

Spatial and temporal variability of leaf gas exchange and temperature responses of apple trees to drought assessed by a 3D turbid medium model

Jérôme Ngao^{1,2}, Boris Adam^{1,2}, Marie Charreyron^{1,2} and Marc Saudreau^{1,2}
¹INRA, UMR 547 PIAF, F-63100 Clermont-Ferrand, France, ²UBP, UMR547 PIAF, F- 63000 Aubière, France

*correspondence: jerome.ngao@clermont.inra.fr

Highlights: Drought stress alters tree carbon and water balance, and it could affect pest and disease development as affected by changes in microclimate. Spatial and temporal variability of leaf gas exchange and microclimate (through leaf temperature) were assessed by adapting a 3D turbid medium model to drought stress and comparing model outputs to drought experiments.

Keywords: canopy microclimate, drought, leaf nitrogen, RATP model, stomatal conductance, transpiration

INTRODUCTION

Tree 3D-structure induces environmental and physiological gradients, which have to be taken into account for understanding the acclimation of various plant processes such as photosynthetic assimilation (A_{net}), stomatal conductance (g_s) and leaf transpiration (TR) to the main driving factors, particularly intra-canopy microclimate. Modelling such variability is also a prerequisite for upscaling to the whole plant or population. Numerous studies have investigated the acclimation of g_s and A_{net} to local light interception (Hollinger 1996; Leuning et al. 1991). Spatial variability of A_{net} has been shown to be tightly related to that of light interception *via* leaf nitrogen distribution expressed per surface area (N_a , Thornley 2004). Characterization of the spatial distribution of g_s within the canopy has been done generally to relate it with hydraulic traits (Sperry et al., 2008), or to A_{net} (Prieto et al. 2012). Another consequence of the canopy light gradient is the spatial variability of the energy balance, particularly that of the latent heat (determined by g_s) and the sensible heat (leaf temperature, T_{leaf}) terms (Monteith and Unsworth 1990). Thus g_s may allow assessing and modelling spatial variability of T_{leaf} , which is an agronomic challenge in fruit tree species as the development of numerous pests are temperature-dependent.

The effects of summer drought on A_{net} , TR and g_s have been widely studied, and various models have been proposed (Damour et al. 2010). However, intra-canopy variability of such responses has received much less attention than temporal dynamics. One major difficulty lies on the tools available for assessing both the processes of interest (light interception, carbon assimilation, etc.) and their spatial distribution in a realistic way (Niinemets, 2012). Moreover, there are still very few models able to simulate T_{leaf} spatially distributed, and include leaf functions together with A_{net} and g_s .

The RATP model (Sinoquet et al., 2001) allows simulating (i) the radiation intercepted by the crown foliage, (ii) leaf temperature (T_{leaf}) and g_s as outputs of the energy balance, and (iii) A_{net} and TR (Fig. 1). It considers the canopy 3D structure by discretizing the crown foliage into voxels as turbid media, and thus allowing simulation of A_{net} and TR at both canopy level and voxel levels. This model has been applied for various aims, for example assessing the foliage randomness (Sinoquet et al., 2005), simulating the thermal microclimate and its effect on leaf miner development (Pincebourde et al., 2007), and disentangling structural and functional effects on TR and A_{net} (Massonnet et al., 2008). But until now, the RATP model relied on optimal water conditions, as the Jarvis g_s submodel (Jarvis, 1976) did not simulate the response to water potential, thus the model was not adapted to drought conditions.

Our aim was to assess spatial variability, and its temporal evolution, of transpiration, stomatal conductance and temperature responses of young apple trees to drought (*Malus pumila* Mill., var. Delbard Jubilé®). We adapted the RATP model to drought by adding a response function to soil water content in the Jarvis sub-model. We tested the TR outputs (TR_{RATP}) against xylem sapflow measurements as proxy values of total tree canopy transpiration (TR_{sap}) during drought experiments.

MODEL DEVELOPMENT AND PARAMETRIZATION

The g_s submodel as formulated by Jarvis (1976) was first parameterized for the photosynthetically active radiation (PAR), T_{leaf} , and vapour pressure deficit (VPD) response functions in optimal irrigation conditions.

Then during a two-week-long drought period, g_s was measured at different dates during which the PAR , T_{leaf} and VPD values were concurrently measured. The residuals between g_s simulated with the measured microclimatic variables and actual g_s , were linearly related to normalized soil water content. This linear relationship was added in the Jarvis subroutine.

