Original article

Dynamics of internode and stem elongation in three cultivars of maize

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Abstract – The kinetics of elongation of individual internodes, the peduncle and panicle of maize were studied in field experiments in Gatton (Australia) using two tropical cultivars, and compared to similar data previously collected in Grignon (France) on a temperate cultivar. Data for phytomer initiation and organ extension and appearance were related to thermal time calculated from the temperature in the growing zone. Extension of internodes was analysed using a four stage framework: – an initial exponential stage, transition to rapid extension, rapid (linear) extension and transition to final length. The kinetics of internode extension were similar in Gatton and Grignon, though the rates of processes differed. Transition from stage 1 to stage 2 coincided with collar emergence. The commencement of rapid extension of the peduncle coincided with a transient reduction in the rates of extension of vegetative internodes. Further work is needed to assess whether they are effects of genotype only, or genotype and environment.

maize / internode / sheath / tassel / elongation

Résumé – Cinétique d'extension des entre-nœuds et de la tige de trois cultivars de maïs. On a caractérisé la cinétique d'extension des entre-nœuds et de la panicule chez le maïs. Les résultats d'expérimentations au champ réalisées à Gatton (Australie) pour deux cultivars tropicaux sont comparés à ceux précédemment obtenus à Grignon (France) pour un cultivar adapté au climat tempéré. L'extension et l'apparition des organes sont analysées en fonction de la somme de température de la zone de croissance. L'extension est analysée selon un schéma en quatre phases : – une phase exponentielle, une phase de transition, une phase linéaire, et une phase de fin d'extension. La fin de la phase 1 coïncide avec l'émergence de la gaine du même phytomère. Les vitesses d'extension relatives (phase 1) ou linéaires (phase 3) diffèrent entre les expérimentations. Des expérimentations complémentaires seraient nécessaires pour déterminer les composantes génétiques et/ou environnementales de ces différences.

maïs / entre-nœud / gaine / panicule / extension

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1. INTRODUCTION

A key process in the development of crop canopies, and particularly the vertical distribution of leaf area is the extension of the stem. Most models of production of canopies by maize and other crops do not consider the dynamics of vertical growth of plants. Also, existing methodologies generally treat the canopy as a homogeneous entity, without considering the details of extension of internodes or leaves. However, these procedures do not provide sufficient detail and resolution for use in models that consider plant and canopy architecture [8, 9, 20]. Plant architectural models could predict vertical distribution leaf area, and thus light interception or insecticide dilution [13], and be applied in modelling intercrops (where a short statured crop relies on light remaining after interception by a taller companion crop) [1] or pastures containing two or more species [16].

Detailed analysis of the extension of internodes in maize has recently been undertaken under field conditions for the short season cultivar Déa [10, 11]. These authors found that the extension of internodes could be described by four consecutive stages of elongation. This paper (i) examines the applicability of the analysis proposed in [10, 11] for two cultivars of maize adapted to the sub-tropics grown in Gatton, Queensland, Australia; (ii) compares the results to those achieved for Déa in Grignon, France; (iii) examines parameter values that describe internode expansion to determine if a generally applicable framework can be developed, and (iv) quantifies vertical extension of individual internodes and of the stem in total, for application in architectural models.

2. MATERIALS AND METHODS

A field experiment was conducted in Gatton, Queensland, Australia (Latitude 27º33' S, Longitude 152º20' E. Two cultivars of maize, both F1 hybrids (Pioneer 3527, CRM 106 d, and Pioneer C87, CRM 130 d, referred to as P3527 and C87) were grown under non-limiting conditions of nutrient and water supply, and pests were rigorously controlled chemically or mechanically (weeds). An area of 32 m × 24 m of two cultivars of maize was planted, of which 4 m at each end and 2 outside rows were guard areas.

The crops were planted at a seed population of 140 000 ha^{-1} on 4th October 1999, and were thinned to 70 000 ha^{-1} (19 cm between plants in 0.75 m rows) once established (3 visible leaves). The soil at the experimental site was a vertisol, with high water holding capacity and moderate fertility. Water stress was prevented by frequent trickle irrigation (lines in each row beside the plants). Nitrogen was applied at 100 kg N/ha as ammonium nitrate before planting and incorporated by irrigation. Two additional applications each of 75 kg N/ha were made 3 and 6 weeks after emergence. Zinc was applied as a foliar spray at 1 kg Zn SO$_4$.7H$_2$O plus 1 kg urea in 100 litres of water per hectare 2 weeks after emergence, and again 4 and 6 weeks after emergence, dissolved in irrigation water and applied through the trickle irrigation system. Other nutrients were adequately supplied by the soil when assessed against standards used for maize in this location.

2.1. Plant sampling and data collection

Plants were sampled from each cultivar regularly from emergence (leaf 1 of 50% of the sown seed population having emerged from the soil) to the end of the expansion of the canopy. When plants had five visible leaves (3 fully expanded), the length of leaf 3 and the visible length of leaf 4 were determined on 32 plants, and 10 reference plants with the lengths of leaves 3 and 4 close to the median value were tagged to be used as reference plants. Adequate borders were retained around the tagged plants (within the row and in neighbouring rows, and around sampled sites to mitigate edge effects).

Samplings were carried out at 07:30 h at 1, 2 or 3 day intervals, the 3 day interval corresponding to weekends. At each sampling, the number of visible and fully expanded leaves and the lengths of the most recently fully expanded leaf and the one above it were measured (from the collar to the tip and from the point of emergence from the whorl to the tip) on the reference plants. The median length was determined for these two leaves and plants with comparable leaf numbers and sizes were harvested for dissection and measurement of visible (LL) and total lamina and sheath lengths, lamina width (LW) at the widest point and internode length of all phytomers that were initiated. 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 peduncle and panicle structure were measured, and the position of the principal ear recorded. A stereomicroscope was used to measure small internodes and leaves (to 1.0 mm) and to observe the plant apex. The

apex was assessed for panicle initiation using the scale in [17], a rating = 2 taken as panicle initiation.

Leaf area index was calculated from plant population and plant leaf area. The area of each laminae (A) was calculated using the method in [18]

$$A = LL \times LW \times 0.75. \qquad (1)$$

The coefficient (0.75) was retained as it is the mean of values used by other authors working in a range of environments, e.g. 0.73 [15] (United States), 0.75 [4] (France), [6] (Canada), 0.75 [19] (Australia), 0.72 [14] (Kenya)) and 0.79 [3] (Australia).

