Shoot Development in Grapevine (Vitis vinifera) is Affected by the Modular Branching Pattern of the Stem and Intra- and Inter-shoot Trophic Competition

ERIC LEBON1, *, ANNE PELLEGRINO2, FRANCOIS TARDIEU1 and JEREMIE LECOEUR1

1Institut National de la Recherche Agronomique – École Nationale Supérieure Agronomique, Laboratoire d’Écophysiologie des Plantes sous Stress Environnementaux, UMR 759, INRA–ENSA.M, 2 place Viala, 34060 Montpellier Cedex 01, France and 2Centre de coopération Internationale en Recherche Agronomique pour le Développement–École Nationale Supérieure Agronomique–Institut National de la Recherche Agronomique, Fonctionnement et Conduite des Systèmes de Cultures Tropicaux et Méditerranéens, UMR 1123, CIRAD–ENSA.M–INRA, TA 179/01, Avenue Agropolis, 34398 Montpellier Cedex 05, France

Received: 25 August 2003 Returned for revision: 15 October 2003 Accepted: 25 November 2003 Published electronically: 28 January 2004

INTRODUCTION

Leaf area plays a key role in determining crop productivity, by controlling the interception of solar radiation (Monteith, 1977). Analysis of plant development is therefore vital if we are to understand the response of plants to their environment and to optimize farming practices. In addition to this direct connection between intercepted solar radiation and plant leaf area, plant architecture may also affect the microclimate surrounding individual organs (temperature, radiation, humidity), with major consequences for fruit ripening and harvest quality (Smart, 1985; Jackson and Lombard, 1993; Dokoozlian and Kileweer, 1996; Mabrouk and Sinoquet, 1998). A thorough knowledge of the quantitative aspects of shoot development is therefore necessary to understand the determination of crop quality and productivity as a function of environment. For example, the duration of branch or individual leaf development is essential for analysis and prediction of the effect of environmental conditions such as soil water deficit on leaf number and leaf area (Lecoeur et al., 1995; Belaygue et al., 1996).

Previous studies have attempted to analyse and predict the establishment of plant architecture by combining four variables: (1) the number of main shoots; (2) the branching rate of these main shoots; (3) the rate of leaf production on all axes; and (4) the rate of expansion of individual leaves. The relative contributions of these variables to plant architecture depend on the species considered. In most woody species [peach tree (Prunus persica), Pagès et al. 1993; kiwi-fruit (Actinidia delicosa), Seleznyova et al., 2002] and in herbaceous indeterminate species [white clover (Trifolium repens), Belaygue et al., 1996; pea (Pisum sativum), Turc and Lecoeur, 1997], plant leaf area depends more heavily on leaf number than on individual leaf area. In contrast, most single-stem species, such as sunflower (Helianthus annuus) and maize (Zea mays), plant

* For correspondence. E-mail lebon@ensam.inra.fr
leaf area depends on individual leaf area because the number of leaves is determined genetically.

In grapevine, like most deciduous woody plants, the current season’s growth consists of shoots growing from latent buds produced during the previous cycle and made up of five to nine phytomers (Huglin, 1958). The number and position of these latent buds are artificially determined by pruning. The stem, which has an indeterminate growth pattern, consists of a succession of elementary modules, each comprising three phytomers (Jaquinet and Simon, 1971; Huglin, 1986). The leaves on the branches account for 10–50 % of the plant leaf area, depending on the training system, plant vigour, pruning intensity and genotype (Williams, 1987; Mabrouk et al., 1997; Palliotti et al., 2000). The effects of these multiple factors on shoot development result in considerable variability in plant architecture in grapevine. Very few quantitative studies have been carried out on shoot development in grapevine, and even fewer have considered branching (Schultz, 1992).

The development of crop plants has classically been analysed and modelled using thermal time (Ritchie and Nesmith, 1991; Bonhomme, 2000). This approach is based on the assumption that responses to air temperature in terms of primordia initiation and leaf production are linear over a wide range of air temperatures. In most previous studies, thermal time has been calculated by integrating air temperature and subtracting a threshold or base temperature, assuming air temperature to be representative of that surrounding the meristems or expanding leaves. Published results suggest that there is a single base temperature for all developmental processes, at least in pea (Turc and Lecoeur, 1991; Mabrouk et al., 1997; Palliotti et al., 2000). The effects of these multiple factors on shoot development result in considerable variability in plant architecture in grapevine. Very few quantitative studies have been carried out on shoot development in grapevine, and even fewer have considered branching (Schultz, 1992).

