GRAPEVINE CULTURE IN TRENCHES. 2. REPRODUCTIVE CHARACTERISTICS AND INTERACTIONS WITH VEGETATIVE GROWTH

CULTURE DE LA VIGNE EN TRANCHÉE. 2. CARACTÉRISTIQUES DU DÉVELOPPEMENT REPRODUCTEUR ET INTERACTIONS AVEC LA CROISSANCE VÉGÉTATIVE

Ch. ZAPATA[1], J.-Cl. AUDRAN[1] and Ch. MAGNÉ[2]

1 : Université de Reims Champagne-Ardenne, UFR Sciences, Laboratoire de Biologie et Physiologie Végétales, UPRES EA 2069 (URVVC), Reims, France
2 : Université de Bretagne Occidentale, IUEM/LEBHAM, Technopole Brest Iroise, 29280 Plouzané, France

Summary : In order to assess the consequence of a strong vegetative growth on inflorescence development and berry setting, two grapevine cultivars differing in their rate of fruit set were grown for 3 years in a greenhouse under semi-controlled conditions. Merlot (low % fruit set) and Pinot noir (high % fruit set) vines produced well-developed clusters in year 3 after planting, thus allowing the study of interactions between vegetative growth and reproductive development over the third growing season. Progress in development of both cultivars was simultaneous until pea berry size and biomass production was similar throughout the season. However, biomass production was negatively correlated to flower differentiation (number of flowers/inflorescence) in Merlot whereas not in P. noir. Possible causes of this interaction are discussed.

Résumé : Dans le but d'étudier les conséquences d'une forte vigueur sur le développement reproducteur (nombre et taille des inflorescences produites, taux de nouaison) chez la vigne, deux cépages différant par leur taux de nouaison moyen ont été cultivés pendant 3 ans dans une serre en conditions semi-contrôlées. Les plantes de Merlot (faible taux de nouaison) et de Pinot noir (taux de nouaison élevé) ont produit des inflorescences normalement développées dès la troisième année après plantation. Ceci nous a permis d'étudier les interactions entre croissance végétative et caractéristiques des grappes au cours de la troisième saison. Le développement des plantes des 2 cépages s'avère synchrone jusqu'à la nouaison. Ensuite, une différence apparaît, le cépage Pinot noir étant plus précoce que le Merlot, mais elle reste faible jusqu'au stade « petit pois ». De plus, la production de biomasse aérienne est similaire chez les 2 cépages à chaque date d'échantillonnage au cours du printemps de la troisième année. La croissance des rameaux est lente jusqu'à l'approche de la floraison, puis s'intensifie nettement lors du développement floral. Bien que la vigueur des plantes soit stimulée dans nos conditions expérimentales, la production d'inflorescences et de baies est très importante. En conséquence, aucune interaction n'a été observée entre la vigueur et les processus d'induction florale ou de nouaison. Cependant, la production de biomasse est négativement corrélée à la différenciation des fleurs (nombre de fleurs/inflorescence) chez le Merlot, bien que le second processus soit antérieur au premier. Une telle interaction n'est pas observée chez le Pinot noir. Les causes possibles de ce type d'interaction sont discutées, de même que les conséquences à prévoir sur le potentiel de chaque cépage au vignoble.

Key words : cv. Merlot, cv. Pinot noir, fruit set, grapevine, inflorescence, reproductive development

Mots clés : cv. Merlot, cv. Pinot noir, développement reproducteur, inflorescence, nouaison, vigne

INTRODUCTION

In higher plants, vegetative organs are generally considered stronger sinks than reproductive structures until fruit set (HO, 1988 and references therein). In grapevine, such relationship between vegetative growth and fruit setting has been reported in some cultivars (COOMBE, 1959 ; WAGNER *et al.*, 1987 ; HUNTER and VISSER, 1990 ; FOURNIOUX, 1997). Accordingly, strong competition for nutrients might occur during flowering and fruit set in grapevines exhibiting excessive vegetative vigour, thus leading to reduced berry set (WAGNER *et al.*, 1987). On the other hand, severe defoliation at bloom was shown to reduce

*Correspondance : christian.magne@univ-brest.fr

fruit set and cause berry drop (COOMBE, 1959 ; HUNTER and VISSER, 1990) unless growing parts were also removed (FOURNIOUX, 1997). Thus, the rate of berry set might be, in some way, the expression of the interactions between vegetative and reproductive development. Since flower differentiation proceeds in latent buds (POUGET, 1981) before and during bud burst, cluster size might be affected by the extent of growth rate during the previous year. Also, a competition for growth substances instead of C or N compounds cannot be excluded.