2.2. Temperature measurements

Maximum and minimum temperatures were recorded at the nearby Lawes Meteorological Station, in a standard Stevenson screen. Also, soil temperature at 5 cm, apex temperature (once the apex was above ground), and air temperature at 20 cm above ground were recorded using copper constantin thermocouples connected to a data logger. For apex temperature, thermocouples were inserted into the plant so that the thermocouple junction was as close to the apex as possible. Thermocouples were relocated to the new apex position determined in each destructive sampling, until the apex was at least 80 cm above the ground. New representative plants were used each time the thermocouple was relocated, to avoid errors caused by damage to the plant causing reduction in the stem elongation rate. Temperature measurements were taken every 10 minutes and averaged over each hour. Elongation was typically 2–6 cm during the interval between positioning of the thermocouples, and thus the thermocouple was in the region of extending internodes below the apex. Temperature gradients in maize plants are small [10], so that the temperatures recorded in this way could be regarded as representative of the apex.

2.3. Thermal time calculations

The temperature of the apex (when under the soil surface or just above the soil) was higher than the temperature of ambient air, thus use of air temperature underestimates thermal time accumulation during early growth. The temperatures used in thermal time calculations were soil temperature, while the apex was below the ground surface, then apex temperature until the apex was 20 cm above the ground, and subsequently, temperatures taken in the Stevenson screen. For 5 days from emergence no soil temperature was available, due to equipment malfunction, so an estimate based on air temperatures on these days and subsequent days and soil temperatures on subsequent days was made.

Analyses of internode elongation were based on thermal time scales, using a base temperature of 9.8 $^\circ$C [2, 5] as used in [10, 11]. This temperature is higher than the widely used base temperature of 8 $^\circ$C (air), which implies that development depends on air temperature [21], whereas the analysis here uses organ temperatures.

## 2.4. Analysis of internode extension

Internode extension in maize has been described in four stages [10]. These are: Stage I, during which elongation is exponential; Stage II, which is short and during which the extension rate increases rapidly; Stage III, during which the extension rate is essentially constant and internode length increases linearly; and Stage IV, during which the extension rate decreases as the internode approaches its final length.

2.4.1. Exponential phase of extension (Stage I)

The natural logarithm of internode and peduncle length was plotted against thermal time since emergence. From these plots, extension of the internodes and peduncle during the exponential stage (Stage I) was examined by linear regression of the natural logarithm of internode lengths of 0.6 to 2.7 cm on thermal time. The upper limit was chosen from graphical analyses of internode length plotted against thermal time from emergence, to ensure the internodes were in Stage I. The regressions were used to calculate the relative rate of extension (RER) of the internodes and peduncle during Stage I.

2.4.2. Linear phase of extension (Stage III)

Provided there were sufficient data in the linear phase, the rate of extension (cm ($^\circ$Cd)$^{-1}$) was calculated for each internode and the peduncle by regressing internode length on thermal time from emergence. The commencement and completion of the linear phase of extension was identified graphically in the manner described in [10] (Fig. 1). The regression equation was then used to determine the intercept (x_1) on the thermal time axis by setting internode and peduncle length = 0. Similarly, x_2 was determined as the intersection of the fitted values of linear regression and the final internode and peduncle length.
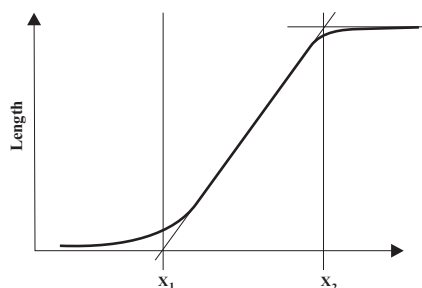
Figure 1. Method of determination of commencement (x_1) and completion (x_2) of equivalent linear extension of internodes.

The equivalent linear duration of extension was calculated as the difference between x_2 and x_1.

2.4.3. End of extension

To examine the behaviour during the end of extension, the extension rate (ER) was normalised by dividing ER values by ER during the linear stage for each internode. This procedure allows comparisons between internodes, should differences exist, or treatment of the data set as a single pool of data, if differences do not occur.

2.5. Data from studies in Grignon, France

Data for the final leaf number, internode length and internode extension rate during Stage III and RER during Stage I from studies with the maize cultivar Déa in Grignon, France (latitude 41°51'N), were incorporated in the relevant figures for comparison with the data from Gatton. The experiments from which these data are drawn are described in [10, 11]. Briefly, though, the maize cultivar Déa was grown at 10 plants·m^{-2} with adequate nutrient and water supplies, and sampled on a similar real time interval to the experiment in Gatton. This resulted in shorter thermal intervals in Grignon, due to lower mean temperatures at this site.