The development of plant material and growing conditions

A wide range of growing conditions in terms of temperature and plant growth was obtained by carrying out four experiments on grapevine, Vitis vinifera L., cultivar ‘Grenache N’, two of them in pots in a glasshouse and outside at the ENSA.M–INRA campus in Montpellier, in the south of France (43°38’N, 3°53’E), and two in a vineyard near Montpellier (43°49’N, 3°54’E).

Pot experiments

In 1999 (expt 1) and 2000 (expt 2), 4- to 5-year-old plants of ‘Grenache N’ (clone 226) grafted onto the rootstock ‘Fercal’ were grown in large pots (0.30 m in diameter and 0.70 m high) in a glasshouse. In expt 2, the pots were removed from the glasshouse at the beginning of plant measurements. This second experiment was designed to ensure that air temperatures were low at the beginning of the plant cycle, resulting in lower mean air temperatures than in other experiments. The pots were filled with a 7 : 2 : 1 mixture of topsoil, sand and organic compost. This soil mixture was covered with a 0.01 m layer of perlite to limit soil evaporation. Plants were pruned before bud burst such that two or three latent buds per plant were retained. The reproductive organs were eliminated as soon as they appeared. At the ‘5 separated leaves’ stage (stage 12 according to the modified Eichron and Lorenz scale; Coombe, 1995), the plants were thinned to two branches and were trained vertically.

Soil water content was measured daily with a time domain reflectometry (TDR) device (Trase System 1; Soil Moisture Equipment Corp., Santa Barbara, CA, USA) following the manufacturer’s instructions. A 0.6-m-long stainless steel guide was installed vertically in each pot. TDR measurements of soil water content were compared with simultaneous direct measurements of soil water content on soil cores from a set of additional pots in both of the pot experiments. Analysis of the regression between indirect and direct measurements of soil water content resulted in a correlation of \( r^2 = 0.920 \) and a slope and an x-intercept that did not differ significantly from 1 and 0, respectively. The pots were irrigated daily with Hoagland N/5 nutrient solution, the pH of which was adjusted to 5.5 with HNO₃, resulting in a final [NO₃] of 2.8 mol m⁻³. Transpirable soil water content was maintained above 75 % of pot capacity. This value is much higher than the thresholds of 25–35 % (Sinclair and Ludlow, 1986) or 40 % (Lecoeur and Sinclair, 1996) below which transpiration and organ expansion are reduced. The pre-dawn leaf water potential of six leaves per treatment was measured using a pressure chamber (no. 3000; Soil Moisture Equipment Corp.).

Air temperature and relative humidity (RH) were measured with a capacitive hygrometer (HMP35A...
Vaisala; Oy, Helsinki, Finland) protected from direct radiation and placed at a height of 1.5 m (expt 1) or 2.5 m (expt 2) from the soil. Photosynthetic photon flux density (PPFD) was measured using silicon cells calibrated in situ with a PPFD sensor (LI-190SB; LI-COR, Lincoln, NB, USA). This device was placed in the middle of the collection of pots. Temperature, PPFD and RH data were collected every 30 s, and means were calculated and stored every 1800 s in a Datalogger (CR10 Wiring Panel; Campbell Scientific Ltd, Shepshed, Leics, UK).

Field experiments

Two experiments were carried out in a vineyard over 2 consecutive years, 1999 (expt 3) and 2000 (expt 4). ‘Grenache N’ (clone 70) grafted onto the rootstock ‘110 Richter’, planted in 1987, was used. The clay loam soil was <1 m deep and contained >60 % stones. Plant density was 0.432 plants m⁻² and the row spacing was 2.35 m. The training system was a short-pruned espalier. The only difference between these two experiments was the crop load, which was managed to analyse the possible effects of berry growth on shoot development. The reproductive organs were retained in expt 3, but were eliminated as soon as they appeared in expt 4. Data were obtained from three replicates of 20 plants. These plots were equipped with drip irrigation on each row and were watered daily. Pre-dawn leaf water potential was also measured once per week on six leaves per plot. In expt 3, air temperature and PPFD were measured with an automatic standard weather station placed at the centre of the field (Pulsonic; Pulsia, Orsay, France). Data were collected every minute and daily means were calculated. In expt 4, the procedure described in expt 1 was used for the measurement and collection of climatic data.

