

# Short-term responses of leaf growth rate to water deficit scale up to whole-plant and crop levels. An integrated modelling approach in maize.

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Physiological and genetic studies of leaf growth often focus on short-term responses, leaving a gap to whole-plant models that predict biomass accumulation, transpiration and yield at crop scale. To bridge this gap, we propose here a model that combines (i) a short-term model of maize leaf expansion that capture genetic and environmental variations (Reymond *et al.*, 2003; Welcker *et al.*, 2007), with (ii) a new model coordinating the development of all leaves of a plant and (iii) the crop model APSIM (Wang *et al.*, 2002; Keating *et al.*, 2003) which takes account of the complex interactions between plants and their environment. The model was tested against final length of all leaves of the plant, leaf area index, biomass accumulation and yield for contrasting field environments.

## MATERIAL AND METHODS

Maize seeds (*Zea mays* L., hybrid Dea) were sown in 12 field experiments in North (Grignon) and South (Montpellier) of France under contrasting temperatures, evaporative demands and soil water conditions. Ten plants were tagged at the appearance of leaf 3 and their visible and ligulated leaves were counted every second or third day. The final length and width of each leaf of these plants were measured. In addition, five to eight plants with similar development stages were sampled every second or third day in order to record the number of initiated leaves and the lamina length of all leaves of a plant. Based on these experimental data, the model estimated leaf initiation, appearance, ligulation and the beginning and end of linear expansion rate for each leaf. Responses of leaf elongation rate to meristem temperature, meristem-to-air vapour pressure deficit (VPD) and soil water deficit (predawn leaf water potential) were determined from growth chamber and greenhouse experiments (Ben Haj Salah and Tardieu, 1995; Reymond, 2001; Reymond *et al.*, 2003). Maximum leaf width of each leaf was estimated as a function of leaf position and the width of the widest leaf on the plant. Lamina area was calculated as the product of lamina length by maximal width, corrected by a shape factor of 0.75 (Zhang and Brandle, 1997).

The leaf model was incorporated as a replacement module for canopy leaf development in the APSIM-Maize model of the APSIM platform (Wang *et al.*, 2002; Keating *et al.*, 2003). A new micrometeorological module was added to APSIM to calculate weather data at an hourly time step and estimate environmental conditions as sensed by leaves (meristem temperature, meristem-to-air VPD and predawn leaf water potential).

The ability of the new model to predict biomass accumulation was tested in three field experiments in Gatton (Australia) with the hybrid Hycorn 53 (Pacific Seeds, Toowoomba, Australia) (Lemaire *et al.*, 2007). Leaf, grain and whole-plant biomass were sampled on 10 plants every 3 to 4 weeks. Leaf area index (LAI) was estimated from measurements of leaf weight and specific leaf area on these plants.

## RESULTS AND DISCUSSION

Stable patterns of leaf development were observed over a large range of field conditions. A stable thermal time was required for initiation of successive leaves, their beginning of linear expansion or their emergence from the whorl. The pattern for cessation of elongation and leaf ligulation was more complex, as thermal time required for these processes decreased for leaves growing after floral transition and nullified for the uppermost leaves.

Stable responses of leaf elongation rate were observed for leaf 6 in growth chamber and greenhouse experiments. Leaf elongation rate linearly increased with meristem temperature. When expressed per thermal time unit, the leaf elongation rate linearly decreased with meristem-to-air VPD in well-watered conditions and it linearly decreased with predawn leaf water potential in the absence of evaporative demand during the night, as previously observed in maize (Ben Haj Salah and Tardieu, 1996 and 1997; Reymond *et al.*, 2003). Large effects of evaporative demand and water deficit were also observed on final leaf area in field experiments (observed data points in Fig 1), consistent with effect on elongation rate in controlled conditions.

