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## A hydraulic model of leaf growth in grasses: reconciling old empirical evidence

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### Introduction

Evidence in grasses, among which tall fescue and maize, has demonstrated a clear link between leaf water potential and leaf elongation rates. More specifically, it has been evidenced that leaf growth results from water deposition in the elongation zone, originating from a quite substantial water potential gradient between xylem and the living cells. Martre et al. (2001) showed that the night-time growth-induced water potential gradient exceeded the gradient during light conditions, suggesting a larger driving force for water deposition and hence growth rate, during the night.

Despite this clear link with water potential, the actual mechanism behind plant cell growth, and by extension organ growth, is turgor pressure (Boyer and Silk, 2004). However, an extensive body of research shows that stem and leaf elongation rates can vary substantially, while concomitant turgor in elongation zones can remain constant (Boyer and Silk; 2004). On the other hand, in mature tissues, substantial variations in turgor have been observed, while these tissues are no longer elongating. Martre et al. (1999) show even that turgor pressure in the elongation zone is lower than in the mature zone of tall fescue leaves under night-time conditions.

Although the mechanism of turgor driven cell enlargement is widely accepted, the link between turgor and growth of grass leaves could not yet be demonstrated explicitly, whereas links with water potential are more prominent.

Therefore, we propose a hydraulic based model for grass leaf growth that reconciles insights collected in former studies in such a way that turgor is indeed the driving force for leaf elongation rate, while accommodating different apparent contradictions and empirical findings: (1) night-time turgor in the mature zone is higher than in the elongating zone; (2) variations in turgor in the elongation zone are smaller than in the mature zone; (3) the growth-induced water potential gradient is larger during the night than during the day.

### Materials and Methods

The grass leaf was conceptualised as presented in Durand et al. (1999), with differentiation between division zone (DZ), an elongation only zone (EOZ) and a mature zone (MZ). Within each of these zones, further differentiation was made between the xylem (X) and the mesophyll (M). The leaf was connected to a root compartment, on which older leaves were already present.

Water flow was modelled based on water potential gradients and hydraulic resistances from the soil through the root and leaf xylem towards the mesophyll. Once the leaf emerged from the sheath, transpiration was modelled from the mesophyll in the MZ, via a simple rectangular function with zero transpiration during the night and a fixed value during the day, proportional to the exposed blade tissue.

Leaf hydraulic resistance architecture was designed following Martre et al. (2001), while assuming that root hydraulic conductance was proportional to the total leaf area on the tiller. The link between water potential, turgor pressure and leaf growth was implemented following the concepts of Coussement et al. (2018), in which variations in water content result in reversible and irreversible variations in organ size.

## Results and Discussion

Fig. 1A shows the simulated complete leaf elongation from the initiation until the final size. Using the model three hypotheses were evaluated. Firstly, Fig. 1B shows that night-time turgor in the mature zone is higher than in the elongating zone. Secondly, Fig. 1B shows that variations in turgor in the elongation zone are smaller than in the mature zone. Finally, results presented in Fig. 1C demonstrate that the growth-induced water potential gradient is larger during the night than during the day.

## Conclusions

The model successfully described short-term variations of leaf elongation rate as a function of turgor pressure, while reconciling apparent contradictory empirical evidence. Furthermore, the model included the division zone of a grass leaf, which allowed to simulate realistic long-term leaf growth, primarily based on leaf hydraulics. These insights are crucial for better understanding of the factors that determine grass leaf growth, both in well-watered and in water-limited conditions.

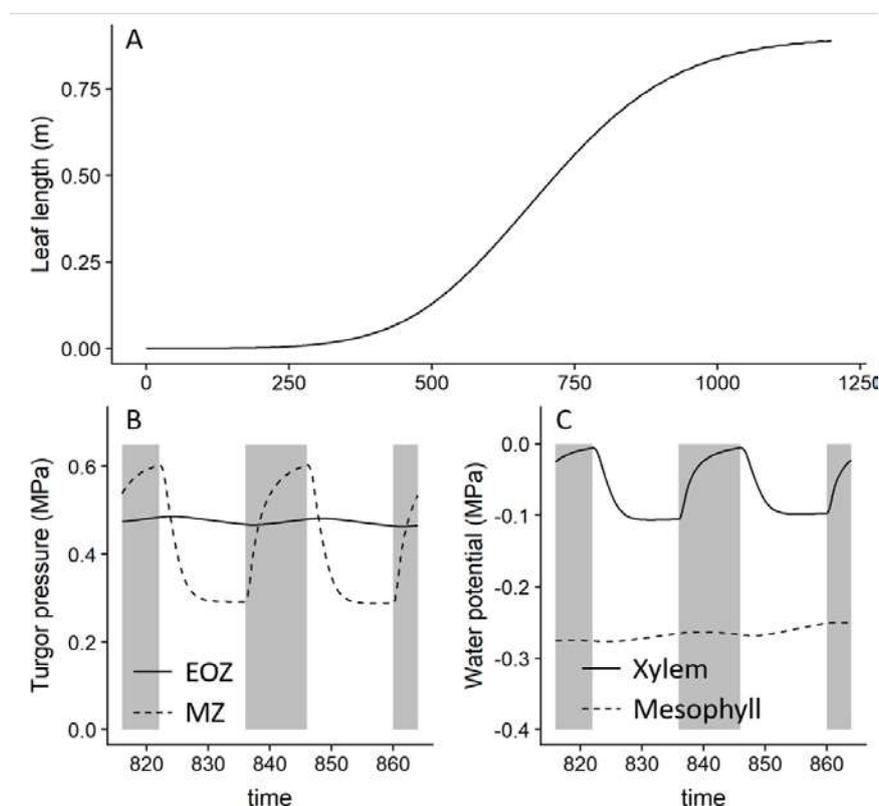


Fig 1: Simulation of (A) Leaf length from initiation to final leaf length as a function of time, in hours, under well-watered conditions; (B) turgor pressure over the 2 days in the elongation zone (EOZ) and the mature zone (MZ); and (C) the water potential in the elongation zone of the xylem and the mesophyll. Grey boxes indicate the night time. Time is expressed in hours.

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