Plant measurements (Table 1)

**Primordium initiation and leaf appearance.** The number of initiated primordia in the apical bud was determined once a week in expt 4. After counting the number of expanded leaves, six shoot tips were immediately placed in storage at 4 °C. The shoot tips were dissected and the initiated primordia were counted up to the meristem under a stereomicroscope (Leica stereomicroscope, wild F8Z; Leica, Wetzlar, Germany) at a magnification of 80×. The numbers of expanded leaves were counted at 3- to 4-d intervals on six shoots in expt 1 and 12 shoots in expt 2, and weekly on nine shoots in expts 3 and 4. The number of expanded leaves on each branch was determined in expts 1, 3 and 4, following the procedure used for the main stem.

The rate of leaf appearance was calculated over short periods (9–15 d) by linear regression between the time in days and the number of produced but unfolded leaves. Three or five consecutive measurements were used in order to generate sufficient data for the fitting of curves with Table Curve 2D (Jandel Scientific Software, Erkrath, Germany).
Leaf area and internode length. Individual leaf areas were estimated from a quadratic relationship between the length of the leaf lamina and the corresponding leaf area, as described by Schultz (1992). The parameters of the relationship were estimated for our experiments from an independent set of 93 leaves, collected from additional plants in expt 3 (LA = 0.0075L^2 + 0.07505L - 29.151, \( r^2 = 0.901 \)). The leaf lamina lengths and leaf areas were measured on each leaf by image analysis (Optimas V6.5; Media Cybernetics, Silver Spring, MD, USA). In expt 3, the final length of all the leaves was measured on six main stems, using a graduated ruler, in order to estimate the leaf area of the main stem. In expts 1 and 4, the lengths of all the leaves on the main stem were measured on six shoots, at 2- to 4-d intervals. For each phytomer position on the main stem, estimated leaf area was plotted against thermal time from leaf appearance. Final leaf area, leaf expansion duration and maximum leaf expansion rate (LER) were estimated by non-linear least-square regression of the change in leaf area with thermal time, using Table Curve 2D, as follows:

\[
\text{Leaf area} = \frac{a}{1 + \exp\left(4c\left(\frac{b - \text{CDD}}{a}\right)\right)}
\]

where \( a \) is the asymptote corresponding to final leaf area, \( b \) is the x-value at the inflexion point corresponding to the midway point in the duration of leaf expansion, and \( c \) is the maximal slope at the inflexion point, corresponding to maximal LER. CDD is thermal time from leaf initiation, calculated as the sum of the daily differences between mean air temperature and a base temperature of 10 °C and expressed in cumulative degree-days (Bonhomme, 2000). The values and confidence intervals of these parameters were estimated with Table Curve 2D. No \( r^2 \) was lower than 0.900 and no coefficient of variation of error was higher than 10%.

In expts 1, 3 and 4, final internode length was measured on all the phytomers of six main stems, using graduated rulers.

Determination of the modular structure of the stem. In expts 1, 3 and 4, the modular structure of the stem was analysed on the first 25 phytomers that had completed their development. The modular structure was built up from three types of phytomer (Fig. 1). The first phytomer of the repeated structure (P0) carried no tendril, whereas the second (P1) and third (P2) phytomers carried tendrils in alternate positions (Jaquinet and Simon, 1971; Huglin, 1986). Phytomers were identified according to their relative positions in an elementary module of three phytomers. All plant measurements were then classified and analysed according to the type of phytomer.

Estimation of base temperature and calculation of thermal time. Grapevine base temperature was estimated by linear regression between air temperature and rate of unfolded leaf production, as follows:

\[
\text{LAR} = aT_m + b
\]

where LAR is the rate of unfolded leaf production (leaf d^{-1}), \( T_m \) is the mean air temperature during the calculation period (°C), \( a \) is the slope and \( b \) is the x-intercept. The base temperature \( (T_b) \) was calculated as the ratio \( -b/a \). The rate of unfolded leaf production, \( a \) and \( b \) were estimated with Table Curve 2D.

