

A framework for quantifying maize leaf expansion and senescence at the individual leaf level

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Abstract

Leaf area index (LAI) is an important component of maize simulation models. Although canopy development processes such as leaf appearance and expansion are well understood, there is lack of quantitative understanding of leaf senescence dynamics. This explains why leaf expansion is simulated at the individual leaf level while leaf senescence is modelled at the canopy level. The life cycle of individual maize leaves (i.e. from leaf tip appearance to physiological maturity) has been intensively measured in a fully irrigated field maize crop at Lincoln, Canterbury, New Zealand. A maximum LAI of approximately 4.5 was achieved at final leaf expansion. The thermal-time requirement for leaf appearance (phyllochron) was constant after the 4th leaf position at 46 °Cd leaf⁻¹. Total leaf expansion, characterised by the appearance of leaf ligules, showed a bi-linear pattern at a rate of 65 °Cd leaf⁻¹ until the 7th leaf position and 26 °Cd leaf⁻¹ after that. The rate of senescence onset was 135 °Cd leaf⁻¹ until the 7th leaf position and 25 °Cd leaf⁻¹ after that. Finally, the rate of complete senescence was 115 °Cd leaf⁻¹ until the 7th leaf. This pattern of differential leaf expansion and senescence for individual leaf positions explained the progression of LAI senescence in two distinct phases. The first phase, from final leaf expansion until approximately the onset of senescence in the 7th leaf, showed a slow rate of LAI decline with negligible changes in light interception. After that, LAI declined at approximately 0.08% per day causing a steep reduction in light interception. The relationships and parameterisation derived from this study can be used to improve the prediction of maize LAI by enabling both the simulation of leaf expansion and leaf senescence at the level of individual leaves.

Additional keywords: corn, modelling, LAI, phyllochron, senescence

Introduction

The simulation of leaf area index (LAI) is a critical component of crop modelling. Biomass accumulation is largely driven by the amount of intercepted light which depends on the pattern of leaf area expansion and senescence. For maize (*Zea mays*), LAI expansion is often simulated as the product of leaf area per plant and plant

population (Muchow *et al.*, 1990). Leaf area per plant is determined by the number of leaves per plant and the size of each leaf. The number of leaves per plant at any given stage is typically calculated using a phyllochron to determine when the tip of each leaf appears. The maximum size of each leaf can be modelled as a function of leaf position using a bell shaped curve

(Dwyer and Stewart, 1986).

Leaves expand in an approximately linear progression from leaf tip appearance until ligule appearance, when the leaf has reached its maximum size. Between ligule

appearance and the onset of leaf senescence, leaf area remains constant. After this, senescence starts and then progresses until the leaf is completely senesced (Figure 1).