3. RESULTS

3.1. Organ temperature

The daily mean temperatures in Gatton for 5 cm below ground, 5 cm above ground, the plant apex (once above the ground) and the standard Stevenson screen are shown in Figure 2. These show that while the apex is below ground level, temperature exceeded the mean air temperature (Stevenson screen) by 2–4 °C. This extended from
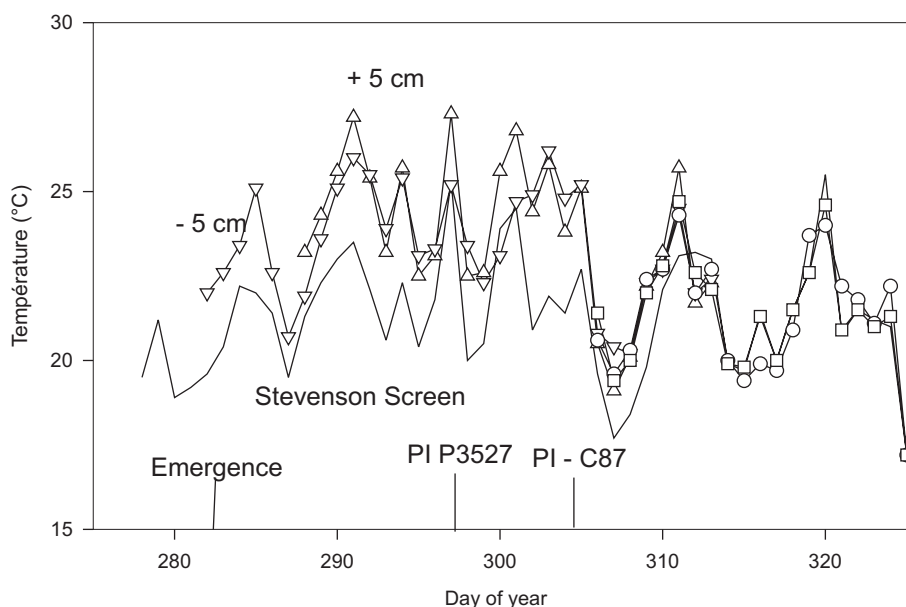
Figure 2. Time course of measure temperatures for P3527 (○) and C87 (□) from planting on day 277 (4 th October 1999) to day 325 (21 November 1999) (a). Temperatures at 5 cm above (△) and 5 cm below (▽) the ground surface, in the apex of P3527 (○) and C87 (□), and in the Stevenson screen (no symbol, line only) in Gatton from planting, shortly after emergence (5 cm above and below ground surface), and from apex elevation above the soil surface (apex temperatures) until day 325. The labelled vertical lines indicate time of emergence and panicle initiation (PI).

seedling to day 302 (330 °Cd after emergence) with LAI < 0.5. During days 303 to 313, differences between soil and air temperatures decreased as leaf area index increased. During that period, the apices were elevated above the soil surface, but apex temperature remained closer to that at 5 cm below the soil surface than air temperature. After day 313, when the apex was 50 cm (P3527) and 20 cm (C87) above ground, and LAI was 2 or greater, soil temperature was no longer measured, and air and apex temperatures were very close.

3.2. Plant level kinetics

3.2.1. Appearance of leaf tips and collars

P3527 and C87 produced 20 and 22 leaves, respectively; the temporal appearance of leaf tips and collars is shown in Figure 3. The number of leaf tips was closely related to the thermal time since emergence, and the two cultivars behaved identically, except for total leaf number. The average rate of appearance calculated from emergence until all tips or collars had appeared were 0.0289 and 0.0259 tips $(°Cd)^{-1}$ and 0.0289 and 0.0265 collars $(°Cd)^{-1}$ in P3527 and C87, respectively.

3.2.2. Stem and panicle elongation

The progressive increase in total height of vegetative internodes is shown for P3527 and C87 in Figure 4. This shows that the apex was below or just at ground level until around 300 °Cd after emergence, and subsequently elevated by elongation of the stem. Both cultivars reached a similar height to the top vegetative internode, though C37 took longer to reach the final height. The similar cumulative total was despite C87 having more internodes than P3527, but several were shorter. Similarly, C87 had shorter shorter panicle and peduncle (Fig. 5).

3.2.3. Final length

In P3527 and C87, the first internode to extend significantly was internode 6, but only to approximately 2.5 cm. Subsequent internodes progressively increased in length until internode 11 in P3527 and 12 in C87, which had lengths of 23.6 and 20 cm, respectively. Above the longest internode, internode lengths initially declined, then increased (internodes 16, 17 and 18 in P3527, and 18 and 19 in C87) and then declined for the topmost vegetative internodes. The peduncle was longer than any vegetative internode.

In Déa, which had 17 vegetative internodes (no peduncle data), internode 6 was the first to elongate, as in P3527 and C87; maximum internode length was similar to that of P3527, but occurred on internodes 9 and 10. Above internode 11, internode length declined. Internodes 6 to 10 were all longer than in P3527 and C87, but higher internodes differed less (Fig. 6a). The pattern of decline from the maximum length was similar to that in P3527 and C87, though the decline was less.
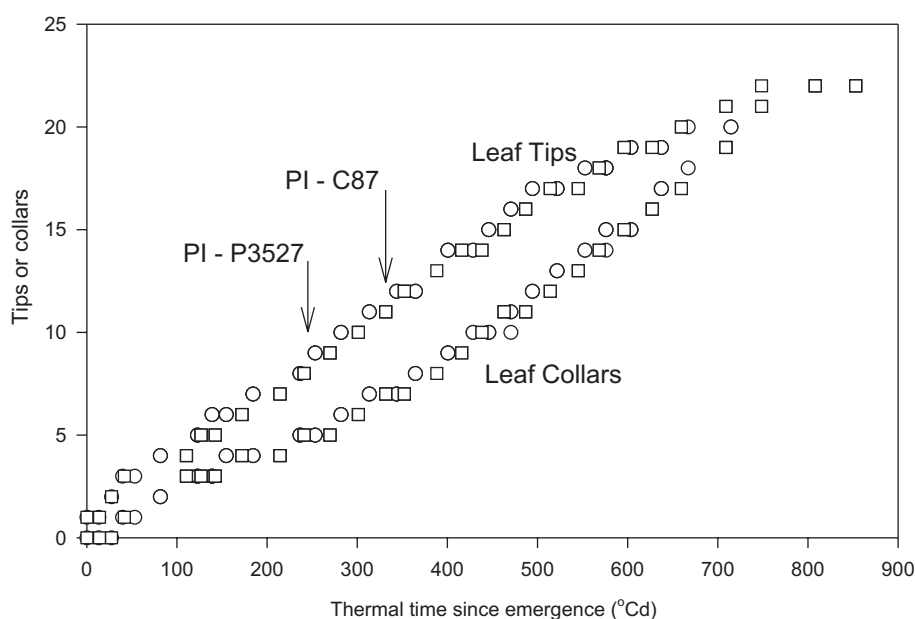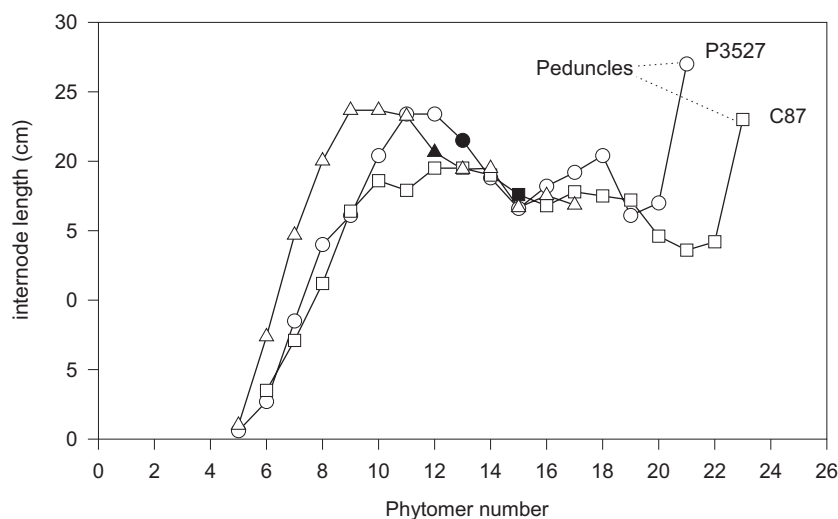