For the foliage structure, only leafy shoots were digitized, and individual leaves were reconstructed by allometric relationships (Sonohat et al., 2006). Computations of transpiration and leaf temperature were performed at a 30-min time step according to the meteorological dataset. The model has been implemented in RATP and integrated into the OpenAlea plant modelling platform (Pradal et al., 2008)

RESULTS AND DISCUSSION

The temporal evolution of TR_{sap} prior the drought was mostly well reproduced by the model. TR_{sap} decreased dramatically eight days after the start of the water shortage and remained very low for several days after the end of the drought (Fig. 2). Driven by soil water content input data, simulated TR_{RATP} decreased dramatically six days after the start of the water shortage. The temporal shift between the TR_{sap} measurements and TR_{RATP} simulations may be attributed to the buffering effect of tree hydraulic capacitance (Sperry et al., 2008), which should be included in the response function, but not represented as input or intermediate data. Furthermore, while TR_{RATP} increased rapidly after irrigation restart, TR_{sap} for unharmed trees remained at very low level, and increased regularly up to five days after restarting irrigation, despite a very fast recovery of g_s . This could be explained by xylem embolism which may have developed during the drought period and decreased the sap flow rate (Cruiziat et al., 2002). Even if g_s recovered quickly to pre-drought levels, xylem vessels have to be refilled by water, but the involved mechanisms are still discussed (Nardini et al., 2011).

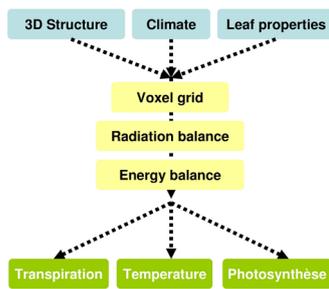


Fig. 1. Main features of the RATP model. The blue boxes are the input data, the main computation processes are in the yellow boxes and the outputs are in the green boxes. Each calculation step is done for each voxel at a 30-min time-step.

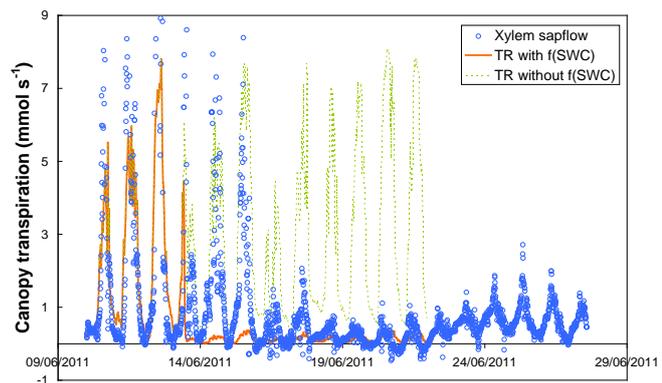


Fig. 2. Temporal course of canopy transpiration (i) as measured by xylem sapflow measurements (blue circles), (ii) as simulated by taking into account soil water shortage (orange lines) or not (green broken lines). The water shortage started on June 7, 2011. The simulations were stopped after June 22 as visible damages on the leaf crown were observed.

As expected, there was a large variability in TR_{RATP} values (Fig. 3a) when the trees experienced optimal irrigation conditions. At the end of the drought experiment, TR_{RATP} values were very low and varied in a very narrow range (Fig. 3b). Further simulations will allow determining the degree of heterogeneity of TR decrease during drought.

On the other hand, the mean T_{leaf} varied temporally according to the air temperature. Moreover, the T_{leaf} range under optimal water conditions varied at the diel scale up to 4°C (Fig. 4a), and according to air temperature. But when both simulations and measurements values of TR were very low, typically at the end of the drought period, the diel range of T_{leaf} decreased, averaging $\approx 2.5^\circ\text{C}$, even if the mean air temperature increased (Fig. 4b). This is in good agreement with measurements done on almond trees under drought by Gonzalez-Dugo et al. (2012).

Among the model parameters, the leaf nitrogen content expressed per area unit (N_a) had an important influence in the simulation outputs. In RATP, N_a drives the maximal g_s (g_{Smax}) which is degraded by the response functions of the Jarvis submodel. Leroux et al (1999) found a linear relationship between the daily cumulated PAR averaged over several days and N_a , allowing a fixed distribution of N_a within the canopy

Prieto et al. (2012) showed that N_a varied over the growing seasons in grapevines. This implies that seasonal changes in N_a distribution within the canopy have to be taken into account, as well its relationship with g_{Smax} for which Leroux et al. (1999) showed seasonal differences.

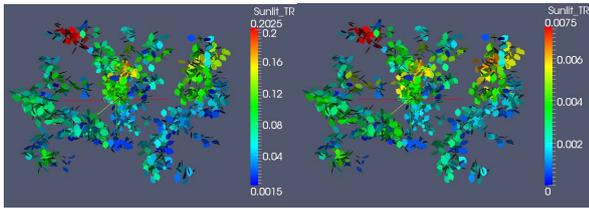


Fig. 3. Example of spatial distribution of sunlit leaf transpiration (a) on June 5th (optimal soil water content) and (b) on June 21st (end of the drought period). Both pictures display transpiration values at 12:00.