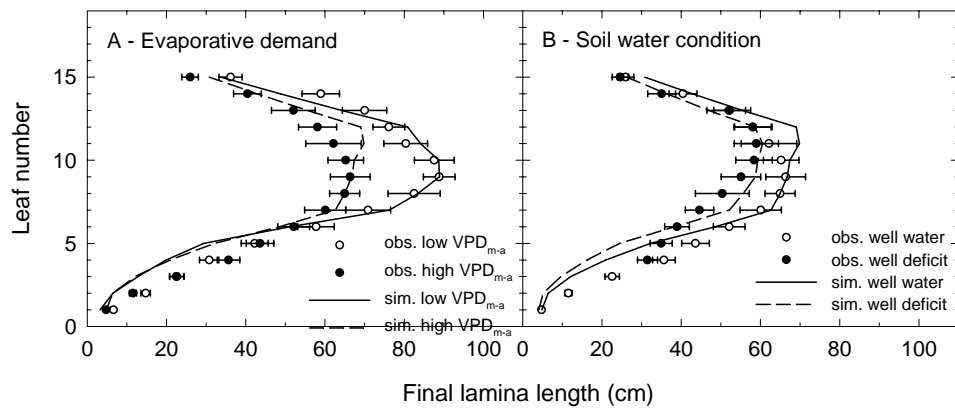


Figure 1. Observed (points) and simulated (lines) final lamina lengths in field plants grown under contrasting evaporative demands (A) and soil water conditions (B). Data for well-watered conditions with meristem-to-air vapour pressure deficit ( $VPD_{m-a}$ ) of 1.1 (○) and 2.6 kPa (●) averaged over the vegetative period (A); well-watered (○) and water deficit (●) conditions (B). Error bars, standard deviations;  $n = 10$ .

The leaf model resulted from a combination between a model that coordinates the development of all leaves of the plant (13 parameters estimated from a single field experiment and data from Andrieu *et al.*, 2006) and a model that predicts leaf 6 elongation rate as affected by environmental conditions (4 parameters estimated from growth chamber and greenhouse experiments). The leaf-coordinating model estimated the beginning and end of linear elongation for all leaves and predicted the variation in leaf elongation rate among leaves of a plant. It thus fixed the time frame of expansion for all leaves, while the leaf growth model simulated the leaf elongation rate as affected by the leaf environmental conditions (meristem temperature, meristem-to-air VPD and predawn leaf water potential) that were estimated using the interface with the APSIM model.

The model was used to predict (with a single set of parameters) the final length of all leaves of a plant in the 12 field experiments carried out in France. Examples of simulations are given for final leaf length of plants grown under contrasting VPD (Fig. 1A) and soil water conditions (Fig. 1B). Effects of changes with time in soil water potential were accurately simulated for reduction in length of individual leaves. Only leaves exposed to water deficit during their development (either hidden in the world or partly emerged) had a reduced final area in the model as in the field experiments. Overall the model adequately simulated the final lamina length for effects of both the environment and leaf position on the stem (for all the tested environments:  $y = 1.018 x$ ,  $r^2 = 0.922$ ,  $CVe = 0.147$ ).

Tests over the crop cycle were performed in the three Australian experiments using a local hybrid. This genotype displayed similar leaf growth than Dea with nevertheless lightly longer lamina for first leaves. Interfacing the leaf model with the crop model APSIM allowed estimation of integrated phenotypes at canopy level. The model adequately predicted leaf area index ( $y = 0.919 x$ ,  $r^2 = 0.619$ ,  $CVe = 0.347$ ), vegetative biomass ( $y = 0.839 x$ ,  $r^2 = 0.955$ ,  $CVe = 0.177$ ) and grain yield ( $y = 0.986 x$ ,  $r^2 = 0.849$ ,  $CVe = 0.432$ ) under well-watered conditions that varied in seasonal temperature and VPD profiles across contrasting sowing dates.

The study presented here shows that it is possible to integrate a leaf growth model with a time scale of hours into a canopy model with a time scale of months. Furthermore the parameters used in the leaf model are stable characteristics of a genotype over a wide range of environments, and can be related to QTL independent of environment (Reymond *et al.*, 2003; Welcker *et al.*, 2007). This study thus opens the way for modeling genetic variability at the whole-plant level under fluctuating conditions and should help in the evaluation of the contribution to yield of QTL for individual leaf traits.

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