DYNAMICS OF PHYLLODE ELONGATION IN TWO TROPICALLY ADAPTED CULTIVARS OF MAIZE – A CONTRIBUTION TO DEVELOPING TECHNOLOGIES FOR PRECISION CROP MANAGEMENT

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Abstract

The kinetics of elongation of individual leaf laminae and sheaths in maize were studied in two field experiments at Gatton (Australia) using two cultivars, Pioneer 3527 and Pioneer C87, in the first experiment and one cultivar, Pioneer C87, in the second. Destructive sampling was used to obtain detailed data on phyllode initiation, leaf tip appearance and extension of laminae and sheaths. Non-destructive observations were used to ensure that destructive sampling represented the median plants of the population. The appearance and expansion of leaves were related to thermal time, calculated from temperature measured in the region of cell division and elongation. Extension of laminae and sheaths was analysed using a four phases framework: two exponential phases, rapid (linear) extension and transition to final organ length.

Relationships among organs were examined, to determine the timing and effect of events at the organ level. The four phases framework was found applicable to leaf and sheath extension, and length of phyllodes and laminae could be related to ordinal position using a modified bell curve. Thresholds on phytomer rank were detected, with differing rates of organ extension, or changes in distribution among component organs of phyllodes occurring consistently at these.

These relations will be used for modification of existing architectural models of maize to contribute to the more precise research and quantification of maize response to environmental characteristics.

Introduction

A key process in the development of crop canopies is the extension of leaves, which with extension of internodes, provides the vertical distribution of leaf area in the canopy. Leaf expansion results from leaf extension and leaf width acquisition, which generally respond differently to environmental factors (Fournier and Andrieu 1999, Tardieu et al. 1999, Fournier 2000; Ljutovac 2002). Most crop models do not consider extension of individual leaves nor do they consider the dynamics of vertical extension of plants. Crop structure measurements generally aim to characterize the canopy as an homogeneous entity, but do not provide sufficient detail and resolution for use in plant models that simulate the dynamics of canopy (eg Fournier et Andrieu 1998, 1999). Plant architectural models could predict spatial distribution in both the vertical and horizontal domains, and thus improve quantification of resource distribution, such as light throughout the canopy (Hanan 1997, Chelle and Andrieu 1999).

Such models could be applied to simulate intercrops (where a short stature crop relies on light remaining after interception by a taller companion crop) (Adiku et al. 1998, Hillier et al 2005) or pastures containing two or more species (Mahalatti 1998).

Developing robust architectural models of a range of species requires developing generic submodels for extension at organ level. Detailed analysis of the extension of internodes in maize has recently been undertaken under field conditions for the short season cultivar Dea (Fournier and Andrieu 2000a, b) and for tropically adapted cultivars (Birch et al. 2002). These authors found that the extension of internodes could be described by four consecutive phases of elongation.

The present paper examines (i) the applicability of the 4 phases analysis of extension to phyllodes, and their constituent laminae and sheaths (ii) the parameter values that describe lamina and sheath extension, (iii) the correlation between parameters and phytomer position and possible relationships among parameters, and (iv) tests the use of parameters as predictors of laminae and phyllode extension using independent data sets.
Materials and methods

Two field experiments were conducted at Gatton, Queensland, Australia (Latitude 27° 33' S, Longitude 152° 20'E). Two cultivars of maize (Pioneer 3527, CRM 106 d, and Pioneer C87, CRM 130 d, referred to as P3527 and C87) were planted on 4th October 1999 (both cultivars, Experiment 1) and on 17th January 2000 (C87 only, Experiment 2) and grown under non-limiting conditions of nutrient and water supply. Pests were rigorously controlled. An area of 32 m x 24 m of each cultivar 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 and thinned to 70 000 ha⁻¹ (19 cm between plants in 0.75m rows) once established (3 visible leaves). The soil at the site was a vertosol, with high water holding capacity and moderate fertility. Water stress was prevented by frequent trickle irrigation. Nutrients applied were: nitrogen at 100 kg N/ha as ammonium nitrate before planting and incorporated by irrigation, and at 75 kgN/ha 3 and 6 weeks after emergence. Zinc was applied as a foliar spray at 1 kg Zn SO₄.7H₂O plus 1 kg urea in 100 litres water per hectare 2 and 4 weeks after emergence. Other nutrients were adequately supplied by the soil when assessed using standards for maize in this location.