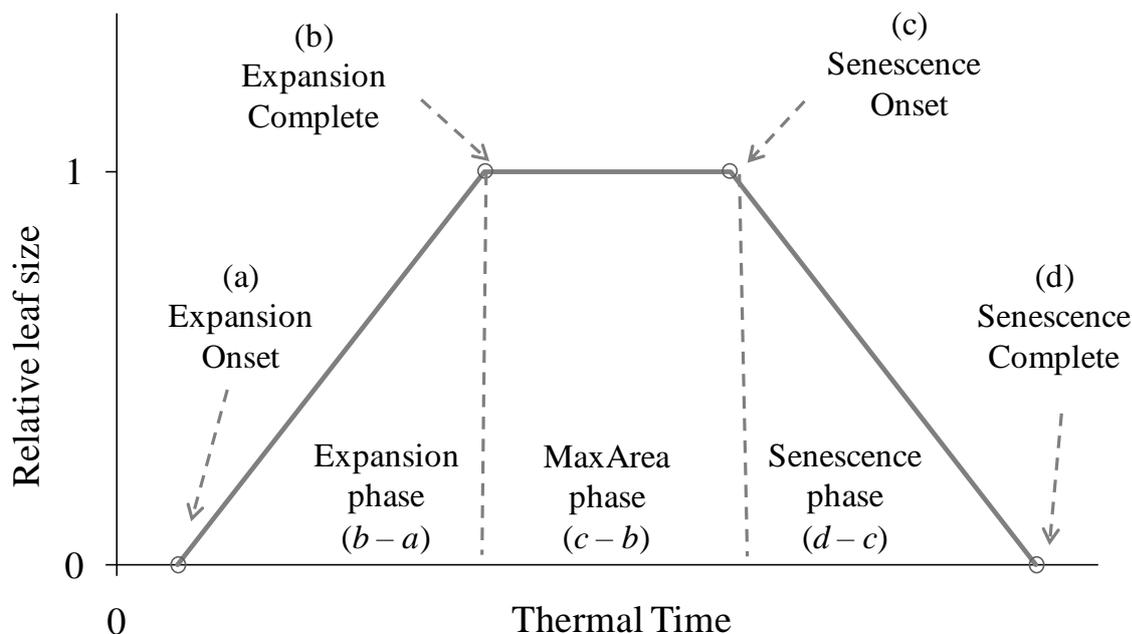


Figure 1: Schematic framework used to model the time course of leaf area of individual leaves showing four different leaf development stages (*a* to *d*) and three phases (expansion, maximum area and senescence).

There is a substantial amount of information available quantifying the appearance of leaf tips and the duration of the expansion phase for maize (Birch *et al.*, 1998; Wilson *et al.*, 1995). However, there is surprisingly little information available quantifying the durations of the maximum leaf size and senescence phases. Therefore, the decline in LAI caused by leaf senescence is often modelled with empirical approaches. For example, both Wilson *et al.* (1995) and Muchow *et al.* (1990) assumed an exponential increase in the senesced fraction of LAI with thermal-time from sowing. There is a clear physiological

disconnect between modelling leaf area expansion on an individual leaf basis and modelling senescence at the whole canopy level.

In this study we present an analysis that links senescence to the individual leaf level approach commonly used for leaf expansion. The aim was to quantify the thermal duration of each of the phases of the relative leaf size progression in Figure 1 so that leaf area expansion and senescence are described at a similar hierarchical level. Data from a preliminary experiment was used to explore this approach.

Materials and Methods

On 26 October 2010, four plots (3.04 m x 9.0 m) were sown with the short maturity maize (*Zea mays* L.) hybrid Pioneer 39V43 on a Templeton silt loam soil at Lincoln (Canterbury, New Zealand, 43°37'S; 172°28'E) at a population density of 12 plants m⁻² with a row spacing of 0.76 m. Crops were fully irrigated (194 mm for the season), received mineral fertilisation (247 kg ha⁻¹ N, 53 kg ha⁻¹ P, 44 kg ha⁻¹ K⁻¹ and 3 kg ha⁻¹ S) and pre-emergence herbicides Lasso Microtech™ @ 5 l ha⁻¹ and Bruno™ @ 3 l ha⁻¹ with 200 l ha⁻¹ water (2.4 kg ha⁻¹ alachlor and 1.5 kg ha⁻¹ cyanazine as active ingredients respectively) to enable unconstrained growth rates. Weather conditions at site were monitored from the Lincoln Broadfields Weather Station (NIWA 17603). Average temperature was 15.4 °C, mean solar radiation was 20.6 MJ m⁻² day⁻¹ and accumulated rainfall was 266 mm respectively.

In each plot, nine plants were marked with coloured rings. These marked plants were monitored weekly for the appearance of leaf tips (i.e. assumed as onset of leaf expansion), leaf ligules (i.e. assumed as the end of leaf expansion) and the fraction of leaf lamina senesced for each leaf position through visual scoring previously calibrated against measurements taken with the image analysis software QUANT v 1.0 (Vale *et al.*, 2001). The maximum leaf area at each leaf position was calculated as the product of maximum leaf width, length and a conversion factor of 0.71 calibrated for the crop. Grain dry matter was sampled seven times during the season from three to six plants per plot by drying cobs at 60°C and then separating grains from rachis by hand. Fractional light interception was measured with a Sunfleck ceptometer (Model SF-80) by taking one reading of incoming

photosynthetically active radiation (PAR) above the canopy and five readings of transmitted PAR below the canopy. Thermal-time (Tt) accumulation was calculated using cardinal temperatures of 0, 8, 26 and 44°C with corresponding Tt accumulations of 0, 8, 26 and 0 °Cd (Wilson *et al.*, 1995). Leaf area index was estimated by integrating the product of the number of leaves (expanding plus expanded) and the area of individual leaves. The area of expanding leaves was linearly interpolated from readings of two consecutive measurements and two or three-stage piecewise functions were fitted to the data using Sigmaplot v.10.