Figure 3. Number of visible leaf tips and leaf collars in P3527 (○) and C87 (□) plotted against thermal time (base temperature = 9.8 °C) from emergence until leaf expansion complete (PI – P3527 and PI – C87 indicate time of panicle initiation in P3527 and C87).
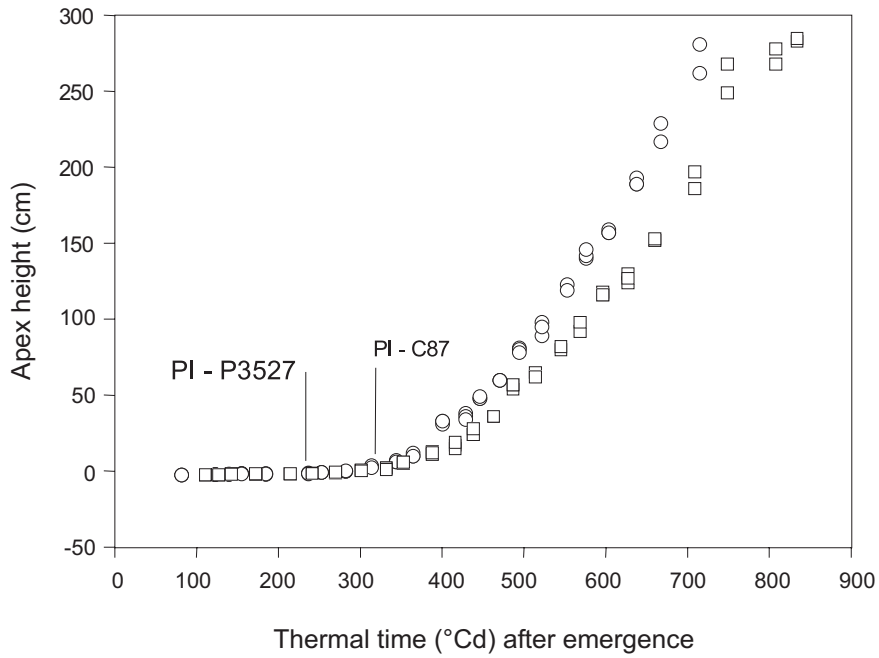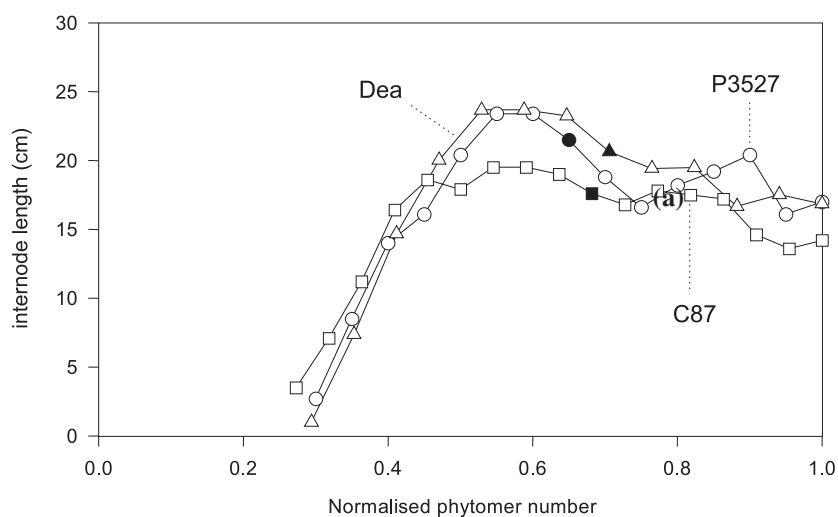
Figure 4. Apex height of vegetative internodes in P3527 (○) and C87 (□) plotted against thermal time (base temperature = 9.8 ºC) from emergence until stem extension complete (Apex height until 420 ºCd after emergence, then base of tassel peduncle, PI – P3527 and PI – C87 indicate time of panicle initiation in P3527 and C87).
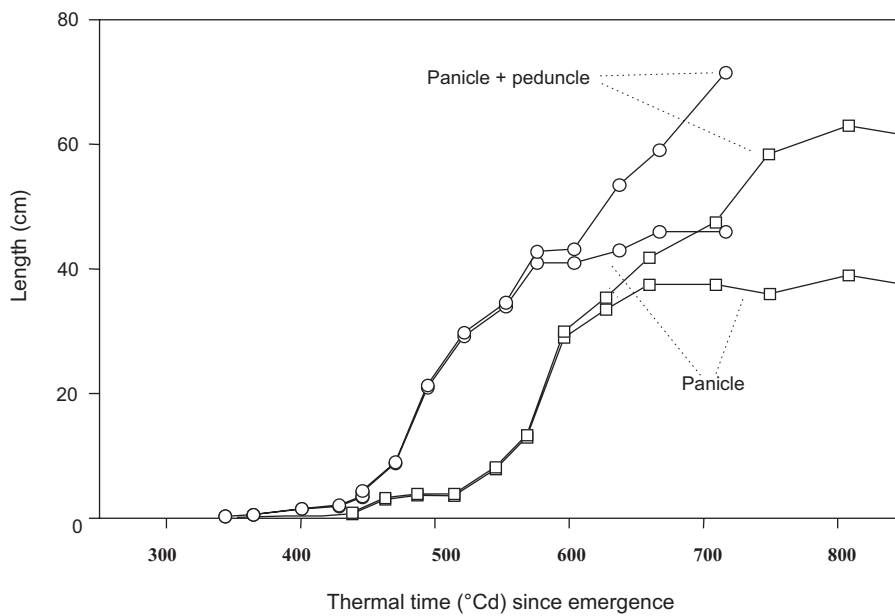
Figure 5. Length of panicle and panicle plus peduncle in P3527 (○) and C87 (□) plotted against thermal time (base temperature = 9.8 ºC) from emergence.

