EFFECTS OF RIPENING CONDITIONS ON THE FOLLOWING SEASON'S GROWTH AND YIELD COMPONENTS FOR PINOT NOIR AND GEWURZTRAMINER GRAPEVINES (*VITIS VINIFERA* L.) IN A CONTROLLED ENVIRONMENT

EFFET DES CONDITIONS DE MATURATION SUR LA CROISSANCE ET LES COMPOSANTES DU RENDEMENT AU COURS DE LA SAISON SUIVANTE POUR DEUX VARIÉTÉS DE VIGNE (*VITIS VINIFERA* L.), LE GEWURZTRAMINER ET LE PINOT NOIR, EN CONDITIONS CONTRÔLÉES

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Abstract: Two levels of leaf/area ratio were created for two varieties of grapevine (*Vitis vinifera* L.) in a glasshouse. Carbohydrate and free amino acids concentrations in the pruning wood were significantly reduced when the leaf/fruit ratio was low. In the following season, growth parameters were affected as well as yield components such as the number of shoots per plant, the number of inflorescences per shoot, the number of flowers per inflorescence and the number of berries per cluster. Fruit set was however not altered. Weight of grapes at fruit set was reduced by 68% for Gewurztraminer and by 46 % for Pinot noir.

Résumé : Deux niveaux de rapport feuille/fruit au cours de la maturation des raisins ont été créés en serre pour deux variétés de vigne (*Vitis vinifera* L.), le Gewurztraminer et le Pinot noir, afin d'évaluer si un faible niveau de réserves hivernales pouvait être à l'origine de situations de coulure au cours de la saison suivante. Les traitements, avec un effet marqué sur les teneurs en sucres des raisins, ont induit de fortes différences dans les teneurs en sucres et en acides aminés libres du bois de taille. Au cours de la saison suivante des paramètres de la croissance tels que le diamètre des rameaux, l'indice de chlorophylle des feuilles, les poids de rognage, ont été nettement plus faibles lorsque la maturation l'année antérieure a été difficile. La croissance végétative a été davantage pénalisée pour le Pinot noir que pour le Gewurztraminer.
Le nombre de rameaux débourrés, d'inflorescences par rameau, de fleurs par inflorescence, de baies par grappe ont été également fortement affectés. Le taux de nouaison et les paramètres de la fécondation sont par contre restés inchangés. Le poids des raisins par plante à la nouaison est au final réduit de 68 % pour le Gewurztraminer et de 46 % pour le Pinot noir.
La variabilité de rendement, qui peut être considérée comme un caractéristique variétale, pourrait être en relation avec la priorité qu'une variété établi entre développement végétatif et développement reproducteur lorsque les ressources, ici les réserves hivernales, sont limitantes.

Key words : *Vitis vinifera*, reserves, growth, yield components, fruit set.

Mots clefs : *Vitis vinifera*, réserves, croissance, composantes du rendement, nouaison.

INTRODUCTION

Grape quality for wine making is closely related to the leaf/fruit ratio during ripening. (CARBONNEAU *et al.*, 1977; MURISIER and ZUFFEREY, 1997). Whereas rules for optimising leaf area and light interception are quite well established (SMART, 1985; CARBONNEAU, 1989), yield level remains a poorly controlled variable.

This yield level greatly depends on the number of flowers but also on the rate of transformation of flowers into berries, known as fruit set (DUCHENE *et al.*, 2001).

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Varieties such as Gewurztraminer or Muscat Ottonel sometimes have very low and even null, fruit set (HUGLIN and SCHNEIDER, 1998). Two groups of hypothesis are raised to explain these production breakdowns.

The first explanations include factors external to the plant and acting directly on the flower. Cold temperatures and/or wet conditions around flowering could induce abnormally low fruit set, as supported by experimental results (KOBLET, 1966; EBADI *et al.*, 1995).

The second group of hypothesis refers to internal causes at the whole plant level. Many authors have shown that the number of berries and fruit set can be modified with variations in incident radiation (DELOIRE *et al.*, 1995; FERREE *et al.*, 2001), leaf area (COOMBE, 1962; KOBLET, 1966; CASPARI *et al.*, 1998), or competitions among vegetative and reproductive organs (COOMBE, 1962; KOBLET, 1966; SMITHYMAN *et al.*, 1998; VASCONCELOS and CASTAGNOLI, 2000) during the berry formation period. Fruit set would then depends on assimilates availability at the flower level. However, the intensities of the treatments required to obtain significant results are unrelated to natural conditions, even unfavourable. We have moreover shown for Grenache that the number of berries per cluster could be influenced by the nitrogen nutrition level during the previous growing season (DUCHENE *et al.*, 2000).