Plant sampling and data collection

Plants were sampled from each cultivar regularly from emergence to the end of the expansion of the canopy. When plants had five visible leaves (3 fully expanded), 10 representative plants were tagged as reference plants in future samplings. Adequate borders were retained around the tagged plants when plants were removed in destructive sampling. At each sampling (at 0730 hrs on 1, 2 or 3 day intervals), three plants with leaf number and sizes comparable to the reference plants were harvested for dissection and detailed measurement of visible and total lamina and sheath (where present) lengths of all phyllodes that were initiated. A stereomicroscope was used measure small leaves, and apex height was determined during plant dissection to assess the position of the growth zone of leaves to position sensors in plants to measure its temperature.

Temperature measurements

Maximum and minimum temperatures were recorded at the nearby Lawes Meteorological Station. 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. 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 at the Lawes Meteorological Station. A base temperature of 9.8°C (Durand et al. 1982, Ben Haj Salah and Tardieu 1996) was used.

Analysis of phyllode extension

Four phases in the extension of maize internodes were described by Fournier and Andrieu (2000a, 2000b), and confirmed on additional cultivars by Birch et al. (2002). These are: Phase I, during which organ extension is exponential; Phase II – extension is also exponential, but with a higher relative extension rate; Phase III – extension rate is essentially constant; and Phase IV, during which extension rate decreases rapidly as final length is approached. In this paper, we apply the four phases analysis to describe the extension of phyllodes, laminae and sheaths of individual maize leaves. Data from the present experiments were insufficiently detailed to examine the extension of organs just after their initiation. Phase I, though, has been detected in another study with maize cultivar Dea in France, and is complete when phyllodes are around 0.5 cm long in leaves 4-9 and around 2.0 cm in higher leaves (Andrieu and Birch unpublished data). Thus, the existence of phase I was accepted, and analyses of Phase II and III of laminae and phyllodes and Phase II for sheaths followed procedures in Fournier and Andrieu (2000a) and Birch et al. (2001). For sheaths, the number of data points in Phase III was mostly insufficient for detailed analysis (Muller et al. 2001).

In this paper, we focus on the analysis of phase III of phyllode and lamina extension. Also, most reference will be to normalised phytomer position (NP), the ratio of phytomer position (numbered from the bottom to top of the plant) to total phytomer number to produce a 0 to 1 scale, as this was found to be more useful than ordinal phytomer position in earlier work of this nature (Birch et al. 2001). Also, the top two leaves are excluded as these have different characteristics of extension (Robertson 1994).
Linear phase of extension

Provided there were sufficient data in Phase III, the rate of extension (LER, cm °Cd⁻¹) was calculated for each organ by linear regression of organ length on thermal time since emergence. The commencement and completion of linear extension was identified graphically (Fournier and Andrieu 2000a, Birch et al. 2002). The lengths of laminae and phyllodes at the start of Phase III were usually near 10% of final length. The regression equation was used to determine the thermal time from emergence to the commencement of effective linear extension (x₁) and completion of extension (x₂) of each organ (by setting organ length = 0 and final length respectively). The equivalent linear duration of extension (LED, °Cd leaf⁻¹) for each organ was calculated as x₂ minus x₁.

Predictive accuracy of constants and equations

The predictive accuracy of constants and equations derived in the analysis described above was assessed by using them to predict values for P3527 (Experiment 1) and C87 (Experiment 2). Predicted values were compared to observed data using Root Mean Square Deviation and regression of predictions on observed data and are presented graphically.