(a)

(b)

Figure 6. Final length (cm) of organs in P3527 (○), C87 (□) and Déa (△) (a) internodes and peduncles plotted against phytomer number and (b) internodes only plotted against normalised phytomer number. The filled symbols show the position of the principal ear on each cultivar.

Internode length was plotted against normalised phytomer number (NP) (NP = phytomer number/total phytomers, producing a scale of 0 to 1) to examine their lengths against relative position on the stem (Fig. 6b). On the normalised scale, the patterns of variation of internode length with rank were similar for all three genotypes : length increased up to NP = 0.45, and then decreased. The principal ear was at 0.65 < NP < 0.7, on the first internode significantly shorter than the internode below it.

3.2.4. Temporal internode, peduncle and panicle extension

The progressive increase in length of the internodes of P3527 and C87 against thermal time are shown in Figures 7a and b, and for peduncles and panicles in Figure 5 (peduncle length the difference between panicle length plus peduncle and panicle lengths). These data show a consistent pattern of sigmoidal increase in the length of each internode, peduncle and the panicle. The graphs also show the sequential commencement of rapid extension of the internodes, panicle and peduncle.
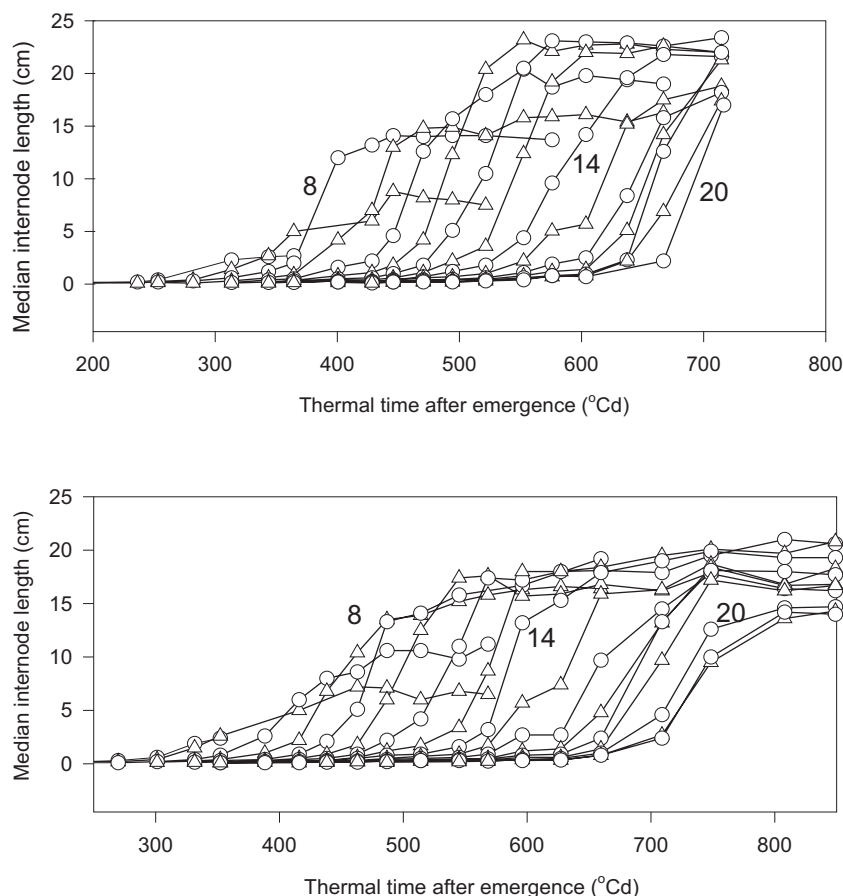
Figure 7. Median internode length (cm) plotted against thermal time (ºCd) after emergence (a) P3527 and (b) C87. Circles are for internodes 8, 10, 12… 20 (or 22 in C87) and triangles for internodes 9, 11, 13… 19 (or 21 in C87).

There is some evidence of departure from the general pattern of extension in internodes 14 to 16 in P3527 and 14 to 17 in C87, from approximately 570 ºCd and 600 ºCd after emergence in P3527 and C87. This coincides with the increasing rate of extension of the peduncle (Fig. 5).

3.3. Analysis of kinetics of individual organs

#### 3.3.1. Relationship between internode extension and collar appearance

The plot of the ratio of the length of internode n and internode $(n + 1)$ against the visible length of sheath n showed a clear change in the ratio when the collar appeared (i.e. sheath visible length = 0 cm) in P3527 and C87 (Fig. 8). Before the sheath became visible, the ratio clustered around 1.6 (range 1 to 2.6), but once the sheath

became visible, the ratio increased. This indicates that the extension rate of internode n increased relative to that of the one above it, and supports the view proposed by [10] that this increase is triggered by the emergence of the leaf collar from the enclosing outer sheath.
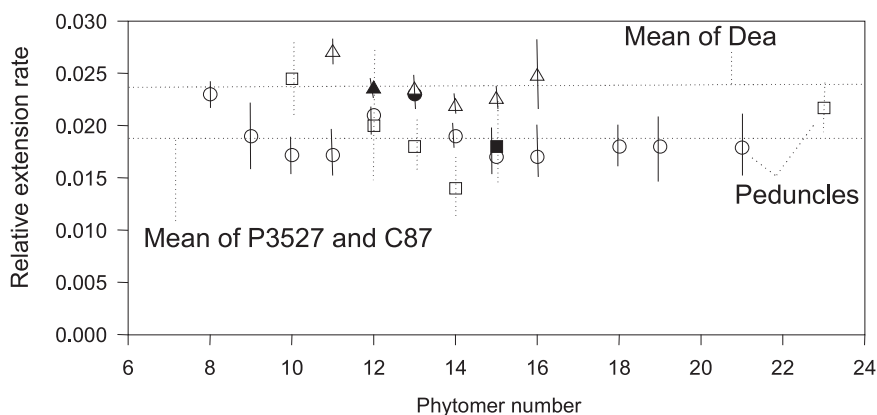
3.3.2. Relative rate of extension of internodes Stage I

