Dynamics of the Elongation of Internodes in Maize (Zea mays L.). Effects of Shade Treatment on Elongation Patterns

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The dynamics of elongation of individual maize internodes have previously been characterized under standard agronomic conditions. In this paper these dynamics are compared with those under a shading treatment. Shading was applied after the tip appearance of leaf 6, using a black net that transmitted 20% of light, without altering spectral composition. Internode length was determined as a function of thermal time by measuring the vertical displacement of individual leaf collars. Shading slowed plant development and caused significant reductions in internode length. The onset of the linear phase of elongation was delayed by shading, but its duration was not affected. The reduction in the linear elongation rate was almost totally responsible for the reduction in the final length of phytomers in the shade treatment. The co-ordination between collar emergence and the onset of linear elongation remained. These results support the contention that the kinetics of internode elongation are controlled by the emergence of leaf collars.

Key words: Zea mays L., internode, elongation, dynamics, model, shade, light, phytomer, stem, thermal time, photomorphogenesis.

INTRODUCTION

In a companion paper (Fournier and Andrieu, 2000), which analysed the elongation kinetics of individual internodes in maize, it was proposed that elongation could be described in four phases. Phase I, during which the elongation of an internode is exponential, appears to be part of an integrated process at the level of the whole apical cone. The relative elongation rate of internodes during this phase was found to be the same for all phytomers. During phase II there is a close relationship between the extension of the sheath and the internode, such that the combined elongation rate of sheath and internode is constant; sheath elongation decreases while the rate of internode elongation increases. During phase III the internode alone elongates at a constant rate, equal to that for sheath and internode in phase II, and in phase IV, there is an exponential decline in the elongation rate, that is similar for all phytomers.

This paper examines the effect of shading on the elongation patterns in phases II to IV. Data for phase I were not collected under shading.

MATERIALS AND METHODS

Cultivation details and experimental design

The full-light treatment corresponds to the 1996 experiment described in the companion paper (Fournier and Andrieu, 2000). The shade treatment was identical, except that plants were shaded from the tip appearance of leaf 6 onwards.

Maize (Zea mays L., Fl ‘Dèa’) was sown at INRA, Bioclimatology Unit of Grignon, France, in a deep silt loam on 2 May 1996. Nitrogen and water were applied to ensure non-limiting conditions. There were no leaf diseases, and weeds were controlled by hand. On 6 June, two plots of ten plants each were chosen for their uniformity in terms of development; the plants were tagged, and a black shading net was placed over one of the plots.

The shading net transmitted 20% of light, neutrally. It was fixed to a 2 m x 3 m rectangular roof, with the long axis parallel to the row orientation. The roof had adjustable legs; its height was 1 m at the beginning of the experiment and it was raised during crop growth, so that the net remained 30 cm above the top of the canopy. Flaps were placed along sides (40-cm wide) and along the ends (30-cm wide). This limited exposure to light early and late in the day, while allowing good ventilation.

Measurements began on 7 June and covered the whole period of stem elongation until 6 August (full light) and 13 August (shade). Every 2 to 3 d, the heights of all the elevating collars of the tagged plants were measured, and visible leaf tips and collars were counted. At the end of the experiments, all the plants were dissected to measure the final lengths of the sheaths and internodes.

Temperature measurements

Mean (hourly) air temperatures at screen height (2 m) were obtained from a meteorological station 500 m from the experiment. In both treatments, organ and soil temperatures were monitored directly on one plant using four small copper-constantan thermocouples. One thermocouple was placed in the soil at a depth of 3 cm, and the...
three others were inserted between the sheath and internode in a zone of active elongation. Their positions were adjusted every 2 to 3 d, to sample the whole region of stem elongation. Measurements were taken every 30 s and averaged over periods of 30 min using a data logger. Temperature profiles along the stem were calculated at hourly intervals using linear interpolation between measurements at different heights. The actual positions of internode meristems were calculated a posteriori from the measurements of internode lengths, and the temperatures for all the meristems were estimated as a function of height above the soil surface.