Thermal time was calculated by daily integration of air temperature minus the base temperature:

\[
\text{CDD} = \int \max(0; (T_m - T_b)) \, dt
\]

where CDD is thermal time expressed in cumulative degree-days.
Durations and rates were then calculated in thermal time, by substituting thermal time for time in the corresponding analyses and equations.

Statistical analysis

The ANOVA/MANOVA procedure of Statistica 6.0 (Statsoft, Tulsa, OK, USA) was used to test for significant differences between means. To test differences of slopes and of intercepts of linear regressions among data sets, SSi (summation of the residual sums of squares for the individual fitting of each data set) was compared with SSC (residual sum of squares for the common fitting to the whole data set) using the statistic

$$F = \frac{|SSC - \sum_{i=1}^{n} SSi| / ((n - 1)k)}{\sum_{i=1}^{n} SSi / (N_{data} - k)}$$

which follows Fisher’s law with (n - 1)k and (Ndata - k) degrees of freedom. Ndata is the total number of data points, n is the number of individual regressions and k is the number of fitted parameters for each regression. The adjustments were made using Table Curve 2D 5.01 (SYSTAT Software Inc., Richmond, CA, USA). To compare the frequency distributions in the rate of leaf production on branches, we used the Kolmogorov–Smirnov test of the Nonparametrics procedure of Statistica 6.0.

RESULTS

Variability of observed plant architectures

The plants were subjected to a broad range of environmental conditions over the four experiments (Table 2). However, none of the plants experienced soil water deficit because mean pre-dawn leaf water potential did not fall below −0.1 MPa in any of the experiments. Mean diurnal air temperature ranged from 9.0 °C in expt 2 to 26.6 °C in expt 4. Daily cumulative photosynthetic photon flux density (PPFD) was the most variable microclimate parameter, with diurnal values ranging from 2.5 mol m⁻² d⁻¹ in expt 1 to 61.1 mol m⁻² d⁻¹ in expt 4. Mean daily cumulative PPFD in expt 1, which was carried out in a glasshouse, was less than half that in the other experiments. The range of daily mean vapour pressure deficit (VPD) was similar in pot and field experiments. Maximal daily mean VPD was about 30 % higher in expt 2 as in expt 1, and twice as high in the field (expts 3 and 4).

Major differences in plant architecture at the end of the experiments were observed (Table 3). Some of this variability may result from the imposed numbers of shoots and clusters. This made it possible to rank our experiments in terms of trophic competition between shoots. Levels of trophic competition were probably lowest in expt 1, with only two shoots per vine and no cluster, intermediate in expt 4, with 12 shoots per vine and no cluster, and highest in expt 3, with 12 shoots per vine and cluster development. This ranking for trophic competition correlates with rankings for architectural variables, except for the number of leaves on the main stem (Table 3).

The number of leaves on the main stem was similar in all experiments, but the number of leaves on branches differed significantly, ranging from 53 in expt 3 to 107 in expt 1. Mean individual leaf areas differed significantly between experiments, resulting in differences in total shoot leaf area. Total shoot leaf area increased exponentially over time from budbreak to the end of the experiment (Fig. 2). During the first third of the experiment, most of the shoot leaf area consisted of leaves of the main axis. The leaf area of the main stem increased almost linearly from the moment at

| Expt | Harvest time (degree-days) | Leaf number on main shoot | Leaf no. on branches | Ratio of leaf no. on branches to main stem | Main stem leaf area (m²) | Branch leaf area (m²)
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>618</td>
<td>29.7a</td>
<td>107.0a</td>
<td>3.60</td>
<td>0.518a</td>
<td>0.777 ± 0.075</td>
</tr>
<tr>
<td>3</td>
<td>603</td>
<td>28.3b</td>
<td>53.5b</td>
<td>1.89</td>
<td>0.280b</td>
<td>–</td>
</tr>
<tr>
<td>4</td>
<td>685</td>
<td>30.3b</td>
<td>65.7b</td>
<td>2.17</td>
<td>0.348b</td>
<td>–</td>
</tr>
</tbody>
</table>

Values followed by different letters are significantly different (P < 0.05).
which the first leaves reached their final area, for at least 60 d. The proportion of leaves corresponding to secondary axes increased exponentially from day 100, and corresponded to more than half the plant leaf area by the end of the experiment.