Results and Discussion

The relative size progression of each leaf from tip appearance to complete senescence was quantified in a thermal-time scale (Figure 2). From the 4th leaf position on, the rate of leaf tip appearance was constant, yielding a phyllochron of 46 °Cd leaf⁻¹, which is consistent with previous literature (Birch *et al.*, 2003). The rate of fully expanded leaf appearance was a bi-linear pattern with a thermal-time requirement of 65 °Cd leaf⁻¹ until the full expansion of the 7th leaf and was faster at 26 °Cd leaf⁻¹ after that (Figure 2, function “b”). This curvilinear pattern agrees with previous observations (e.g. Stone *et al.*, 1999). Approximately at the same leaf position, the rate of progression for the onset of senescence increased from 135 °Cd leaf⁻¹ to 25 °Cd leaf⁻¹ after that (Figure 2, function “c”). Complete senescence was observed in the first seven leaves, because the final six leaves had not reached full senescence at physiological maturity of the crop (black layer stage), at a rate of 115 °Cd leaf⁻¹ (Figure 2, function “d”).

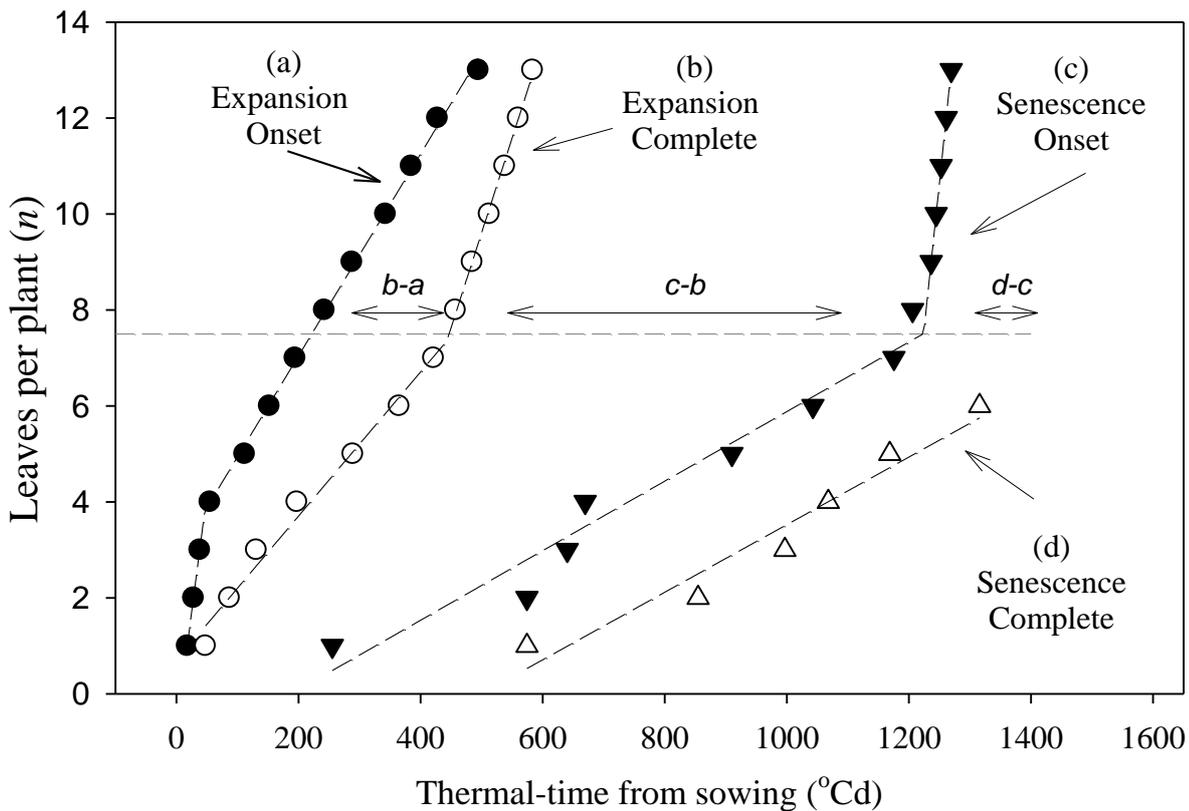


Figure 2: Dynamics of (a) leaf expansion onset (leaf tip appearance), (b) leaf expansion completion (leaf ligule appearance), (c) senescence onset and (d) senescence completion for maize crops at Lincoln, Canterbury, New Zealand. Note: Horizontal dashed line indicates 7.5 leaves for reference and phases are (b-a) expansion phase, (c-b) maximum area (MaxArea) phase, (d-c) senescence phase.

The respective duration of each respective phase could be calculated from the two-stage piecewise functions shown in Figure 3.

