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Modelling water use and carbon assimilation of vineyards with different canopy structures and varietal strategies during water deficit

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Abstract

A model of carbon assimilation and water use for grapevines based in part on mechanistic and empirical relationships linking single leaf responses to environmental variables such as soil water availability (through pre-dawn water potential), temperature, photon flux density (PFD), and relative humidity (via stomatal coupling) was developed based on field data sets from varieties growing over a large climatic transect across Europe. Stomatal coupling to photosynthesis was modelled using the approach of Ball, Woodrow, Berry (1987) which includes variety dependent changes in the stomatal sensitivity factor during drought stress. The geometric model of Riou et al. (1989) was used as a base to describe canopy structure in which leaves are allocated to 8 distinct canopy zones and are classified according to age (using the plastochron concept), and light environment (sunlit or shaded). Leaf area development is temperature driven and coupled to changes in canopy dimensions. The model has been validated using data sets from single leaf – and whole vine gas-exchange and transpiration (sap flow) measurements. Based on historic meteorological data and estimations of soil water status, total plant carbon acquisition was simulated for entire seasons (1961-1998) and compared reasonably with actual measured values of yield and sugar concentration.

Introduction

The geometrical structure of a plant canopy determines its interaction with fluxes of energy. Canopy architecture and density are intimately related to crop productivity since the distribution of leaf and non-leaf surfaces influences light interception and subsequent carbon assimilation and water loss. This has been widely recognized for fruit and grape production (i.e. Wagenmakers 1991, Dokoozlian and Kliewer 1995). Since the large spatial and temporal variations in the radiation regime in different locations of a canopy are difficult to measure, simulation models have become the main tool to integrate the activities of individual leaves and their responses to the natural environment and to evaluate the performance of various plant canopy forms. In most models a scale-up approach from the leaves to the canopy is used (i.e. Caldwell et al. 1986, Harley and Baldocchi 1995, Beyschlag and Rye 1998) with more or less complex descriptions of canopy form and leaf area distribution (i.e. Wang and Jarvis 1990, Tenhunen et al. 1989). Since grapes are grown in a multitude

of different canopy systems across the world, they represent an ideal tool to address the problem of modelling whole vineyard gas-exchange as influenced by canopy structure. In one attempt, the distribution of surfaces (leaves, shoots, fruit) in space has been modelled for two different grapevine canopies (Schultz 1995) using a two-dimensional beta function (Wang and Jarvis 1990). However, the data set required to develop such a model is very complex and difficult to obtain and a simpler approach using a geometrical model may be more adequate (Riou et al. 1989).

Apart from the role in light interception, CO₂ acquisition and water loss, canopy structure mediates whole-plant responses to environmental stresses such as water deficit or high light (or both) (Tenhunen et al. 1990, Werner et al. 2001). Werner et al. (2001) showed that the extent of photoinhibition in oak was strongly dependent on structural parameters of the canopy, such as leaf area index (LAI) and leaf angle. For grapevines, which are grown over a large climatic transect from cool temperate through the dry mediterranean-type climates to the tropics, environmental stresses such as water shortage are a frequent constraint. The type and the velocity of physiological responses to this shortage under field conditions seems to be variety dependent (Chaves et al. 1987, Schultz 1998, Escalona et al. 1999). Our objectives were therefore to develop a model on grapevine gas-exchange capable of integrating effects of canopy structure as well as varietal responses to water deficit.

Material and methods

Radiation model and canopy structure

The canopy radiation and structure model of Riou et al. (1989) was adapted for modelling light interception of- and light distribution within the canopy (Schultz et al. 1997). The model assumes that the geometrical shape of the canopy resembles a hedgerow, thus the trans-section is rectangular. The 2 vertical canopy sides have a certain porosity (or gap fraction) (Po, %) which allows light not intercepted by the foliage to pass through the canopy, where it may be intercepted by a neighbouring row or the soil, depending on solar angle. The horizontal part of the canopy is non-porous by definition. Changes in canopy dimensions and leaf area within the geometrical envelope, i.e. canopy height (H, m), canopy width (L, m), and canopy porosity are modelled as a function of accumulated heat sum (> 10 °C). Direct and diffuse light intercepted by 8 canopy zones, 3 on each of the hedgerow sides (apical, central, basal), 1 on top of the canopy and 1 inside the canopy are calculated separately. By using exposed leaf surface, SFE, in the calculation, we assumed essentially only one exterior layer of leaves. Leaf angle and azimuth can be varied, yet detailed information on varietal differences or responses to drought are lacking. Light attenuation inside the canopy is calculated according to Norman (1982).