Determination of base temperature

A wide range of mean air temperatures was obtained over periods of 9–15 d in the four experiments: from 13-0 to 23-8 °C (Fig. 3). This range encompasses the range of instantaneous air temperatures generally encountered by plants during the cycle. The estimated slopes and intercepts of the linear relationship between the leaf appearance rate and the air temperature of the four data sets corresponding to the four experiments were not significantly different at $P = 0.05$ ($F_{6,368} = 1.22$). A single relationship could be used to describe the change in leaf appearance rate with the air temperature whatever the environmental conditions experienced by the plants. The corresponding rates of unfolded leaf production ranged from 0.097 to 0.770 leaves d$^{-1}$. The linear relationship between mean air temperature and rate of unfolded leaf production can be written as follows:

$$LAR = 0.0430T_m - 0.3946 \quad (r^2 = 0.837, P < 0.0001)$$

The estimated base temperature, $T_b$, was 9.2 ± 0.5 °C. This base temperature is slightly lower than the 10 °C generally used for grapevine (Winkler et al., 1974; Jackson and Cherry, 1988). However, it was considered that the difference between the two estimates was small enough for the standard value of 10 °C to be used in our analysis. This small discrepancy in estimating $T_b$ may result from the high proportion of temperatures close to 10 °C in our data set. It has been shown that estimations of $T_b$ tend to decrease when using low temperatures because of the slight curvilinear tendency of the relationship between plant development and temperature close to $T_b$ (Bonhomme, 2000).

Stable linear relationships between thermal time and the production of leaf primordia, unfolded leaves and fully expanded leaves results in a thermal time-based programme of leaf development on the main stem

The numbers of initiated leaf primordia ($N_{fi}$), unfolded leaves ($N_{fu}$) and fully expanded leaves ($N_{fe}$) were linearly related to the number of cumulative degree-days from budbreak (CDD) (Fig. 4). The three linear relationships applied to data obtained both in the glasshouse and in the field. Greater variability, on both sides of the regression line, was observed for the unfolded leaf stage than for the two other stages. This greater variability may be related to the way in which estimates were made for the unfolded leaf stage. This stage was estimated by eye, whereas initiation is a distinct anatomical event and the end of expansion is statistically determined. The following equations relate to the production of leaves at the three stages:

$$N_{fi} = 0.050CDD + 7.85 \quad (r^2 = 0.993, P < 0.0001)$$

$$N_{fu} = 0.046CDD + 0.36 \quad (r^2 = 0.986, P < 0.0001)$$

$$N_{fe} = 0.038CDD - 5.27 \quad (r^2 = 0.991, P < 0.0001)$$

The combination of the three relationships produce a diagrammatic representation of leaf development on the
main stem (Fig. 4). As the rate of production of fully expanded leaves was lower than the rate of production of leaf primordia, the duration of leaf expansion increased with phytomer position on the main stem. For example, the duration of leaf expansion was 366 and 425 degree-days for the phytomers at positions 10 and 20 on the main stem, respectively.

Differences in individual leaf area between glasshouse and field experiments are due to differences in leaf expansion rate and not to differences in the duration of leaf expansion.

The final leaf area on the main stem was significantly lower in field experiments (expts 3 and 4) than in the glasshouse (Fig. 5A). However, the pattern of the change in individual leaf area with phytomer position was similar in all experiments. Differences between the two field experiments were observed after the 15th leaf had expanded, corresponding to the period of rapid berry growth.

The duration of leaf expansion, expressed in thermal time, was similar in all experiments and seemed to depend on position of the phytomer on the stem, although this trend was not significant (Fig. 5B). From the base of the shoot to the tenth phytomer, the duration of leaf expansion tended to increase by approx. 25 degree-days with position on the main stem. Then there was a smaller increase of approx. 5 degree-days for subsequent phytomers.