**Internode elongation from collar displacement**

For both treatments, internode elongation was estimated using collar displacement, as described in Fournier and Andrieu (2000). This method makes it possible to analyse the combined elongation of sheath and internode during phase II (transfer of extension from sheath to internode), and to estimate internode length after the sheath is fully elongated, i.e. during phase III (linear phase) and phase IV (exponential decline in rate).

**Analysis**

The analysis of internode elongation was performed using thermal time (degree-days), calculated for each internode using the temperature of individual internode meristems. The base temperature for maize is usually taken to be between 6 and 10 °C, with a value of 8 °C being most widely used (Kiniry and Bonhomme, 1991). This variation in estimated base temperatures is a result of the range of temperatures studied (Durand et al., 1982), and of the position of measurement: air, soil or apex (Ben Haj Salah and Tardieu, 1996). In this study, a base temperature of 9.8 °C was used, as established at Grignon for leaf elongation in ‘Dea’ using apex temperature (Durand et al., 1982; Ben Haj Salah and Tardieu, 1996). The existence of temperature gradients within the plant raises questions about the choice of appropriate thermal variables when considering processes at the whole-plant level. However, differences in recorded temperatures for different active zones of the plant were very small. Apical temperature was, therefore, used for analysing processes such as the timing of phytomer development and the rate of stem elongation.

By convention, leaves were numbered acropetally, starting from the first leaf above the coleoptile. Internodes were given the same number as the leaves above them.

**RESULTS**

*Temperatures in the zone of internode elongation*

Before stem elongation, the temperature of the apical region was equal to the surrounding soil temperature, on average 2.7 °C higher (full light) and 0.5 °C lower (shade) than the air temperature at screen height (Fig. 1). After stem elongation had commenced, apical temperature diverged from soil temperature and finally converged with air temperature at screen height after the apex was 25 cm above the soil (full light), or 5 cm above the soil (shade).

The differences in temperature between the apical region and internode meristems were very small. In the full-light treatment a small temperature gradient was found during the elongation of internodes 7 and 8; this was taken into account when calculating thermal time for these internodes. In the shade treatment, the difference in temperature between the apical region and elongating internodes was less than 0.1 °C, except for internodes 7 to 9. Even for these internodes there was no systematic bias, so that the daily mean temperatures for the apex and any elongating internode were equal. Apex temperature was, therefore, used to represent the temperature of the active zones of the stem throughout the experiment.

**Total number of phytomers**

Final leaf number was between 15 and 17 (mean 16.2) in the full-light treatment, and between 15 and 16 in the shade treatment (mean 15.8). This difference was small, and no
difference was observed between the characteristics of phytomers of the same number. Thus data are presented as functions of phytomer number, counted acropetally, independently of the number of leaves produced.

Plant development under the shading net

The plants subjected to the two treatments developed at the same rate until the shading net was installed. Subsequent plant development was slower under the shading net, even when expressed in thermal time (Fig. 2). The rates of tip and collar appearance were lower under shading from phytomer 9 onwards (at 81 °Cd after the beginning of the shade treatment for tip appearance, and 242 °Cd for collar appearance). In neither treatment was the rate of tip or collar appearance a linear function of thermal time: the rate of tip appearance was lower for the upper phytomers, whereas the rate of collar appearance was higher.

Final internode length was strongly affected by shading (Fig. 3A). Internodes 6 and 7 were slightly longer (+2.8 cm on average) under the shading net but later internodes were, on average, 7 cm shorter than in full light. This resulted in a mean final plant height of 220 cm under full light and 150 cm under shaded conditions. The highest internode length was for phytomer 9 in each treatment.

Final sheath length was similarly affected, although the increase in length for the basal phytomers was more marked and involved more phytomers, whereas the reduction in length for later phytomers was smaller for the sheaths than for the internodes.