Gas-exchange

We have followed two different approaches for modelling single leaf photosynthesis. One was based on an empirical model using a set of response functions to environmental variables (Tenhunen et al. 1976), the other was based on the biochemical approach of Farquhar et al. (1980). Parameterisation of the second has not yet been completed for conditions including effects of water deficit on photosynthesis but includes responses to (1) phenological stage (6 phases are distinct) (2) leaf age (3) light intensity and (4) leaf temperature. All necessary parameters have been derived for sun and shade adapted leaves separately. Water deficit is currently modelled through the relationship of maximum quantum saturated rate of photosynthesis (A_{\max}) (under ambient CO₂ concentration) to pre-dawn leaf water

potential (ψ_{PD}). Leaf age is expressed in plastochrons and 4 plastochron classes are distributed within the canopy at each point in time. Light response is described using a non-rectangular hyperbola (McMurtie and Wang 1993) and the response to temperature is modelled according to Tenhunen et al. (1976) and Harley et al. (1992). Since the response of photosynthesis to leaf temperature is not constant, that is, the photosynthetic apparatus may acclimate to higher or lower temperatures, we established a simple relationship between the temperature optimum of photosynthesis measured in the field and the mean air temperature over the 14 days preceding the measurement. The necessary data set was acquired with 2 varieties in 5 locations (Geisenheim, Germany; Davis, Lodi, California, US; Montpellier, Bordeaux, France). Dark respiration is modelled using previously published Q_{10} values as dependent on plastochron index and phenological stage and in relation to ψ_{PD} .

Coupling photosynthesis and stomatal conductance

Photosynthesis was linked to stomatal conductance (g) using the approach of Ball et al. (1987). While the use of relative humidity (h_s) in this model is questionable (Aphalo and Jarvis 1993), we found very good linear correlations between g and the product of A and (h_s/C_a) , where C_a is the CO_2 partial pressure. The slope of this relationship was termed the stomatal sensitivity factor, k , which changes with soil water deficit (Tenhunen et al. 1990) (Fig. 1) and which allowed us to distinguish varietal responses to drought.

Model validation

We have tried to validate the model using different approaches with different varieties in different viticultural regions of Europe. One approach was to measure single leaf A and g throughout the day in different canopy zones of different canopy systems under changing plant water status keeping the leaves in their natural position. The second approach was comparing the calculated transpiration rates by the model for the whole canopy with data from sap flow gauges (Granier type); and the third approach was comparing calculated whole vine net assimilation rates with measurements conducted with a whole plant gas-exchange system. The required input data for the model are global radiation, air temperature, relative humidity, wind speed and ψ_{PD} .

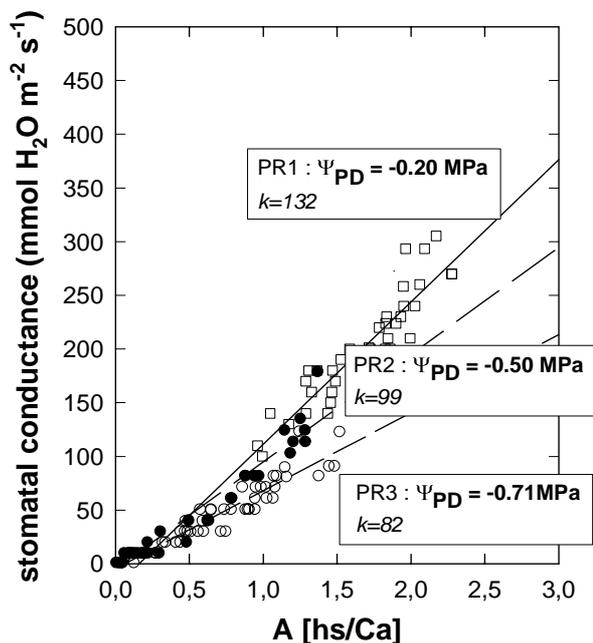


Fig. 1. Measured stomatal conductance to water vapour as a function of the product of assimilation rate and the relative humidity divided by the external CO_2 concentration at different levels of water deficit for the variety Syrah in the field near Montpellier, France. Data are from 1994 and 1995.

Results and Discussion

One of the validation data sets is shown for the 8 canopy zones in Fig. 2. Measured and simulated stomatal conductance in this case were compared for a hedgerow system using the variety Syrah during a water stress experiment ($\psi_{PD} = -0.51$ MPa) in southern France.

