Grape canopy structure, light microclimate and photosynthesis. I. A two-dimensional model of the spatial distribution of surface area densities and leaf ages in two canopy systems

by

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S u m m a r y : The development of a model of the vertical and horizontal distribution of leaf, shoot, and fruit surface area densities, SAD (surface area per unit of canopy volume, m^2 m^{-3}), as well as leaf types (main and lateral leaves) and leaf ages is described for two canopy systems (Espalier-type, S-System, and 3-wire Cordon, C-System). Leaf, shoot and fruit SAD increased towards the canopy interior for both systems and reached maximum values of 12, 0.8, and 1.2 $m^2 \cdot m^{-3}$, respectively, for the S-System, and 10, 0.4, and 1.0 $m^2 \cdot m^{-3}$ for the C-System. The fruit zone was always located near canopy areas of highest density. The distribution of surfaces of leaves of different ages from primary and secondary shoots was distinctly different for the two canopy types tested.

K e y w o r d s : canopy structure, model, surface area density, leaf age, beta function.

Introduction

The geometrical structure of a plant canopy determines its interaction with fluxes of energy (RAUNIER 1976). 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. The structure of grape canopies can influence grape yield and quality through effects on the amount of exposed leaf surface area and thus potential photosynthesis (SMART 1974; CARBONNEAU 1995), and through direct effects on the micro-climate in the immediate vicinity of the fruits (SPARKS and LARSEN 1966; CARBONNEAU et al. 1978; GIORGESSI and DI LEE 1985; SMART et al. 1985; INTRIERI 1987; REYNOLDS and WARDLE 1989; REYNOLDS et al. 1995).

Since the large spatial and temporal variations in the radiation regime inside 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 as well as to describe the efficiency with which different canopy architectures harvest light or distribute light with respect to crop quality (RIOU et al. 1989, WAGENMARKERS 1991; SMITH et al. 1994; PIERI 1995). To adequately address the latter point, models need to incorporate detailed information on the architectural characteristics of the canopies, hence it is necessary to describe the heterogeneous distribution of plant surfaces within the canopy envelope. Several indices are currently used to describe the foliage "density" in grapevine canopies, such as leaf area per m canopy length, leaf area per canopy surface area, projected leaf area index, i.e. leaf area per soil area covered by the canopy, or leaf layer

number (SMART 1985; SMART 1988; DOKOOZLIAN and KLIEWER 1995 b). However, all these indices or parameters give, at best, a rough approximation of "foliage density"and yield no information about the distribution of surface area in space. The term "density" in this context is often used in an ambiguous way, since it should be reserved for expressions of "surface area per unit space volume" as defined by RAUNIER (1976) and Ross (1981). In the present study, the distribution of surface area densities (surface area per unit volume) of leaves, shoots and fruits in two grape canopy systems is described with a model based on the approach of WANG et al. (1990).

Material and methods

E x p e r i m e n t a l c o n d i t i o n s : 9-year-old White Riesling grapevines (clone 198 Gm on 5 C rootstocks) located in a vineyard at the State Research Institute in Geisenheim, Germany were used for canopy analyses from 1987 to 1989. Two common canopy systems were compared: (1) Espalier-type, S-System, cane pruned, spaced 2.0 m x 0.9 m; (2) 3-wire cordon, C-System, cane pruned (non-divided canopy), spaced 2.8 m x 0.85 m. The general outlines of the systems are given in Fig. 1. All systems were dormant pruned to 10 buds $\cdot$ m^{-2} and viticultural treatments were done according to commercial practices.

