Calibration and Evaluation of a STELLA Software-based Daily CO₂ Balance Model in *Vitis vinifera* L.

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ABSTRACT. This paper describes and evaluates the reliability of a model for prediction of daily carbon balance and dry matter (DM) accumulation in vertically shoot positioned grapevine (*Vitis vinifera* L.) canopies based on the user-friendly STELLA simulation software. Validation of the model was produced for potted ‘Cabernet Sauvignon’ grapevines at both low canopy density [LD (≈10 shoots/m of row)] and high canopy density [HD (≈20 shoots/m of row)] by comparing, on a seasonal basis, the modelled daily CO₂ balance with the diurnal net carbon exchange rate (NCER) measured using a whole-canopy enclosure method. Estimated daily total photosynthesis (P_n) was linearly correlated with measured NCER for LD ($r^2 = 0.87$) and HD ($r^2 = 0.86$), thereby indicating that despite its simplicity the model led to a fairly good degree of precision, although it tended to slightly underestimate (5% to 8% less) the measured rates and scattering increased at high values of CO₂ fixations. Daily total respiration (R) for LD treatment was 29.0% of total daily P_n, with clusters, leaves and stems accounting for 11.8%, 46.7%, and 41.5%, respectively. Daily total R was 24.2% of total daily P_n in HD treatment and single organs contributed 22.3% (clusters), 41.6% (leaves), and 36.1% (stems). The model estimated that 1604 and 1893 g DM per vine accumulated at harvest for LD and HD treatment, respectively, whereas destructive sampling of leaves, stems and clusters yielded 1475 ± 64 g per vine for LD treatment and 1730 ± 96 g per vine for HD treatment, respectively, corresponding to the 91% and 92% of the DM estimated with STELLA, which in its present version does not take into account root respiration.

One of the most distinctive features of the cultivated grape (*Vitis* L.) is that it can be trained and pruned to assume various forms and shapes so as to produce canopies with a great variability in size and leaf arrangement (Winkler et al., 1974). The interactions of climate, canopy size, and leaf distribution (vertically positioned shoots vs. sprawling shoots) ultimately define the amount of source (i.e., functional leaf area) for a given canopy. A vine can be viewed as being in balance when the source is adequate to allow both the highest productivity at the desired quality level and proper wood maturation for the following year’s development and cropping (Partridge, 1925).

While it is relatively easy to define “crop load” as the supply–demand balance for carbohydrates, it is decidedly more troublesome to provide accurate estimates or measures of it. A traditional approach is to calculate crop load indices, the most popular being the yield-to-pruning weight ratio (Ravaz, 1911). A general rule states that balanced vines should have yield-to-pruning weight ratios ranging around 5–8 (Smart, 1985). While published reports confirm that this index can be useful as a general warning for excessively high or low crop load situations (Bravdo

et al., 1984; Reynolds and Wardle, 1994), it has also been shown that at very similar yield-to-pruning weight ratios grape quality can also considerably differ (Cavallo et al., 2000). This is mostly due to the lack of sensitivity of pruning weight as an indicator of effective canopy function; a vigorous vine at very high pruning weight can easily have lower net canopy photosynthesis than a more balanced vine, which in spite of a lower pruning weight can benefit from better leaf exposure (i.e., higher diffuse light within the canopy) and less vegetative competition for the accumulation of solutes in the berries after veraison.

Expressing crop load as the leaf-to-fruit ratio would overcome the problem but a review paper by Howell (2001) has reported that its optimum range may actually vary from 7 to 14 cm²·g⁻¹, depending upon how environmental and cultural factors act to make the “total” leaf area somewhat different from the “functional” leaf area. A case in point is a study conducted on ‘Merlot’ grapevines trained to various trellises that used a sophisticated three-dimensional digitising canopy scanning method (Mabrouk and Sinoquet, 1998). It showed that initial values of 1.21–3.35 m²·kg⁻¹ dropped to 0.70–2.27 m²·kg⁻¹ when the external leaf area was calculated and fell further to 0.3–0.7 m²·kg⁻¹ upon estimation of the sunlit fraction. This feature, associated with the objective difficulty of assessing the “exposed” fraction of leaf area, makes this index very site-specific and inherently limits its practical usefulness.

A more objective approach to the estimation of the supply–demand balance may be offered by modelling. Among the modelling applications which have been run to predict canopy photosynthesis

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or dry matter accumulation and/or partitioning in the grapevine, some have reached a good degree of prediction and have also been satisfactorily validated (Schultz et al., 2001; Williams et al., 1985). However, most of them are still quite complex in regard to both input details needed to describe canopy structure and function or the physiological status of vine organs (Bindi et al., 1997; Schultz, 1995; Vivin et al., 2002). Moreover, the model's structure often requires specific computer programming skills and/or familiarity with complex mathematics (Gutierrez et al., 1985; Wermelinger et al., 1991). An ideal model should thus provide a compromise between user-friendliness and reasonable precision of produced outputs. The STELLA software developed by Isee Systems (Lebanon, N.H.) is a user-friendly simulation programming language that only requires algebraic equations and data inputs in graph or table form, thereby facilitating model use and exchange. The first published work on STELLA-based modelling in fruit tree research appeared in 1990 (Lakso and Johnson) and dealt with simulation of the seasonal dry matter production in 8-year-old 'McIntosh' apple trees (*Malus x domestica* Borkh.) in eastern New York State. This initial version has since been improved to include variation of photosynthesis in discontinuous canopy (Lakso, 1993), and sub-models have been added to account for carbon partitioning to specific organs and fruit growth and abscission patterns (Lakso et al., 2001). Simulations have also been produced to integrate the effects of pests, environmental variations, and cultural practices (i.e., crop load adjustments) on seasonal canopy dry matter production and fruit development (Lakso and Nyrop, 2002; Lakso et al., 2001). Attempts to adapt and validate the dry matter production model for 'Concord' grape (*V. labruscana* B.) are in progress (A.N. Lakso, personal communication).

The objectives of the present study were to 1) validate the daily and seasonal canopy photosynthesis values estimated from a modified STELLA-based daily CO₂ balance model for 'Cabernet Sauvignon' (*V. vinifera*) grapevines subjected to either low and high shoot densities by direct comparison to whole-vine gas exchange data, and 2) compare the end-of-season dry matter accumulation outputs with those derived from destructive measurements.

Materials and Methods

STRUCTURE OF THE MODEL. The structure of the model to predict daily CO₂ balance and seasonal dry matter accumulation by grapevine canopies (Fig. 1) has been reworked from the original version published by Lakso and Johnson (1990). Figure 1A, 1B, and 1C are representative of the photosynthesis (P_n), leaf area (LA), and respiration (R) sub-models, respectively. The two primary outputs of the model are the seasonal LA and dry matter (DM) per vine shown as "stocks" (Isee Systems, 2005). The latter is obtained by subtracting daily total R from daily total P_n and then by multiplying the resulting daily balance of CO₂ (Fig. 1D) by a carbon/dry matter conversion factor (Vivin et al., 2003). The list of the model's required inputs and respective units are reported in Table 1. At the moment, the model runs on a daily step and does not take into consideration old wood and root contribution or dry matter partitioning to different vine organs.