The coefficients of determination of regressions (adjusted r^2) used to calculate RER were mostly above 0.90. In P3527, the RER ranged from 0.017 to 0.023. In C87, where only five internodes and the peduncle were examined, the RER ranged from 0.014 to 0.0245 (Fig. 9). There was no significant difference ($P = 0.05$) between the means of value of RER for internodes and peduncles for P3257 (0.0189 ± 0.0006 ºC^{-1}·d^{-1}) and C87 (0.0194 ± 0.0015 ºC^{-1}·d^{-1}), but the mean for Déa (0.0235 ± 0.0008 ºC^{-1}·d^{-1}) was significantly higher ($P < 0.05$)
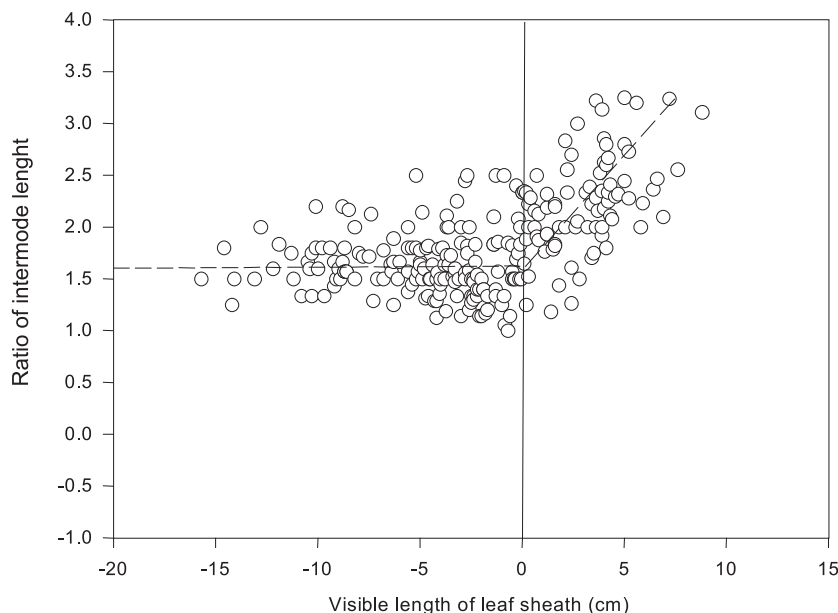
Figure 8. Ratio of length of internode (n) to that of internode (n+1) plotted against visible length of sheath of leaf (n). Negative visible length of sheath is the distance the ligule on leaf (n) is below that of the collar of the sheath of leaf (n–1).

Figure 9. Relative extension rates of internodes and peduncles during Stage I in P3527 ($\bigcirc$), C87 ($\square$) and Déa ($\triangle$) plotted against phytomer number. The filled symbols show the position of the principal ear on each cultivar, and the vertical dotted or solid bars the 95% confidence interval.

(Fig. 9). Finally, during Stage I, the internodes (and peduncles) extended similarly in P3527 and C87, but more slowly than in Déa.

3.3.3. Change to linear extension (Stage III)

During the short Stage II, RER increased rapidly after about 50 °Cd prior to x_1 to about 0.06 near x_1, the commencement of effective linear extension (detailed data not shown). This pattern was very similar to that reported in [10].

3.3.4. Rate of extension during Stage III

There was important variability of the rate of extension during Stage III among phytomers and among cultivars : from 0.06 cm (°Cd)$^{-1}$ (internode 7, C87) to 0.38 cm (°Cd)$^{-1}$ (internode 9, Déa), and was usually lower in C87 than P3527 and Déa. The rate increased to phytomer 9 (Déa), 11 (P3527), and 12 (C87), and declined for higher phytomers (Fig. 10). The rate of extension was much higher in Déa than in P3527 and C87 up to phytomer 10, but for higher phytomers was either slightly lower than or similar to P3527. The rates of
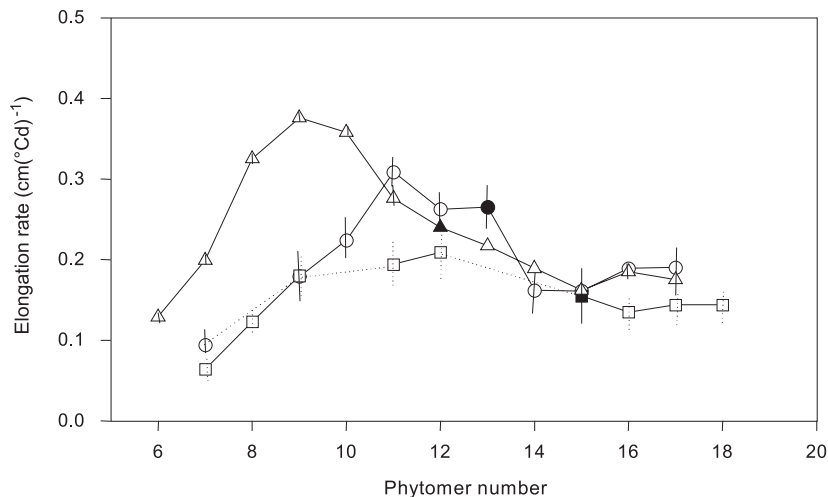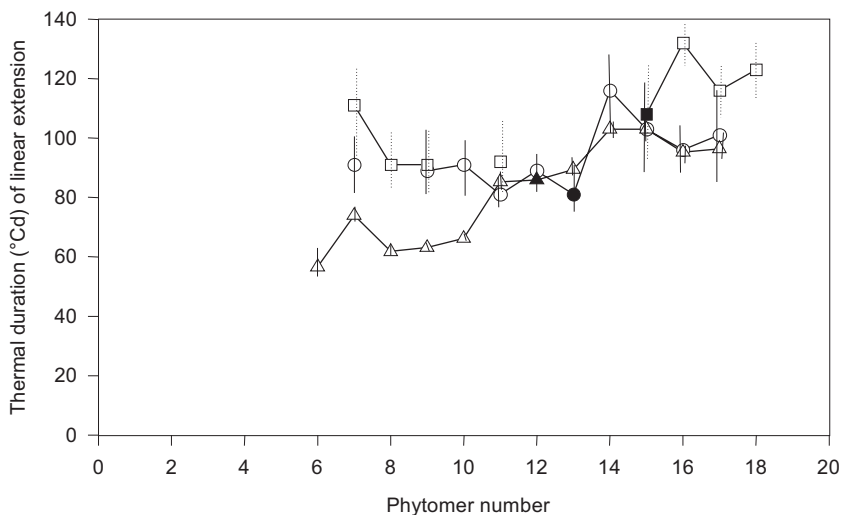
Figure 10. Elongation rates (cm (°Cd)$^{-1}$ of internodes during Stage III in P3527 (○), C87 (□) and Déa (△) plotted against phytomer number. The filled symbols show the position of the principal ear on each cultivar, and the vertical dotted or solid bars the 95% confidence interval.