M e a s u r e m e n t s o f s u r f a c e a r e a d e n s i t i e s : The vertical and horizontal distribution of the surface area densities (SAD, surface per unit volume, $m^2 \cdot m^{-3}$) of leaves, shoots and fruits were determined at

the end of August (approx. 2 weeks after veraison) using a 3-dimensional grid system. Three to 4 representative vines were chosen and the canopy divided into 15 cm x 15 cm x 15 cm cells using a steel-grid cage which enclosed the vines from all directions (Fig. 1). Horizontal and vertical divisions were made with thin wires. Thus, the discrete two-dimensional distribution of all surfaces was represented by a matrix of n x n values (6 x 11 for the Espalier-System, 10 x 16 for the 3-wire Cordon-System, Fig. 1) representing the surface area index (SAI, $m^2 \cdot m^{-2}$) in n x n cube cells in the row. Measurements were conducted in a total of 1320 and 3200 cells in the S- and the C-System, respectively.
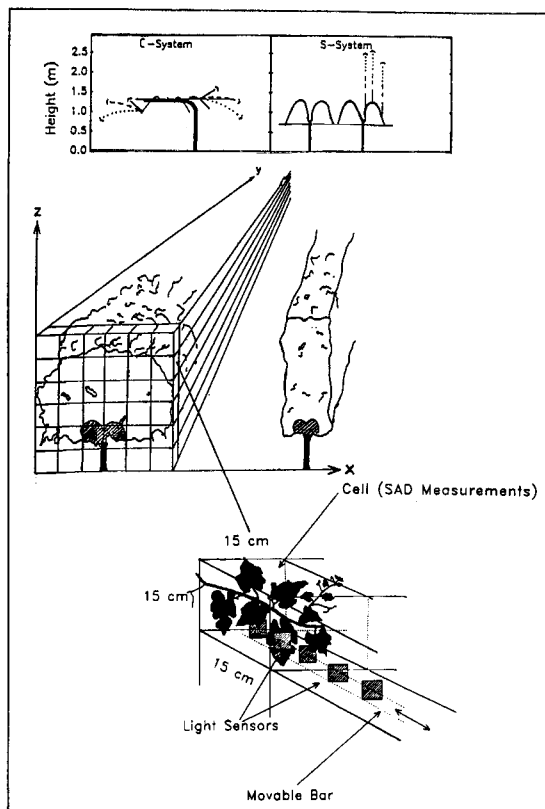

Fig. 1: Schematic presentation of the grid-cell system used to obtain surface area density distributions for two canopy systems; a 3-wire-Cordon-System, C-System (inset left), and an Espalier-type-System, S-System (inset right). The enlarged cell shows how and where radiation measurements were conducted within the same system using 6 Li-Cor quantum sensors mounted on a movable rod.

In each cell, the length of each individual leaf lamina was measured to calculate leaf area ($R^2=0.97$, SCHULTZ 1992) and the leaf plastochron noted to indicate leaf age (SCHULTZ 1993 a). In cases where leaves extended over more than one aggregate, the approximate proportion of surface area attributable to each cell was estimated. Additionally, the lengths and diameters of all shoot axes within a respective cell were measured to calculate shoot surface areas assuming the shape of a frustum of a cone. The surface area of fruits was calculated from measurements of the length and the proximal diameter of the cluster assuming a conical fruit shape. Leaf, fruit and shoot axis surface values are given as half the total surface. If present within

the canopy, the outlines of permanent wood structures (i.e. cordon) were also determined.

The grid cell system also allowed the measurement of photon flux densities (μmol photons $\cdot m^{-2} \cdot s^{-1}$, PFD) within each cell in the canopy (Fig. 1). Using 6 Li-Cor quantum sensors mounted onto a movable rod and connected to a Li-Cor data-logger, an entire canopy (1200-3200 cells) could be sampled within 30 min. Data will be presented in a forthcoming publication.

Theory - The canopy structure model: The distribution of surfaces in space was modelled using the approach of COHEN and FUCHS (1984) and WANG et al. (1990). The model assumes that the surface area within a vineyard row crossection varies in two dimensions, vertically with height of the canopy, and horizontally with the radius from the trunk. The distribution along the length of the row is taken as constant for the time after canopy closure (Fig. 1), since there were no larger gaps between individual vines. The distribution of surface area density, SAD, in both horizontal and vertical directions was described with a two-dimensional beta function:

$$SAD = B_1 \cdot h^{B_2} \cdot (h)^{B_3} \cdot B_4 \cdot r^{B_5} \cdot (1-r)^{B_6} \qquad (1)$$
$$(0 < r, h < 1), r = f(R)$$

where h and r are relative canopy height (starting where foliage begins) and radial distance, respectively (WANG et al. 1990), and B_1 to B_6 are parameters. Total canopy height was 1.5 m for the C- and 1.65 m for the S-System. For the C-System, r depends on the absolute canopy radius (R) which changes as a function of relative canopy height. The canopy envelope is modelled as a half-ellipsoid according to:

$$R'(h) = R \cdot \sqrt{(1+h) \cdot (1-h)} \qquad (2)$$

where
R' = radius at height h (m),
R = radius at the base of the canopy (h=0), set at 1.2 m.