PHOTOSYNTHESIS SUB-MODEL. The daily integral of canopy photosynthesis (P_n) is computed according to Charles-Edwards (1982) as:

$$P_n = \alpha ShP_n \max [1 - \exp(-K L)] / (\alpha KS + hP_n \max) \quad \text{Eq. [1]}$$

where α is the quantum yield in $\mu\text{g}\cdot\text{J}^{-1}$, S is the daily integral of

total radiation on a horizontal surface in $\text{MJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, h is day length in seconds, P_n max is the rate of light saturated leaf photosynthesis in $\text{mg}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, K is the canopy light extinction coefficient and L is the leaf area index. This original formulation derives light interception as $1 - \exp(-KL)$, thereby implying continuous canopies. In wine grape, this pattern can be realistic for overhead or, to some extent, pergola-trained vines that shade close to 100% of the soil at full canopy, but it would introduce a considerable error for any hedgerow-trained vineyard, for which estimates of maximum 65% to 75% light interception at full canopy have been reported (Poni et al., 1996; Smart, 1985). Therefore, it was decided to enter light interception (as percentage of ground area allotted per vine) to the model, considering also that this parameter can be measured via quite straightforward and inexpensive methods (Wünsche et al., 1995) or estimated by fairly simple models requiring latitude, time of year, and hedgerow configuration and orientation (Jackson and Palmer, 1979).

The model was made less conservative as to temperature effects on photosynthesis since work on grapevines has shown that optimal or high photosynthesis can still be sustained at temperatures exceeding 30 °C (Zufferey et al., 2000). The equation currently entered in the model for calculating the fractional reduction of daily P_n as a function of air temperature was derived from Intrieri and Poni (1998) and gives no fractional reduction of P_n till about 31.5 °C and a 7% decrease at 34 °C.

LEAF AREA DEVELOPMENT SUB-MODEL. Estimates of leaf area development (Fig. 1B) rely upon the well-established relationship between grapevine shoot development and degree-day (DD) temperature accumulation (10 °C base), which has been shown to be linearly correlated throughout the budbreak-bloom period (Due et al., 1993; Williams et al., 1985b). The model thus uses leaf area (square centimeters) formed per DD as a primary input. Another input, called "fraction of growing shoots" (FGS) multiplied by total shoot number, gives the number of effectively growing shoots. The FGS can be estimated as a function of accumulated DD (Williams et al., 1985b) or quickly calculated by visually counting the green-like turgid apices vs. yellowish or desiccated ones.

Modifications introduced into the leaf area development sub-model as compared to the version proposed by Lakso and Johnson (1990) now make it possible to include the situation of trimmed grapevine shoots, thereby representing a second wave of growth depending upon number and vigor of developing lateral shoots. The model has thus added an outflow (LA removed as percent of the amount accumulated the day before trimming) and has been made sensitive to the number of potentially growing shoots (laterals) after trimming (Fig. 1B). For example, if the initial shoot number per vine is 15 and trimming is performed to retain 12 main leaves, the post-trim shoot number will be increased by 165 to 180 potentially growing shoots. Then, a FGS multiplier sets in to account for dynamics and duration of lateral regrowth of the second wave.

RESPIRATION SUB-MODEL. While there are many data in the literature on the photosynthesis components that can be used to compile the model (Williams et al., 1994, and literature cited therein), those regarding the respiratory activities of grapevine organs at varying temperature are not as prevalent (Blanke and Lenz, 1989; Higgins et al., 1992; Kriedemann, 1968; Palliotti and Cartechini, 2001; Zufferey et al., 2000). The respiration sub-model (Fig. 1C) has not been substantially modified since Johnson and Lakso (1990), and the daily total respiration is computed as the summation of stem, cluster and leaf respiration. In each vine organ

Fig. 1. Core model structure of the STELLA programming language for prediction of leaf area (LA) and dry matter (DM) production in grapevine canopies. P_n = net photosynthesis, P_n max = rate of light saturated leaf photosynthesis, K = canopy light extinction coefficient, DD = degree days, T min = minimum daily temperature, T max = maximum daily temperature, FGS = fraction of growing shoots, LA/DD = leaf area formed per degree day, R = respiration rate, T = temperature. Refer also to Tables 1 and 2 for model inputs, abbreviations and STELLA manual (Isee Systems, Inc., 2005) for details about building blocks.

Table 1. List of model inputs (single value or interval) and units used for dry matter simulations run at low (10/m of row) and high (20/m of row) shoot densities in 'Cabernet Sauvignon' grapevines.

Sub model	Parameter input ^z	Unit	Shoot density	
			10 shoots/m	20 shoots/m
Canopy leaf area	Maximum daily T	°C	7.4–36	7.4–36
	Minimum daily T	°C	0.6–22	0.6–22
	Leaf area/DD – pre-trimming	cm ² /°C	3.31	1.34 ^w
	Leaf area/DD – post-trimming	cm ² /°C	0.726	
	Initial shoot no. per vine	no.	21	52
	Increment of shoot no. after trimming	no.	231	---
	LA removed with trimming	% of pre-trimming LA	27.7	---
	FGS before trimming	%	0–100	0–100 ^w
Photosynthesis	FGS after trimming	%	0–13.4	
	Daylength	S	46140–56568	46140–56568
	Total radiation	MJ·m ⁻² ·d ⁻¹	1.5–28.51	1.5–28.51
	Maximum leaf P_n	mg·m ⁻² ·s ⁻¹	0–0.569	0–0.501
	Canopy light interception	% of allotted ground area per vine	0–43.1	0–42.4
	Light extinction coefficient (K)	dimensionless	0.60	0.55
	Quantum yield	μg·J ⁻¹	0–3.25	0–2.95
	Allotted ground area per vine ^x	m ²	4.63	5.73
Respiration ^y	Leaves	Slope	dimensionless	0.056–0.044
		Intercept	mg·m ⁻² ·s ⁻¹	0.024–0.0018
	Clusters	Slope	dimensionless	0.069–0.046
		Intercept	mg·g ⁻¹ ·h ⁻¹	0.048–0.016
	Stems	Clusters per vine	no.	18
		Cluster weight	g	35
	Stems	Slope	dimensionless	0–138
		Intercept	mg·m ⁻² ·s ⁻¹	0–126
	Stems	Slope	dimensionless	0.072–0.054
		Intercept	mg·m ⁻² ·s ⁻¹	0.072–0.054
	Stems	Slope	dimensionless	0.073–0.010
		Intercept	mg·m ⁻² ·s ⁻¹	0.073–0.010

^zT = air temperature, DD = degree days; LA = leaf area; FGS = fraction of growing shoots; P_n = net photosynthesis.

^yRespiration sub models use also minimum daily temperature (T min), maximum daily temperature (T max) and day length, as specified in Fig. 1.

^xAllotted ground area per vine calculated as the product of light bar length (2.205 m) by total cane length per vine (2.1 m for low shoot density and 2.6 m for high shoot density).

^wSingle value due to absence of trimming.

the respiration sub-model is based on the Arrhenius's equation, which describes the exponential response of the respiration rate (R) to temperature as:

$$R = a \exp^{(k \cdot T)} \quad \text{Eq. [2]}$$

where a and k are the intercept and slope of $\ln R$ vs. T , respectively, and T is the temperature in degrees Celsius. For each vine organ, the temperature coefficient Q_{10} was then calculated using the slope coefficient k , which is defined as the increase in the respiration rate resulting from a temperature increase of 10 °C, according to:

$$Q_{10} = \exp^{(10 \cdot k)} \quad \text{Eq. [3]}$$

The respiration rates of attached leaves, stems (main axes of leaf-stripped shoots) and clusters of 15 four-year-old potted 'Sangiovese' (*V. vinifera*) grapevines housed in a 12-m³ controlled chamber (Angelantoni Industria, Massa Martana, Italy) and subjected to 5 °C heating steps within the 10 to 35 °C interval were measured in conditions of complete darkness at varying developmental stages throughout the season. These vines were grown outside in 40-L pots filled with a substrate comprising a mixture of 1 soil : 1 peat : 1 fine sand (by volume). Pots were fully irrigated 3–4 times per week and fertilized in late April with Osmocote Plus (Scotts Co., Marysville, Ohio) containing 15N–4.8P–10.8K–1.2Mg. Surface temperatures of the different vine organs were monitored using a copper–constantan thermocouple attached to them by means of a small strip of surgical tape. The time needed by a given organ to reach the desired temperature level ranged from 3 to 5 h, the vines being kept during this period at a light intensity of 200–250 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ so as to avoid interference on the R rate due to change on substrate availability. Carbon dioxide efflux was measured using two open system LCA3 portable infrared gas analysers (Analytical Development Co., Hoddesdon, U.K.) connected to a leaf (PLC3N) and a fruit chamber (PLC-3FM), respectively. For the measurements taken 3 weeks after budbreak, when the young shoots averaged 15 cm in length, the whole stem was entirely enclosed in the PLC-3FM chamber; the median zone of the stem, ≈ 15 cm in length without leaves, was used in all other measurements. The gas exchange measurements were taken by enclosing the vine organ in a chamber, flushing it for 20 min in dark conditions with air flow at 500 mL·min⁻¹ and then recording CO₂ efflux; the equilibrium state at a given temperature threshold was attained in 2–6 min.