The Tt length of the expansion phase (stages *b-a*) showed an increase to a maximum of approximately 200 °Cd at approximately leaf position 7. The length of the maximum leaf area phase (stages *c-b*) increased from 300 at the first leaf to approximately 760 °Cd at leaf 7 and declined slowly to 680 °Cd at the final leaf. This highlights the importance of the larger leaves in the middle of the canopy profile as main providers of photosynthates during grain filling, as these maintain light

interception at later development stages and also show the highest relative CO₂ exchange rates (Thiagarajah *et al.*, 1981). Finally, the length of the senescence phase declined from 300-330 °Cd for the first leaves to 155 °Cd. At the proximity of crop maturity, senescence progressed from top to the middle of the plant suggesting even lower thermal-time requirements for the senescence of leaves on the top. This pattern is in agreement with observations in other modern hybrids and seems to be a consequence of selection for high yielding genotypes at high plant populations (Valentinuz and Tollenaar, 2004).

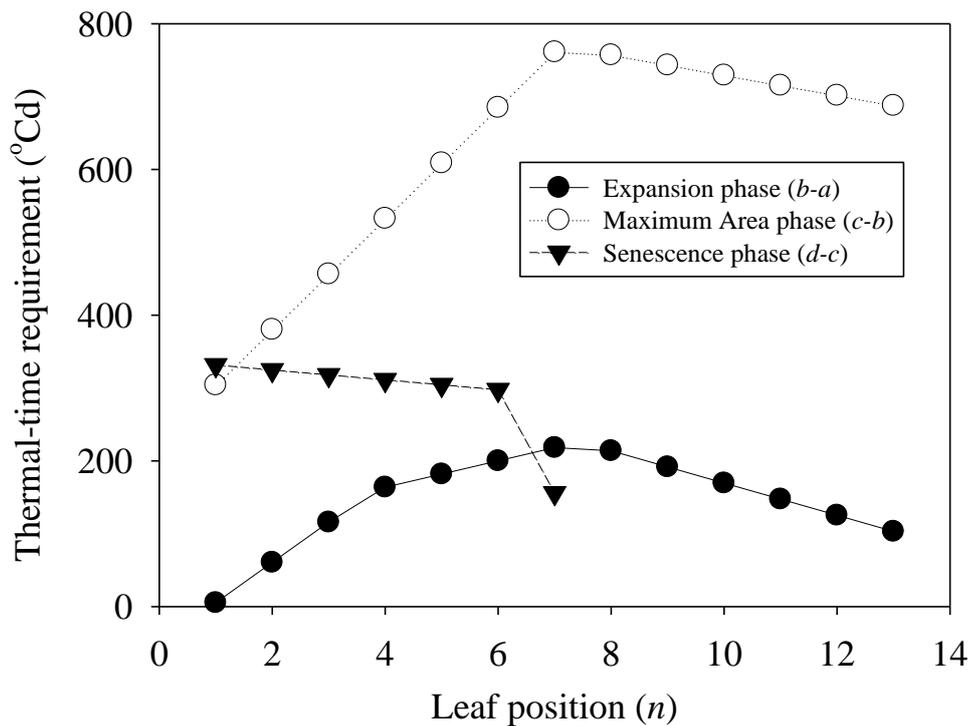


Figure 3: Thermal-time requirement (Tt) for each leaf stage of development and senescence in maize crops at Lincoln, Canterbury, New Zealand.

Using the relationships and parameters in Figures 2 and 3 in conjunction with maximum individual leaf size, it was possible to simulate the time course of LAI (Figure 4a). At the whole canopy level there were two distinct stages of leaf senescence. In the first stage from maximum LAI to approximately 1200 °Cd from sowing (15 January to 15 March) there was a slow decline in LAI at a rate of 0.01 m² leaf m⁻² soil day⁻¹ (Figure 4a). During this period, light interception remained constant at approximately 0.85 (Figure 4b) because senescence was only occurring on basal leaves before leaf position 7 which contributed to a small fraction of LAI. In contrast, at the onset of senescence in leaf position 7 (approximately 1200 °Cd from sowing) there was an eightfold acceleration

in senescence rate. This caused a fast decline in light interception at a rate of 0.08% per day, reaching a minimum interception of 0.60 at the moment of harvest.

Grain filling is strongly dependent on photosynthetic activity after anthesis. At the moment of transition from the slow to the fast senescence period, grain dry matter accumulation had reached approximately 80% of its maximum (Figure 4c). This highlights the importance of having an accurate simulation of the timing and rate of senescence to be able to predict grain yield and harvest index correctly.

Future work may test the robustness of observed senescence patterns in hybrids with contrasting maturity rates, ‘stay-green’ characteristics and N supply regimes.