extension were similar within variety for internodes 14 or 15 and above, and closer across cultivars than for lower phytomers. The highest rate of internode extension occurred in the internodes 2 to 3 below the position of the principal ear.

By normalising phytomer number, the maximum rate of internode extension during Stage III occurred near NP = 0.55. Elongation rates were generally similar across cultivars for 0.4 < NP and NP > 0.7. For 0.45 < NP < 0.7 elongation rates differed between cultivars in the order C87 < P3527 < Déa.

3.3.5. Equivalent linear duration of internode extension

In both P3527 and in C87 the equivalent linear duration of extension of internodes below the ear was nearly the same for all internodes for which it could be calculated, with a mean value of 92 °Cd (Fig. 11). Higher internodes, especially in P3527, had longer equivalent linear duration. The maximum duration occurred one (in P3527 and C87) or two (in Déa) internodes above the ear. For internodes below or at the ear (P3527 and C87), the duration of extension was consistently 70 to 80% of the

Figure 11. Equivalent linear duration (°Cd) of internode extension in P3527 (○), C87 (□) and Déa (△) plotted against phytomer number. The filled symbols show the position of the principal ear on each cultivar, and the dotted or solid vertical bars the 95% confidence interval.

maximum duration. However, in Déa, four of the six internodes for which data were available had equivalent linear durations < 65% of the maximum.

3.3.6. End of extension

The normalised values of RER plotted against thermal time since x_2 (using x_2 as the time origin) show that until around 40 ºCd before x_2, the normalised values were around unity, with no differences that could be attributed to internode number or cultivar, and then declined to around zero (Fig. 12). The decline was complete by about 20 ºCd after x_2, meaning the change from linear extension to final length (Stage IV) occurs in a relatively short period of about 60 ºCd, similar to the estimated value for Déa (50 ºCd).

## 4. DISCUSSION

4.1. Organ temperature

The mean daily temperature of the soil at 5 cm depth was on average 3–4 ºC higher than air temperature at 1.5 m. This confirms that Stevenson screen temperature may differ significantly from the temperature of the meristematic zones, at least while the apex is below ground. Thus, when detailed studies of specific organs are undertaken, the temperature at the zone/s of meristematic activity should be measured or estimated by a model such as that in [12].

4.2. Plant level kinetics

Stem elongation

The height of the top vegetative node, top of the peduncle and tip of the panicle progressed similarly in both P3527 and C87, though C87 was shorter at all times. The final height of the top vegetative internode was similar for both cultivars, despite the higher number of internodes in C87. This arose because internodes were shorter, especially near the ear. The shorter length of upper internodes in C87 was principally due to the lower rate of extension during Stage III, as effective linear duration was similar to or higher than that of P3527 for the same relative position on the stem. Finally, the tassel and tassel peduncle were also shorter in C87, resulting in a lower plant height (to the top of the tassel).

After tassel initiation (236 ºCd and 315 ºCd after emergence in P3527 and C87), stem extension was initially more rapid in C87, but slower for most of the time from panicle initiation to final stem height. This early difference is due to the stage of extension of two internodes (6 and 7) at tassel initiation. In C87, they had median lengths of median 0.7 and 0.4 cm and were approaching Stage III of extension when panicle initiation occurred. However, in P3527, both internodes 6 and 7 were very short (< 0.2 cm) and still within Stage I, and thus some delay in stem extension would be expected. However, the higher rate of extension of internodes in P3527 than in C87 (see later) meant that both cultivars reached similar final height (of the top vegetative internode) around 450 ºCd after tassel initiation. These
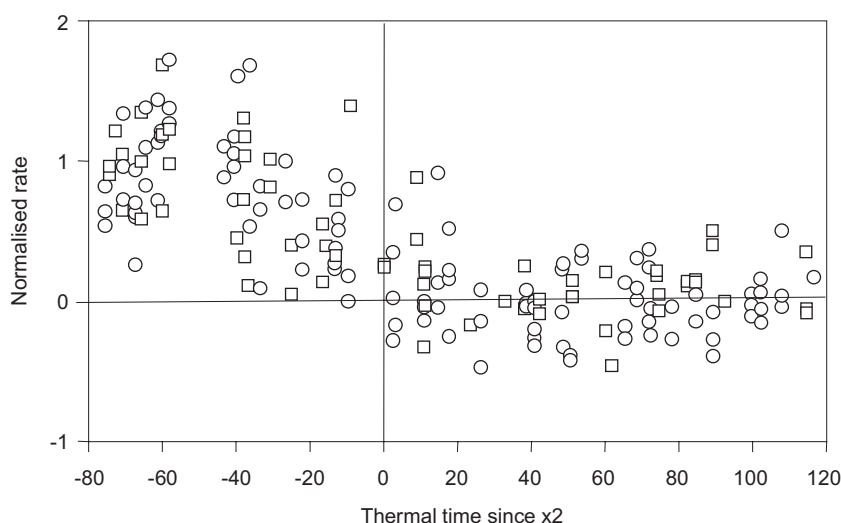
Figure 12. Normalised extension rate of internodes from 80 ºCd before to 120 ºCd after completion of equivalent linear duration (x_2) in P3527 (○) and C87 (□).

findings point to genetic differences affecting the dynamics of internode and thus stem extension, through the coordination of vegetative and reproductive development. The rate of extension was significantly higher in Déa than in P3527 and C87. Further experiments are required to elucidate the role of genotype and environment in such differences.

