

## Simulating the impact of (“long-distance” or “root-to-shoot”) hormonal signaling and non-uniform soil water distribution on plant transpiration

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**Highlights:** In response to non-uniformly distributed soil water, root water uptake and actual (whole plant) transpiration was simulated using R-SWMS as part of the soil dried. These variables varied widely (reduction between 10 and 55 percent) between plants with different controls of stomatal conductance, i.e. controlled by leaf pressure and/or by the concentration of a hormonal signal triggered by low root water potentials in dry soil regions. Hormonal regulation of transpiration was effective only for a limited time, when water flow out of drying soil regions was sufficient to transport hormones to the shoot.

**Keywords:** R-SWMS, hormonal signaling, transpiration reduction, stomatal conductance

### THEORY

Low soil water availability causes most plants to reduce their actual transpiration,  $T_{act}$ , via stomatal closure. Tardieu and Simmoneau [1998] classified stomatal adjustments for several different species and distinguished between isohydric and anisohydric plant types, the first type keeping leaf water pressure  $h_{leaf}$  constant via stomatal closure during drying and the latter type showing decreasing  $h_{leaf}$  for higher transpiration rates and lower soil water contents.

The triggers for stomatal closure that reduce  $T_{act}$  compared with the potential transpiration,  $T_{pot}$  can be driven either by plant hydraulics, hormonal signaling or a combination of both (Equation 1) [Tardieu and Davies, 1993].

$$\alpha = \left( g_{s,min} + (g_{s,max} - g_{s,min}) e^{\beta[signal]e^{\delta h_{Leaf}}} \right) \frac{1}{g_{s,max}} \quad (1)$$

where  $g_{s,min}$  and  $g_{s,max}$  are minimal and maximal stomatal conductances [ $\mu\text{mol cm}^{-2} \text{d}^{-1}$ ], [signal] is the hormone concentration in the leaf [ $\mu\text{mol cm}^{-3}$ ],  $h_{Leaf}$  [cm] is the pressure head in the leaves, and  $\beta$  [ $\text{cm}^3 \mu\text{mol}^{-1}$ ] and  $\delta$  [ $\text{cm}^{-1}$ ] are empirical parameters. The reduction factor  $\alpha$  [-] is the ratio between  $T_{act}$  and  $T_{pot}$  and takes values between 0 and 1.

The most common studied plant hormone that is responsible for stomatal closure is abscisic acid (ABA) [Davies *et al.*, 2005]. As the soil dries, the rate of ABA produced by the roots increases and is proportional to the root water pressure [Simonneau *et al.*, 1998]. It is assumed that the ABA is transported with the xylem water flow towards the leaves to trigger stomatal closure.

### SIMULATIONS

Virtual experiments were simulated using R-SWMS, which describes the water flow in the soil, towards, and in the 3-D network of roots mechanistically and based on basic laws of fluid dynamics [Javaux *et al.*, 2008]. This model simulates the soil, root, and leaf water pressure heads. To model the hormonal signal concentrations in the leaf, [signal], a transport equation in the root network with signal mass production rate at the root tips,  $M_{signal}$  [ $\mu\text{mol d}^{-1}$ ], and advection terms in the root xylem segments that are derived from the flow equation was solved using a particle tracking algorithm.  $M_{signal}$  is a function of the pressure head at the root tips,  $h_{root}$  (Eq. 2).

$$M_{signal} = \begin{cases} 0 & \text{for } |h_{Root}| < |h_0| \\ a h_{Root} - b & \text{for } |h_{Root}| \geq |h_0| \end{cases} \quad (2)$$

where  $a$  [ $\mu\text{mol cm}^{-1} \text{d}^{-1}$ ] and  $b$  [ $\mu\text{mol d}^{-1}$ ] are production factors and  $h_0$  is a threshold potential that triggers the signal production. The particle tracking algorithm simulates the mass flux of the signal at the root collar

which is divided by the transpiration stream to obtain the signal concentration in the leaf. The signal concentration may also be calculated by assuming that all produced signal arrives instantaneously at the root collar by dividing the sum of the signal production rates at the root tips by the transpiration stream (Eq. 3)

$$[signal] = \frac{\sum M_{signal}}{T_{act}} \quad (3)$$

Stomatal conductance is not modeled explicitly but as a reduction factor (varying between 0 and 1) for  $T_{pot}$  using Equation 1.