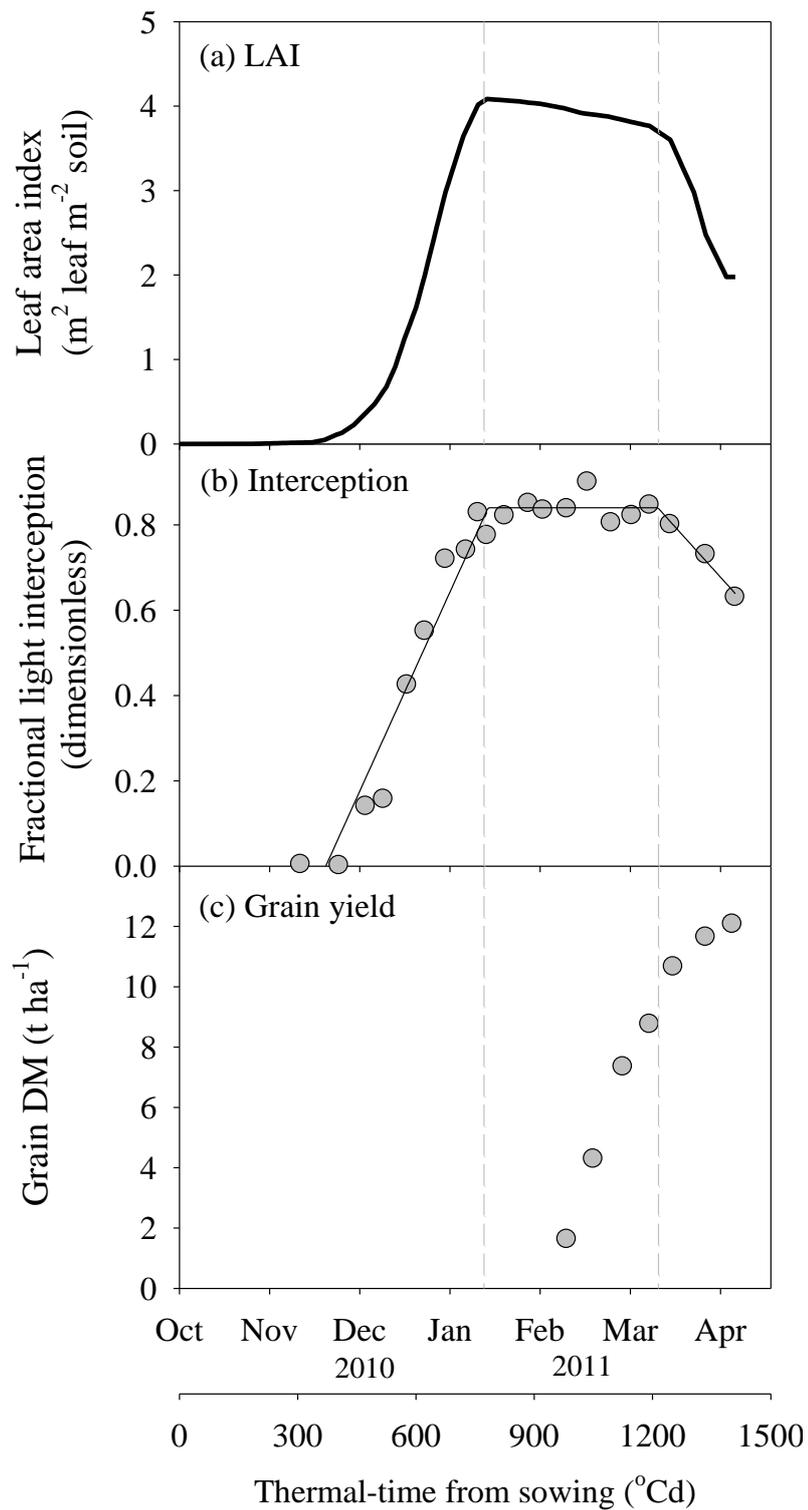


Figure 4: Dynamics of (a) simulated leaf area index (LAI), (b) measured light interception and (c) measured grain dry matter accumulation in maize crops at Lincoln, Canterbury, New Zealand as a function of thermal time (Tt).

Conclusions

The dynamics of leaf development and senescence for individual leaf positions in maize crops have been quantified. These relationships and coefficients can be used to develop more mechanistic modelling approaches to simulate maize LAI where both leaf area expansion and senescence are calculated at the hierarchical level of individual leaves.

Acknowledgements

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