For the S-System, R was 0.45 m at all heights. Both forms closely approximate the actual canopy envelope (Fig. 2).

Leaf age distribution: Leaf age was determined according to the plastochron concept (SCHULTZ 1993 a). Five leaf age or plastochron classes were formed. They were based on the previously determined development of leaf area and photosynthetic capacity (SCHULTZ 1990). Leaf age classes on primary, main shoots comprised leaf plastochron indices (LPI) 6-10, i.e. the youngest remaining leaves after hedging; LPI 10-25, i.e. the middle portion of the shoot, and LPI > 25, i.e. the basal leaves on the shoot (SCHULTZ 1992). Leaves on secondary, lateral shoots were classified into apical, growing and basal, nongrowing leaves.

Total leaf area of each leaf age class within each grid cell was calculated and equation (1) used to model its two-dimensional distribution. The model was parameterized using SAS and Sigma-Plot statistical procedures.
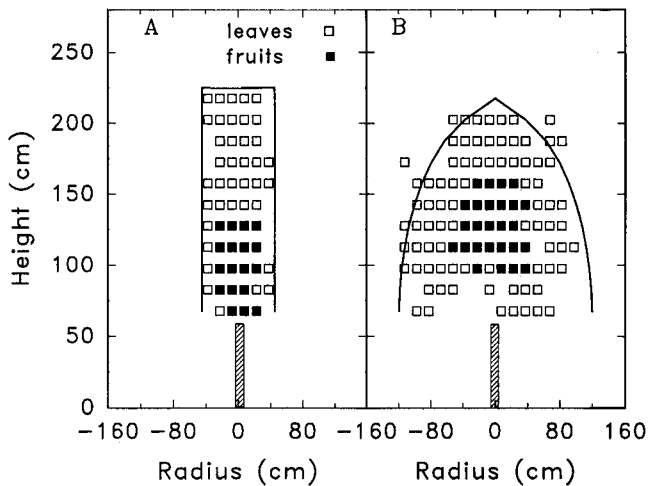
Fig. 2: Modelled canopy envelopes (lines) of the S- (A) and C-System (B) canopies. Open squares indicate aggregates within the canopy trans-section where leaves or shoots were found, closed squares indicate the location of fruits.

Results and discussion

Fig. 3 shows the average vertical and horizontal distribution of foliage, shoot (+ wood), and fruit area densities for the 2 canopy types as determined with the grid cell system in the field. Leaf area densities (LAD, $m^2 \cdot m^{-3}$) of main and lateral leaves were higher in the S-System (Fig. 3 B) than in the C-System over all canopy heights (Fig. 3 A, B). The average LAD for the entire canopy was 3.71 $m^2 \cdot m^{-3}$ for the S-System (leaf area index, LAI = 2.79 $m^2 \cdot m^{-2}$) and 2.02 $m^2 \cdot m^{-3}$ for the C-System (LAI = 2.03 $m^2 \cdot m^{-2}$). These values are within the range normally found for grape (SMART et al. 1985) and dense apple canopies (KAPPEL and QUAMME 1993), yet they are substantially above those found in coniferous and deciduous forests (WANG et al. 1990; RAUNIER 1976). The S-System had ca. 80 % more lateral leaf area than the C-System, mainly located in the upper third of the canopy (Fig. 3 B). The ratio of main to total leaf area was smaller in the S- than in the C-System indicating higher vigour and a higher growth capacity of the former (DOKOOZLIAN and KLIEWER 1995 a). The radial distribution of the leaf area densities in the C-System was bimodal with high densities on each side of the cordon and trunk (trunk position=radius 0) (Fig. 3 C). Highest densities in the S-System were concentrated near the canopy centre at the trunk (Fig. 3D). The fruiting zones of both systems were always located near canopy areas with high densities (Fig. 3 A-D).