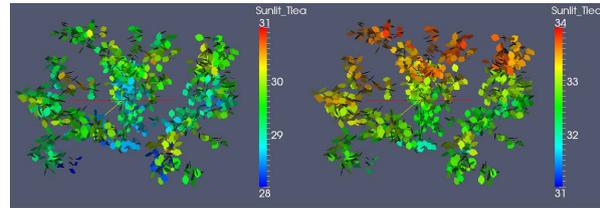


Fig. 4. Example of spatial distribution of sunlit leaf temperature (a) on June 5th (optimal soil water content) and (b) on June 21st (end of the drought period). Both pictures display transpiration values at 12:00.

LITERATURE CITED

- Cruziat P, Cochard H, Ameglio T. 2002.** Hydraulic architecture of trees: main concepts and results. *Annals of Forest Science* **59**:723-752.
- Damour G, Simonneau T, Cochard H, Urban L. 2010.** An overview of models of stomatal conductance at the leaf level. *Plant, Cell & Environment* **33**:1419–1438.
- Gonzalez-Dugo V, Zarco-Tejada P, Berni JAJ, Suarez L, Goldhamer D, Fereres E. 2012.** Almond tree canopy temperature reveals intra-crown variability that is water stress-dependent. *Agricultural and Forest Meteorology* **154**:156-165.
- Hollinger DY. 1996.** Optimality and nitrogen allocation in a tree canopy. *Tree Physiology* **16**:627-634.
- Jarvis PG. 1976.** The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Philosophical Transactions of the Royal Society B* **273**:593–610.
- Le Roux X, Sinoquet H, Vandame M. 1999.** Spatial distribution of leaf dry weight per area and leaf nitrogen concentration in relation to local radiation regime within an isolated tree crown. *Tree Physiology* **19**: 181-188.
- Leuning R, Wang YP, Cromer RN. 1991.** Model simulations of spatial distributions and daily totals of photosynthesis in *eucalyptus-grandis* canopies. *Oecologia* **88**:494-503.
- Massonnet C, Regnard JL, Lauri PE, Costes E, Sinoquet H. 2008.** Contributions of foliage distribution and leaf functions to light interception, transpiration and photosynthetic capacities in two apple cultivars at branch and tree scales. *Tree Physiology* **28**:665–678.
- Monteith JL, Unsworth MH. 1990.** Principles of Environmental Physics. Edward Arnold, London, p.291.
- Nardini A, Lo Gullo MA, Salleo S. 2011.** Refilling embolized xylem conduits: Is it a matter of phloem unloading? *Plant Science* **180**:604-611.
- Niinemets Ü. 2012.** Optimization of foliage photosynthetic capacity in tree canopies: towards identifying missing constraints. *Tree physiology* **32**:505-509.
- Pincebourde S, Sinoquet H, Combes D, Casas J. 2007.** Regional climate modulates the canopy mosaic of favourable and risky microclimates for insects. *Journal of Animal Ecology* **76**:424-438.
- Pradal C, Dufour-Kowalski S, Boudon F, Fournier C, Godin C. 2008.** OpenAlea: a visual programming and component-based software platform for plant modelling. *Functional Plant Biology* **35**:751-760.
- Prieto JA, Louarn G, Pena JP, Ojeda H, Simonneau T, Lebon E. 2012.** A leaf gas exchange model that accounts for intra-canopy variability by considering leaf nitrogen content and local acclimation to radiation in grapevine (*Vitis vinifera* L.). *Plant Cell & Environment* **35**:1313-1328.
- Sinoquet H, Le Roux X, Adam B, Ameglio T, Daudet FA. 2001.** RATP: a model for simulating the spatial distribution of radiation absorption, transpiration and photosynthesis within canopies: application to an isolated tree crown. *Plant Cell & Environment* **24**:395-406.
- Sinoquet H, Sonohat G, Phattaralerphong J, Godin C. 2005.** Foliage randomness and light interception in 3-D digitized trees: an analysis from multiscale discretization of the canopy. *Plant Cell & Environment* **28**:1158-1170.
- Sonohat G, Sinoquet H, Kulandaivelu V, Combes D, Lescourret F. 2006.** Three-dimensional reconstruction of partially 3D-digitized peach tree canopies. *Tree physiology* **26**:337-351.
- Sperry JS, Meinzer FC, McCulloh KA. 2008.** Safety and efficiency conflicts in hydraulic architecture: scaling from tissues to trees. *Plant Cell & Environment* **31**:632-645.
- Thornley JHM. 2004.** Acclimation of photosynthesis to light and canopy nitrogen distribution: an interpretation. *Annals of Botany* **93**:473-475.