Maximal leaf expansion rate (LER) showed the opposite trend, decreasing steadily with leaf position after the fifth phytomer (Fig. 5C). It was lower in the field than in glasshouse experiments for all phytomer positions. The differences were significant for 14 of the 23 phytomers studied ($P < 0.05$).

Shoot architecture is strongly related to the modular structure of the main stem.

The final characteristics of the shoot may be analysed by dividing the stem into two parts: a proximal part, corresponding to the first eight phytomers, and a distal part, corresponding to the remaining phytomers (Fig. 6). Internode length tended to increase until phytomer 12 and then fluctuated around a mean value of 100 mm (Fig. 6A). For the distal part of the stem, the repeated ternary structure (Fig. 1) influenced the internode lengths and branch development of successive phytomers. The elementary modules of the pre-existing part of the stem were not regular. The internodes of P0 phytomers were shorter and presented more developed branches in terms of leaf number than did the other types of phytomer (Fig. 6A and B). The internodes of P2 phytomers were longer, with short branches. P1 phytomers had intermediate internode lengths but branches of similar length to P2 phytomers.

The rate of unfolded leaf production on a branch depends on the position of that branch in the modular structure of the main stem and on growing conditions.

Branches derived from P0 phytomers (R0) presented higher rates of unfolded leaf production than did branches derived from P1 and P2 phytomers (R1 and R2) of the same modular unit (Fig. 7). We therefore distinguished two types
of branch in our analysis of branch development: R0 and R1/R2, which were pooled because they were not significantly different. In contrast to what was observed for the main stem, the rate of production of unfolded leaves ($N_{fu}$) was not linearly related to thermal time from bursting of the corresponding axillary bud (Fig. 7). Rates of unfolded leaf production were highly variable and similar to or lower than those of the main stem. These rates were affected by growing conditions because $N_{fu}$ was much lower in the field (expt 4) (Fig. 7B and D) than in the glasshouse (expt 1) (Fig. 7A and C) for thermal times from budbreak exceeding 100 CDD.

$N_{fu}$ at a given thermal time was highly variable in all experiments. This variability in $N_{fu}$ resulted from large variability in the rate of unfolded leaf production. Therefore the rate of unfolded leaf production was not analysed in terms of mean traits, but instead frequency distributions were considered for short successive periods of thermal time for each type of branch (Fig. 8).

During the first 100 CDD, there were no significant differences in the distribution rate of unfolded leaf production in the glasshouse and in the field, except for the R0 branches in expt 1 which were significantly higher ($P < 0.05$). These rates were significantly lower than the corresponding rate for the main stem, except for the fastest R0 branches. The frequency distribution was normal ($P = 0.05$), indicating uniform behaviour.

During the second 100 CDD period (Fig. 8B and E), the rate of unfolded leaf production decreased significantly ($P < 0.05$), except for R0 branches in expt 1, for which it remained stable. Furthermore, the frequency distribution remained normal in expt 1 ($P < 0.05$), whereas it was no longer normal in expt 4 with development stopping completely in about 15% of the branches. This indicated that the branches could no longer be considered as a homogeneous population in expt 4.

During the third 100 CDD period (Fig. 8C and F), major differences were observed in the behaviour of branches in the glasshouse and in the field. In expt 1, the mean rate of development of the R0 population slightly increased as compared with the first period ($P < 0.05$), with 25% of these branches having rates similar to those of the main stems. On the other hand, R1 and R2 branches showed a significant tendency to develop more slowly ($P < 0.05$), with an increase in the proportion of branches that stopped growing. In expt 4, all branches developed significantly more slowly ($P < 0.05$), and up to 25% of the R0 branches and 50% of the R1 and R2 branches completely stopped growing.

**DISCUSSION**

*Individual shoot architecture is highly variable, even in the absence of soil water deficit and mineral deficiency*

All the architectural characteristics of the shoots studied, with the exception of the number of leaves on the main stem, were highly variable. The plants studied experienced no soil water deficit or mineral deficiency. Such variability among grapevine plants at a given time after budbreak has been reported elsewhere (Williams, 1987; Kliwer et al., 1989; Miller et al., 1996). Two types of limitation may have affected plant architecture in our experiments: (1) trophic competition between the shoots, depending on the number...
of latent buds retained at pruning, and plant reserves, which differed in glasshouse and field experiments; and (2) environmental conditions.

