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Decomposing grass leaf elongation rate: hydraulics, visco-elasticity and ontogeny

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Introduction

To increase crop productivity, we need to improve our understanding on how growing organs (sinks) utilize photoassimilates, nutrients and water, and thus we need to better grasp the mechanisms underpinning growth.

In grasses, leaf and tiller initiation and appearance are remarkably coordinated with the onset and cessation of cell division in the leaf meristem. Therefore, the growth kinetics of a specific leaf have important consequences on the development rate of successive leaves and, consequently, on plant and crop productivity. Based on Lockhart's equation (1965), (linear) cell growth has been described as the wall extensibility (ϕ ; in $\text{MPa}^{-1} \text{h}^{-1}$) times the difference between turgor pressure (P ; in MPa) and a threshold for wall yielding (Y ; in MPa):

$$\frac{1}{L} \frac{dL}{dt} = \phi \cdot \max(P - Y, 0)$$

In the growth zone of grasses, turgor has been reported to be rather constant across day and night, and even under progressive drought (Michelena and Boyer, 1982). This low variability in turgor does not map onto the recorded growth dynamics of grass leaves, which show very strong day-night variations and strong effects of withholding water. To explain this mismatch, it has been proposed that ϕ and/or Y should be variable, or that the water potential gradient (and not turgor) is the actual driving force of growth. However, in these analyses, the augmented growth equation by Ortega (1985), which includes elastic effects, is often overlooked. This model describes the 'Maxwell-type' visco-elastic behaviour:

$$\frac{1}{L} \frac{dL}{dt} = \phi \cdot \max(P - Y, 0) + \frac{1}{\varepsilon} \frac{dP}{dt}$$

where the second term is purely elastic, using the elastic modulus (ε ; in MPa).

To improve our understanding of growth, we aim (1) to decompose the short-term dynamics in grass leaf elongation rate into meaningful components, using a model based on hydraulic, visco-elastic and ontogenetic components, (2) to translate insights from short-term dynamics to overall leaf growth, and (3) to infer the impact on the coordination system of grass tillers.

Materials and Methods

We have developed a grass leaf model, parameterized for *Festuca arundinacea*, that scales short-term growth dynamics (minutes-to-hours) to the whole leaf growth period (days-to-weeks). Thereto, the growing leaf is split into four zones, differing in hydraulic, visco-elastic and meristematic properties. Closest to the leaf base, there is the cell division zone (DZ), which is meristematic, highly elastic, a strong sink for carbohydrates and not transpiring, as it is fully enclosed by the sheaths of the leaves on the tiller. Distal to the cell division zone, there is the cell elongation-only zone, where cells have stopped dividing, but are still highly elastic, are elongating, are strong sinks and fully enclosed. In the third zone, cell elongation has stopped, and cells have become less elastic, but are still enclosed and not transpiring. In the fourth zone, cells are mature (and thus no longer growing and less elastic), but are exposed to the atmosphere, and thus transpiring and photosynthesizing. Using the hydraulic architecture presented by Martre et al. (2001) flows of water between connecting zones are modelled according to gradients in water potential. Flows of cells through the different consecutive zones are modelled via the ontogenetic model of Durand et al. (1997). That latter

model has been extended with the functionality of triggering cell division cessation by leaf tip appearance. This growing leaf is inserted on a tiller with three older leaves.

Results and Discussion

Under a day-night regime (Fig. 1A), our simulations show a rather stable growth zone turgor pressure compared to the mature zones turgor (Fig. 1B). The model also allows to decompose grass leaf elongation rate into cell growth and the size of the growth zone components (which results from the newly produced cells via division), but also into the elastic component due to the response of maturing tissue to transpiration (Fig. 1C). This suggests that the actual, irreversible growth rate is masked by substantial elastic dynamics. This may provide a (partial) explanation for the stored growth phenomenon. Because cessation of cell division in the model is triggered by leaf tip emergence from the whorl, leaf growth is enhanced by (artificially) lengthening the pseudostem (Fig. 1D), as has been shown experimentally.

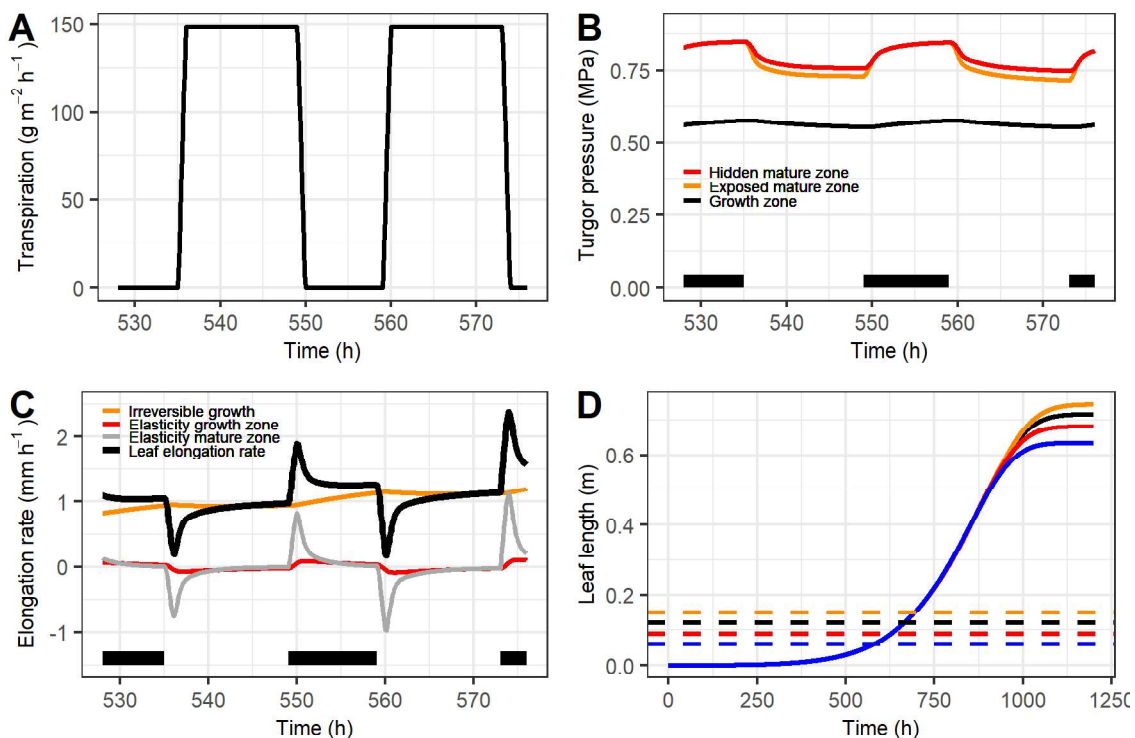


Figure 1: Two-day pattern of the input signal (Transpiration; panel A), turgor pressure simulation in three compartments (panel B), and components of the leaf elongation rate (panel C). Panel D shows the effect of changes in pseudostem length (dashed lines) on the final leaf length.

Conclusion

We provide a hydraulic framework, that predicts constant growth zone turgor, while showing strong day-night dynamics in leaf elongation rate. As such, this model predicted short-term fluctuations in leaf elongation rate without the need for rapid adaptations in cell wall extensibility or turgor threshold, while turgor was still the driver for growth. Furthermore, this model is compatible with the coordination rules in grasses for leaf initiation and appearance, facilitating its inclusion in a full FSPM.

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