Results

Final length of phyllodes, laminae and sheaths

Median final length of phyllodes, laminae and sheaths (numbered bottom to the top) followed a similar pattern of increasing length of phyllodes and laminae to phyllode number 11 to 14, depending on final leaf number (20, 22 or 24) for P3527 and C87 (Experiment 1) and C87 (Experiment 2). Figure 1 shows the data for C87 experiment 1. For leaves above this level, length decreased approximately linearly with position, except for the top 1 or 2 leaves that were shorter. Sheath lengths increased to phyllode 6, then several of similar length, followed by 3 or 4 that were progressively shorter and most of the remainder being of similar and slightly shorter length.

Percentage of phyllode length present as lamina

The percentage of phyllode present as lamina had an initial rapid increase to 75% at around NP = 0.2 followed by a decline from 0.2<NP<0.3 This was followed by a curvilinear pattern above NP = 0.3 (Figure 2). The relationship for C87 was described by 2 quadratic equations for NP < 0.3 and NP >= 0.3 (Figure 2), with maxima near NP = 0.2 and 0.65 (74 and 83%).

Figure 1. Final phyllode (O), lamina (ð) and sheath (D) length in Pioneer C87 (Experiment 1) at Gatton, Australia. Figure 2. The percentage of phyllode length present as laminae in Pioneer C87 (Experiment 1)
**Temporal pattern of extension of phyllodes, laminae and sheaths**

The progressive increases in total length of phyllodes, laminae and sheaths followed a similar pattern in all phyllodes, a slow initial phase being followed by an increasing rate of extension, then an effectively linear phase, and finally slowing as final organ length was approached, as shown for phyllodes of C87 (Experiment 1) (Figure 3).

Figure 3. Median length (cm) of even numbered phyllodes from 4 to 20 plotted against thermal time (°Cd) after emergence for Pioneer C87 (Experiment 1)

**Rate of linear extension**

There was considerable variation in LER of laminae and phyllodes. Extension rates for laminae increased from 0.35 to around 0.5 to 0.55 cm °Cd⁻¹ for most laminae from leaf position 9 to around 15, then declining to around 0.25 cm °Cd⁻¹. For phyllodes, extension rates increased from 0.35 to around 0.55 to 0.60 cm °Cd⁻¹ for most phyllodes from leaf position 9 to around 15, then declining to values around 0.3 cm °Cd⁻¹. The relationship of LER to NP for laminae and phyllodes for 0.3<NP<0.9 (Figure 4a, for laminae) were described by quadratic equations:

- for laminae: \( y = -0.17 + 2.3*NP - 1.9*NP^2 \) \( r^2 = 0.91 \) (4) and
- for phyllodes: \( y = -0.04 + 2.1*NP - 1.8*NP^2 \) \( r^2 = 0.84 \) (5)

with maxima of 0.55 cm °Cd⁻¹ (laminae) and 0.61 cm °Cd⁻¹ (phyllodes) near NP = 0.6.

**Equivalent linear duration of phyllode and lamina extension**

Effective linear duration (ELD, °Cd) of laminae increased from 125 °Cd for leaf 4 to around 180 to 210 °Cd for leaves midway up the stem and then declined for higher leaves (Figure 4b). Though around 30°Cd longer, a similar pattern was present for phyllodes. The equations were:

- for laminae: \( ELD = 20.9 + 519*NP - 416*NP^2 \) \( r^2 = 0.80 \) (5) and
- for phyllodes: \( ELD = 50.0 + 548*NP - 477*NP^2 \) \( r^2 = 0.75 \) (6),

with maxima of 182 °Cd and 210 °Cd for laminae and phyllodes near NP=0.6.

Figure 4. Extension (a) rates and (b) duration of Phase III of laminae of Pioneer C87 (Experiment 1) against normalised leaf position. Vertical error bars represent ± s. e.
Predictive accuracy of derived functions

When equations for LER and ELD were applied to independent data sets for P3537 and C87 (Experiment 2), predictions were quite sound when assessed by Root Mean Square (Figure 5 a-d), but coefficients of determination of regressions were only modest for LER of phyllodes and laminae, though the points were distributed along and close to the 1:1 line and the range in predicted values and observed data were similar.