Collar elevation

Figure 4 presents the data for collar elevation in full light (A) and shade (B). In each, the distance between collars increased linearly with thermal time, from collar appearance onwards. To analyse more precisely the variation in the rate of elevation around collar appearance, instantaneous rates of collar elevation for individual phytomers were plotted against distance between collars (Fig. 5). In each treatment, the elevation rate remained constant from collar appearance onwards. This occurred even though collar elevation initially represented the combined elongation of the sheath and the internode (from collar appearance up to the completion of sheath extension, i.e. when the collar was a few centimetres above the level of the enclosing sheath) but, thereafter, represented internode elongation only. This confirms the finding of the previous paper that there is transfer of extension from sheath to internode without any change in meristematic activity. Thus, the internode elongation rate during the linear phase (phase III) was the same as the combined rate of sheath and internode elongation during phase II.

Linear elongation phase

The beginning of the linear phase can only be exactly determined from direct measurements of the early stages of internode development; such measurements were not made.
for the shade treatment. The linear phase of internode elongation was analysed using the three phytomer-dependent parameters that define the linear approximation of the internode length time course: $x_1$, thermal time when linear approximation is zero; $x_2$, thermal time when linear approximation is the final internode length; and $u$, the slope of linear approximation. As discussed in the companion paper:

$x_1$ is within phase II, i.e. slightly before the beginning of linear elongation.

$x_2$ is slightly after the end of linear elongation; it is shown below that there is a nearly constant delay (11°Cd) between the end of linear elongation and $x_2$ in both treatments.

$u$ is the elongation rate of the internode during the linear phase.

Linear regressions of the course of collar elevation against thermal time provided excellent fits ($R^2 > 0.97$). From these regressions and final internode lengths, the parameters $x_1$, $x_2$, and $u$ were obtained. Figure 6 shows the timing of collar emergence and $x_1$ for each phytomer number. In full light, the time of collar emergence was calculated from direct measurements (Fournier and Andrieu, 2000). For the shade treatment, the time of collar emergence was estimated from the observed date of collar appearance, by assuming the delay between collar appearance and collar emergence to be the same as in the full-light treatment.

The emergence of collars was significantly delayed in the shade treatment, but the synchronization of $x_1$ and collar emergence was observed for phytomers 7 to 14 in each treatment. This reinforces the notion that collar (or sheath) emergence triggers the beginning of the linear phase. In both treatments, for phytomer 6, $x_1$ was significantly delayed after collar emergence. This atypical behaviour is
not unexpected as internode 6 was the first to elongate significantly. This point was discussed in the companion paper, but here a more precise explanation is proposed. The ability of an internode cell to elongate is not a property of the phytomer, but rather is dependent on the availability of gibberellin, and correlated with the floral development of the apex (Martin, 1988). Thus, the ability of an internode to respond to collar emergence by cell elongation probably arises only after some discrete event has occurred at the whole-plant level. The fact that this event occurred only after the emergence of the collar of leaf 6 would explain why phytomers 1–5 did not exhibit cell elongation, and why the onset of cell elongation in phytomer 6 is delayed compared with collar emergence.

The difference $d_1 = x_2 - x_1$ represents the equivalent linear duration that would be required for the internode to reach its final length, if all the extension occurred at a constant rate, $v$. Figure 7 shows that the equivalent linear duration was not significantly, if at all, affected by shading. The maximum difference occurred for phytomers 9 and 10. However, this could simply be an effect of there being different number of phytomers between the shade and light treatments, as almost all differences disappear if phytomers are numbered basipetally rather than acropetally.

The linear elongation rates of internodes are shown in Figure 8. As expected from the constancy of elongation duration, considerable differences in elongation rate exist between treatments. These are responsible for most of the differences in final internode length (Fig. 3A). Figure 9 shows the elongation rate during the linear phase in relation to the final internode length. The relationship between elongation rate and final length is linear for the upper internodes (0.011 $\pm$ 0.0002°C$^{-1}$ d$^{-1}$) in both treatments. The lower internodes show another linear relationship (0.0158 $\pm$ 0.0005°C$^{-1}$ d$^{-1}$), which is also identical in both treatments. This indicates the existence of two groups of internodes on the stem which behave differently, possibly due to a phase change at the plant level.

End of elongation

In the companion paper we proposed a model of exponential decline in the elongation rate of internodes, constrained by continuity at the end of the linear phase, to fit the last phase of elongation:

$$l = L - \frac{v_n}{k} e^{-k(d-x_2+\frac{1}{2})}$$

(1)

where $l$ is the internode length, $L$ is the final internode length, $v_n$ is the elongation rate during the linear phase, $k$ is a parameter, and $d$ is thermal time. In this parameterization, $k$ is the only free parameter; it represents the inverse of
the thermal time interval between the end of the linear phase and $x_2$.

Figure 10 shows the value of this interval (i.e. $1/k$), estimated by fitting eqn (1) independently for the different phytomers and the different treatments. There was no significant variation between treatments (Student’s $t$-test at the 5% level, $P = 0.73$). Some systematic variation in $1/k$ with phytomer number cannot be excluded. However, using a constant value for $1/k$ (11°Cd) did not significantly reduce the fit.

Succession of elongation between phytomers

From the results presented in this paper and in the companion paper, the onsets of phases I to IV in the elongation of individual internodes are as follows: phase I, at the initiation of the internode, approximately half a plastochron after the initiation of the leaf primordium; phase II, at the emergence of the collar; phase III, at the end of sheath elongation; and phase IV, at the end of the linear phase. Figure 11 shows the sequence of three events, as determined for both treatments, i.e. initiation of the internode, $x_1$ and the end of the linear phase. In the shade treatment, the initiation of the last three internodes could not be estimated, as only twelve internodes had been initiated by the beginning of the shade treatment.

There were no significant differences between plants that produced 15, 16 or 17 phytomers, within each treatment, in the times of phase changes; however, there were differences between the treatments. Shading delayed collar appearance and the beginning of the linear phase, thus delaying the onset of phase IV, due to the unchanged duration of the linear phase. However, because there were slightly fewer phytomers in the shade treatment, the elongation of the last internode in the two treatments ended almost simultaneously.

The end of elongation was synchronous for internodes 14 to 16 in the shade treatment and internodes 15 to 17, for seven out of ten plants in the full-light treatment. This confirms the idea that phytomers in shade and full-light treatments behave similarly if numbered basipetally.

The number of simultaneously-growing internodes varied with thermal time and between treatments. This indicates that no direct synchronization exists between the end of elongation of one phytomer and the beginning of elongation of another.

Stem elongation rate

The elongation rate for the whole stem was calculated by summing the elevation rates of all the collars that were
visible. This meant that internodes in the exponential phase were not taken into account, but the end of sheath elongation was included. For the full-light treatment, data from the X-ray experiment show that there was almost exact compensation between these two approximations (data not shown), and it is assumed that compensation also occurred in the shade treatment.

As expected from the analysis of successive elongation of phytomers, the time course of the stem elongation rate was similar in both treatments (Fig. 12). In each treatment, stem elongation began 300 °Cd after plant emergence, and the elongation rate reached a maximum around 390 °Cd after emergence. This was followed by a period of constant elongation rate (linear phase of stem elongation), up to 500 °Cd, and then a period of rapid reduction in rate. Elongation ceased about 615 °Cd after emergence for both treatments. The main difference between treatments was the much lower elongation rate during the linear phase of stem elongation in the shade treatment.

**DISCUSSION**

The results of this study support the patterns of internode elongation presented in the companion paper (Fournier and Andrieu, 2000), and provide additional information. Shading resulted in significantly shorter internodes, and changed the timing of $x_i$ (which represents a good approximation for the onset of linear elongation). Despite this, the coordination between collar emergence and $x_i$ remained, suggesting that collar emergence triggers phase changes in internode elongation kinetics. No synchronization could be found to indicate the existence of a trigger for the end of the linear phase of elongation. However, since the duration of this phase was unaffected by shading, it could be taken to be a function of phytomer number, preferably counted basipetally. Further work is required to investigate whether this relationship holds over a large range of conditions. Finally, the parameterization of phase IV was also confirmed, as an exponential decline function described this period equally well for the full-light and shade treatments.

The variation in linear elongation rate explained a significant proportion of the variation in final internode length with phytomer number, and it was the only parameter necessary to account for differences in internode length between the full-light and shade treatments. An interesting point is the correlation between the combined elongation rate of the sheath plus internode, and the linear elongation rate of the internode alone. This was observed from shortly after collar emergence, and it occurred for all the internodes in both the full-light and shade treatments, over a large range of internode elongation rates. In the full-light treatment, X-ray measurements showed that, at collar appearance, the internode elongation rate was less than 0.5 times the linear rate for internodes 11 to 15. This does not imply that the linear elongation rates for the internode and the sheath were equal, but rather that the linear rate of internode elongation was not set independently from that of the sheath. Both probably reflect a level of phytomer meristematic activity which is not specific to the type of material (sheath or internode) produced. This does not preclude a relationship between final internode length and internode size at the end of phase I (reported in the companion paper), but no data were obtained in the present study to permit analysis of the stability of this relationship under shaded conditions. Further work is required to establish how phytomer meristematic activity and the timing of events are inter-related and how they determine final internode length. Clearly, a detailed analysis of sheath elongation kinetics would help in defining these relationships.

The assumption that internode length is directly related to carbon availability has been included in the crop models of Grant and Hesketh (1992) and Kropff and van Laar (1993). However, Pattanaik and Mohapatra (1988) failed to relate differences in the length of rice internodes to a difference in carbohydrate and phosphate availability during elongation. The increase in internode length observed here for the lower phytomers in the shade treatment does not support the hypothesis of trophic limitation. It is proposed that changes in internode length in the shade treatment reflect the length of the sheaths within which they grow. This is at least qualitatively substantiated by Fig. 3. This mechanism might also be relevant for modelling leaf elongation. Wilson and Laidlaw (1985) and Davies et al. (1983) controlled the size of leaves experimentally with artificial whorls that delayed their exposure to light.

**CONCLUSION**

This study has provided several concepts for modelling the dynamics of plant architecture. First, thermal time was found to be appropriate for modelling kinetics occurring within each of the elongation phases, provided that it is calculated using the temperature of the plant organs, rather than the air. However, defining the thermal time for a plant requires that the temperature gradients within the plant are small, as in the present experiment and probably in maize crops in general. This may not be true for plants in which elongation occurs simultaneously at points separated by some distance, e.g. tillering grasses or dicots. Second, the ‘transfer of rapid extension’ between organs appears to be triggered by exposure to light or other environmental signals, and thus is related to the morphology of older organs. Taking this into account, rather than using thermal time parameters, in modelling the kinetics of elongation of a series of organs would help to improve understanding of plant adaptation to varied environmental conditions, as plasticity in morphology is one of the major sources of variation involved in such adaptation. Third, it seems that there is also a dependence of the final length of the organ on the time of triggering the ‘transfer of rapid extension’. This could explain how a plant maintains allometric relations among organs of different types, and the strong correlations that exist between the size of similar organs among successive phytomers (Buis et al., 1978; Dwyer and Stewart, 1986; Dwyer et al., 1992). Finally, this work demonstrates relationships between development and triggers which depend upon interactions between morphology and environment. Incorporating such relationships into...
simulation models of the whole plant can be carried out using process-based architectural plant models (Fournier and Andrieu, 1998, 1999) that take into account the three-dimensional shape of organs in characterizing exchanges with the external environment.

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LITERATURE CITED