The changes in leaf R rates as per temperature were measured 3 weeks after budbreak [day 87 of the year (87 DOY)], flowering (153 DOY), veraison (213 DOY), ripening (263 DOY), and senescence (302 DOY). The cluster measurements were taken at 153, 213, and 263 DOY, whereas stem respiration was checked at 87, 153, 213, and 263 DOY. Refixation ability of respired CO₂ in green vine organs was not considered. The time between two sampling dates was separated at midpoint and the corresponding a and k coefficients were applied to each period in order to run the model and, hence, to estimate the current season respiration rate in leaf, stem and cluster.

After each sampling, the vine organ was cut and its fresh weight immediately registered, the surface area of leaves and stems was measured and their R rate expressed as $\mu\text{g} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Cluster R rates were instead given as $\text{mg} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$.

PLANT MATERIAL AND VINE GROWTH. The validation study was conducted in Piacenza (lat. 45°1'N, long. 9°6'E, Italy) on 6-year-old fruiting 'Cabernet Sauvignon' grapevines grafted to 'SO4' rootstock and grown outside in large pots (70-L) filled with a mixture of 1.5 sand : 1 peat : 2.5 soil (by volume). To create more variability as pattern of leaf area development and hence strengthen

validation, it was decided to work on two different growth habits represented by a low shoot density [LD (≈ 10 shoots/m of row)], requiring shoot trimming at a given time during the season, and a high shoot density [HD (≈ 20 shoots/m of row)] without trimming. Four vines were selected in winter and pruned to retain either two to four long canes per vine. All the vines were then trained to a vertically shoot-positioned bilateral Guyot (Smart, 1985) to form the test row along which vines with two or four canes were alternated. Mean cane length per vine was 2.1 m for LD and 2.6 m for HD. This test row was 35° northeast–southwest oriented and one extra vine was added as front- and end-row buffers. The fruiting canes were trained horizontally along a main supporting wire placed 80 cm from the ground; single catch wires were placed 30, 70, and 110 cm above the main wire to allow a maximum canopy height of ≈ 2.2 m. To mimic a field situation, border rows of similar shape were created using extra-vines and spaced 2.2 m from the test row, yielding a canopy height-intra-row spacing ratio of about 1:1.

Two weeks after budbreak, estimated to occur around 1 Apr., shoot thinning was applied to set the LD and HD treatments as described above. On the same date, to warrant proportional sampling, three and six shoots per vine were tagged for LD and HD, respectively, and thereafter used for vegetative growth measurements. Total shoot length, length, and maximum width of any expanded leaf (either main or lateral) were measured at intervals on each tagged shoot beginning from 9 May to the end of the experiment (3 Sept.). Final sampling consisted of defoliating the whole vines and processing each leaf through a portable leaf area meter, keeping the leaves from primary shoots separated from the lateral population. All removed leaves were then dried till constant weight in a ventilated oven at 70 °C. At intermediate dates, an estimate of the total leaf area per vine was obtained by multiplying leaf area per shoot and total shoot number per vine. The former parameter was obtained by nondestructively calculating single leaf areas with a well-established linear model ($y = 0.45 + 0.957x$; $r^2 = 0.98$) relating actual leaf area (y) and length $\times$ maximum width (x). To enlarge the database dealing with leaf area (square centimeters) formed per DD (an input for the model), the same growth measurements were also taken on four extra-vines adjacent to the test vines of variable shoot number.

According to the experimental layout, the more vigorous shoots that developed on the two LD canopies were trimmed above leaf 12 on 17 June, when shoots had formed an average of 21 visible main leaves; the amount of leaf area removed from each vine was determined via leaf area meter. No trimming was applied to shoots of the HD canopy vines.

Veraison occurred on 17 July, when at least 10% of the berries on each vine had shown initial pigmentation. Seasonal berry growth was monitored by taking the fresh weight of 10 and 20 berries per vine for the LD and HD treatments, respectively, at 10-d intervals from veraison through harvest. At harvest, cluster number and yield per vine were recorded. Two 100-berry samples per vine were processed for fresh weight and then freeze-dried to estimating the DM partitioned to clusters. After leaf fall, all the 1-year-old wood (main and lateral formations) was removed from each vine, weighed and oven dried at 70 °C to constant weight. Twenty two-node stem cuttings were also taken from each vine and their diameter measured at two different points. The exposed stem surface [y (in square centimeters)] of each cutting was then calculated on the basis of a round shape (diameter ratio was 0.93 for both treatments) and regressed over fresh weight [x (in grams)] to give the following relationships: $y = 4.43 + 10.06x$; r^2

= 0.93 for LD; $y = 4.61 + 6.64 x$; $r^2 = 0.96$ for HD). Eventually, the seasonal stem surface needed by the model was recalculated from relationships between shoot fresh weight [x (in grams)] and leaf area [y (in square centimeters)] based on sampling from extra vines which yielded $y = 26.46 x$, $r^2 = 0.97$ for primary shoots and $y = 44.08 x$, $r^2 = 0.94$ for laterals. The stems were then oven-dried at 70 °C to constant weight. Vines were irrigated to pot capacity twice per day from fruit-set till harvest to avoid interference due to transient water stress. Pot sides were wrapped with foil to minimize radiation-induced heating of the root system.

TOTAL CANOPY LIGHT INTERCEPTION. The method used to quantify the total solar radiation intercepted by the grapevine canopies was that of Giuliani et al. (2000) with modifications. Light readings were taken using a multiple line sensor equipped with 64 low-cost photodiodes (BPW20R Silicon PN Photodiode; Vishay Telefunken, Heilbronn, Germany) with a spectral sensitivity in the 300–1100 nm waveband. The sensors were embedded in a lightweight aluminium bar (1.5 cm wide, 3.5 cm thick), spaced at 3.5 cm to yield a total maximum measuring length of 220.5 cm, and covered with a Teflon layer for Lambert's cosine law correction. Measurements of total canopy light interception were taken eight times throughout the season (1, 15, 24 May, and 14 June as pre-trim dates and 17 June, 7 July, 5 Aug., and 2 Sept. as post-trim dates) under clear-sky conditions and negligible wind speed. On each date, readings were taken at about solar noon and at about 3 h before and after solar noon by moving the horizontally held light scanner below the main supporting wire at a step length of 10 cm. This step length allowed each canopy to be monitored in about 2 to 3 min. The number of data sets per canopy varied between 24 and 32, depending upon canopy length and sun position, for a total number of measuring points per canopy varying from 1536 to 2048. At each measurement the light scanner was shifted across the row line to include the entire canopy shadow projection; the solar irradiation hitting the canopy top was monitored by holding the scanner horizontally about 50 cm above the canopy top. Five sets of data were recorded to estimate the reference value of the incoming light intensity as a mean of all sensor readings. The percentage of canopy light interception was calculated by dividing the summation of the difference between the reference (external) incoming light (I_r) and the value for each pixel of the under-canopy light intensity (I_t) by the summation of the reference incoming light hitting the allotted vine area. The area of canopy-projected shade was found by multiplying the number of the shaded pixels on the ground by the grid area of each pixel. The grid area was calculated by multiplying the step length (0.1 m) by the space between one sensor and the next (0.035 m) along the scanner. Dividing total leaf area per vine by the area of the canopy-projected shade yielded an adjusted leaf area index (LAI'), which was used to calculate the light extinction coefficient (K) as $\ln(I_r/I_t)/LAI'$.