Discussion

This study has extended the applicability of the four phase analysis of organ extension from internodes of maize (Fournier and Andrieu 2000, Birch et al. 2002) to phyllodes and laminae and probably sheaths, though data for sheaths is limited.

Figure 5. Predicted (a) percentage of phyllodes present as laminae, (b) duration of linear extension (“Cd”), (c) linear extension rate (cm “Cd”−1) of phyllodes and (d) linear extension rate (cm “Cd”−1) of laminae based on normalised position against respective observed data for P3527 (O) (Experiment 1) and C87 (experiment 2).

When expressed as a function of NP, the proportion of phyllodes present as laminae was described by two quadratic equations that corresponded to the bottom 6 leaves and to all upper leaves respectively. These equations could provide a useful means of apportioning phyllode length, and be an indicator of other processes occurring at phyllode or whole plant level. The percentage of phyllode represented by laminae increased to NP = 0.2, then declined to NP=0.3, coinciding with the first internode to extend significantly, then increased almost linearly to 85% over the range 0.3 < NP < 0.55, the range over which final internode length also increased (Birch et al. 2002), followed by a plateau and then decline.

Final organ length and linear elongation rate

Fournier and Andrieu (2000a,b) identified two subsets of phytomers differing in the relation between internode extension rate and final length in cultivar Dea. We also identified two subsets of phyllodes and laminae, corresponding to lower (NP<=0.6)and upper phytomers (0.6<NPO<=0.9), in which rates of extension were related to final length of organs (data not presented). The NP of 0.6 that separate the two subsets is close to or above the position of the longest or equally so lamina on maize with 18 to 23 leaves (Birch 1996) and here (20 to 24 leaves). Thus this study confirms NP = 0.6 as a useful threshold for change in behaviour of plant organs, since internode length also declined near NP = 0.65 (Birch et al 2002).
Predictive accuracy of relationships

The predictions of the equations derived from C87 (Experiment 1) when assessed by linear regression of predicted values on observed data and RMSD (Figure 4a-d) indicate that the equations can be used for modelling kinetics of phyllode extension and distribution of component laminae and sheaths. Equations based on NP rather than analogous equations using LN should be applicable for plants with total leaf number outside the range used here, as they allow the position of maximum rates and durations of processes to remain at NP = 0.6, and hence at a different LN. Using equations based on LN would have a set position for maxima to occur, be biologically inaccurate as the position of the largest leaf varies with total leaf number (Birch et al. 1998, Keating et al. 1992) and would produce unrealistic values if extrapolated beyond the experimental range in total leaf number used to develop them. However, use of NP is not without limitations, as using NP means that any differences in leaf extension associated physiological functions or the functions themselves that are independent of leaf number e.g. floral initiation that depends on temperature and photoperiod will not be accurately modelled, consequently an alternative or supplementary approach would be needed.

Conclusions

The approach of Fournier and Andrieu (2000) proposed for internodes was found appropriate for analysis of phyllode, laminae and sheath lengths for plants with 20 to 24 leaves, as had previously been reported for internodes in maize (Birch et al. 2002) grown in a much warmer environment than used by Fournier and Andrieu (2000). Changes in parameters describing internodes (Birch et al. 2002) and phyllodes in this study consistently occur near NP = 0.6 (close to the position of the primary ear and longest laminae on maize with 18 to 23 leaves (Birch 1996) and here (20 to 24 leaves) indicates that NP=0.6 is a useful threshold for change in behaviour of plant organs. Total number of phyllodes largely determines the schedule of organ extension, and reflects the genotype and environmental conditions that lead to tassel initiation. This, and the regular patterns presented in this work, suggests that total number of phyllodes may be a useful parameter on which to base a description of extension of phyllodes, laminae and sheaths. The concept should be tested on a wider range of genotypes, for example groups adapted to temperate and tropical conditions, and environmental conditions such as water supply and temperature.

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References