Considering that fruit set could be related to assimilate availability during the budbreak-flowering period and that there are some evidences that varieties mobilise their reserves for spring growth in different ways (ZAPATA *et al.*, 2001), our aim was to investigate whether low over-wintering reserves levels could induce low fruit set for Gewurztraminer vines.

This paper presents the effects on growth and yield components of treatments where we altered reserves level by reducing the leaf/fruit ratio during the previous ripening period. We compared Gewurztraminer to Pinot noir, less susceptible to yield variations.

MATERIAL AND METHODS

I - EXPERIMENTAL CONDITIONS

This study was conducted in a glasshouse on Gewurztraminer clone 47 (GW) and Pinot noir clone 162 (PN). The plants, grafted onto SO4, were 4 years old in 2001.

They were grown in 80 l containers in a sand/perlite mixture (50/50, v/v) and irrigated with a complete nutritive solution (129 mg N/l, 397 mg P_2O_5/l, 95 mg K_2O/l).

Each plant was pruned in order to leave a long-wood and one spur for renewal. At the 5-6 leaves stage, only 6 shoots were left per vine and further trained on 2 m stalks.

Bibliographic data show that modifying leaf/fruit ratio during the ripening phase can induce contrasted reserves levels. (KOBLET *et al.*, 1993; CANDOLFI-VASCONCELOS *et al.*, 1994; MURISIER and AERNY, 1994; KOBLET *et al.*, 1997; BENNETT *et al.*, 2002).

In order to obtain such effects, the following operations were applied on July 24, 2000 when 97 % of Gewurztraminer berries and 90 % of Pinot noir ones had started softening :

R+ (favourable Ripening or Reserves) : only one cluster left per shoot as well as all the leaves,

R- (unfavourable Ripening or Reserves) : all the clusters left, 50 % of the leaves (1 out of 2 along the shoot) as well as laterals removed.

Year 2000 will be considered as year *n*.

R+ grapes were harvested on August 28, 2000 and R- grapes only on October 30, 2000 in order to amplify the expected effects.

Each of the 4 combinations (variety (GW/PN)* ripening (R+/R-)) was represented by 7 plants. They were randomly distributed in three lines of 10, 8 and 10 plants respectively, where all the treatments were represented. These lines can be considered as blocks.

In 2001, the plants were grown and conducted exactly as in 2000, especially in regard to the nutritive solution.

II - MEASURES AND NOTATIONS

During the 2000 ripening period, about 100 berries per plant were picked up for acidity and total soluble solids determination.

The number and weight of clusters was controlled at harvest as well as the weight of remaining and removed leaves.

Weight, dry matter, carbohydrates and amino acids contents of the pruning wood were assessed after pruning on January 10, 2001. Total carbohydrates and free amino acids concentrations of the pruning wood were determined as follow :

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Samples of pruning wood were dried and finely crushed (< 100 µm). Reserve carbohydrates, starch, sucrose, glucose and fructose, were extracted and their concentration determined by an enzymatic method. A sample of powder was humidified and autoclaved 2 h at 130 °C. Starch and sucrose were hydrolysed 2 h at 55 °C by an amyloglucosidase and invertase solution (acetate buffer, pH 4.6). Glucose and fructose were extracted by water and titrated by spectrophotometry with an enzymatic method (kit CETIM, Cergy Pontoise, France).

Free amino acids of another sample of wood powder were extracted by ethanol 80 % at 50 °C. α-amino acids were titrated with a spectrophotometer after a reaction with ninhydrine for 15 mn at 100 °C.

During the *n+1* season (2001) the number of appearing shoots was counted every 2-3 days in order to determine the 50 % budbreak date. At the 5-6 leaves stage, inflorescences were counted and the number of shoots was then adjusted to 6 shoots per plant.

The number of unfolded leaves was recorded at two dates for each remaining shoot and the percentage of open flowers of all the inflorescences evaluated twice a week during the flowering period.

Growth was monitored following the diameter of the shoots base.