The large standard errors reflect the substantial variability of the SAD within the canopy (Fig. 3). This suggested that the density distributions in vertical and horizontal direction were non-uniform. In models of tree canopy architecture, the density distribution of leaves (or needles), which are by far the largest component of all surfaces in a canopy (Fig. 3), is usually assumed to be uniform or random (CHARLES-EDWARDS 1982), an assumption also intrinsic to all the indices used to characterize grape canopy structures (SMART 1985; SMART 1988; DOKOOZLIAN and KLIEWER 1995 b). However, it has been shown that this

assumption can lead to underestimates of the radiation flux density within the canopy (NORMAN and JARVIS 1975), and subsequently of photosynthesis (WANG and JARVIS 1990). Since light has a direct and positive effect on fruit composition and wine quality (MORRISON and NOBLE 1990), it is of importance to adequately describe the surface distribution of leaves and fruits in order to model the radiation flux density within the canopy, especially within the fruiting zone.

In the present study, the density distribution in vertical and horizontal direction within the two grape canopy systems was modelled by fitting equation (1) to leaf, shoot, and fruit surface data representing the average densities measured in row direction. Since the LAD distribution was bimodal for the C-System, the fitting was done separately for each canopy side. Measured and fitted SAD values agreed well for the S-System (data not shown), but leaf and shoot axes area densities were underestimated for the C-System when measured SAD was very high (> 8 $m^2 \cdot m^{-3}$ for leaves, and > 0.25 $m^2 \cdot m^{-3}$ for shoots). This suggested a larger degree of leaf and shoot clumping for the C- compared to the S-System and might necessitate the introduction of a clumping factor into the model (OKER-BLOM and KELLOMÄKI 1983; WANG and JARVIS 1990).

Useful practical indices proposed to assess for canopy density of grapevines (e.g. SMART 1988) do not consider within canopy variations in SAD, thus are one-dimensional, and do not consider the distribution of the fruits. Modelling the 2- or 3-dimensional distribution of surfaces is more
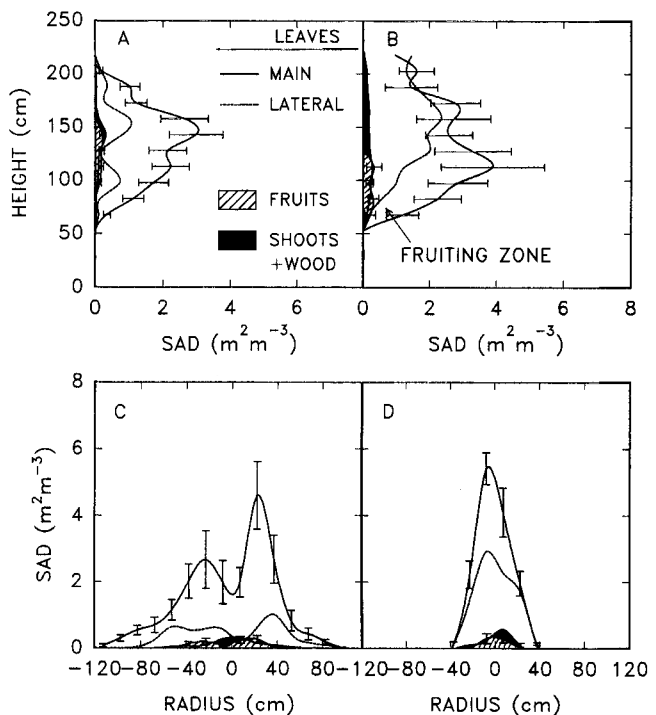

Fig. 3: Average (over the whole canopy) vertical (A, B) and horizontal (C, D) surface area density SAD distribution of lateral and main leaves, and shoots (+wood) and fruits of the C- (A, C) and the S-System (B, D). Measurements were conducted in late August in a 3-dimensional grid-cell system. A radius of 0 indicates the position of the trunk. Bars denote Standard Errors for main leaf surface distribution. Others Standard Error bars were omitted for clarity.

complex. Cohen *et al.* (1987) used a photographic method to determine leaf area density in 0.125 m³ cells (cell size in the present study was 0.0034 m³) across the rows in an orange grove and used the data to draw 2-dimensional contours showing the LAD distribution (Cohen and Fuchs 1987). They found highest LAD values near the canopy envelope, with decreasing densities towards the crown centre.