WHOLE-CANOPY AND SINGLE-LEAF GAS EXCHANGE. Validation of a model running on a daily basis requires methodology capable of providing continuous or high-frequency canopy gas exchange readings on a 24-h time span. Whole-canopy net CO_2 exchange rate (NCER) records were thus taken throughout the season using the custom-built, flow-through system adapted by Poni et al. (1997) to run multiple and automated NCER readings on grapevine canopies. The chambers were set up on 9 May, then dismantled and repositioned again several times throughout the season till harvest in order to yield continuous and automated gas exchange readings for time lengths varying from 2 to 15 d. The system featured four air-feed centrifugal blowers, four flexible,

inflated, transparent polyethylene chambers, an EGM3 infrared gas analyzer (PP-System, Hertfordshire, U.K.) and a CR10 datalogger (Campbell, Logan, Utah) for system programming and data storing and processing. The chambers enclose the entire canopy with the exclusion of the trunk. Reference inlet and outlet CO_2 air streams were switched at 2-min intervals to the EGM3 by a solenoid valve and the differential CO_2 was recorded automatically at 10-min intervals in association with air temperature measured by polyvinyl chloride-insulated, copper-constantan thermocouples placed at the reference inlet and chamber outlets; total radiation was measured by a cosine-corrected RG030 pyranometer (Silimet, Modena, Italy) placed horizontally on top of a support stake next to the chambers. This support also mounted a BF2 sunshine sensor (Delta-T Devices, Cambridge, U.K.), which uses an array of cosine-corrected photodiodes and a shading pattern to produce two analogue outputs corresponding to the diffuse and total light components both converted into photosynthetically active radiation (PAR) quanta ($PAR \approx 400\text{--}700$ nm). The BF2 sensor was wired to the CR10 data logger and data recorded at 10-min intervals. The flow rate fed to the chambers varied throughout the season depending upon the amount of leaf area enclosed in the chamber; it was adjusted at 12–14 $L \cdot s^{-1}$ at the beginning of measurements and then raised to 46–48 $L \cdot s^{-1}$ at full canopy. Whole-canopy NCER ($\mu mol \cdot s^{-1}$) was then calculated from dawn to dusk from differential CO_2 and flow rates after Long and Hallgren (1985). Overnight variability in ambient CO_2 and the practical difficulties of lowering flow rates every night for better detection of CO_2 differential made it unfeasible to measure night respiration.

To satisfy inputs needed by the model, estimates of maximum leaf P_n were taken during the morning hours (0900 to 1300 HR) on three clear days before (29 Apr., 15 May, 14 June) and after (18 June, 5 Aug., 2 Sept.) trimming on the southeast side of each test vine using a portable flow-through CIRAS-2 (PP-System) gas exchange system. The system featured a broad leaf chamber with a 2.5-cm² window and all readings were taken at ambient relative humidity with an air flow adjusted to 400 $mL \cdot min^{-1}$. To procure the most representative leaves of the population composing the canopy, two shoots per canopy were chosen and every other main leaf measured acropetally starting with the first normally developed basal leaf. On each shoot of the LD treatment, two leaves of a lateral shoot inserted at basal and distal position on the main stem were selected and measured accordingly after trimming. On each date, three nonsenescent mature leaves per vine were progressively shaded with neutral light filter to plot light response curves. Quantum yield was then calculated as the slope of P_n against total PAR within the 0–200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ interval. All remaining input parameters needed to run the model are reported for the low and the high shoot density treatments in Table 1.

Results and Discussion

LEAF AREA DEVELOPMENT. The precision by which the model predicted leaf area development was high for both shoot density treatments (Fig. 2), indicating that the modifications introduced to account for dynamic changes in canopy development caused by trimming were effective. Trimming removed 27.5% of LA in LD treatment (Fig. 2A), with laterals accounting for 47% of final leaf area as compared to 14.7% for HD treatment. Although the focus of this study was not on comparing vine performance at different shoot densities, it has to be noted that if final LA per canopy is expressed per meter of row basis, the resulting values of $2.13 \pm$

Fig. 2. Seasonal evolution of canopy leaf area (LA) per vine for (A) low canopy density [LD (≈ 10 shoots/m of row)] and (B) high canopy density [HD (≈ 20 shoots/m of row)] in 'Cabernet Sauvignon' grapevines. Each data point is the mean of the two-vine replicates. Dashed lines represent the modelled trends. Pre-trimming actual LA data for LD were fitted to $y^{0.5} = -1.90 + 0.023x$, $r^2 = 0.96$; post-trimming actual LA data for LD were fitted to $y^2 = 50.85 - 7291.9/x^{-1}$, $r^2 = 0.90$. Actual LA data for HD were fitted to $\ln y = 0.1007 + 19460x^{-1.5} - 213327x^{-2}$, $r^2 = 0.97$. Shoot trimming in LD was performed 17 June (168 day of the year).

0.20 m² and 2.03 ± 0.38 m² for LD and HD, respectively, indicate that pot constriction induced a strong growth compensation in spite of the doubling in the initial shoot number per row length. The square centimeters of leaf area formed per DD decreased exponentially with shoot number per vine (Fig. 3), evincing that little response was found beyond the threshold of 40 shoots per vine, which likely represents a limiting growth threshold under the conditions of the present trial.

CANOPY LIGHT INTERCEPTION. The trend of seasonal canopy light interception essentially followed that of leaf area development (Fig. 4), although the observed decrease over the last reading (245 DOY) was caused by a lower maximum incoming light intensity. At full canopy, while the maximum fraction of intercepted light did not exceed 43% of allotted vine area in both treatments, the recorded values seem coherent with the leaf area densities reached in the present study (≈ 2 m²·m⁻¹), which are to be considered representative of moderate vigor as pointed out by Dokoozlian and Kliewer (1995).

LEAF PHOTOSYNTHESIS RATE. Maximum leaf P_n rates measured early in the season showed more variability in both treatments

Fig. 3. Relationship between leaf area formed per degree day (LA/DD) and shoot number per vine determined in 'Cabernet Sauvignon' grapevines. Data were fitted to the following equation: $y = 0.154 + 57.6/x$; $r^2 = 0.96$.

Fig. 4. Seasonal evolution of canopy light interception (given as percent of maximum allotted by vine ground area) for low canopy density [LD (≈ 10 shoots/m of row)] (●) and high canopy density [HD (≈ 20 shoots/m of row)] (○) in 'Cabernet Sauvignon' grapevines. Each data point is the mean of two-vine replicates $\pm$ SE. Arrows indicate date of shoot trimming in LD [day 168 of the year (168 DOY)] and date of veraison (198 DOY), respectively.

due to larger variation in the demography of leaf samples (Fig. 5). For the remainder of the season, leaf P_n in LD was higher than in HD as it benefited from the rejuvenating effect of lateral leaves (Poni and Giachino, 2000). In LD treatment, the peak of P_n (13.2 ± 0.7 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was reached 2 d after trimming, when sampling regarded only fully expanded main leaves. In HD treatment, mean leaf P_n reached its maximum values at 217 DOY, corresponding to 11.4 ± 0.8 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

WHOLE-VINE GAS EXCHANGE. The whole-vine gas-exchange system provided 39 d of valid records to be used for validation within the 9 May–3 Sept. interval. This time span made it possible to include the largest variability in terms of total radiation (1.5–28.5 MJ·m⁻²·d⁻¹), total PAR (327–1173 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), diffuse PAR (217–609 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), ratio of diffuse-to-total PAR (18.5% to 90.7%), mean daily air temperature (18.6 to 34.8 °C) and VPD (0.41 to 2.71 kPa). Of the 39 d available for validation, only 11 (28%) had a diffuse-to-total PAR ratio lower than 50%, thereby well describing the summer weather of the experimental site (Po

Fig. 5. Seasonal evolution of maximum single leaf net photosynthesis (leaf P_n) for low canopy density [LD (≈ 10 shoots/m of row)] (●) and high canopy density [HD (≈ 20 shoots/m of row)] (○) in 'Cabernet Sauvignon' grapevines. Each data point is the mean of two-vine replicates $\pm$ SE. Arrows indicate date of shoot trimming in LD [day 168 of the year (168 DOY)] and date of veraison (198 DOY), respectively.

Valley), which typically showed a prevalence of hazy days with light cloudiness.

Validation of the estimated total daily P_n by the model was carried out by regression vs. the whole-canopy net CO_2 exchange rate measured via the enclosure method from dawn to dusk (Fig. 6). Since the gas exchange readings inherently include the contribution of all vine organs enclosed in the chamber, the estimated daily total P_n by the model was corrected for daily respiration of clusters and stems. Estimated daily total P_n was linearly correlated with measured NCER for both the low ($r^2 = 0.87$, Fig. 6A) and the high ($r^2 = 0.86$, Fig. 6B) shoot loads, indicating that despite its simplicity the model can lead to a fairly good degree of precision. The equations of the linear trends forced to the origin suggest, however, that the model tends to slightly underestimate the measured rates and that scattering increases at high values of CO_2 fixations. This effect probably becomes more pronounced with canopy development and progressive accumulation of leaf layers, thus making the role played by diffuse light scattered on the shaded side of the canopy wall throughout the day increasingly important. The model accepts total daily radiation as the primary regulator of total daily photosynthesis, but on days with haze and/or light clouds that reduce the total daily photosynthesis there can be quite a high amount of diffuse light available to the leaves on the shaded side of the canopy which the model cannot "see." It is therefore likely that for upright, thin grapevine canopies the diffuse light component might be more important than expected and the model is being modified to introduce a correction factor of total daily P_n proportional to the amount of diffuse light as a whole.

Another point to be stressed is that the model's precision in estimating whole-canopy NCER changed but slightly with the growth system (low vs. high shoot density) despite the fact that the vines differed markedly as to shoot number per unit length, vigour of individual shoots, presence/absence of trimming and fraction of lateral leaf area-to-total leaf area. This outcome is encouraging in terms of model sensitivity and it confirms that canopy total light interception is well correlated to canopy photosynthetic efficiency (Poni et al., 2003). As a matter of fact, we deliberately avoided including total leaf area (although estimated by the model in the LA sub-routine) in the computation of total daily P_n . Indeed, a

Fig. 6. Relationship between measured whole-canopy net CO_2 exchange rate (NCER) and estimated daily total net photosynthesis (P_n) for (A) low canopy density [LD (≈ 10 shoots/m of row)] and (B) high canopy density [HD (≈ 20 shoots/m of row)] in 'Cabernet Sauvignon' grapevines. Linear equation fitted to LD was: $y = 0.954x$, $r^2 = 0.87$, $n = 39$. Linear equation fitted to HD was $y = 0.922x$, $r^2 = 0.86$, $n = 39$. Empty symbols represent days with a diffuse-to-total PAR ratio lower than 50%.

considerable error might occur in all cases where leaf area keeps accumulating in the canopy beyond the point of optimal canopy filling, resulting in aggravation of internal mutual shade and negligible increase in total light interception and photosynthesis (Intieri et al., 2001). In our study shoot trimming performed on LD induced a decrease in light interception (-12.3% , Fig. 4) and in whole-canopy NCER (-15.1% , calculated as the difference in grams per day measured on 13 and 21 June under mostly clear days) less than proportional to the amount of total leaf area removed with trimming (-27.7% as compared to pre-trimming values, Fig. 2A). This lack of proportionality between removed leaf area and canopy photosynthesis is caused because trimming applied at this stage removes a fairly high portion of young, low functional apical leaves and allows, especially at high sun angles, the re-exposure to full light of partially shaded leaves.

RESPIRATION RATE OF DIFFERENT VINE ORGANS. The R rates in all vine organs were positively correlated to temperature and negatively to aging (Fig. 7). The R-response to temperature on all measurements dates was well described by Arrhenius's equation, with coefficient of determination (r^2) higher than 0.81. The seasonal mean of Q_{10} values, which indicate the sensitivity of R rate

Fig. 7. Leaf (A), cluster (B), and stem (C) respiration-temperature response functions according to phenological stage of 'Sangiovese' grapevines. Each data point is the mean of four measurements $\pm$ SE. In the leaf (A), nonlinear regression of respiration (R) vs. temperature (T) at 3 weeks after budbreak ($\bullet$), flowering ($\blacksquare$), veraison ($\blacktriangle$), ripening ($\blacklozenge$), and senescence ($\blacklozenge$) stages are: $R = 25.22 e^{(0.0428 T)}$ ($r^2 = 0.971$), $R = 14.99 e^{(0.0539 T)}$ ($r^2 = 0.974$), $R = 16.93 e^{(0.0415 T)}$ ($r^2 = 0.945$), $R = 3.38 e^{(0.0509 T)}$ ($r^2 = 0.956$), and $R = 2.17 e^{(0.0426 T)}$ ($r^2 = 0.945$), respectively. In the cluster (B), nonlinear regression of R vs. T at flowering ($\blacksquare$), veraison ($\blacktriangle$), and ripening ($\blacklozenge$) are: $R = 0.288 e^{(0.0508 T)}$ ($r^2 = 0.903$), $R = 0.0204 e^{(0.0519 T)}$ ($r^2 = 0.810$) and $R = 0.0096 e^{(0.0691 T)}$ ($r^2 = 0.945$), respectively. In the stem (C), nonlinear regression of R vs. T at 3 weeks after budbreak ($\bullet$), flowering ($\blacksquare$), veraison ($\blacktriangle$), and ripening ($\blacklozenge$) are: $R = 81.17 e^{(0.0685 T)}$ ($r^2 = 0.987$), $R = 66.85 e^{(0.0659 T)}$ ($r^2 = 0.976$), $R = 14.71 e^{(0.0555 T)}$ ($r^2 = 0.985$) and $R = 11.68 e^{(0.0509 T)}$ ($r^2 = 0.980$), respectively. ($1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} = 44 \mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$).

to T, were 1.90 for stem, 1.77 for cluster and 1.66 for leaf (Table 2). The stem and cluster Q_{10} values progressively decreased over the season, registering the lowest value at ripening; the mean leaf Q_{10} was quite stable throughout the season. The leaf Q_{10} values were generally lower than those reported in literature. Schultz (1991) found Q_{10} values above 3 early in the season and at the beginning of fruit ripening, whereas at other times the Q_{10} ranged between 2.4 and 2.7. Using mature grapevine leaves, Williams et al. (1994) calculated a Q_{10} of ≈ 2.0 in the temperature range of 10 to 42 °C. A Q_{10} of ≈ 2.0 has also been reported for cluster and stem respiration in the grapevine (Frieden et al., 1987) and in other fruit (Grossman and De Jong, 1994) and woody species (Damesin et al., 2002; Edwards et al., 2002; Linder and Troeng, 1981).