4.3. Kinetics of individual organs

The number of leaves was higher in Gatton (20 and 22, P3527 and C87) than in Grignon (17). Thus, the total range in leaf number provides the opportunity to examine the applicability of the analysis proposed in [10] for internode extension for cultivars with more internodes.

The synchronisation between the onset of rapid extension of internodes and collar appearance (Fig. 8) was observed for the three genotypes regardless of the environmental conditions under which the crops were grown. This confirms that the appearance of the collar, and thus its exposure to light and/or possibly other changes in its microenvironment triggers the onset of the phase of rapid extension of the internode that subtends the sheath.

This study also confirms that there is no significant variation among phytomers in the relative rate of extension of internodes during Stage I, for a larger range in total number of phytomers than in the study of [10], and also for peduncles. Further, there were no significant differences in the mean RER values for P3527 and C87, but RER for Déa was higher, suggesting that RER and linear extension may share some common genotypic and/or environmental determinants.

It was proposed in [10, 11] that internode length at the end of Stage I determined both the final length of the internode and the linear elongation rate: the longer the internode at the end of Stage I, the longer the internode at the end of elongation, and the higher the rate at which it elongates during Stage III. It is not possible to verify directly these relationships here because the determination of internode length at the end of Stage I was not sufficiently accurate. However, the correlation between linear elongation rate and the final length was examined (Fig. 13). A small departure from the linear relationship occurred for phytomers 14 to 18, that extend simultaneously with the tassel peduncle. This departure is consistent with departures from the general pattern of internode extension (Fig. 7a,b). The regression of elongation rate (y) on final internode length (x) for all cultivars and treatments (excluding the phytomers below 11 in Déa and 14 to 18 of P3527 and C87) was:

$$y = 0.014 \ (+/- \ 0.012) + 0.0114 \ (+/- \ 0.007)x,$$
$$r^2 = 0.92, P < 0.001. \tag{2}$$

The atypical behaviour of the lower internodes in Déa was not observed in P3527 and C87 (Fig. 13). This questions the hypothesis in [10] that an ontogenic phase change at the plant level was responsible for contrasting behaviour between lower and upper internodes. It appears that environmental conditions, or genotypic characteristics, or both play a role together with – or instead of – ontogenic change.

In P3527 and C87, the internodes that were extending rapidly at the onset of tassel peduncle extension, around 570 °Cd for P3527 and 600 °Cd for C87, showed a significant break in their phase of linear extension (Fig. 7). As shown in Figure 13, these internodes also had an average
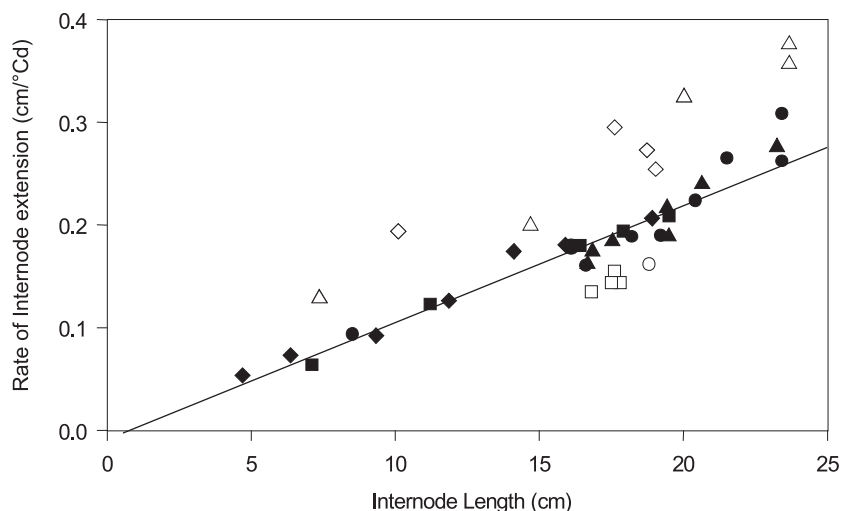
Figure 13. Relationships between final internode length and linear elongation rate in P3527 (○), for C87 (□), Déa grown in full sun (△) and Déa under 80% shading (◇). In Déa, open symbols are for the lower internodes (6–10 under full sun and 6–9 under shading). In C87 and P3527, open symbols are for phytomers whose extension Stage II or III takes place during tassel panicle elongation. Filled symbols are for all other cases, for which the line shows regression between elongation rate and final length.

extension rate slightly below what would be predicted from their final length. Close examination of data from Déa suggests that these patterns also exist, but less pronounced. The coincidence of these events indicates that extension of the peduncle takes precedence over the extension of vegetative internodes. For either final length or rate of extension to be reduced, the ratio for these internodes would need to differ from that in other internodes. As the ratios did not differ, final length as well as rate of extension is probably reduced in these internodes.

5. CONCLUSIONS

The approach in [10] was found appropriate for analysis of internode extension of cultivars producing substantially more internodes than in their study and grown in a much warmer environment. The kinetics of internode extension were similar in Gatton and Grignon, though the rates of processes differed, but generally not greatly. The position of internodes relative to the ear is important, with rates of at least some processes differing below and above it. However, these positional dependant differences may actually reflect the time of extension of the internodes relative to that of the tassel peduncle, as the onset of panicle and peduncle extension modifies the rate of extension of at least three or four internodes that are extending simultaneously with it. Differences between cultivars may occur, or be a result of environmental effects or genotype by environmental interaction. It would be useful to be able to describe the pattern of internode extension by using only one or a few easily measurable plant parameters, similar to the bell-shaped curve of [6, 7] for the final size of individual laminae as a function of total leaf number. The total number of phytomers largely determines the schedule of internode extension, and its relation to the time of peduncle extension and thus competition between these organs for assimilates and growth substances. The total number of phytomers also reflects the genotype and environmental conditions that lead to tassel initiation, and involve the production of growth substances such as gibberellin that are also important for internode cell elongation. This, and the regular patterns presented in this work, suggests that the total number of phytomers may be a useful parameter on which to base a description of the vertical distribution of internode size and extension rate. This should be tested on a wider range of genotypes and environmental conditions.

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