



## Modelling of root ABA synthesis, stomatal conductance, transpiration and potato production under water saving irrigation regimes

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### ABSTRACT

Application of water saving irrigation strategies in agriculture has become increasingly important. Both modelling and experimental work are needed to gain more insights into the biological and physical mechanisms in the soil–plant system, which regulates water flow in the system and plays a central role in reducing crop transpiration. This paper presented a mechanistic model (Daisy) developed based on data obtained in the SAFIR project on measured leaf gas exchange and soil water dynamics in irrigated potato crops grown in a semi-field environment subjected to different irrigation regimes. Experimental data was compared to simulated results from the new enhanced Daisy model which include modelling 2D soil water flow, abscisic acid (ABA) signalling and its effect on stomatal conductance and hence on transpiration and assimilation, and finally crop yield. The results demonstrated that the enhanced Daisy model is capable of simulating the mechanisms underlying the water saving effects of the partial root-zone drying (PRD) irrigation as compared with the conventional full irrigation (FI). However the simulated effect on both crop yield and water use in this particular experiment was negligible indicating more experimental studies are necessary in order to improve on the model.

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### 1. Introduction

Irrigated agriculture is the biggest consumer of available fresh-water resources and accounts for about 70% of the total water withdrawals and 60–80% of total consumptive water use (Huffaker and Hamilton, 2007). It has been estimated that in order to produce enough food for eight billion people by 2025, the irrigated area must expand more than 20% and at the same time the irrigated crop yields should improve 40% above the current level (Lascano and Sojka, 2007). This dramatic demand in agricultural production calls for developing novel irrigation strategies to utilize the current available water resources more efficiently (English, 1990; Geerts and Raes, 2009; Strzepek and Boehlert, 2010). Application of advanced irrigation techniques like drip irrigation and adoption of water-saving irrigation strategies (Jensen et al., 2010), as well as breeding towards crops with high water use efficiency are potential approaches achieving this goal. Sub-surface drip irrigation can be applied as deficit (DI) and regulated deficit irrigation

(RDI) and as partial rootzone drying (PRD) irrigation, a new method, which has been demonstrated to increase product quality and allow considerable water savings—in some cases almost a doubling of irrigation water-use-efficiency (Davies and Hartung, 2004; Liu et al., 2006). Early split-pot experiments have suggested a mechanism for this, namely generation of ABA in the drying roots, which acts as a root-to-shoot chemical signal inducing stomatal closure (Davies and Zhang, 1991). The stomatal conductance is a crucial factor controlling both photosynthesis and transpiration of the plants, and therefore to the whole energy balance in the soil–plant–atmosphere-continuum. In order to explore the mechanistic effects of abscisic acid (ABA) signalling on plant water use and yield at a field scale, the SAFIR project has extended the agro-ecological model Daisy (Hansen et al., 1991; Abrahamsen and Hansen, 2000) with a new integrated framework for predicting stomatal conductance, transpiration and crop production.

The original Daisy is a 1D Soil–Plant–Atmosphere system model designed to simulate water balance, heat balance, solute balance and crop production in agro-ecosystems subjected to various management strategies. The water balance model comprises a surface water balance and a soil water balance. The surface water balance model includes a model for snow accumulation and melting, a model for interception, through-fall, and evaporation of water

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in the crop canopy, and a model for infiltration and surface runoff. The soil water balance model includes water flow in the soil matrix (based on a numerical solution to Richards's equation) as well as in macropores. In addition, it includes water uptake by plants and water drainage to pipe drain. The solute balance model simulates transport, sorption and transformation processes. Special emphasis is put on nitrogen dynamics in agro-ecosystems. Mineralization–immobilization, nitrification and denitrification, sorption of ammonium, root uptake of nitrate and ammonium, and leaching of nitrate and ammonium are simulated. The crop production model simulates plant growth and development, including the accumulation of dry matter and nitrogen in different plant parts. Furthermore, the development of leaf area index and the distribution of root and root density are also simulated.

The functionality of the original Daisy model has been extensively tested in a wide range of applications (Svendsen et al., 1995; Petersen et al., 1995; Müller et al., 1997; Jensen et al., 1997; Djurhuus et al., 1999; Van der Keur et al., 2001; Boegh et al., 2004, 2009; Heidmann et al., 2008; Gjettermann et al., 2008). The new extended version of Daisy has preserved the well tested functionality of the previous version.

The present study presents the extension of the Daisy model based on data obtained from a semi-field experiment with potatoes subjected to different subsurface drip irrigation regimes. The objective was to develop new sub-models which are capable of simulating 2D soil water dynamics, ABA signalling, leaf gas exchange, and crop yield. The simulated results were compared with the observed values from the field experiments. Perspectives of the models and its limitations are discussed and further investigations for improving the performance of the developed models are suggested.

## 2. Theory and model description

The extension to the existing Daisy model comprises:

1. An extension of the transport processes in the soil (water, solutes and heat) from 1D to 2D.
2. A stomatal conductance model that takes the effect of the ABA signalling into account.
3. A model for generating ABA in the root system and transportation of the ABA to the leaves.
4. A soil–vegetation–atmosphere transfer (SVAT) model.