Simulations were conducted in a virtual split root setup in a soil domain of 15.5 cm depth and 21 cm<sup>2</sup> soil surface with a top soil boundary condition (irrigation) of 10 cm<sup>3</sup>d<sup>-1</sup> and an upper root boundary condition ( $T_{pot}$ ) of 9.9 cm<sup>3</sup>d<sup>-1</sup>. Initial soil water content was uniformly distributed over depth. The irrigation was uniform over the total soil domain for the first 5 days. Then the same irrigation rate was applied only to one side of the soil domain. Hence only the water distribution changed; the plants had always sufficient water to maintain  $T_{pot}$ .

Five different cases were compared (Table 1). For the first case, denoted as '**PH (pressure head)**', the upper root boundary condition ( $h_{leaf}$ ) cannot be lower than a critical water potential  $h_{crit}$ . If  $h_{leaf}$  reaches  $h_{crit}$  the type of the upper boundary condition is switched from flow to constant water potential. For '**Signal**',  $T_{act}$  is calculated with Equation 1 and  $\delta$  zero so that the leaf water pressure has no influence on stomatal closure. For '**PH+Signal**' also the influence of  $h_{leaf}$  on stomatal conductance is considered. To compare the impact of signal transport towards the leaf '**PH+Signal**' is also calculated assuming an instantaneous signal without simulating transport ('**PH+Sign inst.**'). Those four cases are compared with '**No Regulation**', where stomata remain fully open.

Table 1. Model parameters\*

	<b>PH</b>	<b>Signal</b>	<b>PH+Signal</b>
$ \psi_{crit} $	-7100	-	-
$\beta$	-	$1 \cdot 10^{-3}$	$1 \cdot 10^{-3}$
$\delta$	-	0	$1 \cdot 10^{-5}$
<b>a</b>	-	$1.5 \cdot 10^{-4}$	$1.5 \cdot 10^{-4}$
<b>b</b>	-	1.065	1.065
$ \psi_0 $	-	-7100	-7100

\* Orders of magnitude from *Tardieu and Davies* [1993]

## RESULTS AND DISCUSSION

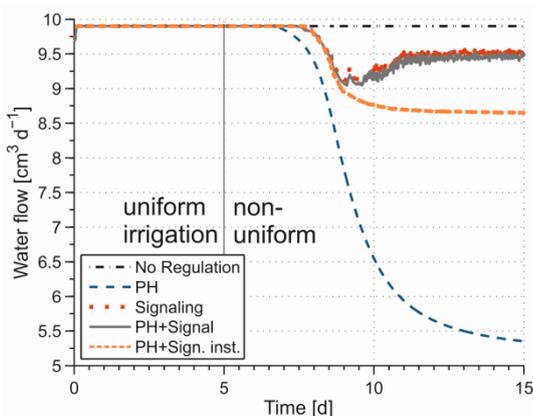


Fig. 1. Comparison of actual (whole plant) transpiration rate for the five different cases

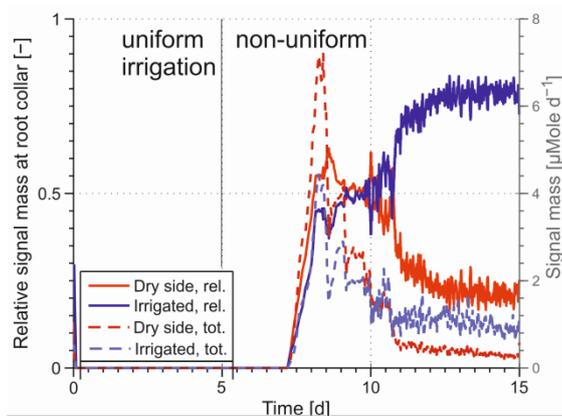


Fig. 2. Rates of signal mass arriving at the root collar and originating from the dry and irrigated side for PH+Signal case: left axis; relative signal mass rates normalized by the total signal mass rates, right axis: absolute signal mass rates.