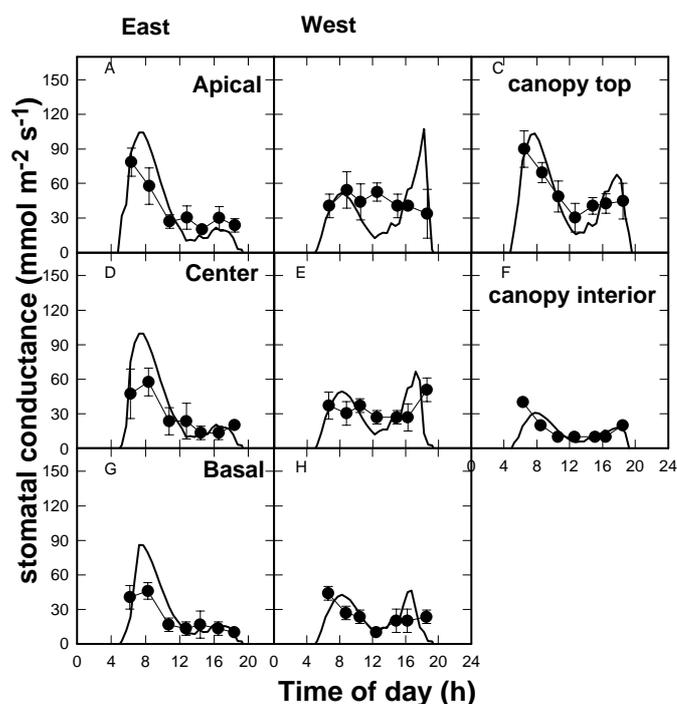


Fig. 2. Measured (symbols) and simulated (lines) stomatal conductance for 8 zones of a Syrah canopy on August 3, 1995 at Roujan, France. The ψ_{PD} was -0.51 MPa. Leaves were kept in their natural position.

Measured and simulated values were in good agreement (Fig. 2). Photosynthesis and stomatal conductance was slightly underestimated on

the West side in the morning but the strong afternoon depression in both photosynthesis and stomatal conductance on the East side were simulated accurately (Figs. 2 B, E, H). However, in order to ultimately evaluate model performance, we compared model calculations with whole plant measurements of gas-exchange in the field using an automated polyethylene chamber system (Poni et al. 1997). The experiment was part of a study comparing two different canopy systems with the variety Chardonnay in Bologna, Italy. One of the systems studied resembled the hedgerow, vertical shoot positioned system used in many European vineyards, the other was a minimal pruning system, which develops very large canopies with hanging shoots. Figure 3 shows some results for a diurnal time course of net CO_2 exchange rate (NCER) of the two systems during a clear day in September. With the exception of some discrepancies between measured and simulated NCER values early in the morning, agreement was excellent. The complex canopy structure of the minimal pruning system probably contributed to these differences, and more complex approaches to describing leaf area distribution may improve performance of the model (Wang and Jarvis 1990). The consistent early morning underestimation of photosynthesis may also be related to a currently insufficient account of the temperature dependence of quantum yield in the model (McMurtie and Wang 1993).

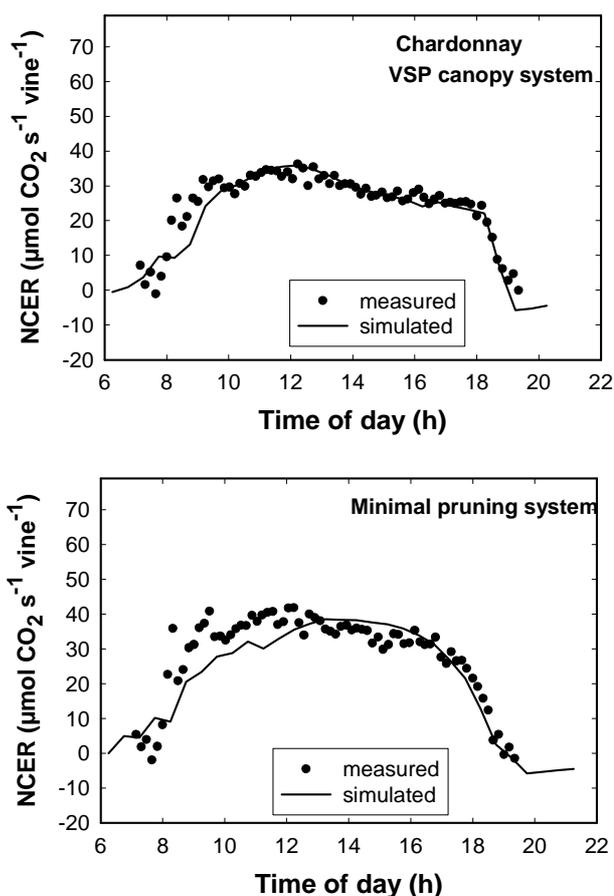


Fig. 3. Simulated (lines) and measured (symbols) whole-vine net CO₂-exchange rate for 2 canopy systems on a clear day in September in Bologna, Italy. Measurements were conducted with a whole-plant polyethylene chamber system at 10minute intervals in the field.

Simulations of whole-vine CO₂ assimilation based on historical meteorological data over entire seasons (1961-1998) compared reasonably well with actual measured values of yield and sugar concentration (harvest carbohydrates).

The model through its incorporation of different stomatal sensitivity factors can be used to simulate the effect of different strategies with

respect to water stress on whole-vine carbon balance and water consumption. However, there are several points in our modelling efforts which still need substantial improvement, respectively development in order to arrive at a complex and flexible model. A more sophisticated energy balance sub-routine is needed to calculate leaf temperature in different canopy zones based on physical principles and inputs of air temperatures, wind speed and boundary layer conductance, i.e. leaf size. This will be one of the model parts to be worked on in the near future.

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