Previous studies have shown an effect of trophic competition, with the final area of leaves and the level of branch development higher in plants carrying fewer shoots (Sommer et al., 1995; Miller et al., 1996) and lower in vineyards in which minimal pruning is practised, resulting in four times the normal number of growing shoots (Downton and Grant, 1992). Hedging also results in an increase in the area of expanding leaves not removed by pruning (Fournioux, 1996). Similar results were obtained for branch development. Variability in branch development is partly due to differences in the timing of budbreak on different shoots (Kliwer et al., 1989), which results in differences in their developmental stages. The more developed shoots take advantage of their higher sink strength, and absorb more nutrients (Williams, 1987; Miller et al., 1996). Trophic competition also depends on the number of clusters per shoot. The shoots with strong fruiting development display a lower level of vegetative development (Edson et al., 1993). Similar results have been obtained in other woody species, such as peach (Génard et al., 1998), indicating that branch development is very sensitive to plant trophic status. These previous results are in agreement with our proposed ranking of our experiments in terms of trophic competition between shoots: in ascending order, the glasshouse experiments (expts 1 and 2), the second field experiment (expt 4) and the first field experiment (expt 3). Cumulative solar radiation may also affect trophic competition between shoots. In our experiments, cumulative PPFD was much lower in glasshouse experiments than in field experiments. This trend is opposite to that for trophic competition based on the number of remaining shoots and may have reduced differences in plant architecture between experiments.

Vapour pressure deficit (VPD) patterns differed between the first glasshouse experiment and experiments in which the plants were outside [expt 2 (pots outside) and the two field experiments]. Mean VPDs were similar, but maximal daily mean VPD ranged from 1.5 kPa in expt 1 to 2.8 kPa for expt 4. In our experiments, evapotranspiration rates were high outside the glasshouse and lower within it. Although VPD was not measured in experiment 3, the similarity in the other weather variables measured for the two field experiments suggests that VPD was probably also similar in these

![Figure 8](https://example.com/image8.png)

**Figure 8.** Changes in the frequency distribution of leaf appearance rate (LAR) on secondary shoots during three 100°Cd periods after budbreak for (A–C) the glasshouse (expt 1), and (D–F) the field (expt 4) experiments. Secondary axes are labelled R0, R1 and R2 according to their position in the ternary sequence (P0–P1–P2). Note that R1 and R2 types were pooled because they behaved in a similar manner (see Fig. 6B). Open bars correspond to R0 branches and solid bars to R1 and R2 branches.
two experiments. These high VPD values may have affected vegetative development. It has been suggested for various species, including maize (Ben Haj Salah and Tardieu, 1997) and rice (Tivet, 2000), that high VPD may reduce leaf expansion rate, even in well-watered plants.

Analysis of shoot development at phytomer level, using thermal time, identifies constants in the grapevine shoot development programme

It was found that air temperature played an important role in development of the main axis. The rates of production of leaf primordia, unfolded leaves and fully expanded leaves on the main axis, expressed as functions of thermal time, were constant over a wide range of situations, including fluctuating environmental conditions, glasshouse and field locations, and at various plant ages. The linear relationships obtained for each stage of leaf development were stable throughout shoot development, from budbreak to veraison. Similar results have been obtained for kiwi-fruit, another cultivated liana, in constant temperature experiments (Greer, 1996; Seleznynova and Greer, 2001). However, Schultz (1992) showed that the rate of unfolded leaf production of the main axis decreased gradually during shoot development for plants in the vineyard. This difference from our results, which were also obtained in a vineyard, may be due to (a) higher fructing levels resulting in stronger trophic competition between the vegetative and reproductive parts of the shoot (Edson et al., 1993; Hardie and Martin, 2000), and (b) probable soil water deficits in a productive vineyard, the intensity of which would have increased during the cycle, reducing the rate of unfolded leaf production.