Contour plots based on the results from fitting equation (1) showed that LAD increased in both canopy systems with decreasing distance to the centre (Fig. 4 A, B), which is exactly opposite to the results of Cohen *et al.* (1987), but in accordance with a detailled study on *Pinus radiata* canopies (Wang *et al.* 1990). A large proportion of the S-System canopy had LAD values > 8 m² ·m⁻³, which is much higher than the LAD of other perennial plants, where LADs typically range from 1 to 2 m² · m⁻³ for deciduous forest species (Raunier 1976) and rarely exceed 3 m² · m⁻³ in citrus orchards (Cohen *et al.* 1987).

ported for apple trees by Wagenmakers (1991). Shoot surface areas are usually neglected in canopy models, yet the present results showed that they contributed 0.15 m² per m of canopy length to the total surface area for both canopy systems, thus about the same amount as the fruits, albeit more dispersed in space (Fig. 4 C, D). Woody structures may contribute substantially to canopy density in localized areas (Fig. 4 C).

The similar leaf areas per unit canopy length, yet very dissimilar average leaf area densities for the two canopy systems (3.71 m² · m⁻³ S-System, 2.02 m² · m⁻³ C-System) demonstrate that leaf area per m of canopy length is not a good indicator of canopy density as suggested by Dokoozlian and Kliewer (1995 a, b). Nevertheless, they found good correlations between leaf area per canopy length and several indicators of fruit zone light microclimate.

The distribution of leaves of different physiological ages within the canopy can play a role in whole-canopy photosynthesis (Hodonova 1979; Wang and Jarvis 1990). Leaf age distribution analyses of the two canopy types revealed that in the C-System up to 40 % of the primary leaf area near the canopy envelope were in leaf age class LPI 6-10, i.e. the physiologically youngest remaining primary leaves after hedging, whereas this leaf age class was concentrated on the canopy top in the S-System (Fig. 5 A, B). Since leaves of this age class have high photosynthetic rates until harvest (Schultz 1990), their position within the canopy in relation to light microclimate may influence whole-canopy performance. Basal leaves
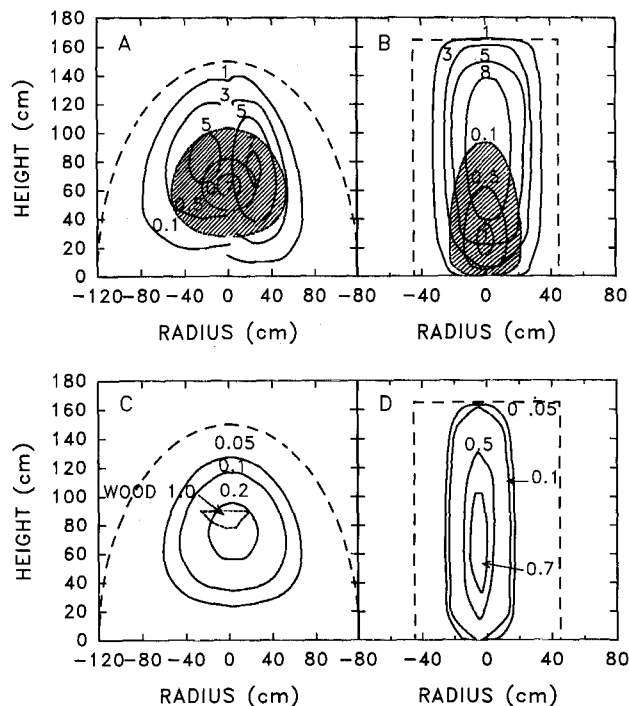

Fig. 4: Contour plots of the calculated 2-dimensional SAD distribution for the C- (A, C) and the S- (B, D) canopy systems. The SAD values near the contours have units of m² · m⁻³. A, B: Leaf and fruit (hatched circles) surface distribution. C, D: Shoot and wood surface distribution. Dashed lines denote canopy envelopes.