### 2.1. Soil water model

Soil water dynamics is simulated by a numeric solution (finite volume technique) to Richards equation:

$$\frac{\partial \theta(h_p)}{\partial t} = \frac{\partial}{\partial x} \left[ k_{xx}(h_p) \frac{\partial h_p}{\partial x} \right] + \frac{\partial}{\partial z} \left[ k_{zz}(h_p) \frac{\partial h_p}{\partial z} + 1 \right] - S \quad (1)$$

where  $\theta(h_p)$  is volumetric soil water content at the head  $h_p$  and  $S$  is water uptake by plants.  $k_{xx}(h_p)$  and  $k_{zz}(h_p)$  are the hydraulic conductivity in the  $x$ -direction and  $z$ -direction, respectively. The model for the water uptake of plants uses the functionality in the 1D Daisy. This model is based on the single root concept, hence the water uptake model requires information on the root length density distribution and the driving force is the crown potential (see Hansen et al., 1991 or Hansen and Abrahamsen, 2009).

### 2.2. Stomatal conductance model

Stomatal conductance ( $g_s$ ) is an important factor for both transpiration and photosynthesis. Daisy allows for the implementation of several models for calculating  $g_s$ .

The Ball–Berry stomatal conductance model (Ball et al., 1987; Collatz et al., 1991) describes the stomatal conductance as a function of the net  $\text{CO}_2$  assimilation rate ( $A_n$ ). Therefore, it is customary to combine the Ball–Berry model with a biochemical model of photosynthesis (Farquhar et al., 1980). We have implemented a photosynthesis model based on the model of de Pury and Farquhar (1997). The model of de Pury and Farquhar (1997) is a single-layer model which considers the sunlit and shaded leaves separately. We have divided canopy in several layers and the cumulative absorbed photosynthetic active radiation (PAR) (from the top to the bottom of the canopy) in the model was applied for each canopy layer. Next, the net  $\text{CO}_2$  assimilation rate ( $A_n$ ) of shaded and sunlit leaves was calculated for the whole canopy.

We have implemented the Ball–Berry stomatal conductance model adjusted for drought stress, both based on hydraulic signalling (crown water potential,  $\psi_c$ ) and chemical signalling (xylem ABA concentration,  $c_{ABA}$ ):

$$g_s^{\text{CO}_2} = mA_n \frac{h_s}{c_s} e^{-\beta(c_{ABA} - c_{ABA}^{\min})} e^{-\delta|\psi_c|} + g_{s0}^{\text{CO}_2} \quad (2)$$

where  $g_s^{\text{CO}_2}$  is stomatal conductance [ $\text{mol m}^{-2} \text{s}^{-1}$ ],  $A_n$  is the net  $\text{CO}_2$  assimilation rate [ $\text{mol m}^{-2} \text{s}^{-1}$ ],  $c_s$  is the leaf surface  $\text{CO}_2$  concentration,  $h_s$  is the relative humidity at the leaf surface,  $c_{ABA}$  is the ABA concentration in the xylem sap [ $\text{ng cm}^{-3}$ ],  $c_{ABA}^{\min}$  is the minimum ABA concentration in the xylem sap [ $\text{ng cm}^{-3}$ ],  $\psi_c$  is the crown water potential [MPa],  $g_{s0}^{\text{CO}_2}$  is the stomatal conductance as  $A_n \rightarrow 0$  when  $\text{PAR} \rightarrow 0$ ,  $m$ ,  $\beta$  and  $\delta$  are empirical constants. The exponential form of the influence of leaf water potential and xylem ABA concentration was suggested by Tardieu (1993). With  $\delta=0$  Eq. (2) becomes equal to the equation proposed by Gutschick and Simonneau (2002), and with both  $\delta=0$  and  $\beta=0$  it becomes equivalent to the original Ball–Berry model (Ball et al., 1987).

The unit of stomatal conductance, i.e.  $\text{mol m}^{-2} \text{s}^{-1}$ , can be converted to [m/s] by:

$$g_{s,i}^{\text{CO}_2} = \frac{RT}{P_{\text{surf}}} g_{s,i}^{\text{CO}_2} \quad (3)$$

where  $R$  is the gas constant ( $8.314 \text{ J mol}^{-1} \text{ K}^{-1}$ ),  $T$  is temperature [K] and  $P_{\text{surf}}$  is atmospheric pressure [Pa]. Up-scaling from leaf to canopy yields the stomatal conductance for water vapor:

$$g_s^w = \begin{cases} 2(D_w/D_C) \sum_i^{n_{LAI}} \Delta L_{ai} g_{s,i}^{\text{CO}_2} & \text{hypostomatous leaves} \\ (D_w/D_C) \sum_i^{n_{LAI}} \Delta L_{ai} g_{s,i}^{\text{CO}_2} & \text{amphistomatous leaves} \end{cases} \quad (4)$$

where  $D_w$  is the diffusion coefficient of water vapour (see Appendix C),  $D_C$  is the diffusion coefficient of  $\text{CO}_2$ ,  $n_{LAI}$  is the number of leaf layers and  $\Delta L_{ai}$  is the size of the leaf layer.

### 2.3. ABA generation in the root system and transport of the ABA to the leaves

It is assumed that ABA is generated in the root tips in response to soil drying and is transported to the leaves through the xylem system with the transpiration stream. In addition, it is assumed that the ABA concentration in the leaf apoplast is identical to the ABA concentration in the xylem sap. Storage, degradation, and transportation time were ignored. The ABA production in the roots is assumed to be a function of the water potential in the soil surrounding the roots. Since the soil water potential varies within the root zone, the ABA concentration in the xylem  $c_{ABA}$  [ $\text{ng cm}^{-3}$ ] is

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