This stability of the progression of developmental stages along the main stem, modelled with three linear relationships, results in a thermal-time-based programme of leaf development on the main axis. This type of representation has already been developed for annual plants (Rickman and Klepper, 1995; Belaygue et al., 1996; Turc and Lecoeur, 1997; Granier and Tardieu, 1999; Granier et al., 2002; Lafarge and Tardieu, 2002). A vertical reading of this representation indicates the number of phytomers forming the main stem and their developmental stage at a given thermal time. A horizontal reading indicates the timing of the developmental stages for a given phytomer. The development of the main axis of the grapevine shoot system is comparable to the stem development of most of annual plants. Thus, the duration of leaf expansion at a given phytomer position on the main axis is constant when expressed in thermal time in various environmental conditions, as shown previously for several annual species.

The modular structure of the main stem affects development of the secondary axis

Quantitative analysis of shoot development was improved by distinguishing pre-existing (proximal) from newly produced (distal) parts of the main axis and by locating the modular ternary structures on the newly produced parts of the plant. According to Bouard (1966) and Jaquinet and Simon (1971), the modular structure accounts for a large part of the observed variability in shoot architecture. These three types of phytomer produce populations of branches differing considerably in development potential. The actual development of these populations of branches depends on intra- and inter-shoot trophic competition and on environmental conditions. However, branches derived from P0 phytomers (R0) always showed higher levels of development than those derived from the P1 and P2 phytomers (R1 and R2) of the corresponding modular structure.

In contrast to the production of phytomers and the development of individual leaves on the main axis, the rate and duration of branch development are not stable when expressed as functions of thermal time. After a short initial period, corresponding to the production of the two first phytomers, in which all branch populations, in most cases, had similar rates of development, the rates of branch development differed between the R0, R1 and R2 populations and between situations for a given population. In situations of strong trophic competition (expt 4), rates of unfolded leaf production decreased until a large proportion of the branches stopped producing leaves, between 200 and 300 CDD after budbreak. In conditions of weaker trophic competition (expt 1), the rates of unfolded leaf production of the R1 and R2 branches gradually decreased, whereas that of the R0 branches increased. Some of these R0 branches reached rates of development similar to those of the main axis, and their $N_{\text{ph}}$ increased linearly with thermal time. These results show that there is a hierarchy of shoot axes in which each type of axis has its own development potential, which is affected by intra- and inter-shoot competition and environmental conditions. In most growing conditions, the main axis achieves its development potential because at least 90% of the buds are removed by winter pruning. In contrast, the higher order axes generally have lower and less stable development rates than the main axis, as shown, for example, for the peach tree (Pagès et al. 1993). As the development of the main axis is stable, the shoot architecture of grapevine appears to depend principally on the presence of pre-existing and newly produced parts, including modular ternary structure and a hierarchy of the axes. This confers a high level of architectural plasticity on the grapevine, enabling it to respond to environmental conditions.

CONCLUSIONS

A distinctive feature of grapevine is that the growth produced each year is then removed by pruning. Consequently, the architecture of this plant does not result from the stacking and reiteration of annual structures as in trees. In this manner, grapevine development is more comparable to the development of an annual plant, with latent buds equivalent to seeds, except that the development of each bud is affected by the level of plant reserves and by trophic competition between the various shoots. Thus, shoot development in pruned grapevine can be analysed using approaches originally developed for annual plants. These approaches make it possible to describe the response, in
well-watered conditions, of grapevine shoot development to pruning and environmental conditions. It is therefore possible to simulate the number and development stage of the phytomers on the main axis, and to characterize branch development. The proposed quantitative analysis of shoot development is a useful first step towards the analysis and modelling of the effects of abiotic stresses, particularly water deficit, on the growth and architecture of shoots. However, this model cannot be used to predict leaf area and leaf production on the branches. In contrast with the main axis, the development of branches seldom achieves its potential, even in the absence of soil water deficit or mineral deficiency. Plant trophic status must be taken into account, together with intra- and inter-shoot competition, in order to develop a more complete model.

ACKNOWLEDGEMENTS

We thank Philippe Naudin for his help during the set-up of the experiments and for technical assistance with micro-meteorological measurements, and Géraldine Farges and Laurence Delbac for data collection during expts 3 and 4.

LITERATURE CITED


Seleznyova AN, Greer DH. 2001. Effects of temperature and leaf position on leaf area expansion of kiwi-fruits (*Actinidia delicosa*) shoots:


