

# An empirical model for the simulation of leaf appearance and leaf area development of primary shoots of several grapevine (*Vitis vinifera* L.) canopy-systems

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## ABSTRACT

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A simple empirical model for leaf appearance and leaf area formation of primary grapevine shoots with different growth orientation is presented. The growth orientations characterize two groups of canopy-systems; one group with upright-growing shoots, represented by the Espalier-type system and the Vertical cordon system; and one group with hanging shoots, represented by the Geneva-Double-Curtain and unilateral cordon systems. Thermal time in degree days ( $^{\circ}\text{C day}$ ,  $> 10^{\circ}\text{C}$ ) was used as the driving variable starting at bud burst. Leaf appearance and leaf area expansion were linked to thermal time via the plastochron concept. A subroutine was devised to model hedging effects on shoot leaf area. Canopy-systems with hanging shoots exhibited fewer leaves per shoot and smaller individual leaf areas. Simulation runs on datasets from 2 years showed that the model closely describes leaf area development of whole shoots throughout the growing season for both groups of canopy-systems under cool climate conditions (Geisenheim, Rheingau, Germany). The model underestimated leaf number and leaf area of shoots during the latter part of the season when tested on a dataset from a hot climate (Davis, CA).

Keywords: canopy-systems; leaf appearance; leaf area; model; *Vitis vinifera*.

## INTRODUCTION

The growth and development of a crop involves a large number of processes which are influenced by environmental factors and stage of development. It has long been recognized that the key process controlling plant dry matter production in agronomic and horticultural commodities, including grape, is the formation of leaf area as primary photosynthetic surface (Ravaz, 1912;

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Kroemer et al., 1923). Dry matter accumulation and economic (fruit) yield are often directly proportional to the amount of light intercepted by the leaf surface (Monteith, 1965; Jackson, 1980; Smart et al., 1982a,b). In grape, canopy shape and leaf area displacement can significantly influence light interception and fruit quality (Smart et al., 1982a; Smart 1985). In recent years several models for the simulation of grapevine growth have been developed, each one mainly focusing on describing the accumulation of dry weight or its main components, carbon and nitrogen, in the various plant parts (Gutierrez et al., 1985; Crespin et al., 1987; Wermelinger et al., 1991). None of these models, however, takes into account that shoot and leaf area development and leaf area distribution depend on the type of canopy-system used (Smart, 1985; Kliewer et al., 1989). This limits their application in evaluating the efficiency of light interception of different canopy-systems, which is needed in order to optimize canopy structure with respect to fruit yield and quality. This is especially important in northern grape growing areas where light is often limiting or under conditions where excessive vigor limits light penetration into the canopy.

Efforts to simulate leaf area in relation to phenology have resulted in many models, especially for agronomic crops, which vary considerably in complexity. In its simplest form, leaf area index (LAI) is modeled as a direct function of total number of leaves or duration of the period of vegetative growth (Dale et al., 1980; Flesch and Dale, 1987). Some of the more complex modeling approaches include modeling areas of single leaves and incorporate simulations of leaf initiation or leaf appearance, leaf expansion and possibly leaf senescence (Mutsaers, 1983; Porter, 1984).

The latter approach was adopted in part for grape in the present study, because this allows the possibility of incorporation of changing leaf size with plant age or light environment.

Since temperature has been demonstrated to be the dominant environmental factor controlling shoot development and leaf growth in grape (Buttrose 1968, 1969), this study reports an effort to model these relationships for primary shoots of different canopy-systems.

## MATERIALS AND METHODS

### *Experimental sites*

Two 9-year-old vineyards of White Riesling grapevines (*Vitis vinifera* L.) clone 198 Gm on 5C rootstocks located at the State Research Institute in Geisenheim, Germany (50° North, 8° East) were used for growth analyses in 1986. In 1987 and 1988 growth data were collected at only one of these sites (Table 1).

For validation of the model under different climatic conditions, a dataset

TABLE 1

Within row and between row spacings of the investigated canopy-systems at the two vineyard sites in Geisenheim, Germany (1, 2) and the validation site in Davis, USA

Spacing/location	Canopy-system						Davis
	S-System		V-System	G-System	U-System		
	1	2	1	1	1	2	
Between rows (m)	2.00	2.00	2.00	2.80	2.80	3.20	3.60
Within rows (m)	0.90	1.50	0.90	0.85	0.85	1.20	2.10
(m <sup>2</sup> per vine)	1.80	3.00	1.80	2.38	2.38	3.80	7.56

(1) Exposure south-west, slope 15°, soil type loam, soil pH neutral.

(2) Southern exposure, slope 0°, soil type sandy-loam, soil pH neutral.

Davis: exposure west, slope 0°, soil type deep sandy-loam, soil pH neutral.

was obtained from 17-year-old White Riesling grapevines clone 110 Gm on AxR1 rootstock grown at the University of California, Davis, USA (38° North, 122° West) in 1991 (Table 1).

### *Description of the canopy-systems*

Figure 1 shows a schematic presentation of the four canopy systems included in the study, indicating the dominant pattern of shoot growth and the approximate change in general shoot orientation during the growing season (Figs. 1(A), 1(C), 1(E), 1(G)), as well as the dimensions of canopy cross-sectional areas (Figs. 1(B), 1(D), 1(F), 1(H)). The systems were divided into two groups according to the main direction of shoot orientation: (1) upward-oriented: Espalier-type, S-System, cane pruned (Figs. 1(A), 1(B)); Vertical cordon, V-System, spur pruned (Figs. 1(C), 1(D)). (2) Horizontal- and downward-oriented, i.e. 'hanging' shoots: Geneva Double Curtain, G-System, cane pruned (Figs. 1(E), 1(F)); 3-wire cordon, U-System, cane pruned (Figs. 1(G), 1(H)).

At the German sites, all systems were dormant pruned to 10 buds m<sup>-2</sup> in January. Individual vines carried between 18 and 30 buds because planting density differed among systems and between locations (Table 1). Summer pruning (hedging, removal of apical portion of the shoot) and suckering was done according to commercial practices or as required by experimental design. Depending on the canopy-system, 18–32 shoots per vine were retained.

Vines at the California site were dormant pruned to approximately 3 buds m<sup>-2</sup> and carried 23 buds per vine (28–32 shoots). The canopy-system resembled the 3-wire cordon (Figs. 1(G), 1(H)) but shoots originated from spurs, were trained upright and remained unhedged. Because of the upright shoot orientation, the system was categorized as Group 1.

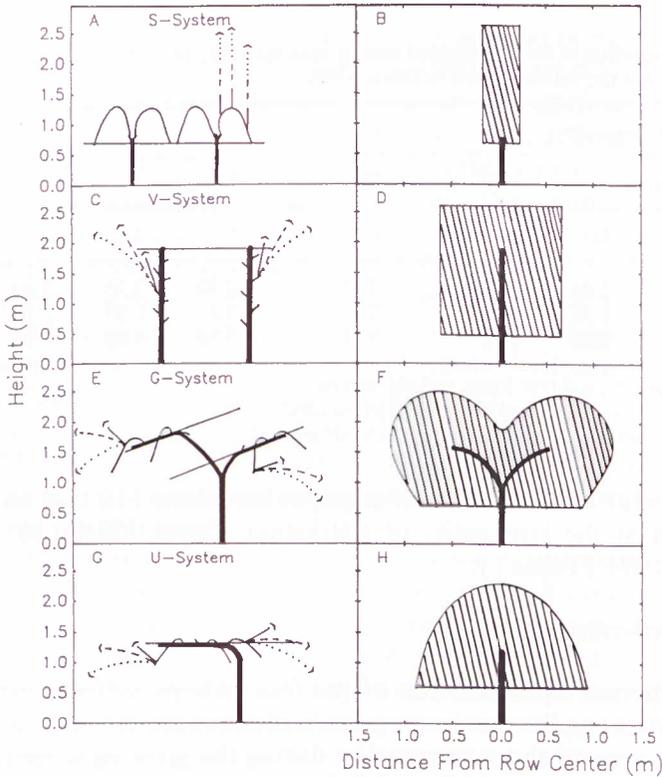


Fig. 1. Schematic presentation of main growth direction of primary shoots, (A), (C), (E), (G); and the approximate canopy dimensions of the four canopy-systems studied, (B), (D), (F), (H).

### *Growth measurements*

Internode and leaf lamina lengths of all primary shoots on two to four vines per canopy-system were measured at irregular intervals (2–60 days) with a hand-held micrometer during the 1986 and 1987 growing seasons. Measurements commenced shortly after bud break and were conducted until September in 1986 and until late October in 1987. Whole vines, rather than selected shoots, throughout a vineyard were used in order to maximize the variation among shoots. In 1988, five upward-oriented shoots from vines trained in the V- and S-Systems were selected and the lamina length of all leaves on these shoots was measured at 2–3 day intervals throughout the season until mid-October. An additional five shoots from the canopy interior (two in the V-System, three in the S-System) were selected in June of the same year and the same measurements performed. These ‘shade’ shoots, grew in canopy zones where photosynthetic photon flux density, PPFD, averaged less than  $150 \mu\text{mol}$

$\text{m}^{-2} \text{s}^{-1}$  at noon of a clear day. Table 2 lists the total number of shoots per canopy system monitored.

Leaf area ( $LA, \text{cm}^2$ ) was estimated non-destructively from measurements of leaf lamina length ( $L, \text{mm}$ ) using a quadratic model of the form

$$LA = \max(0, a \times L^2 + b \times L - c) \quad (1)$$

The calibration of this equation was based on the length and area measurements of randomly selected leaves of all sizes, 61 from the canopy exterior and 55 from the canopy interior, using a custom leaf area meter. Since differences in the relationship of  $L$  to  $LA$  between sun and shade leaves were non-significant (Table 3), one quadratic model was used for all leaves (Fig. 2). Based on the numerical values of  $a$ ,  $b$  and  $c$ ,  $LA$  is set to 0 at  $L$  of 26 mm (Table 3). If  $L$  is expressed in cm rather than mm,  $LA = 1.18 \times (L - 2.6) \times (L + 8.75)$  (Fig. 2).

The validation dataset from Davis was collected on 27 shoots on nine vines. Shoots were selected randomly at bud break and leaf lamina lengths measured 11 times until fruit maturity (29 September 1991). Leaf area was estimated based on a separate calibration of eqn. (1) using 119 leaf samples (Table 3).

### Model development

Table 4 gives a list of the variables used in the model.

*Driving variable.* - Thermal time (THT), or heat units (Winkler and Williams 1939; Gallagher, 1979), expressed in degree days ( $^{\circ}\text{C day}$ ) was calculated daily from:

$$\text{THT} = \sum_{i=1}^n 0.5 \times (T_{\max,i} + T_{\min,i}) - T_b \quad (2)$$

TABLE 2

Number of primary shoots used for collecting growth data

Year/location	Canopy-system						Davis
	S-System		V-System	G-System	U-System		
	1	2	1	1	1	2	
1986	49	24	50	40	-	64	-
1987	53	-	35	49	54	-	-
1988	5	-	5	-	-	-	-
(shade shoots)	(3)		(2)				
1991	-	-	-	-	-	-	27

TABLE 3

Estimates of parameter values and coefficients

Experimental site	Parameter			$R^2$					
	<i>a</i>	<i>b</i>	<i>c</i>						
<i>Ratio of leaf length, L, to leaf area, LA, (eqn. (1))</i>									
Geisenheim									
Sun leaves	0.0115	0.8095	-30.14	0.97					
Shade leaves	0.0110	0.7867	-28.19	0.96					
Davis									
Sun leaves	0.0135	0.2488	-11.44	0.93					
Shade leaves	0.0103	0.6479	-19.44	0.95					
Sun+Shade	0.0111	0.5485	-17.93	0.95					
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Growth direction	Parameter			$R^2$					
	<i>a</i>	<i>b</i>	<i>c</i>						
<i>Relationship between PDR and THT (eqn. (5))</i>									
Upright	$-3.35 \cdot 10^{-8}$	$-9.52 \cdot 10^{-6}$	$5.05 \cdot 10^{-2}$	0.83					
Hanging	$-7.84 \cdot 10^{-8}$	$1.17 \cdot 10^{-5}$	$4.56 \cdot 10^{-2}$	0.77					
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Growth direction									
Upright					Hanging				
THT	$LA_{max}$	$LA_0$	$\alpha$	$R^2$	THT	$LA_{max}$	$LA_0$	$\alpha$	$R^2$
<i>Relationship between leaf leaf area and LPI for leaves unfolding at different times during the season (eqn. (6))</i>									
1.0	47.1	3.1	1.06	0.82	1.0	52.6	4.0	0.78	0.73
20.4	89.3	11.8	0.76	0.92	24.8	86.3	7.5	1.02	0.93
41.9	109.3	7.9	1.02	0.97	41.9	118.4	11.8	1.22	0.89
50.7	128.2	9.7	1.34	0.98	76.8	131.3	12.5	1.37	0.89
65.0	171.3	12.1	1.09	0.98	107.9	126.3	12.8	1.60	0.92
80.3	162.3	11.3	1.16	0.96	127.9	114.7	13.1	1.33	0.95
187.0	164.8	11.4	1.10	0.98	166.9	118.5	16.4	0.86	0.95
238.1	132.0	10.7	1.13	0.97	217.1	109.4	11.6	0.94	0.96
371.9	115.4	8.2	1.12	0.96	256.7	95.9	9.7	1.10	0.94
434.8	101.3	9.3	0.93	0.99	323.0	85.5	9.3	1.21	0.94
559.0	87.0	10.6	0.82	0.97	408.8	68.7	8.6	1.35	0.90
674.9	62.6	7.9	1.22	0.98	535.7	38.7	8.0	1.30	0.91
760.6	47.4	7.6	1.56	0.95	565.8	43.5	6.9	1.30	0.81
893.6	42.2	8.8	1.46	0.95					

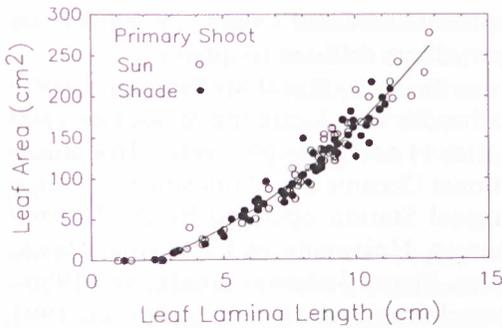


Fig. 2. Relationship of leaf lamina length (cm) to leaf area (cm<sup>2</sup>) of sun and shade leaves in the field. Data are from 10 to 12 different plants per canopy-system.

TABLE 4

List of variables and abbreviations used

Symbol	Meaning
$\alpha$	Parameter of logistic growth curve
$L$	Leaf length (mm)
$LA$	Leaf area (cm <sup>2</sup> )
$LA_{max}$	Maximum leaf area (cm <sup>2</sup> )
$LA_0$	Leaf area at LPI=0 (cm <sup>2</sup> )
LPI	Leaf plastochron index
PI	Plastochron index
PR	Plastochron rate
PDR	Plastochron development rate
Phyllochron	Plastochron per unit THT
RLN	Remaining leaf number after hedging
$T_{max}$	Maximum air temperature (°C)
$T_{min}$	Minimum air temperature (°C)
$T_b$	Base temperature (10°C)
THT	Thermal time, degree days (°C day <sup>-1</sup> )
THT day <sup>-1</sup>	Thermal time per day (°C day <sup>-1</sup> )

where  $T_{max}$  and  $T_{min}$  are the daily maximum and minimum temperatures, respectively, and the base temperature,  $T_b$ , is 10°C (Winkler and Williams, 1939; Horney, 1966; Guitierrez et al., 1985). Leaf initiation has been demonstrated to approach negligibly small rates at temperatures below 10° (Schultz, 1989). In the present study the accumulation of THT ( $i=1$ ) was started at phenological Stage 5 according to the Eichhorn and Lorenz (1977) development scale. This stage, hereafter referred to as bud burst, occurs when 50% of the shoots are 2 cm long and their first leaves have unfolded and reached a length of approximately 20 mm. Choosing this stage allowed a defined start-

ing point for following shoot development since leaf length can actually be measured, whereas earlier stages of growth are difficult to quantify.

Temperature data were obtained from the Agricultural Meteorology Experiment Station, National German Weather Service, Geisenheim, located 1500 m and 400 m from the experimental sites (1 and 2, respectively). In California, data were obtained from the National Oceanic and Atmospheric Association (NOAA) Reference Climatological Station operated by the Department of Land, Air and Water Resources, University of California, Davis, located 1000 m from the validation site. Figure 3 shows cumulative (1986–1988) and daily (1986) values of thermal time for Germany and for the 1991 season in California.

*Leaf appearance.* – Grape has a distichous phyllotaxy with alternate leaves (Pratt, 1974). Therefore, the plastochron concept can be used to quantify leaf initiation rate and leaf age (Askenasy, 1880; Erickson and Michelini, 1957). The plastochron index (PI) denotes the number of leaves on a shoot. It is made a continuous function of time by logarithmic interpolation between the leaf indices of the two top leaves at either side of a reference length (Erickson

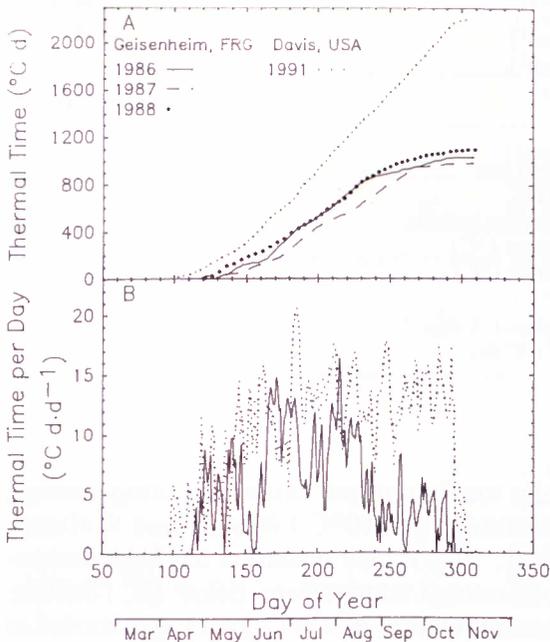


Fig. 3. Accumulation of thermal time, °C day ( $> 10^{\circ}\text{C}$ ); (A) during the 1986, 1987 and 1988 growing seasons in Geisenheim, Rhg., Germany and during the 1991 season in Davis, CA, USA; (B) daily thermal time values for the 1986 season in Germany and the 1991 season in California. Thermal time was calculated beginning at observed bud burst and ending at harvest.

and Michelini, 1957). Based on earlier results with grape, 30 mm was chosen as reference length (Freeman and Kliewer, 1984). Erickson and Michelini (1957) also defined a leaf plastochron index (LPI) which allows the developmental age of all leaves on a shoot to be expressed on a common scale of plastochrons. The LPI of a given node position is calculated

$$\text{LPI} = \text{PI} - i \quad (3)$$

where  $i$  is the number of nodes basipetal to the position in question. Snyder and Bunce (1983) defined a plastochron rate (PR), i.e. plastochron(s) per day, where higher values indicate faster rates of leaf appearance and PR has units of  $\text{PI day}^{-1}$ . Chronological time can be substituted by physiological time to define a plastochron rate as a function of temperature, which was termed plastochron development rate, PDR, thus

$$\text{PDR} = \frac{\text{PI}_{\text{END}} - \text{PI}_{\text{INIT}}}{\text{THT}_{\text{END}} - \text{THT}_{\text{INIT}}} = \frac{d \text{PI}}{dTHT} \quad (4)$$

where  $\text{PI}_{\text{END}}$ ,  $\text{PI}_{\text{INIT}}$ ,  $\text{THT}_{\text{END}}$  and  $\text{THT}_{\text{INIT}}$  are plastochron indices and thermal time values before (INITIAL) and after (END) the time interval in question and PDR has units of plastochrons per degree day,  $\text{PI} \times (^\circ\text{C day})^{-1}$ .

The PDR represents the first derivative, i.e. slope, of the relationship between PI and THT (Figs. 4(A) and 4(B)) and can be calculated for any point during a growing season (Figs. 4(C) and 4(D)). The main assumption was that PDR or its reciprocal, here termed phyllochron,  $(^\circ\text{C day}) \text{PI}^{-1}$ , used

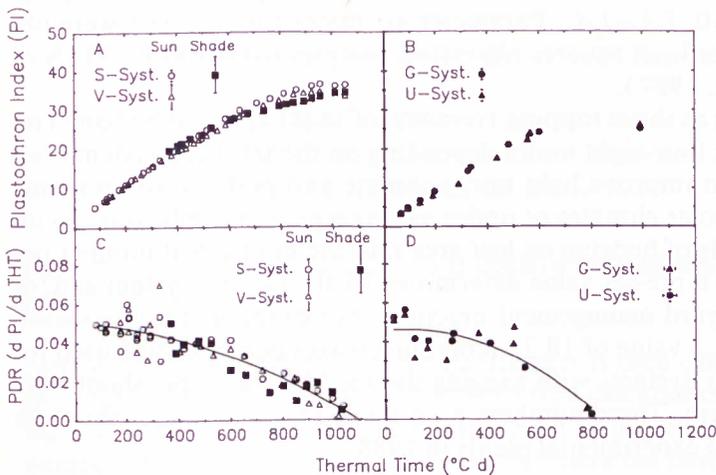


Fig. 4. Relationship of plastochron index, PI, and plastochron development rate, PDR, to thermal time for canopy-systems with upward-oriented shoots during 1988, (A), (C); hanging shoots during 1987, (B), (D). Shoots were not hedged. Lines represent fitted curves of quadratic models. The average standard error for each treatment is indicated.

in some models to denote the heat unit requirement per plastochron (Porter, 1985; Alm et al., 1991), is solely dependent on shoot orientation and physiological time, but is independent of the year. Subsequently, a quadratic model

$$\text{PDR} = a \times \text{THT}^2 + b \times \text{THT} + c \quad (5)$$

was fitted to data grouped according to the main direction of shoot orientation (Fig. 4(C), 4(D)) (Table 3). The consistency of quadratic fits of PDR versus THT in different years was evaluated using an analysis of covariance (ANOCOVA) model that allowed for interactions between parameters of the quadratic and the year (SAS-Statistics package, Statistical Analysis Institute, 1987).

*Individual leaf area development.* – To simulate leaf area development, a sub-model was constructed which could be linked to the plastochron model (eqn. (3)–(4)) and thus be driven by temperature. Leaf area development of groups of 10–22 leaves unfolding at 14 different times during the growing season was followed until maturity for both types of shoot orientation. The shoots studied were not hedged so that leaves unfolding late in the season could be monitored. Leaf area was expressed as a function of LPI using a logistic growth equation:

$$LA = \frac{LA_{\max}}{[1 + (LA_{\max}/LA_0 - 1) \times e^{-\alpha \times \text{LPI}}]} \quad (6)$$

where  $LA_{\max}$  denotes the final leaf size ( $\text{cm}^2$ ), i.e. the upper limit of the growth function,  $LA_0$  is the leaf area ( $\text{cm}^2$ ) at  $\text{LPI}=0$  and  $\alpha$  represents the shape of the curve; if  $\text{LPI}=0$ ,  $LA=LA_0$ . Parameter estimates for eqn. (6) were obtained by non-linear least squares regression analyses using PROC NLIN of SAS (SAS Institute, 1987).

Summer pruning as shoot topping (removal of shoot apex) or hedging (removal of the upper four-eight nodes depending on the trellising system) is a frequent practice to improve light micro-climate and pest control in grapevine canopies in cooler climates or under vigorous growth conditions. To incorporate the effects of hedging on leaf area into the model, leaf number per shoot is reduced to a pre-set value determined by the canopy-system and/or the particular vineyard management practices. For example, for late-season hedging or topping, a value of 18.25 remaining leaves per shoot was used for the G and U canopy-systems with hanging shoots, 15.5 leaves per shoot were used for the S-system. These numbers were the average nodes per shoot on vines other than the experimental plants in 1988.

*Model structure.* – The simulation sequence of the model is outlined in Fig. 5. Inputs required are maximum and minimum air temperature, observed date of bud burst, and date of hedging.

The model calculates the PI to determine the appearance of new leaves. For

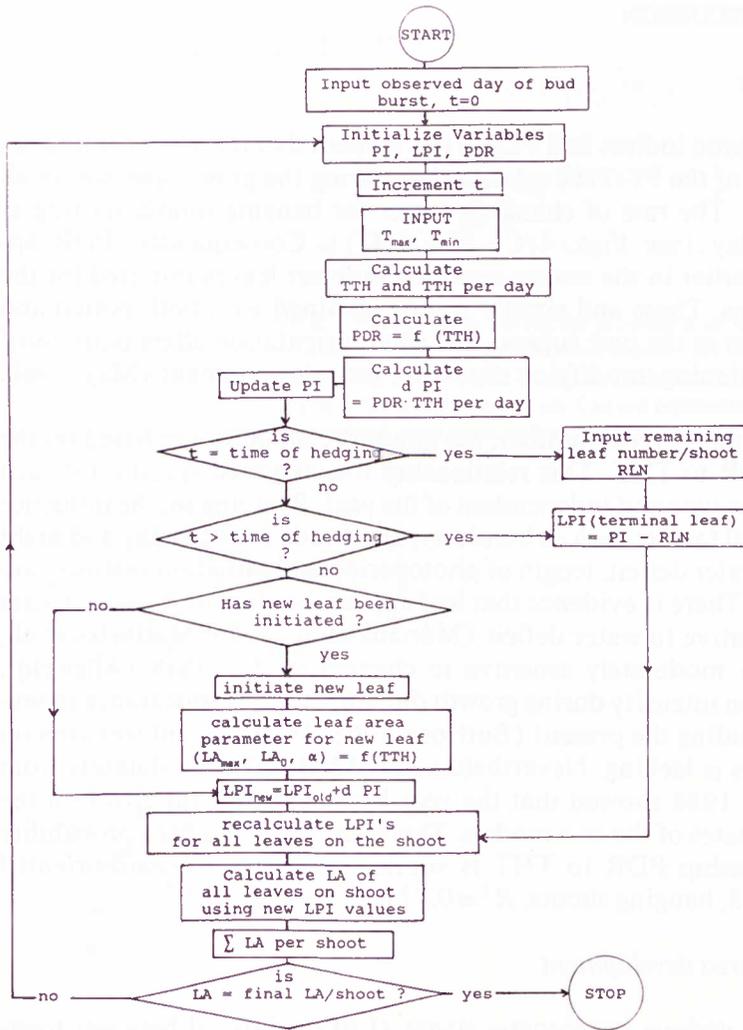


Fig. 5. Flow diagram of the simulation of leaf appearance and leaf area development of primary grapevine shoots.

each leaf a specific set of leaf area parameters is then calculated. At hedging, two routines run in sequence. The model first calculates the PI as if no hedging had occurred, the second retrieves this PI value from the first, deduces the number of remaining leaves (RLN) to calculate the new LPI of the terminal leaf, then 'ages' the other remaining leaves accordingly. Finally the remaining leaf area per shoot is calculated. This hedging subroutine is similar to the one outlined by Williams et al. (1985b) with the major difference being that a certain leaf number instead of dry mass is removed.

## RESULTS AND DISCUSSION

*Leaf appearance*

From plastochron indices and PDR's it is evident that there is a continuous change in slope of the PI-THT relationship during the growing season in all canopy systems. The rate of change is larger for hanging shoots starting at about 500°C day (see Figs. 4(C) and 4(D)). Consequently, PDR approaches zero earlier in the season resulting in fewer leaves initiated for the G and U systems. These and similar results obtained with both potted and field-grown vines in the past suggest that shoot orientation alters patterns of assimilate partitioning, modifying shoot and fruit development (May, 1966; Currie, 1973).

For the prediction of leaf number, the quadratic models were based on the relationship PDR to THT. This relationship was assumed specific for each shoot orientation type and independent of the year. By doing so, the influence of environmental factors such as humidity, amplitude between day and night temperatures, water deficit, length of photoperiod and radiation intensity are largely ignored. There is evidence that leaf appearance rate in *Vitis vinifera* is relatively insensitive to water deficit (Mériaux et al., 1976; Matthews et al., 1987) and only moderately sensitive to changes in daylength (Alleweldt, 1960). Radiation intensity during growth did not alter leaf appearance in several studies including the present (Buttrose, 1968, 1969) but information on the other factors is lacking. Nevertheless, the ANOCOVA on datasets from 1986, 1987 and 1988 showed that the year had no significant effect on the parameter estimates of the two models. Therefore, there is a high probability that the relationship PDR to THT is similar each year (upward-oriented shoots,  $R^2 = 0.78$ ; hanging shoots,  $R^2 = 0.77$ ).

*Individual leaf area development*

Leaf areas at various ontogenetic stages (LPI's) differed between treatments, i.e. shoot orientation, and unfolding times (in THT) (see brackets, Fig. 6(A) and 6(B)). Upright-growing shoots had larger individual leaf areas throughout the season with the exception of leaves appearing very early in shoot development (Fig. 6(A), Fig. 7(A)). For both types of shoot orientation, leaves unfolding at about THT 100 attained the largest final leaf area, (Fig. 7(A)). Thereafter,  $LA_{max}$  decreased continuously (Fig. 7(A)). The other parameters characterizing leaf expansion ( $LA_0$  and  $\alpha$ ) also increased from the beginning of the season until about 100 THT, but showed no consistent pattern thereafter (Figs. 7(B) and 7(C)). Differences in growth duration were the main cause of differences in size, since expansion rates in the linear growth phase were similar for leaves unfolding at similar THT's over

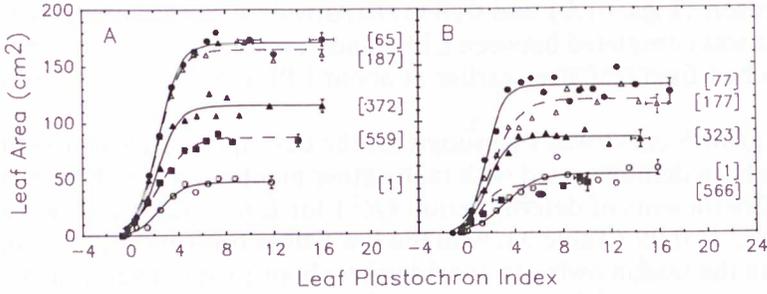


Fig. 6. Area of leaves unfolded at different times during the growing season at different ontogenetic stages (leaf plastochron indices): (A) upright-oriented shoots; (B) hanging shoots. Thermal time values, °C day, at unfolding are given in brackets. Each datum is the mean of measurements on 10–22 leaves, each from a different shoot. Curves represent model calculations from eqn. (8). Two times the standard error is given for each leaf type at the end of the curves.

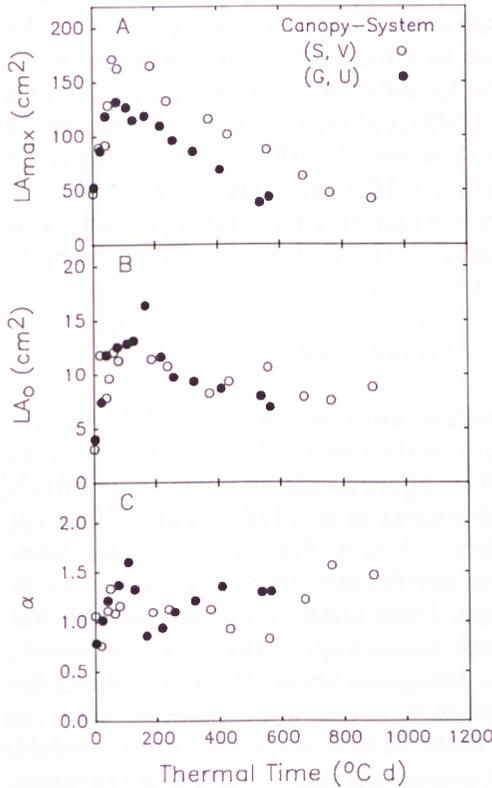


Fig. 7. Estimated parameter values of the logistic growth equation for leaves of different unfolding times and different shoot orientations. Canopy-system S and V represent upright-oriented shoots, G and U represent hanging shoots.

most of the season (Figs. 6(A) and 6(B)). Expansion of leaves on upright growing shoots was completed between LPI 6 and 7, whereas leaves on hanging shoots reached final leaf sizes earlier at about LPI 4–5 (Figs. 6(A) and 6(B)).

The logistic growth curve was well suited for the description of leaf growth in grape as has been demonstrated with many other plants (Charles-Edwards et al., 1986). Coefficients of determination ( $R^2$ ) for  $LA_{\max}$ ,  $LA_0$ ,  $\alpha$  (Fig. 7) ranged from 0.73 to 0.99 (Table 3), with the low values for leaves appearing early and late in the season owing to considerable shoot-to-shoot variability.

There are various simplifying assumptions involved in expressing leaf expansion solely based on the sequence of emergence on single shoots and physiological time. This implies that final leaf size, growth rate and growth duration are largely independent of temperature experienced which is true for some plants (Dale, 1982) but not for others (Friend and Pomeroy, 1970). Generally, final leaf size increases with increasing growth temperature up to an optimum (Monteith, 1979) but ontogenetic changes may override such a relationship (Dennet et al., 1979). Ontogenetic size gradients for leaves of the grape shoot similar to the results shown here have been demonstrated for different varieties in different climates and for different shoot orientations (Vereš and Valachovič, 1975; Kliewer et al., 1989) and may be related to changes in assimilate partitioning and hormonal relations (Currle, 1973) causing alterations in cell number at the apical meristem (Ong and Baker, 1985).

Final leaf size can also be altered by low light intensity during growth (Fitter and Hay, 1983), however at present there is no simple way to implement adaptive processes of this detail into the model.

### *Simulation of leaf appearance and leaf area per shoot*

In contrast to other grape growth models (Guitierrez et al., 1985; Crespin et al., 1987), the one presented here requires the observed date of bud burst as an input. By using variety-specific values of accumulated degree days after a certain calendar date as parameters, Guitierrez et al. (1985) and Williams et al. (1985a) predicted bud break within  $\pm 3$  days. Pouget (1967) and Swanepol et al. (1990) calculated cultivar coefficients for both cold and warm climates in order to predict bud break from temperature summation but pointed out that considerable variation depending on the clone, rootstock, vigor, trellising system and time of pruning can occur. It was therefore decided to focus on the time after bud break to avoid obscuring simulation results of leaf area formation with lack of fit of bud break prediction models. Nevertheless, eventually a bud break prediction routine has to be incorporated to make the model independent of phenological observations.

The plastochron sub-model was tested using data on leaf appearance rates collected in 1987 and 1986 (Fig. 8). Note that for upright-growing shoots

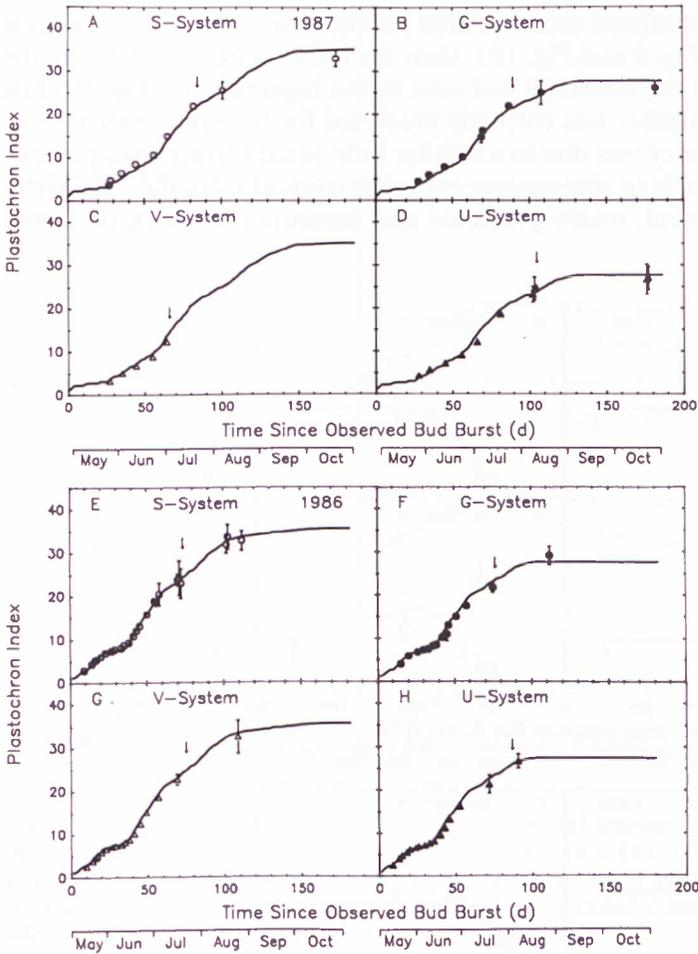


Fig. 8. Observed (symbols) and predicted (lines) plastochron indices for primary shoots of four canopy-systems for the 1987, (A), (B), (C), (D); and 1986, (E), (F), (G), (H), growing season. Each datum represents the mean  $\pm 2 \times$  SE of 40–64 measured shoots. Arrows indicate time of hedging.

both years constitute independent datasets (model was developed based on 1988 data), whereas for hanging shoots only the 1986 data can be considered independent (model was developed based on a 1987 dataset). For both years the model predictions closely tracked the observed data for all four canopy-systems. It closely described fluctuations in leaf appearance as reflected by PI owing to low or high temperature periods, such as in 1986, when cool temperatures (around  $10^{\circ}\text{C}$ ) slowed development considerably between Day 25 and 40 (Figs. 8(E)–8(H)).

Simulation runs of the complete leaf area prediction model for all canopy-

systems accurately predicted total leaf area per shoot before and after hedging in all but one case (Fig. 9 and Fig. 10). Only for the U-system in 1987 did the model overestimate the observed leaf area at the beginning of August (Fig. 9(D)). Since leaf number was correctly predicted for the same system (Fig. 8(D)), the discrepancy was due to a smaller individual surface area per leaf. That this is not specific to this canopy-system is evident from the 1986 dataset for the same system, where predicted and measured leaf area per shoot agree well.

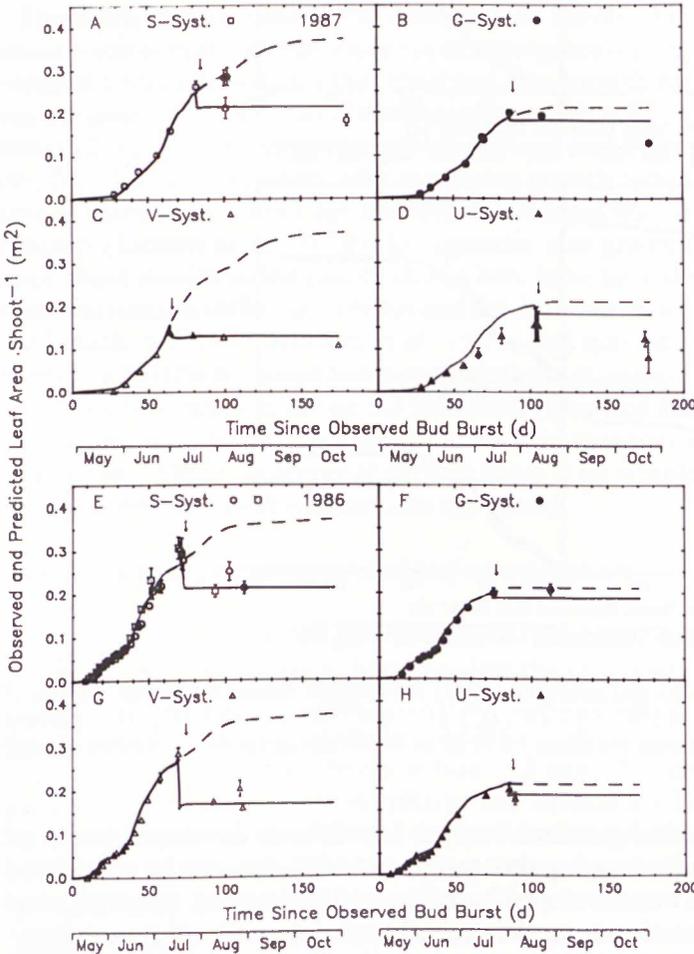


Fig. 9. Observed (symbols) and predicted (lines) leaf area per primary shoot of four canopy-systems for the 1987, (A), (B), (C), (D); 1986, (E), (F), (G), (H), growing season. Dashed and solid lines represent model predictions for unhedged and hedged shoots, respectively. Each datum represents the mean  $\pm 2 \times$  SE of 40–64 measured shoots. Note that two datasets from two different locations are shown in (E). Arrows indicate time of hedging.

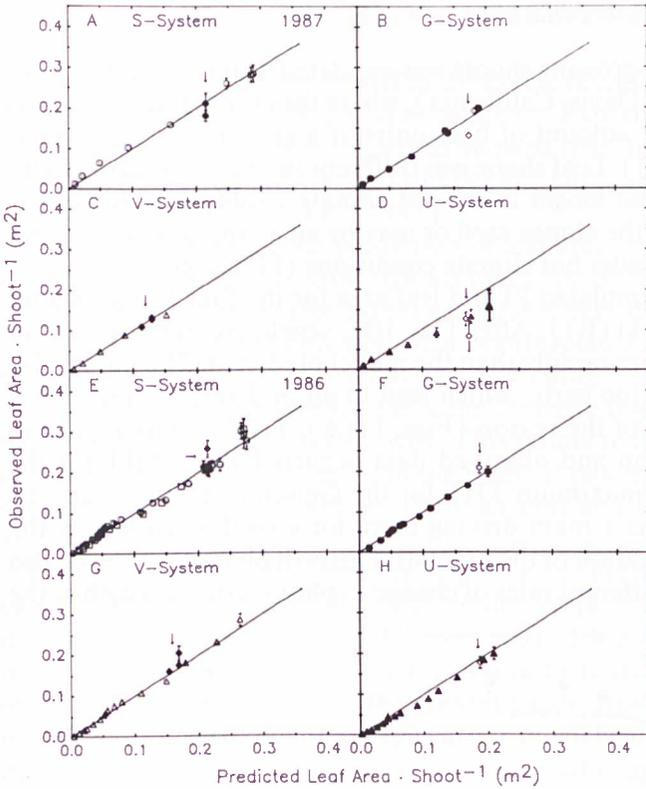


Fig. 10. Relationship between observed and predicted leaf area per primary shoot of four canopy-systems for the 1987, (A), (B), (C), (D); 1986, (E), (F), (G), (H), growing season. Lines represent a 1:1 relationship. Each datum is the mean  $\pm 2 \times$  SE of 40–64 measured shoots. Note data collected after hedging are shown as open or closed symbols (diamonds). Arrows additionally indicate the location of these data points.

For the S-system in 1986, datasets from the two different vineyard locations were used for testing the model. Despite the differences in vine spacing between the two locations (see Table 1), leaf area development was not different and was well approximated by the model (Fig. 9(E)). This indicates that single shoot vigor did not respond to an increase from 18 to 30 buds per vine (20 to 32 shoots per vine), which reflects the range of common pruning levels in Germany for the S-system.

The consistent overestimation of leaf area per shoot late in the 1987 season (Fig. 9(A)–9(D)) was due to leaf fall and indicates the need to account for this in future versions of the model. Nevertheless, agreement between simulated and measured leaf area was generally very good (Fig. 10).

### Validation under hot climate conditions

The model for upright-growing shoots was validated against a dataset from a hot, dry environment (Davis, California), where the crop typically receives approximately twice the amount of heat units of a growing season in Germany (see also Fig. 3(A)). Leaf shape was different in the two locations with laminae being thinner and longer in the hot climate (Table 3). This difference may be inherent to the clones used or may be an adaptation to improve the leaf energy balance under hot climate conditions (Ehleringer, 1989).

The model correctly simulated PI and leaf area for the first 100 days after budburst (Figs. 11(A), 11(B)). After Day 100, vegetative development of the plants progressed more rapidly than the model predicted. The model also stopped leaf production too early, which lead to an underestimation of leaf area during the late part of the season (Figs. 11(A), 11(B)). Discrepancies between model prediction and observed data occurred when THT for the Davis site exceeded the maximum THT for the Geisenheim site suggesting that temperature remains a main driving force for growth even late in the season. However, the duration of the vegetative growth phase could have also been influenced by the different rates of change in photoperiodic length at the

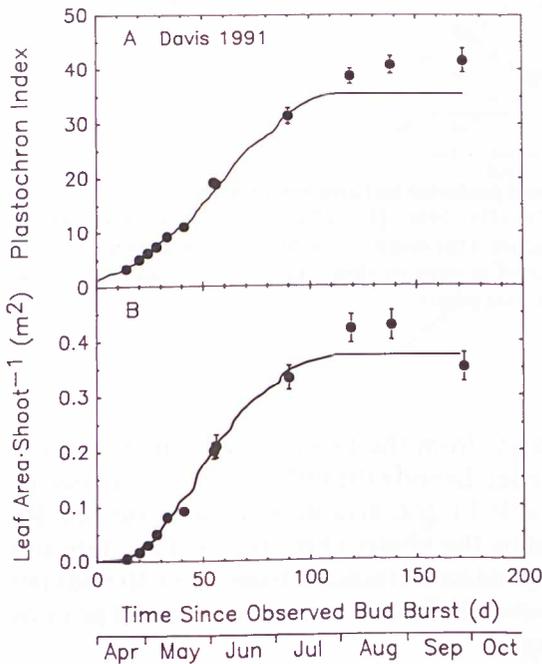


Fig. 11. Simulation run on a 1991 dataset from a hot dry environment (Davis, CA, USA). Observed (symbols) and predicted (lines), (A) plastochron indices for upright-growing primary shoots; (B) leaf area per shoot. Each datum represents the mean  $\pm 2 \times$  SE of 27 measured shoots.

two locations (Hodges and Ritchie, 1991) or by differences in vine vigor (Winkler et al., 1974).

In order to calibrate the model to the Davis situation, PDR or phyllochron ( $1/\text{PDR}$ ) values would have to be adjusted. Experience with models of agronomic crops and competing weeds showed that different phyllochron values have to be used for different latitudes and cultivars (Porter, 1985; Hodges and Ritchie, 1991; Alm et al., 1991).

It is remarkable that the prediction of leaf area formation solely based on temperature is possible with high accuracy for different years within a climatic region and to a large extent even for a very different climate. On the other hand, the onset of phenological events related to the fruit after bloom, such as veraison (fruit coloration, fruit softening), differed by as much as 70 °C day between years within the same climatic region and by 260 °C day between climates (data not shown). This points to other factors gaining importance on fruit development in the interval bloom to ripeness as has been suggested previously (Coombe, 1973; Klenert and Rapp, 1985; Williams et al., 1985a).

Problems can be anticipated in applying the model to other varieties because of the large genetic disparity among grape-cultivars and the inherent differences in development (McIntyre et al., 1982). Additionally, development may also be influenced by the choice of rootstock and canopy-system other than those dealt with in the present paper. However, once an algorithm is created for the growth of a grape variety it will be useful because of the long life span (25–40 years) of grapevines compared to agronomic crops.

Lateral leaves can make up from 10 to more than 50% of the final leaf area per vine depending on the canopy-system and management (hedging) practices (Williams, 1987; Wermelinger and Koblet, 1990). Thus, a model to describe lateral shoot growth is needed. However, modelling of lateral branch or shoot initiation and growth has not been well developed, particularly because of mostly irregular growth habits. There are only few crop models dealing with this issue (Wilson, 1975; Baker et al., 1981; Hodges and Ritchie, 1991).

Whereas shoot and leaf growth in production models are usually based on dry matter accumulation (Curry et al., 1975; Guitterez et al., 1985), the present models describe leaf area development. Leaf surfaces are the primary site for light interception and photosynthesis and leaf area and its distribution are important in determining the light environment in the canopy. Although leaf distribution has not been addressed in this paper, knowledge of leaf area expansion allows leaf area-based photosynthesis and respiration models of sun and shade shoots (Schultz, 1989) to be linked to the growth model. Finally, descriptive translation techniques using morphological response functions for converting increments in size to increments in dry weight can be used to con-

sider dry weight partitioning and hence, develop a dry weight production model (Loomis et al., 1979).

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