Trench culture has been reported as a convenient model to study water and nutrient uptake by grapevine (CONRADIE *et al.*, 1996 ; MYBURGH *et al.*, 1996). Recently, we have further developed this experimental method to investigate dry matter partitioning in two varieties (Merlot and Pinot noir) throughout the season (ZAPATA *et al.*, 2001). Since the extent of shedding differs greatly between these two varieties in their production regions (OLLAT, 1992 ; BROQUEDIS *et al.,* 1996; HUGLIN and SCHNEIDER, 1998 ; PANIGAI and MONCOMBLE, 1999), we investigated the interactions between vegetative and reproductive development using such trench culture design. For that purpose, vines were grown in semi-controlled conditions under greenhouse to induce strong vegetative growth.

With the objective to examine possible cause of variations of flower differentiation and berry setting in grapevine, we report here comparative results on the influence of vegetative growth on reproductive development of Merlot and Pinot noir varieties grown under the same semi-controlled conditions, these conditions inducing strong vegetative growth.

MATERIALS AND METHODS

I - EXPERIMENTAL LAYOUT

Plants of Pinot noir (clone 521) and Merlot (clone 181) cultivars grafted onto SO4 (clone 5) rootstock were grown in trenches under semi-controlled conditions over three years (ZAPATA *et al.*, 2001). During that period, vines were supported vertically. Two shoots/plant were allowed to grow in year 1, three in year 2 and four in year 3 after planting. Vines were irrigated daily from bleeding sap (mid March) to leaf fall (late October) with nutrient solution (COÏC and LESAINT, 1971) by means of a drip system. Winter pruning was carried out each year in February.

II - REPRODUCTIVE DEVELOPMENT

In year 3 after planting, date of appearance of each developmental stage, as well as daily mean temperatures exceeding 10°C, were noted until veraison. The following reproductive characteristics were recorded on nine vines of each variety: number of flowers per inflorescence, number of berries per bunch, and percentage fruit set (defined as the ratio of berries to flowers). For the latter, inflorescences were bagged in muslin in order to assess the number of fallen flowers.

III - VEGETATIVE GROWTH

Nine plants of each cultivar were pulled out at the end of year 2, and during the third year at the following stages: first leaf fully expanded, early bloom (first flower opened), and berries at pea size. These 3 stages correspond to stages 7, 19 and 31 according to EICHHORN and LORENZ (1977). From these plants, the annual tissues (shoots, leaves, tendrils and clusters) were collected, oven dried at 70°C for 72 hours and subsequently weighed. The rate of shoot growth was assessed during the 4 weeks preceding bloom by measuring the length of all four shoots from nine vines per cultivar.

When indicated, standard errors to the means were calculated and data from the two cultivars were compared with pairwise t tests. Difference between the two cultivars was considered significant at the $P<0.05$ level.

RESULTS

I - DEVELOPMENT RATE

During the first year after planting, vines were not pruned and exhibited 3 m long shoots on average. Some vines produced small inflorescences which were removed before bloom. During the second and third growing seasons, budbreak occurred at the same time (early April) for both cultivars (fig. 1). Afterwards, stage 7 (first leaf fully expanded) was reached simultaneously. At stage 19 (first flower opened), a difference of three days was found between cultivars, P. noir being earlier than Merlot. This small difference remained unchanged until stage 31 (pea berry size) but increased thereafter, reaching ten days at veraison.

II - VEGETATIVE GROWTH

Vegetative growth was very strong under our greenhouse conditions. Accordingly, vines had to be summer-pruned twice in year 2. During the third growing season, shoots of the two cultivars exhibited the same pattern of growth rate (fig. 2). Thus, aerial biomass production increased slowly until early bloom, then rapidly (+ 5 gDW/day in average) throughout anthesis and berry setting (stages 19 to 31) (fig. 2a). Shoot growth rate of the two cultivars increased slightly until one week before bloom, then markedly (fig. 2b).

III - INFLORESCENCE PRODUCTION

In the second season, inflorescences were produced on every plant in both cultivars but their size was small. In year 3, inflorescence production in the two varieties showed a high variability of the number of inflorescences per vine, ranging from 2 to 12. Most of the shoots carried two inflorescences (fig. 3a). However, a high frequency of shoots had three clusters, especially in Merlot. Basal inflorescences of Merlot had more flowers than those of Pinot noir (fig. 3b). Moreover, the number of flowers per cluster was highly variable in Merlot as compared to Pinot noir. The same observation could be made with the rate of berry set in basal inflorescences (fig. 3c). On a per-vine basis, percent berry set was less variable and ranged between 41-60 % and 48-69 % in Merlot and Pinot noir, respectively (fig. 3d).

Cluster data showed that the number of inflorescences per plant was higher in Pinot noir than in Merlot in year 2, but similar in year 3 (table 1). A marked (3-fold) increase in the inflorescence size (number of flowers per cluster) was recorded for Pinot noir in year 3 compared to year 2. This increase was even more pronounced (6.5-fold) for Merlot, leading to inflorescences larger than those of Pinot noir. However, clusters obtained in each cultivar after pollination showed comparable size (160-170 berries/bunch). The mean fruit set was similar (63-64 %) in both cultivars in year 2. Then, it was lower in year 3, when the inflorescences were significantly larger. We found that the fruit set in year 3 was lower in Merlot (44 %) than in Pinot noir (56.5 %).

Competition between vegetative and reproductive tissues: In both cultivars, no significant correlation was found between inflorescence size in year 3 and plant growth over the previous season (fig. 4a). However, inflorescence size and aerial vegetative growth over the same year were negatively correlated in Merlot (fig. 4b). Such relationship could not be found in Pinot noir. Moreover, we did not find any significant correlation between vegetative growth and fruit set during the same year (fig. 4c).

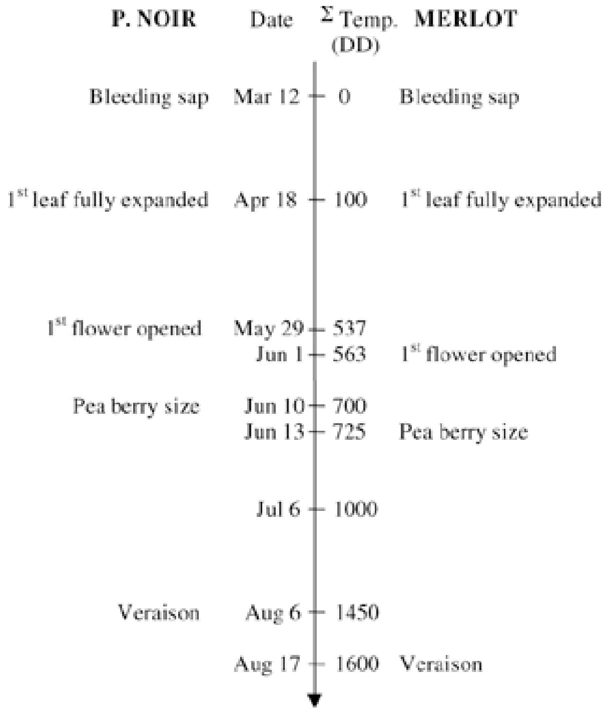

Fig. 1 - Development of Pinot noir and Merlot cultivars during the third year after planting.

Temperature summation in degree-days (DD) is shown in parallel with the progress in development.

Chronologie du développement des plantes de Pinot noir et de Merlot au cours de la troisième année.

La somme des températures en degrés-jours (DD) est indiquée en parallèle.

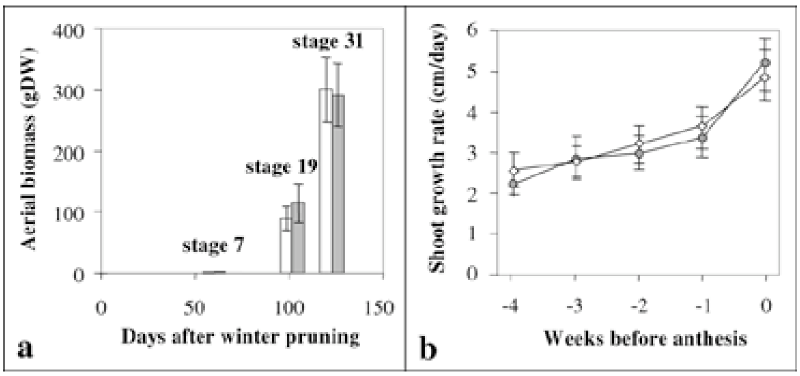

Fig. 2 - Vegetative growth of Pinot noir (❐) and Merlot (■) cultivars during the third growing season. a: changes in biomass production; b: shoot growth rate before anthesis.

Data are mean of 9 plants ± SE.

Croissance végétative des plantes de Pinot noir (❐) et de Merlot (■) au cours de la troisième année. a: production de biomasse ; b : vitesse de croissance avant l'anthèse.

Les valeurs sont la moyenne de 9 plantes ± écart-type.

Table I - Inflorescence characteristics of Merlot and Pinot noir in year 2 and 3 after planting.
Data are mean ± SE of 9 plants. For each year, data within a line followed by the same letter are not significantly different (P<0.05).

Caractéristiques des inflorescences de Pinot noir et de Merlot produites au cours de la deuxième et de la troisième années.
Les valeurs sont la moyenne de 9 plantes + écart-type. Pour chaque année, les valeurs d'une même ligne suivies de la même lettre ne sont pas significativement différentes au seuil de 5 %.

	Year 2		Year 3	
	Pinot noir	Merlot	Pinot noir	Merlot
No inflo./vine	5.4 ± 0.6 a	4.3 ± 0.5 b	7.6 ± 0.8 a	8.0 ± 1.0 a
No flowers/inflo.	91 ± 19 a	60 ± 12 b	278 ± 30 a	391 ± 78 b
No flowers/vine	430 ± 87 a	238 ± 53 b	2249 ± 202 a	3127 ± 384 b
No berries/bunch	56 ± 11 a	38 ± 8 b	157 ± 18 a	172 ± 30 a
No berries/vine	256 ± 49 a	147 ± 32 b	1309 ± 139 a	1378 ± 154 a
Fruit set (%)	64 ± 4 a	65 ± 3 a	56.5 ± 2 a	44 ± 3 b

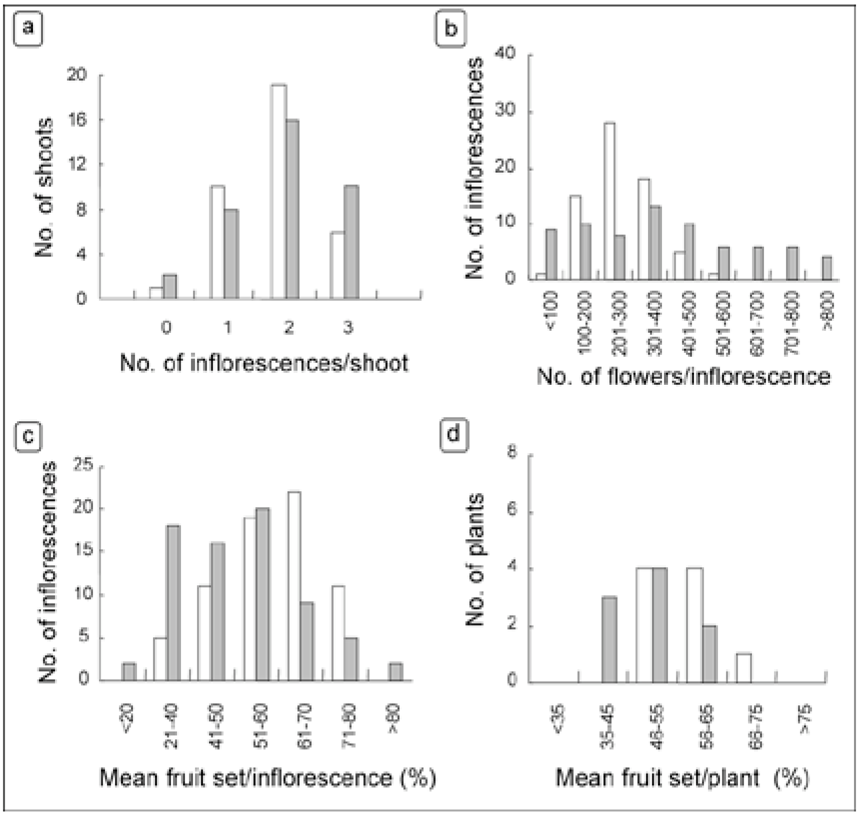

Fig. 3 - Characteristics of Pinot noir (❒) and Merlot (■) inflorescences produced in year 3. a: no. of inflorescences/shoot; b: no. of flowers/inflorescence; c: fruit set at the inflorescence level; d: fruit set at the plant level.

Caractéristiques des inflorescences de Pinot noir (❒) et de Merlot (■) produites lors de la troisième année. a: nombre d'inflorescences/rameau; b: nombre de fleurs/inflorescence; c: taux de nouaison par inflorescence; d: taux de nouaison par plante.

DISCUSSION

Our experimental system (trench culture under greenhouse) allowed vines to grow under « non-limiting » conditions (higher temperatures than in the vineyard, saturating light, water availability and nutrients in excess). Accordingly, greenhouse grown plants exhibited a significantly stronger vegetative growth than that of vines grown outside. Even, greenhouse conditions resulted in the early development of vines, budbreak occurring 3 to 4 weeks in advance compared to plants grown outside. In our experiment, budbreak appeared at the same time in both cultivars. Then, Pinot noir and Merlot development progressed in synchrony until pea berry size, the last sampling stage in our experiment. Moreover, three-year old vines grown in trenches exhibited clusters similar in size to those of plants in commercial vineyards (BROQUEDIS *et al.,* 1996 ; HUGLIN and SCHNEIDER, 1998 ; PANIGAI and MONCOMBLE, 1999).

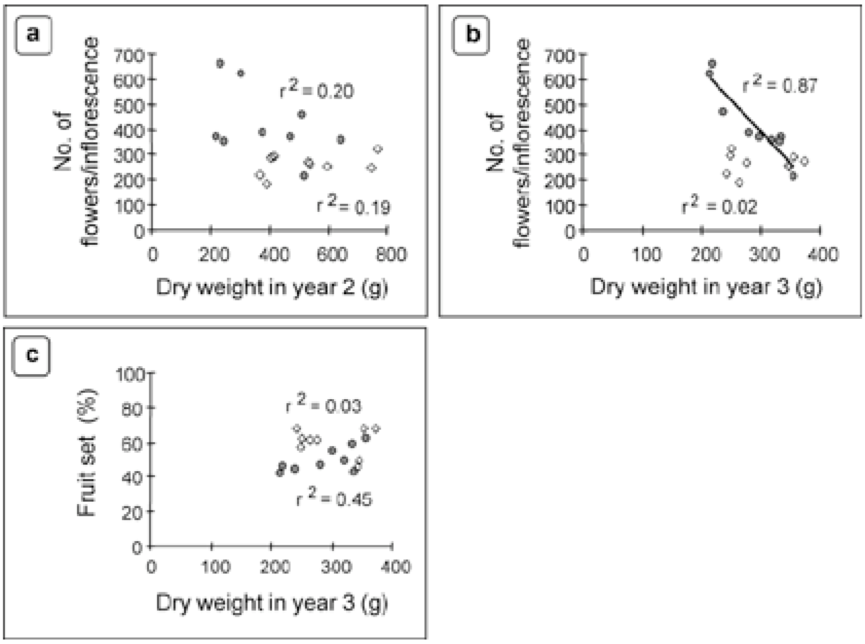

Fig. 4 - Relationships between aerial vegetative growth and reproductive characteristics in Pinot noir ( ) and Merlot (●) cultivars. r2: coefficient of determination.
a: no. of flowers/inflorescence and dry weight of annual tissues produced in year 2;
b: no. of flowers/inflorescence and dry weight of annual tissues produced in year 3;
c: fruit set rate and dry weight of annual tissues produced in year 3.

Relations entre croissance aérienne et caractéristiques du développement reproducteur chez les cépages Pinot noir ( ) et Merlot (●). r2: coefficient de corrélation.
a : no. de fleurs/inflorescence et biomasse sèche des rameaux produits dans l'année 2 ;
b : no. de fleurs/inflorescence et biomasse sèche des rameaux produits dans l'année 3 ;
c : taux de nouaison et biomasse sèche des rameaux produits dans l'année 3.

In grapevine, the spring growth flush is generally described through a two-phase process, the first being characterized by a slow daily growth and the second by a rapid one (HUGLIN and SCHNEIDER, 1998). Assuming that the curve between stage 7 and stage 19 would certainly not have been linear, the fast rate of shoot expansion likely starts about one week before stage 19, thus 2-3 weeks before anthesis.

Inflorescence characteristics of the two cultivars were different. Number of clusters per shoot and that of flowers per basal inflorescence were more homogenous in Pinot noir than in Merlot. The mean numbers for these two traits were higher in Merlot than in P. noir, in agreement with the observations usually made in commercial vineyards (BROQUEDIS *et al.*, 1996 ; HUGLIN and SCHNEIDER, 1998 ; PANIGAI and MONCOMBLE, 1999). In particular, they confirmed the higher potential to produce flowers in Merlot than in Pinot noir. However, fruit set was lower in Merlot (44 %) than in Pinot noir (56.5 %). Moreover, % berry set was higher (64-65 %) in the inflorescences produced in year 2, which were smaller than those in year 3. This is in good agreement with the reported negative correlation between the number of flowers/inflorescence and % berry set (HUGLIN and BALTHAZARD, 1975). Thus, it is likely that through the fruit setting process, vines adjust berry yield to a potential defined by the conditions of the early growth period, as it has been suggested earlier (OSBORNE, 1989 ; CARBONNEAU and OLLAT, 1993).

With respect to the stimulation of vegetative growth under greenhouse, one could expect a poor berry set for both varieties. On the contrary, the observed %set in both varieties was close to, or even higher than, those usually observed under natural conditions (OLLAT, 1992 ; BROQUEDIS *et al.*, 1996 ; HUGLIN and SCHNEIDER, 1998 ; PANIGAI and MONCOMBLE, 1999). Thus, it is likely that strong vegetative growth, as induced in our experiment, may not cause flower and berry drop as long as environmental conditions (including climatic factors and soil nutrients) are favourable. On the other hand, vigour was negatively correlated to flower differentiation during the same growing season in Merlot, although the latter proceeds before the former. This interaction could be the result of a strong competition for growth substances, presumably cytokinins. Accordingly, these hormones are well known to activate shoot growth, and they have been reported to induce flower initiation (BERNIER *et al.*, 1993).

CONCLUSION

The present work report the comparative results on interactions between vegetative and reproductive development of two grapevine varieties grown in trenches under semi-controlled conditions. Those conditions resulted in the same difference of earliness between cultivars as that observed in their respective production region. However, flowering and berry set occurred simultaneously in the two cultivars, thus allowing the comparison of developmental processes (floral induction or initiation, rate of fruit set) under similar environmental conditions. Strong vegetative growth induced under greenhouse conditions did not affect inflorescence initiation in latent buds. However, in Merlot, it was shown to interfere with flower differentiation. Such interference might, in turn, account for the higher susceptibility of this cultivar to shedding, compared to Pinot noir. To elucidate the possible relationship between nutrient status during inflorescence development and shedding, further work on the management (storage and subsequent mobilization) of C and N reserves upon the spring growth flush in our two model varieties is under progress.

Acknowledgements : The authors are indebted to S.A. Mumm Perrier-Jouët Vignobles et Recherches, Epernay (France) for funding the Ph.D. grant to C. Zapata and the inter-region VVS research network for financial support.

REFERENCES

BERNIER G., HAVELANGE A., HOUSSA C., PETITJEAN A. and LEJEUNE P., 1993. Physiological signals that induce flowering. *Plant Cell*, **5**, 1147-1155.

BROQUEDIS M., LESPY-LABAYLETTE P. and BOUARD J., 1996. Les polyamines et leur effet anticoulure chez la vigne. *J. Int. Sci. Vigne Vin*, n° h. série, 55-58.

CARBONNEAU A. and OLLAT N., 1993. Étude de la coulure et maîtrise de la production. *Progrès Agric. Vitic.*, **13**, 331-340.

COÏC F. and LESAINT L., 1971. Comment assurer une bonne nutrition en eau et en ions minéraux en horticulture. *Hortic. Français*, **8**, 11-14.

CONRADIE W.J., VAN ZYL J.L. and MYBURGH P.A., 1996. Effect of soil preparation depth on nutrient leaching and nutrient uptake by young *Vitis vinifera* L. cv. Pinot noir. *South Afric. J. Enol. Vitic.*, **17**, 43-52.

COOMBE, B.G., 1959. Fruit set and development in seeded grape varieties as affected by defoliation, topping, girdling and other treatments. *Amer. J. Enol. Vitic.*, **10**, 85-100.

EICHHORN K.W. and LORENZ D.H., 1977. Phänologische Entwicklungsstadien der Rebe. *Nachrichtenbl. Dtsch. Pflanzenschutzdienstes (Braunschweig)*, **29**, 119-120.

FOURNIOUX J.C., 1997. Influences foliaires sur le développement et la maturation des grappes. *Progrès Agric. Vitic.*, **114**, 359-372.

HO L.C., 1988. Metabolism and compartmentation of imported sugars in sink organs in relation to sink strength. *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, **38**, 355-378.

HUGLIN P. and BALTHAZARD J., 1975. Variabilité et fluctuation de la composition des inflorescences et des grappes chez quelques variétés de *V. vinifera*. *Vitis*, **14**, 6-13.

HUGLIN P. and SCHNEIDER C., 1998. *Biologie et écologie de la vigne*. Ed. Tec. & Doc., Paris.

HUNTER J.J. and VISSER J.H., 1990. The effects of partial defoliation on growth characteristics of *Vitis vinifera* L. cv Cabernet sauvignon. II. Reproductive growth. *South Afric. J. Enol. Vitic.*, **11**, 26-32.

MYBURGH P.A., VAN ZYL J.L. and CONRADIE W.J., 1996. Effect of soil depth on growth and water consumption of young *Vitis vinifera* L. cv. Pinot noir. *South Afric. J. Enol. Vitic.*, **17**, 53-62.

OLLAT N., 1992. Nouaison chez *Vitis vinifera* L. cv Merlot noir : rôle de l'intensité lumineuse et de la photosynthèse à la floraison. *In : 4th Int. Symp. Grapevine Physiol.*, Turin, Italy. p. 113-116.

OSBORNE D.J., 1989. Abscission. *Crit. Rev. Plant Sci.*, **8**, 103-129.

PANIGAI L. and MONCOMBLE D., 1999. La coulure : une épée de Damoclès sur la Champagne. *Le Vigneron Champenois*, **120**, 35-41.

POUGET R., 1981. Action de la température sur la différenciation des inflorescences et des fleurs durant les phases de pré-débourrement et de post-débourrement des bourgeons latents de la vigne. *Connaissance Vigne Vin*, **15**, 65-79.

WAGNER R., VERGNES A. and DELMAS P., 1987. Influence de la vitesse de croissance pendant la floraison sur la nouaison de variétés de *Vitis vinifera* L. sensibles à la coulure. *In : 3rd Int. Symp. Grapevine Physiol.*, Bordeaux, France. p. 16-18.

ZAPATA C., MAGNÉ C., DELÉENS E., BRUN, O., AUDRAN J.C. and CHAILLOU S., 2001. Grapevine culture in trenches. I. Root growth and dry matter partitioning. *Aust. J. Grape Wine Res.*, **7**, 127-131.

Manuscrit reçu le 19 juillet 2002 ; accepté pour publication le 27 mars 2003