The lack of agreement on Q_{10} values may be explained by difference in experimental conditions, especially growth temperature and plant acclimation, use of air or organ temperatures and, above all, the range of temperature used to calculate this coefficient. Given the 10 to 35 °C temperature range in mature leaves, the specific R rates between 25.5 and 72.2 $\mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at veraison and between 5.3 and 19.8 $\mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at ripening (Fig. 7A) are consistent with previous measurements (Higgins et al., 1992; Schultz, 1991; Williams et al., 1994; Zufferey et al., 2000). Even the specific cluster R rates (Fig. 7B) were similar to those already reported for grapevine varieties (Blanke and Lenz, 1989; Frieden et al., 1987; Palliotti and Cartechini, 2001); from 10 to 35 °C, the minimum and maximum values ranged at flowering between 0.470 and 1.7 $\text{mg}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$, and at ripening between 0.019 and 0.106 $\text{mg}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$.

In our study, as temperatures rose from 10 to 35 °C, the stem R rates ranged from 161 to 889 $\mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in very young stems (3 weeks after budbreak), and from 19.4 to 69.2 $\mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in mature stems at ripening stage (Fig. 7C). Given the same temperature range, Brayman and Schaedle (1982) reported that dark R rates ranged in aspen (*Populus tremuloides* Michx.) from 194 to 667 $\mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in very young internodes and from 55.6 to 194 $\mu\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in older internodes.

Unfortunately, previous data available on stem R rates in grapevine, reported by Kriedemann and Buttrose (1971), are very difficult to compare since the basis of their calculations is not explained, and at a temperature of 24 to 25 °C huge differences in cane R rates among lab and open field experiments are reported. Recently, Smart (2004) has shown that in grapevine the cane wood R rates expressed on a volume basis ranged from 1.4 to 3.4 $\text{mmol}\cdot\text{m}^{-3}\cdot\text{s}^{-1}$, which is higher than stem R rates found in many other woody species (Damesin et al., 2002; Edwards et

Table 2. Temperature coefficient (Q_{10})² values calculated by respiration measurements in 'Sangiovese' grapevine organs according to phenological stage. Values are means $\pm$ SE, n = 4.

Phenological stage	Leaf	Cluster	Stem
3 weeks after budbreak (87 DOY) ³	1.55 (0.04)	---	2.05 (0.09)
Flowering (153 DOY)	1.77 (0.12)	2.01 (0.14)	2.00 (0.06)
Veraison (213 DOY)	1.59 (0.09)	1.71 (0.08)	1.82 (0.11)
Ripening (263 DOY)	1.75 (0.05)	1.60 (0.10)	1.72 (0.04)
Senescence phase (302 DOY)	1.64 (0.08)	---	---

²Indicate the sensitivity of respiration process to temperature (i.e., the augment in the respiration rate resulting from a temperature increase of 10 °C).

³DOY = day of the year.

al., 2002). At 30 °C, we measured stem R rates of 0.70 and 0.49 mmol·m⁻³·s⁻¹, at veraison and ripening, respectively.

In agreement with data reported for apple (Butler and Landsberg, 1981; Jones, 1981; Proctor et al., 1976), the slope (k) of leaf dark respiration rates (Fig. 7A) changed slightly throughout the season (from 0.0438 to 0.0572), whereas the intercept (a) markedly decreased with leaf aging. In the cluster, both a and k coefficients decreased over time, although the drop observed from fruit set to veraison as compared to the records taken around flowering was more pronounced for the intercept than for the slope (Fig. 7B). Stem respiration showed a moderate seasonal decrease in the slope values (0.0720 measured after bud-burst vs. 0.0541 at the end of the season), whereas the intercept showed a sharp drop for measurements taken from flowering to veraison (Fig. 7C).

SEASONAL DM PRODUCTION MODELLED BY STELLA SOFTWARE. The modelled seasonal trends (from budbreak to harvest) of daily total P_n and R rate in the two shoot densities treatment are reported in Fig. 8; the respiratory contribution of each organ is shown in Fig. 9. In the LD treatment, daily total R was 29.0% of total daily P_n, with clusters, leaves and stems contributing 11.8%, 46.7%, and 41.5%, respectively. In the HD treatment, total daily R was 24.2% of total daily P_n, and single organs contributed 22.3% (clusters), 41.6% (leaves) and 36.1% (stems). In young apple trees, a 27% respiratory loss was found during the growing season (Wibbe et al., 1993), whereas higher percentages were reported in mature apple (40% to 45% by Lakso and Johnson 1990), and apricot (*Prunus armeniaca* L.) (40% to 50% by Evenari et al., 1977). Williams (1996), who included roots and trunk, calculated that in three different phenological stages (147, 206, and 253 DOY), ≈50% of the total CO₂ required by ‘Chenin blanc’ grapevines grown in California was used for respiratory purposes. On mature vineyards of ‘Sangiovese’ grown in central Italy, excluding the roots, a range of 36% to 49% of DM produced by the vine during the season was lost by respiration processes (Pallioti et al., 2003).

On a seasonal basis, the leaves were the organ with higher respiration activity, followed by the stem and then by the cluster. In apple, Proctor et al. (1976) also found that R rates in leaves and stems were very similar, and, when roots were included, they accounted for ≈40% and 39%, respectively, of the total plant R rates.

Fig. 8. Simulated seasonal trends of daily total photosynthesis [P_n (g/vine per day)] and daily total respiration [R (g/vine per day)] for low canopy density [LD (≈10 shoots/m of row)] (—, ●) and high canopy density [HD (≈20 shoots/m of row)] (---, ○) in ‘Cabernet Sauvignon’ grapevines. Trends are averaged over the two-vine replicates. Arrows indicate date of shoot trimming in LD [day 168 of the year (168 DOY)] and date of veraison (198 DOY), respectively.

While the seasonal daily P_n trends also typically reflect fluctuations in incoming radiation, the daily R pattern shows a marked decrease at about 175 DOY for both treatments, which was mostly due to cluster and stem R and, to a lesser extent, leaf R (Figs. 8 and 9). The time from 175 to ≈200 DOY roughly corresponds to the lag-phase of berry growth and includes the beginning of cane ripening. Both phenomena, characterized by a reduction in growth rate, were promptly detected by the model. During the lag-phase, the relative growth rate of ‘Cabernet Sauvignon’ berries (dry

Fig. 9. Simulated seasonal trends of daily total respiration [R (g/vine per day)] for leaves, stems and clusters in low canopy density [LD (≈10 shoots/m of row)] (■, ●, ▲) and high canopy density [HD (≈20 shoots/m of row)] (□, ○, △) in ‘Cabernet Sauvignon’ grapevines. Trends are averaged over the two-vine replicates. Arrows indicate date of shoot trimming in LD [day 168 of the year (168 DOY)] and date of veraison (198 DOY), respectively.

weight basis) dropped from 90 to 10 mg·mg⁻¹·d⁻¹ (Pallioti and Cartechini, 2001). Likewise, model sensitivity was also shown in patterns of daily stem R, which was consistently higher in LD treatment at both pre- and post-trimming due to bigger individual shoot size and the presence of a higher proportion of growing lateral shoots late in the season.

The model estimated that at harvest (3 Sept.), 1604 and 1893 g DM per vine were accumulated in the LD and HD treatments, respectively (Fig. 10), whereas destructive sampling of leaves, stems and clusters yielded 1475 ± 64 g per vine in LD treatment and 1730 ± 96 g in vine in HD treatment, corresponding to 91% and 92% of the total DM estimated by STELLA. Again, these comparisons look very encouraging since Williams et al. (1994) reported that DM stored in stems, leaves and clusters of grapevine cultivars represent ~88% to 93% of the total current-year's biomass. Interestingly, the trends of accumulated DM (Fig. 10) show that the difference between the LD and HD treatments starts widening from veraison onward. Most of this response is due to very little vegetative growth in HD at post-veraison, with consequent lower respiratory costs. The model, despite the absence of any sub-routine specifically dedicated to DM partitioning, can indirectly account for effects dependent upon the source-sink balance of the vine.

Indeed, an objective limit of the current model is the lack of a root component due largely to the lack of quantitative knowledge of the mass and physiological activity of grape roots, although recent efforts have begun to gather useful data (Anderson et al., 2003; Volder et al., 2005). Roots appear to have a quite large sink capacity, but not much sink strength, and the carbon costs of root turnover are difficult to obtain.

Although the model still awaits refinements (e.g., inclusion of the diffuse light factor), the quite promising validation obtained either as prediction of daily CO₂ balance and of end-of-season DM accumulation already makes two valuable applications feasible. The model can be used 1) as a tool for dynamic (seasonal) estimation of the CO₂ canopy balance as a function of training system (e.g., hedgerow or pergola) and/or pruning techniques, and 2) due to the very friendly interface of the model, sensitivity analyses can be run by changing specific inputs and the resulting outputs can be attained in real time. For example, the model can aid training and pruning strategies in vineyard planning by simulating how daily and seasonal P_n could be affected by an increased light interception achieved by modifying row spacing, canopy height or canopy thickness.

A potential point of criticism to the user-friendliness of this model is that numerous parameter have to be known. However, some of them (maximum leaf P_n, quantum yield, light extinction coefficient, the response to temperature of different vine organs) can be computed from the literature, while others (light interception, FGS) are linked to quite straightforward measurements. Yet, the model also allows daily estimates of the source potential of a given grapevine canopy at crucial phenological stages (e.g., bloom or veraison) without necessarily implying tedious and time consuming seasonal measurements. On the other hand, the model itself meets the demand for tools that provide reliable estimates of both photosynthesis and respiration on a whole-canopy basis and which are notoriously very difficult to derive from single-leaf based approaches.

Literature Cited

Anderson, L.J., L.H. Comas, A.N. Lakso, and D.M. Eissenstat. 2003. Multiple factors in root survivorship: A four-year study in Concord

Fig. 10. Simulated seasonal dry matter (DM) accumulation for low canopy density [LD (~10 shoots/m of row)] (■) and high canopy density [HD (~20 shoots/m of row)] (□) in 'Cabernet Sauvignon' grapevines. The single points at day 246 of the year (harvest) represent mean ± SE of DM stored into stems, leaves, and clusters (destructive estimates) for LD (▲) and HD (△) treatments.

- grape. *New Phytol.* 158: 489–501.
- Bindi, M., B. Miglietta, B. Gozzini, S. Orlandini, and L. Seghi. 1997. A simple model for simulation of growth and development in grapevine (*Vitis vinifera* L.). II. Model validation. *Vitis* 36:73–76.
- Blanke, M.M. and F. Lenz. 1989. Fruit photosynthesis. *Plant Cell Environ.* 12:31–46.
- Brayman, A.A. and M. Schaedle. 1982. Photosynthesis and respiration of developing *Populus tremuloides* internodes. *Plant Physiol.* 69:911–915.
- Bravo, B.A., Y. Hepner, C. Loinger, S. Cohen, and H. Tabacman. 1984. Effect of crop level on growth, yield and wine quality in a high yielding Carignan vineyard. *Amer. J. Enol. Viticult.* 35:247–252.
- Butler, D.R. and J.J. Landsberg. 1981. Respiration rates of apple trees estimated by CO₂-efflux measurements. *Plant Cell Environ.* 4:153–159.
- Cavallo, P., S. Poni, and A. Rotundo. 2000. Ecophysiology and vine performance of cv. "Aglanico" under various training systems. *Scientia Hort.* 87:21–32.
- Charles-Edwards, D.A. 1982. The light use efficiency, p. 65–86. In: D. Edwards, D.A. Charles-Edwards, G. Rimmington, and D. Doley (eds.). *Physiological determinants of crop growth*. Academic, Sidney.
- Damesin, C., E. Ceschia, N. Le Goff, J.M. Ottorini, and E. Dufrene. 2002. Stem and branch respiration of beech: From tree measurements to estimations at the stand level. *New Phytol.* 153:159–172.
- Dokoozlian, N.K. and W.M. Kliewer. 1995. The light environment within grapevine canopies. II. Influence of leaf area density on fruit zone light environment and some canopy assessment parameters. *Amer. J. Enol. Viticult.* 46:219–226.
- Due, G., M. Morris, S. Pattison, and B.G. Coombe. 1993. Modelling grapevine phenology against weather: Consideration based on a large data set. *Agr. For. Meteorol.* 65:91–106.
- Edwards, N.T., T.J. Tschaplinski, and R.J. Norby. 2002. Stem respiration increases in CO₂-enriched sweet gum trees. *New Phytol.* 155:239–248.
- Evenari, M., O.L. Lange, E.D. Schultze, L. Kappen, and U. Buschbom. 1977. Net photosynthesis, dry matter production, and phenological development of apricot trees (*Prunus armeniaca* L.) cultivated in the Negev highlands (Israel). *Flora* 166:383–396.
- Frieden, K.H., F. Lenz, and H. Becker. 1987. CO₂-exchange of grape berries in different cultivars as affected by temperature, light and water supply. *Wein-Wissenschaft* 42:382–390.
- Giuliani, R., E. Magnanini, C. Fragassa, and F. Nerozzi. 2000. Ground monitoring the light-shadow windows of a tree canopy to yield canopy light interception and morphological traits. *Plant Cell Environ.* 23:783–796.
- Grossman, Y.L. and T.M. DeJong. 1994. Carbohydrate requirement for

- dark respiration by peach vegetative organ. *Tree Physiol.* 14:37–48.
- Gutierrez, A.P., D.W. Williams, and H. Kido. 1985. A model of grape growth and development: The mathematical structure and biological considerations. *Crop Sci.* 25:721–728.
- Higgins, S.S., F.E. Larsen, R.B. Bendel, G.K. Radamaker, J.H. Bassman, W.R. Bidlake, and A. Al Wir. 1992. Comparative gas exchange characteristics of potted, glasshouse-grown almond, apple, fig, grape, olive, peach and Asian pear. *Scientia Hort.* 52:313–329.
- Howell, G.S. 2001. Sustainable grape productivity and the growth-yield relationship: A review. *Amer. J. Enol. Viticult.* 52:165–174.
- Intrieri, C. and S. Poni. 1998. Misura di scambi gassosi su chiome intere di vite: bilancio di un quadriennio di esperienze. *Frutticoltura* 11:69–83.
- Intrieri, C., S. Poni, G. Lia, and M. Gomez del Campo. 2001. Vine performance and leaf physiology of conventionally and minimally pruned Sangiovese grapevines. *Vitis* 40:123–130.
- Isee Systems, Inc. 2005. STELLA. System thinking for education and research. 20 Aug. 2005. <<http://www.hps-inc.com/software/Education/StellaSoftware.aspx>>.
- Jackson, J.E. and J.W. Palmer. 1979. A simple model of light transmission and interception by discontinuous canopies. *Ann. Bot.* 44:381–383.
- Jones, H.G. 1981. Carbon dioxide exchange of developing apple (*Malus pumila* Mill.) fruits. *J. Expt. Bot.* 32:1203–1208.
- Kriedemann, P.E. 1968. Observation on gas exchange in the developing Sultana berry. *Austral. J. Biol. Sci.* 21:907–916.
- Kriedemann, P.E. and M.S. Buttrose. 1971. Chlorophyll content and photosynthetic activity within woody shoots of *Vitis vinifera* (L.). *Photosynthetica* 5:22–27.
- Lakso, A.N. and R.S. Johnson. 1990. A simplified dry matter production model for apple using an automated programming simulation software. *Acta Hort.* 276:141–148.
- Lakso, A.N. 1993. A simplified dry matter production model for apple: Estimation of canopy photosynthesis in discontinuous canopies. *Acta Hort.* 313:45–50.
- Lakso, A.N., M.D. White, and D.S. Tustin. 2001. Simulation modelling of the effects of short and long-term climatic variations on carbon balance of apple trees. *Acta Hort.* 557:473–480.
- Lakso, A.N. and J.P. Nyrop. 2002. Carbon balance modelling approaches to integrating the effects of foliar pests, environment, and cultural practices in apples. *Acta Hort.* 584:221–228.
- Linder, S. and E. Troeng. 1981. The seasonal variation in stem and coarse root respiration of a 20-year-old scots pine (*Pinus sylvestris* L.). *Mitteilungen der Forstlichen Bundes-Versuchsanstalt* 142:125–134.
- Long, S.P. and J.E. Hallgren. 1985. Measurement of CO₂ assimilation by plants in the field and the laboratory, p. 62–93. In: J. Coombs, D.O. Hall, S.P. Long, and J.M.O. Scurlock (eds.). *Techniques in bioproductivity and photosynthesis*. Pergamon Press, Oxford.
- Mabrouk, H. and H. Sinoquet. 1998. Indices of light microclimate and canopy structure of grapevines determined by 3D digitising and image analysis, and their relationship to grape quality. *Austral. J. Grape Wine Res.* 4:2–13.
- Pallioti, A. and A. Cartechini. 2001. Developmental changes in gas exchange activity in flowers, berries, and tendrils of field-grown Cabernet Sauvignon. *Amer. J. Enol. Viticult.* 52:317–323.
- Pallioti, A., O. Silvestroni, A. Cartechini, D. Neri, S. Mattioli, and L. Nasini. 2003. Seasonal carbon balance of Sangiovese grapevines in two different central-Italy environments. *Acta Hort.* 652:183–190.
- Partridge, N.L. 1925. The use of growth-yield relationship in field trials with grapes. *Proc. Amer. Soc. Hort. Sci.* 23:131–134.
- Poni, S., A.N. Lakso, C. Intrieri, B. Rebutti, and I. Filippetti. 1996. Laser scanning estimation by canopy components in different grapevine training systems. *Vitis* 35:177–182.
- Poni, S. and E. Giachino. 2000. Growth, photosynthesis and cropping of potted grapevines (*Vitis vinifera* L. cv. Cabernet Sauvignon) in relation to shoot trimming. *Austral. J. Grape Wine Res.* 3:216–226.
- Poni, S., E. Magnanini, and F. Bernizzoni. 2003. Degree of correlation between total light interception and whole-canopy net CO₂ exchange rate on two grapevine growth systems. *Austral. J. Grape Wine Res.* 9:2–11.
- Poni, S., E. Magnanini, and B. Rebutti. 1997. An automated chamber system for measurements of whole-vine gas exchange. *HortScience* 32:64–67.
- Proctor, J.T.A., R.L. Watson, and J.J. Landsberg. 1976. The carbon balance of a young apple tree. *J. Amer. Soc. Hort. Sci.* 101:549–554.
- Ravaz, M. 1911. L'effeuillage de la vigne. *Annales d'Ecole Nationale d'Agriculture de Montpellier* 11:216–244.
- Reynolds, A.G. and D.A. Wardle. 1994. Impact of training system and vine spacing on vine performance and berry composition of Seyval blanc. *Amer. J. Enol. Viticult.* 45:444–451.
- Schultz, H.R. 1991. Seasonal and nocturnal changes in leaf age dependent dark respiration of grapevine sun and shade leaves: Modelling the temperature effects. *Viticult. Enol. Sci.* 46:129–141.
- Schultz, H.R. 1995. 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. *Vitis* 34:211–215.
- Schultz, H.R., P. Pieri, S. Poni, and E. Lebon. 2001. Modelling water use and carbon assimilation of vineyards with different canopy structures and varietal strategies during water deficit. In: PS2001 Proc.: 12th Intl. Congress on Photosynthesis. Paper No. S34-002, CSIRO Publ., Melbourne. 23 Aug. 2005. <<http://www.publish.csiro.au/nid/197/issue/1342.htm>>.
- Smart, D.R. 2004. Exposure to elevated carbon dioxide concentration in the dark lowers the respiration quotient of *Vitis* cane wood. *Tree Physiol.* 24:115–120.
- Smart, R.E. 1985. Principles of grapevine canopy manipulation with implications for yield and quality. A review. *Amer. J. Enol. Viticult.* 36:230–239.
- Vivin, P., M. Castelan-Estrada, and J.P. Gaudillere. 2002. A source-sink model to simulate seasonal allocation of carbon in grapevine. *Acta Hort.* 584:43–56.
- Vivin, P., M. Castelan-Estrada, and J.P. Gaudillere. 2003. Seasonal changes in chemical composition and construction costs of grapevine tissues. *Vitis* 42:5–12.
- Volder, A., D.R. Smart, A.J. Bloom, and D.M. Eissenstat. 2005. Rapid decline in nitrate uptake and respiration with age in fine lateral roots of grape: Implications for root efficiency and competitive effectiveness. *New Phytol.* 165:493–502.
- Wibbe, M.L., M.M. Blanke, and F. Lenz. 1993. Effects of fruiting on carbon budgets of apple tree canopies. *Trees* 8:56–60.
- Wermelinger, B., J. Baumgartner, and A.P. Gutierrez. 1991. A demographic model of assimilation and allocation of carbon and nitrogen in grapevines. *Ecological Modelling* 53:1–26.
- Williams, D.W., L.E. Williams, W.M. Barnett, K.M. Kelley, and M.V. McKenry. 1985a. Validation of a model for the growth and development of the Thompson seedless grapevine. I. Vegetative growth and fruit yield. *Amer. J. Enol. Viticult.* 36:275–282.
- Williams, D.W., H.L. Andris, R.H. Beede, D.A. Luvisi, M.V.K. Norton, and L.E. Williams. 1985b. Validation of a model for the growth and development of the Thompson Seedless grapevine. II. Phenology. *Amer. J. Enol. Viticult.* 36:283–289.
- Williams, L.E., N.K. Dokoozlian, and R.L. Wampler. 1994. Grape, p. 85–134. In: B. Schaffer and P.C. Andersen (eds.). *Handbook of environmental physiology of fruit crops. Volume I. Temperate crops*. CRC Press, Boca Raton, Fla.
- Williams, L.E. 1996. Grape, p. 851–881. In: E. Zamski and A.A. Schaffer (eds.). *Photoassimilate distribution plants and crops: Source-sink relationship*. Marcel Dekker, New York.
- Winkler, A.J., J.A. Cook, W.M. Kliewer, and L.A. Lider. 1974. *General viticulture*. Univ. of California Press, Berkeley.
- Wünsche, J.N., A.N. Lakso, and T.L. Robinson. 1995. Comparison of four methods for estimating total light interception by apple trees of varying forms. *HortScience* 30:272–276.
- Zufferey, V., F. Murisier, and H.R. Schultz. 2000. A model analysis of the photosynthetic response of *Vitis vinifera* L. cvs. Riesling and Chasselas leaves in the field: I. Interaction of age, light and temperature. *Vitis* 39:19–26.