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

HR Schultz¹, P. Pieri², S. Poni³, E. Lebon⁴
¹Forschungsanstalt Geisenheim, Fachgebiet Weinbau, D-65366 Geisenheim, Germany, email: h.schultz@geisenheim.fa.fh-wiesbaden.de
²INRA, Centre de Recherches de Bordeaux, Bioclimatologie, F-33883 Villenave d’Ornon Cédex, France
³Istituto di Frutti-viticoltura, via Emilia Parmense, 84, I-29100 Piacenza, Italy
⁴INRA, Agro Montpellier, LEPSE, 2 place Viala, F-34060 Montpellier Cédex, France

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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 Ryel 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 extend 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
where 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 (Aₘₐₓ) (under ambient CO₂ concentration) to pre-dawn leaf water
potential ($\psi_{PD}$). Leaf age is expressed in plastochns and 4 plastochn class 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 proceeding 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 plastochn index and phenological stage and in relation to $\psi_{PD}$.

**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 ($hs$) in this model is questionable (Aphalo and Jarvis 1993), we found very good linear correlations between $g$ and the product of $A$ and ($hs/Ca$), where $Ca$ is the CO2 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 $\psi_{PD}$.

![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 CO2 concentration at different levels of water deficit for the variety Syrah in the field near Montpellier, France. Data are from 1994 and 1995.](image-url)
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 $\psi_{PD}$ was –0.51 MPa. Leaves were kept in their natural position.](image)

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 CO$_2$-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 10-minute intervals in the field.

Simulations of whole-vine CO$_2$ 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.

References