Fruit surface areas were concentrated near canopy zones with high leaf area densities (Fig. 4 A, B), suggesting that surface areas of fruits could contribute significantly to light attenuation (Wagenmakers 1991) and that fruit zone location was not optimal in the studied canopies. Dokoozlian and Kliewer (1995 a) also reported high densities near the fruiting zone in grape canopies in California. The projected fruit surface itself amounted to 0.14 and 0.20 m² per m of canopy length, and the leaf area to 5.6 and 5.7 m² per m of canopy length for the S- and the C-System, respectively. Total fruit surface was thus between 2.4 and 3.5% of total leaf area, about half the values re-
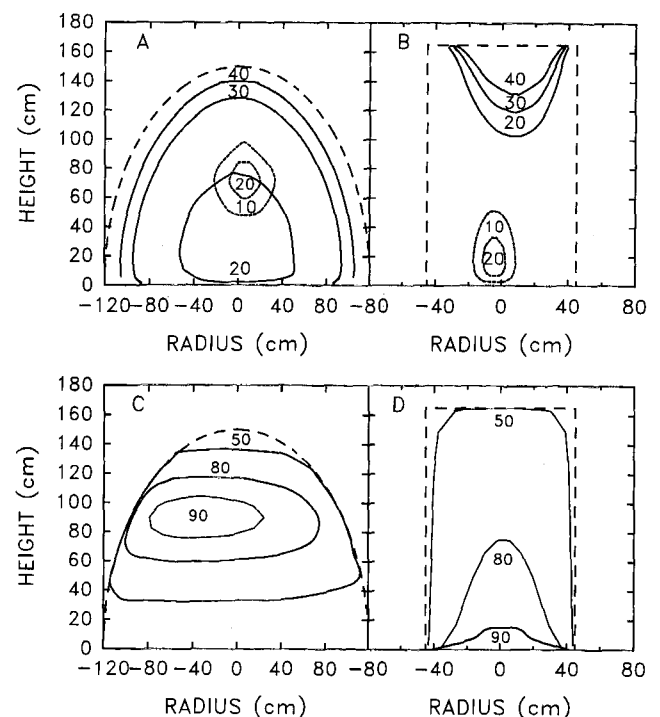

Fig. 5: Contour plots of leaf age distribution within the modelled canopy envelopes (long dashed lines). A, B: Percentage of total primary leaf surface area density in leaf age classes of leaf plastochron indices LPI 6-10 (solid lines), and LPI > 25 (basal leaves, short dashed lines). C, D: Basal (non-growing) lateral leaf surface area density expressed in percent of total lateral leaf area density. (A, C) C-System; (B, D) S-System.

were mainly concentrated in the interior canopy zones of both systems (Fig. 5 A, B), suggesting that their potential contribution to whole-plant photosynthesis was strongly penalized.

Lateral leaves play an important role in berry maturation (KOBLET 1971). Most of the actively photosynthesising, mature (basal) lateral leaves were found in the upper, potentially more sun exposed, part of the C-System (Fig. 5 C), whereas a larger proportion of these leaves was found in the lower part of the S-canopy.

The calculations of canopy SAD and leaf age distributions in this study are based on field-experimental data, and are therefore not entirely symmetric with respect to the vertical canopy axis (Fig. 4, Fig. 5). However, in order to develop a general model for several canopy structures, symmetry will have to be assumed (COHEN et al. 1987). Additionally, canopy development during the season has to be taken into account before any coupling with models of light interception and distribution (RIOU et al. 1989; PIERI 1995; CARBONNEAU 1995), carbon and nitrogen allocation (WERMELINGER et al. 1991), and individual leaf photosynthesis and stomatal conductance (SCHULTZ 1993 b) can be attempted.

Acknowledgements

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