Figure 1 shows that the onset of transpiration reduction is earlier for the purely hydraulic regulation ('PH'). Transpiration for the signaling cases with transport first decreases but start to increase around day 9. This seems counter-intuitive as the stress for the drying part of the soil system is still increasing. Through comparison with the 'PH+Sign.inst.' case, this effect can be related to particle transport. Initially the relative signal mass (solid lines in Figure 2) arriving at the root collar from the dry side is higher than that arriving from the wet side. But around day 9 the ratios change and about 75% of the signal arriving at the leaves originates from the irrigated part of the root system. After four days of drying there is no more water uptake from the dry soil part. Therefore the water velocity inside the dry roots is close to zero so that produced signal is not transported anymore. This leads to a distinct maximum in the signal concentration when plotted versus water content in the dry soil compartment (Figure 3). This behavior was reported previously in plants exposed to partial [Dodd *et al.*, 2008, Figure 5] or alternated root zone soil drying [Stoll *et al.*, 2000].

However, the relation between leaf signal concentration and root zone water content is expected to depend on the soil water distribution. Due to internal water redistribution within the plant from deeper roots located in wet soil, flow velocities might not reach zero even in some very dry parts of the root system. Also the diurnal dynamics of the transpiration rates were not considered in the simulation. During the night when transpiration is diminished, water can redistribute within the root system (according to plant water potential gradients), increasing signal transport in the morning when stomata re-open and the redistributed water is transported from dry root zones to the shoot. Simulations using R-SWMS to evaluate these effects are currently being carried out.

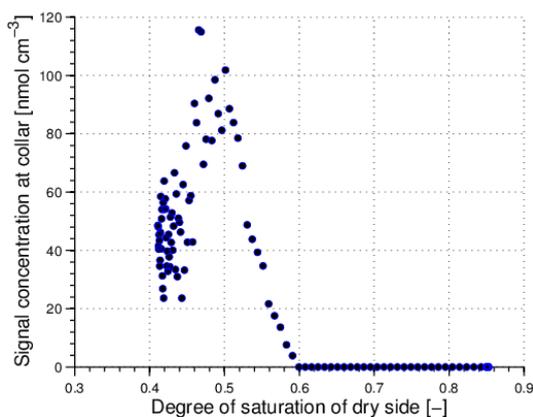


Fig. 3. Relationship between hormone concentration arriving in the leaves and soil water content of the drying part of the soil domain

#### LITERATURE CITED

- Davies, W. J., G. Kudoyarova, and W. Hartung 2005. Long-distance ABA signaling and its relation to other signaling pathways in the detection of soil drying and the mediation of the plant's response to drought, *Journal of Plant Growth Regulation*, **24**(4), 285-295.
- Dodd, I. C., G. Egea, and W. J. Davies 2008, Abscisic acid signalling when soil moisture is heterogeneous: decreased photoperiod sap flow from drying roots limits abscisic acid export to the shoots, *Plant Cell Environ.*, **31**(9), 1263-1274.
- Javaux, M., T. Schröder, J. Vanderborght, and H. Vereecken 2008. Use of a Three-Dimensional Detailed Modeling Approach for Predicting Root Water Uptake, *Vadose Zone Journal*, **7**(3), 1079-1079.
- Simonneau, T., P. Barrieu, and F. Tardieu 1998, Accumulation rate of ABA in detached maize roots correlates with root water potential regardless of age and branching order, *Plant Cell Environ.*, **21**(11), 1113-1122.
- Stoll, M., B. Loveys, and P. Dry (2000), Hormonal changes induced by partial rootzone drying of irrigated grapevine, *Journal of Experimental Botany*, **51**(350), 1627-1634.
- Tardieu, F., and W. J. Davies 1993., Integration of Hydraulic and Chemical Signaling in the Control of Stomatal Conductance and Water Status of Droughted Plants, *Plant Cell Environ.*, **16**(4), 341-349.
- Tardieu, F., and T. Simonneau 1998, Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours, *Journal of Experimental Botany*, **49**, 419-432.

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