 15%, while the reduction was up to 25% for internodes 13 and 14 and 35% for internodes 15 and 16.

Kinetics analysis of individual organs

Relative elongation rate: The analysis of the regression coefficients shows that relative elongation rate (RER) for phytomers don't present a significant difference (P=0.05) between the means of value of RER for pair internodes $(0.0181\pm0.00027)°C^{-1}d^{-1}$ and for odd internodes $(0.0149\pm0.00058)°C^{-1}d^{-1}$, respectively (Fig. 6). Stem and panicle extended similar to the pair internode $(0.0179\pm0.0039)°C^{-1}d^{-1}$. Under drought stress, in T_2 treatment, the RER for odd and pair internodes decreases and becomes to vary linearly on phytomer number with a slope of -0.0006 and -0.0005 $(°Cd)^{-1}$ per phytomer number until to reach a minimum in the internode 11 and 12 (end of stress), restarts to grow with same slope 0.0004 for the remainder of internode then. For stem and panicle, RER

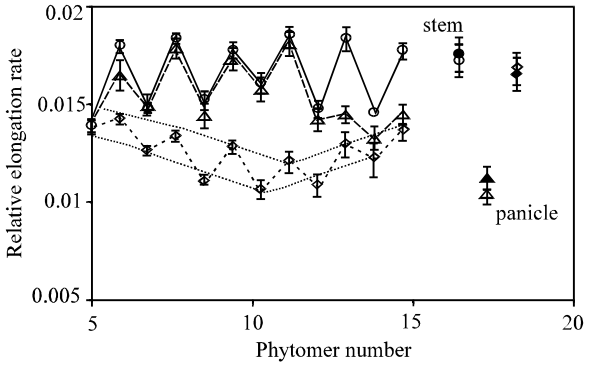

Fig. 6: Relative elongation rate of internodes, stem (filled symbols) and panicle (open symbols) during the exponential phase in each treatment plotted against phytomer number. The line represents the linear regression between the RER and phytomer number. Verticals bars represent 95% confidence intervals

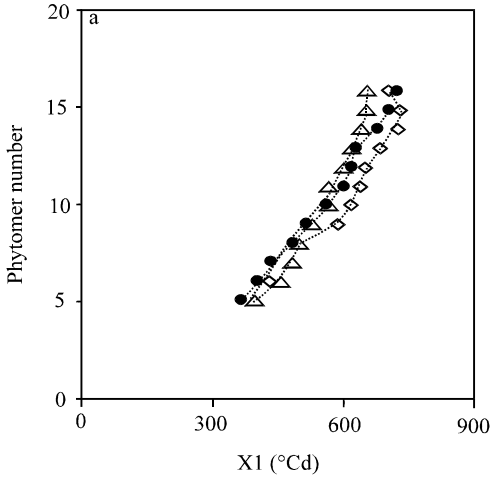

Fig. 7a: Ranks of the phytomer attaining the date X_1 or having the collar emerged in function of thermal time

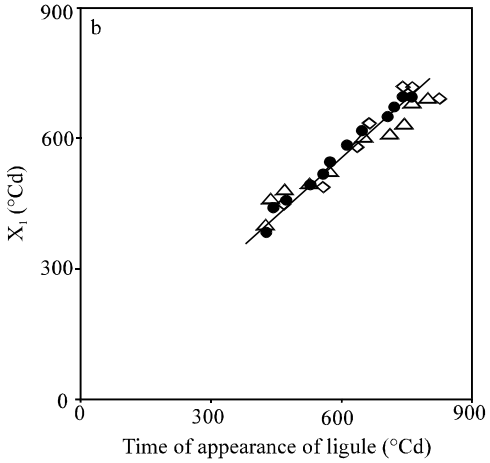

Fig. 7b: Relation between the date of emergence of the collars and the date X_1, for three treatments. (●) Control T_1, (◊) T_2, (△) T_3

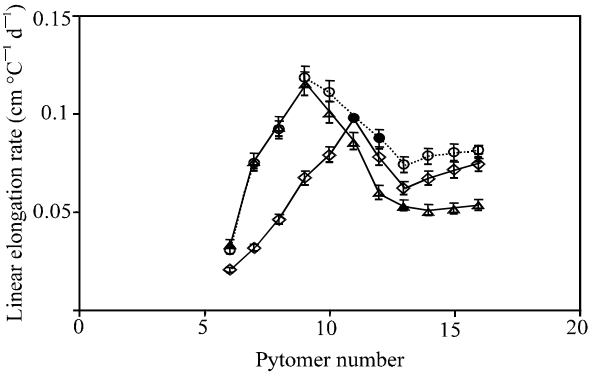

Fig. 8: Elongation rate (cm (°Cd)$^{-1}$ of internodes during Phase III for each treatment plotted against phytomer number. The fitted symbol shows the position of the principal ear. Values are means of six plants and bars represent 95% confidence intervals (●) Control T_1, (◊) T_2, (△) T_3

decreased and becomes (0.0109±0.00056)°C^{-1}d^{-1}. In T_3 the RER start to decrease only at the four last internodes and slightly for stem and panicle, this is due to the fact that during the water stress in T_3, phase I had already been finished for internodes 11 to 12 whereas it had just begun for internodes 13 to 16.

Relation between internode extension and collar appearance: Figure 7a shows the thermal date time of the end of the exponential phase for all phytomers in different treatments. There is a linear relation between the number of phytomer and X_1 (thermal time when linear approximation is zero), (Fig. 1). The resulting slope did not vary significantly with treatment, with a mean value of (0.034±0.009) node°Cd^{-1}. The rate of collar appearance on the leaves coincides with the thermal time corresponding to the end of the exponential phase. For all phytomers of the control plants, the end of the exponential period showed a narrow synchronism with the time the collar of this phytomer reached the ligule, which surrounded it (i.e. emergence) (Fig. 7b). In the case of treatments T_2 and T_3, the collar synchronization with X_1 is maintained, in spite of the differences existing between treatments in the dates of appearance of the collars. The data consolidate the assumption: the end of the exponential phase was triggered by the emergence of the collars[8,9,25].

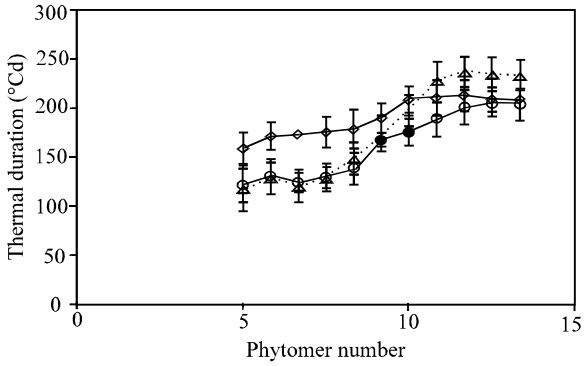

Fig. 9: Equivalent linear duration (°Cd) of internode extension plotted against phytomer number, in each treatment. The fitted symbol shows the position of the principal ear. Values are the means of six plants and bars represent 95% confidence intervals. (●) Control T_1, (◊) T_2, (△) T_3

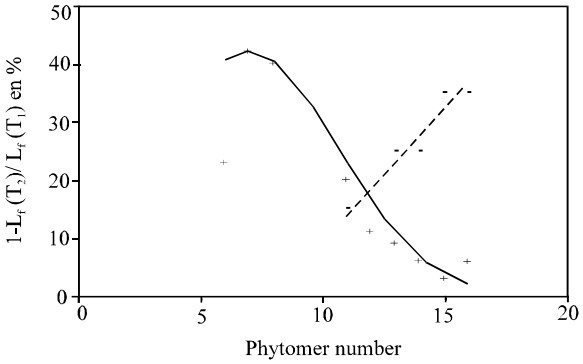

Fig. 10: Relationship between final internode length and linear elongation rate in each treatment. The curve lines show regression between elongation rate and final length

Rate of extension during phase III: The linear elongation rate ($cm°C^{-1}d^{-1}$) during phase III was calculated by a linear regression between the internode length and thermal time. During the linear phase, in contrast to the exponential phase, elongation rate was significantly different between phytomers and between each treatment (Fig. 8). Changes in elongation rate were related to changes in final length: elongation rate increased from 0.0313 cm $(°Cd)^{-1}$ (internode 6) to 0.1188 cm $(°Cd)^{-1}$ (internode 9) then decreased to 0.0747 cm $(°Cd)^{-1}$ (internode 13), grows then slightly to 0.0819 cm $(°Cd)^{-1}$ for the last three internodes. The highest rate of internode extension occurred in the internodes 2 to 3 below the position of the principal ear. Under drought stress, the elongation rate in T_2 was quite lower than in the control treatment. It increased from 0.0212 cm $(°Cd)^{-1}$ (internode 6) to 0.095 cm $(°Cd)^{-1}$ (internode 11), then decreased to 0.063 cm $(°Cd)^{-1}$ (internode 13), grows then slightly to 0.0716 cm $(°Cd)^{-1}$ (internodes 14 to 16) as in the case of the control treatment. In treatment T_3, the elongation rate decreased linearly from internode 11 to 14 with a slope of -0.0167 and stays approximately constant for the last four internodes.

Equivalent linear duration of internode extension: In the control treatment, the duration of the elongation of internodes below the ear was almost constant with a mean value of 129°Cd (Fig. 9). Higher internodes had longer equivalent linear duration with a mean value of 204°Cd. The maximum duration occurred one or two internode above the ear. For internode below or at the ear, the duration of elongation was consistently 85% of the maximum duration.

Most of the internode extension takes place during the linear phase; therefore the final internode length depends mainly on the rate and duration of this phase. In treatment T_2, the duration of elongation for internodes 6 to 11, whose fast extension takes place during stop irrigation, presented an increase comparing to the control with a mean value of 172°Cd. For internode 12 to 16, the linear duration was nearly the same when the irrigation has been taken with a mean value 211°Cd. The duration of elongation for first internodes below the ear becomes 81% of the maximum duration in T_2. In treatment T_3, the duration of elongation was longer than that of the control treatment after the 12th internode with a maximum for the four last internodes with a mean value 234°Cd. Subsequent the duration of elongation for first internodes below the ear becomes only 54% of the maximum duration.

DISCUSSION

The temporal appearance of leaf tips wasn't affected with water stress, but the temporal appearance of the collar was affected from 8th internode. The water stress reduced the internode length. In T_2, the reduction of the length internode (Fig. 10) (internode 6 to 13) can be expressed by:

$$1 - L_{fn}(_{T2}) / L_{fn}(_{T1}) = 42\exp(-0.037 (N_p - 75)^2) R^2=0.99 \quad (5)$$

Where $L_{fn}(_{T2})$ is the final length of internode n in $_{T2}$, N_p is the phytomer number. The maximum reduction was 50% on internode 7 and 8.

In $_{T3}$, the final length internode was reduced for the topmost vegetative internode (11 to 16) and can be expressed by a linear function:

$$1 - L_{fn}(_{T3}) / L_{fn}(_{T1}) = 4.57N_p - 36.71 \quad R^2=0.92 \quad (6)$$

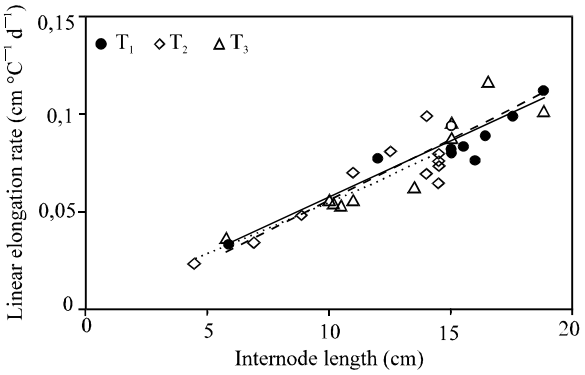

Fig. 11: Relationships between final internode length and linear elongation rate in each treatment. The lines show regression between elongation rate and final length

The coordination between leaf appearance and internode elongation was not affected. This confirms, that the appearance of the collar under drought stress and/or possibly other changes in its micro environment, triggers the onset of the phase of rapid extension of the internode.

Our results confirm the existence of a relationship between the linear elongation rate during phase III and the final length of the internodes (Fig. 11). If all the measurements are considered, the main parts of the length's variations are explained by the variations of the duration of elongation. Fournier and Andrieu[9] found a linear relationship for the upper internodes ((0,011±0,0002)°C^{-1}d^{-1}) and for the lower internodes ((0,0158±0,0005)°C^{-1}d^{-1}) Birch *et al.* [10] proposed a relation for three cultivars for all phytomers below ear ((0,0114±0,007)°C^{-1}d^{-1}) . These relationships are the only parameter that accounts for differences in internode length. In our results the relationship between elongation rate and final length was linear (r^2=0.80) from 6th to 16th internode ((0,0059±0,0001)°C^{-1}d^{-1}) in control T_1, ((0,0055±0,00051°C^{-1}d^{-1}) in T_2 and ((0,0064±0,0001)°C^{-1}d^{-1}) in treatment T_3.

Our results also show that there is one rather precise period of sensitivity of the internodes to the water stress: the lengths were strongly affected each time water stress was started before the beginning of the linear phase and was prolonged during its totality. Other configurations, for which one could expect sensitivity to the water stress, a priori, do not show significant impact. In particular, when only phase I, is affected by the period of water stress, final lengths are only slightly affected (case of internodes 12 to 16 in T_2). Similarly, when the water stress extends over one period between the ends of phase I, but ceases before the middle of phase III; the final reduction in the length is weak (case of internodes 9, 10 and 11 of the T_2 treatment).

Finally, it appears that the strongest reductions occur for the internodes, which underwent the water stress during the totality of the linear phase of growth, that is to say internodes 13 to 16 in treatment T_3 and internodes 7 to 10 in treatment T_2. The effect of the drought was strongly mitigated when an even weak fraction of the linear phase of extension proceeds before the period of the stress (internode 6 of treatment T_2, internodes 9 to 11 of treatment T_3). The effect of the stress was also mitigated if the period of stress covers the exponential phase and the beginning of the linear phase. A significant fraction of the linear period of extension proceeds after the period of stress (internode 10 to 12 of the T_2 treatment). In particular, there is no significant reduction in the final length in the case of internodes 13 to 16 of the T_2 treatment, for which the period of application of the stress relates to only the first phase of extension.

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