Vegetative parts removed during hedging operations were weighed before and after having been dried 48 h at 80 °C.

Three 8 mm samples were picked on each leaf facing a basal inflorescence at the onset of flowering in order to assess their weight per area.

At the end of summer, all the vines were completely defoliated. Limbs of the main shoot and of laterals were weighed separately. Samples of known surfaces allowed the calculation of leaf weight per area and then of total leaf area per plant.

Starting at the 5-6 leaves stage, 3 measurements with a Minolta SPAD 502 chlorophyll meter were taken at regular intervals on the leaves opposite to the basal inflorescence. This measure is correlated with the chlorophyll concentration in the leaves (KELLER and KOBLET, 1995).

Fruit set was evaluated on all inflorescences, wrapped in fine-mesh nylon bags just before flowering. About one month after flowering, fallen organs, small berries (<3-4 mm) and normal berries were counted. The number of seeds was also recorded for each berry.

Statistical analyses were performed by SAS system for Unix (6.12 release) using the glm procedure.

Similar experiments were conducted in the vineyard and will be further reported.

RESULTS

I - CHARACTERISATION OF THE TREATMENTS

The number of removed clusters was approximately 2 out of 3 in the R+ treatment. The leaf weight

Table I - Fruit composition on August 23, 2000 (year *n*)

Caractéristiques des raisins le 23 août 2000 (année *n*)

	"Reserves"	Gewurztraminer		Pinot noir	
		R-	R+	R-	R+
Single berry weight (g)	*	1.24 b (2)	1,38 a	1.13	1.19
Total soluble solids (° Brix)	***	16.1 b	21,5 a	16.6 b	20.3 a
Titrable acidity (eq. g H_2SO_4/l)	NS	4.81 a	4,19 b	5.41	5.43

Table II - Characteristics of the pruning wood (January 2001)

Caractéristiques du bois de taille (janvier 2001)

Variable	"Reserves" effect (1)	Gewurztraminer		Pinot noir	
		R-	R+	R-	R+
Dry weight per plant (g)	***	129.7 b (2)	175.2 a	125.9 b	169.8 a
% Dry matter	***	43.3 b	48.9 a	44.7 b	49.0 a
Total carbohydrates concentration (glucose eq. in mg/g)	***	103.7 b	129.0 a	97.2 b	119.7 a
Free amino acids concentration (alanine eq. in mg/g)	***	0.15 b	0.19 a	0.17 b	0.21 a

(1) NS : Non Significant. *, **,*** : significant at $p \leq 0.05$, $p \leq 0.01$, $p \leq 0.001$ respectively. (2) different letters indicate that the R+/R- difference for a variety is significant at $p \leq 0.05$.

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Table III - Plant architecture in 2001 (year *n+1*)

Architecture des plantes en 2001 (année *n+1*)

Variable (per plant)	"Reserves" effect (1)	Gewurztraminer		Pinot noir	
		R-	R+	R-	R+
Number of buds left after pruning	NS	13.1	13.3	11.7 b	13.1 a
Number of growing shoots	**	11.4 b (2)	13.3 a	9.0 b	11.6 a
Budbreak rate (%)	*	87.6 b	100.0 a	77.2	88.8
Initial number of inflorescences	***	9.7 b	22.3 a	14.3 b	21.4 a
Number of inflorescences after the choice of 6 shoots	**	8.0 b	11.7 a	11.0	12.4
Number of flowering inflorescences	**	5.6 b	11.6 a	9.7	12.4
Fruitfulness (all shoots)	***	0.85 b	1.68 a	1.59 b	1.86 a
Fruitfulness (chosen shoots)	***	1.36 b	1.95 a	1.83 b	2.07 a

(1) NS : Non Significant. *, **,*** : significant at $p \leq 0.05$, $p \leq 0.01$, $p \leq 0.001$ respectively.
(2) different letters indicate that the R+/R- difference for a variety is significant at $p \leq 0.05$.

Table IV - Dry weight of hedging per plant (g) in 2001 (year *n+1*)

Poids sec de rognage par plante (g) en 2001 (année *n+1*)

	"Reserves" effect (1)	Gewurztraminer		Pinot noir	
		R-	R+	R-	R+
Hedging 1 (June 5, 2001)	***	33.4 b (2)	65.4 a	24.9 b	71.9 a
Hedging 2 (July 16, 2001)	NS	98.5	101.6	49.8 b	65.3 a
Total dry weight	***	131.9	167.0	74.7 b	137.3 a

reduction, 1 leaf out of 2 on the main stem and the laterals, was around 70 %.

Ripening conditions in the R- treatment were very harsh (table I), hence inducing a difference corresponding to 2 to 3 degrees in potential alcohol between both treatments. The effect was a little more important for Gewurztraminer, which also showed a lower weight per berry and a higher acidity in the R- treatment. This variety also clearly exhibited difficulties to accumulate colour in the berry skin upon adverse ripening conditions.

II - CHARACTERISTICS OF THE PRUNING WOOD

In the R- treatment, the dry matter content, the total carbohydrates and free amino acids concentrations were significantly lower (table II). Evaluation of the total weight of pruning wood was however biased by the removal of laterals in the R- treatment. R+/R- differences were about the same for the two varieties.

III - DEVELOPMENT STAGES

No effects, neither on average budbreak date nor on the number of leaves per shoot, were noticed (data not shown). However, as there were less growing shoots per plant in the R- treatment (table III), the total number of leaves per plant before shoot removal was about 15 % lower ($p = 0.01$).

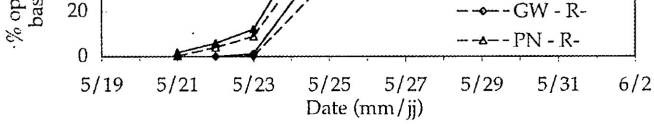


Fig. 1 - Course of flowering in 2001 (year *n + 1*)

Cinétiques de floraison en 2001 (année *n + 1*)

Figure 1 shows a delay of approximately 1 day in flowering in the R- treatment for both GW and PN.

IV - PLANT ARCHITECTURE

Yield components were severely affected by the ripening conditions during the previous season. Before the choice of 6 shoots per plant, there were less shoots per plant, less inflorescences per shoot and consequently less inflorescences per plant in the R- treatment (table III). Even after adjusting the load to 6 shoots per plant, difference in the number of inflorescences per shoot was still highly significant. Moreover, some inflorescences counted as such at the beginning of the gro-

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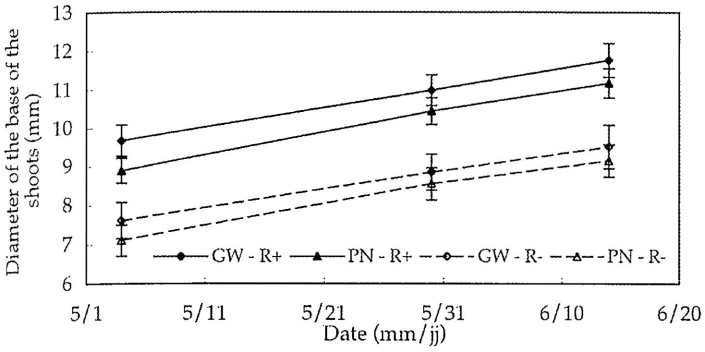


Fig. 2 - Growth the base of the shoots
(bars represent confidence intervals at $p = 0,05$)

Croissance de la base des rameaux
(les barres représentent les intervalles de confiance pour $p = 0,05$)

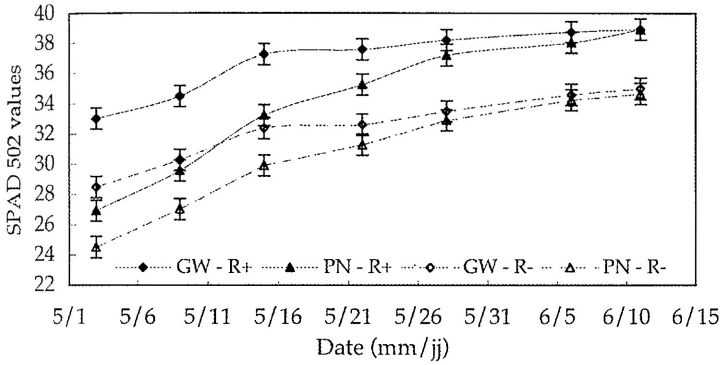


Fig. 3 - Chlorophyll index of the leaves opposite to the basal inflorescences in 2001
(bars represent confidence intervals at $p = 0,05$)

Indice de chlorophylle des feuilles en face des inflorescences basales en 2001
(les barres représentent les intervalles de confiance pour $p = 0,05$)

wing season did never reach the flowering stage in the R- treatment. At flowering, R- Gewurztraminer vines bore half the inflorescences of R+ vines.

V - GROWTH

Figure 2 clearly shows that the bases of the shoots were thinner in the R- treatments for both varieties. The SPAD 502 values, indicating of the leaves chlorophyll content, were also lower in the R- treatment (figure 3). These data indicate that vines were weaker in the R- treatment and weights of vegetative parts cut at the first hedging, significantly lower in the R- treatment (table IV), confirm this idea. At the second hedging, differences were still significant for Pinot noir. Although the "Reserve*Variety" interaction was not significant, it can be noticed that the overall decrease in dry weight of hedging for R- was greater for Pinot noir (-46 %) than for Gewurztraminer (-21 %).

The leaf weights per area of the same leaves, expressed in dry or fresh weight, were higher in the R+ treatment (table V). It is noteworthy that the observed values are consistent with those found by KELLER and KOBLET, 1995 or FERREE *et al.*, 2001.

Significant differences of the weight of leaves on the main stem were still noticeable at the end of summer (table VI) for both varieties. This was partly compensated for Gewurztraminer by a lower weight per area of the leaves in the R- treatment so that no significant differences were found on leaf area for the main shoot. This compensation was not significant for Pinot noir, and leaf areas for the main stem followed hence the pattern of leaves weight. Leaf areas on laterals were similar and overall effect on total leaf areas, less than 10%, was not significant for both varieties.

VI - FRUIT SET AND GRAPE WEIGHT

The cluster weight was significantly reduced in the R- treatment. This was due to a lower number of flowers and berries, but also because remaining berries were smaller (table VII). However, neither the fruit set ratio nor the average number of seeds per berry were modified. The fecundation process did not appear altered as shown by the calculation of the Pe and Ps parameters (DUCHENE *et al.*, 1999) (table VII) corresponding respectively to the probability to form an endosperm and to form moreover an embryo. The observed difference for Pinot noir, although significant, is biologically not important.

Table VIII shows that the main yield component affected by the 2000 treatments at the plant level was the number of flowers per plant. Fruit set being similar, the total number of berries per plant was reduced, which lowered the weight of grape at fruit set by 68 % for Gewurztraminer, 46 % for Pinot noir, in the R- treatment.

DISCUSSION

The treatments applied to the plants at the end of the "véraison" process in 2000 significantly modified the leaf/fruit ratio. They led, as expected (CARBONNEAU *et al.*, 1977; KOBLET *et al.*, 1994; MURISIER and ZUFFEREY, 1997), to major differences in the sugar concentrations of the grapes. A rough approximation shows that grapes in the R- treatment, because of the total weight of grapes, contained about three times more sugar, expressed on a whole plant basis, than the R+ ones. These sugars partly come from photosynthesis but CANDOLFI-VASCONCELOS *et al.*, 1994 clearly showed that defoliation could induce a remobilisation of carbohydrates from the perennial parts. In our case, total carbohydrate concentrations in

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Table V - Leaf dry weight per area for the leaves opposite to the basal inflorescences at flowering in 2001 (three 8 mm diameter samples)

Poids sec des feuilles par unité de surface pour les feuilles en face des inflorescences basales à la floraison en 2001 (trois échantillons de 8 mm de diamètre)

	"Reserves" effect (1)	Gewurztraminer		Pinot noir	
		R-	R+	R-	R+
Leaf fresh weight per area (g/m²)	***	143.3 b (2)	160.0 a	126.4 b	140.2 a
Leaf dry weight per area (g/m²)	***	35.2 b	41.7 a	33.4 b	37.2 a

(1) NS : Non Significant. *, **,*** : significant at $p \leq 0.05$, $p \leq 0.01$, $p \leq 0.001$ respectively. (2) different letters indicate that the R+/R- difference for a variety is significant at $p \leq 0.05$.

Table VI - Leaf weight, weight per area and leaf area per plant on September 19, 2001 (MS = main stem, FW= fresh weight)

Poids des feuilles, poids par unité de surface et surfaces foliaires par plante le 19 septembre 2001

	"Reserves" effect (1)	Gewurztraminer		Pinot noir	
		R-	R+	R-	R+
MS limb weight (g FW)	***	218.1 b (2)	254.2 a	202.5 b	264.4 a
MS leaf fresh weight per area (g/m²)	0.08	182.8	198.6	186.3	189.1
MS leaf dry weight per area (g/m²)	*	52.0 b	57.3 a	52.0	53.4
MS total leaf area (m²)	**	1.20	1.29	1.10 b	1.41 a
Laterals limb weight (g FW)	NS	193.8	207.7	168.6	150.4
Laterals leaf fresh weight per area (g/m²)	0.07	139.2	144.5	145.5	145.5
Laterals leaf dry weight per area (g/m²)	NS	38.0	40.4	41.8	40.4
Laterals total leaf area (m²)	NS	1.39	1.44	1.18	1.04
Total leaf area (m²)	NS	2.59	2.73	2.27	2.45

(1) NS : Non Significant. *, **,*** : significant at $p \leq 0.05$, $p \leq 0.01$, $p \leq 0.001$ respectively.
(2) different letters indicate that the R+/R- difference for a variety is significant at $p \leq 0.05$.

the pruning wood were significantly lower (-20 %) in the R- plants. In other experiments where reserves levels have been modified, (MURISIER and AERNY, 1994; KOBLET *et al.*, 1997) this variable appeared less sensitive than the carbohydrate concentrations in the roots. It is likely that in our case reserve levels in the roots were also affected.

The differences R+/R- were similar for free amino acids (about - 20 % for R-) as for carbohydrates, which was less expected. Half of the leaves were removed when they were still active and still contained nitrogen in the chloroplasts (BROUQUISSE *et al.*, 2001). The lower content of nitrogen in the pruning wood of R- plants can be linked to this leaf removal but also to the presence of grapes, which mobilised nitrogen as well.

Early spring growth relies on carbohydrate and nitrogen reserves accumulated during the previous season. (SCHOLEFIELD *et al.*, 1978; CONRADIE, 1992). Root pruning (MCARTNEY and FERREE, 1999), shading (MCARTNEY and FERREE, 1999) high yield level (MURISIER, 1996) or limiting nitrogen nutrition (KELLER and KOBLET, 1995) can affect the reserves level and subsequently reduce growth during the following season. Consistently with these data, we registered lower hedging weight and shoot diameters in R- plants. The total mass of limbs on the main shoot was also affected but the effects on the leaf area were significant only for Pinot noir (table VI). The leaf weight per area of the leaves opposite to the basal inflorescence at flowering was lower for R- plants (table V). This means that when carbon supply is limited the increase in leaf area is enhanced. KELLER and KOBLET, 1995 showed a similar effect in the case of limiting irradiance. This difference in leaf weights per area remained significant for Gewurztraminer at the end of the season and despite differences in the leaves weight, this led to an equivalent leaf area in both treatments (table VI). For Pinot noir, this compensation did not occur and leaf areas on the main shoot were different at the end of the season (table VI). This can explain why effects of the treatments on growth were observed later in the season for Pinot noir than for Gewurztraminer (table IV).

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Table VII - Fruit set and fecundation process in 2001 (year *n+1*)

Nouaison et processus de fécondation en 2001 (année *n+1*)

	"Reserves" effect (1)	Gewurztraminer		Pinot noir	
		R-	R+	R-	R+
Number of berries per cluster (> 3 mm)	***	55.4 b (2)	77.0 a	76.4 b	103.0 a
Number of flowers per cluster	***	114.6 b	167.4 a	200.0 b	247.7 a
Fruit set (%)	NS	58.9	53.1	42.9	44.8
Total berry weight per cluster (g)	***	17.4 b	26.2 a	33.2 b	48.5 a
Single berry weight (mg)	***	294.6 b	340.4 a	414.6 b	473.4 a
Number of seeds per cluster	***	71.0 b	101.5 a	133.3 b	175.7 a
Number of seeds per berry	NS	1.29	1.27	1.73	1.74
Pe (%)	NS	42.6	41.4	36.4	36.2
Ps (%)	NS	70.6	71.0	98.8 b	99.5 a

(1) NS, *, **,*** : Non Significant at $p = 0.05$, significant at $p \leq 0.05$, $p \leq 0.01$, $p \leq 0.001$ respectively. (2) different letters indicate that the R+/R- difference for a variety is significant at $p \leq 0.05$.

On the other hand, nor the weight neither the leaf area of the laterals were affected. This can be explained by a delay in their development compared to the main shoot (LEBON *et al.*, 2001), when growth less relies on reserves, but also by hedging operations which contributed to equalise the treatments.

It should be noticed that total hedging weight (table IV) or total leaf area (table VI) for GW, R- is equivalent to PN, R+. Moreover, Gewurztraminer showed higher chlorophyll index and laterals weight as well as a greater capacity than Pinot noir to compensate a decrease of leaves weight by lower leaf weight per area. Even in optimal conditions this variety has a more important vegetative development than Pinot noir. In the stressed conditions R-, its vegetative growth is less affected than for Pinot noir but this is not true for reproductive development as will be discussed later.

Before discussing about the number of flowers per shoot, it is relevant to note that as stated by many authors (MANSFIELD and HOWELL, 1981; REYNOLDS and WARDLE, 1989; CANDOLFI-VASCONCELOS and KOBLET, 1990; HOWELL *et al.*, 1994), we observed a lower budbreak rate in the R- treatments which induced a lack of primary shoots for Gewurztraminer. Low temperatures, not below –0.2 °C during the 2000/2001 winter, cannot be responsible. However, the fact that all the buds don' t follow the same pattern of unfolding (acrotonie) is important for grapevine and seems more accurate when the plant vigour is low (HUGLIN and SCHNEIDER, 1998). Figure 4 shows that lower budbreak rate were observed on the buds closest to the trunk. A competition for assimilates between buds is possible but the observation that "acrotonie" depends on the orientation of the shoot (HUGLIN and SCHNEIDER, 1998) is an argument for a hormonal control of budbreak. Cytokinins, which are known to play a role in apical dominance (CLELAND, 1999), could be candidates. These growth regulators are partly synthesised in roots (CLELAND, 1999) and their concentration in the xylem sap of grapevine at budbreak can vary according to root temperatures or fertilisation (ZELLEKE and KLIEWER, 1981). They are also suspected to mediate the response of plants to nitrogen availability (STITT and SCHEIBLE, 1998). The better budbreak rate in R+ plants could therefore be explained by a higher cytokinins concentration in the sap flow, related to an increase in nitrogen availability in the roots as observed in the pruning wood. We chose 6 shoots per plant and hence the pattern of budbreak did not finally influence this yield component.

Despite the choice of the most fruitful shoots, our data showed that the number of inflorescence per shoot as well as the number of flowers per inflorescence was strongly affected by the R- treatment. Inflorescences are initiated in the buds during the previous growing

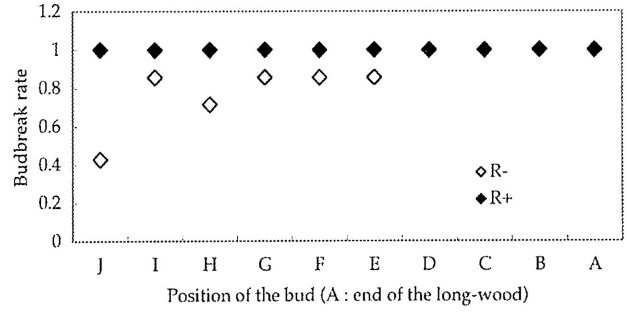


Fig. 4 - Budbreak rate in 2001 (year *n + 1*) according to the position of the bud on the long-wood (Gewurztraminer)

Taux de débourrement en 2001 (année *n + 1*) en fonction de la position du bourgeon sur le long-bois (Gewurztraminer)

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Table VIII - Yield components at the plant level in 2001 (year *n+1*)

Composantes du rendement au niveau de la plante entière en 2001 (année *n+1*)

	"Reserves" effect (1)	Gewurztraminer		Pinot noir	
		R-	R+	R-	R+
Number of flowers	**	638.3 b (2)	1936.7 a	1971.0	3078.6
Number of berries (>3mm)	***	308.7 b	890.9 a	753.1 b	1279.9 a
Weight of berries (g)	***	97.0 b	303.7 a	327.1 b	602.6 a

(1) NS : Non Significant. *, **,*** : significant at $p \leq 0.05$, $p \leq 0.01$, $p \leq 0.001$ respectively.
(2) different letters indicate that the R+/R- difference for a variety is significant at $p \leq 0.05$.

Table IX - Covariance analysis on 2001 yield components : *p* values associated with variables or cofactors

Analyses de covariance sur les composantes du rendement de 2001 : valeurs de la probabilité *p* associée aux variables ou co-facteurs

Variable or cofactor	Number of flowers per shoot (including non fruitful shoots)	Number of berries per shoot (without shoots without berries)
Variety	0.0001	0.0287
Reserves	0.5859	0.8232
Rank of the shoot on the long-wood	0.0001	-
Average diameter of the shoot	0.0001	0.0385
SPAD 502 values at flowering	0.0122	0.0212
Number of flowers per shoot	-	0.0001

season (CAROLUS, 1970; SRINIVASAN and MULLINS, 1981). This process starts around flowering time and ceases when buds enter into dormancy (CAROLUS, 1970). HUGLIN, 1958 showed that for Gewurztraminer in the Alsatian vineyard at least 10 buds from the base of the shoot are fruitful in July and Pinot noir has presumably the same behaviour. Our treatments were applied at the end of July at véraison in a glasshouse, at a later stage of development of the plants; they cannot hence be responsible for the observed lack of fruitfulness, with sometimes no inflorescence at all.

Non-development of inflorescences is common on fruitful cuttings (MULLINS and RAJASEKARAN, 1981), or in the case of early and heavy vineyard defoliation (FOURNIOUX, 1997). In our case, the absence of inflorescences has to be related to a lack of flower differentiation.

Previous experimental results (POUGET, 1981; EZZILI, 1993) have shown that the air temperature around budbreak could influence the number of inflorescences per shoot and the number of flowers per inflorescence. A direct effect of carbohydrate availability seems also possible. MOREAU and VINET, 1932 reported that they could increase the number of inflorescence per plant with an artificial supply of glucose to the plants. More recently, in leaf area or leaf/fruit ratio experiments, an effect on the fruitfulness and/or the number of flowers in the next year has been described (CARBONNEAU *et al.*, 1977; MANSFIELD and HOWELL, 1981; MURISIER, 1996) although not systematic (HUGLIN, 1958; HOWELL *et al.*, 1994; KOBLET *et al.*, 1997). (BENNETT *et al.*, 2002), after a defoliation experiment, show a positive correlation between the starch content of the roots at budbreak and the number of flowers per inflorescence.

The energy cost of building is higher for flowers than for other organs of grapevine (CASTELAN-ESTRADA, 2001) and the level of carbon and nitrogen flux in the early stages of growth is likely to influence the number of differentiated flowers as already observed in other plants (HALEVY, 1987). A hormonal effect is also possible as the floral differentiation process is under the control of cytokinins (SRINIVASAN and MULLINS, 1981). As for the budbreak rate, an effect of our treatments on the root cytokinins metabolism in spring could be an explanation for the observed differences on the number of flowers per inflorescence. Both the presence of cytokinins and an adequate assimilate supply are likely to be two necessary, also individually not sufficient, conditions for flowers differentiation.

A covariance analysis with our data shows that the number of flowers is well explained by growth parameters and that a «reserve» effect, independent from growth, is not significant (table IX). The number of flowers is better explained by the availability of assimilates during the budbreak-flowering period than by the conditions during the floral initiation process.

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Although the impact of the treatments on reserves levels seemed similar (table III) the two varieties showed contrasted reactions on reproductive development. Fruitfulness and number of flowers per inflorescence were more severely affected by the R- treatment for Gewurztraminer than for Pinot noir. The final number of flowers per plant was reduced by 67 % for the former one, by 36 % for the later.

On the other hand, we observed greater reactions of Pinot noir on vegetative development. These elements can explain the generally greater variability in yields for Gewurztraminer : in case of low assimilate supply the vegetative development seems to have a greater priority than the reproductive development whereas this would not be the case for Pinot noir. It should be noticed than even in optimal conditions (R+), vegetative growth is greater and number of flowers lower for Gewurztraminer than for Pinot noir. It could be interesting to test whether the ratio weight of the inflorescences (or number of flowers per shoot)/total weight of the shoot at flowering for instance is related to yield variability. It is possible that, under a certain level of this ratio, the strength of the vegetative sink is such that it can be detrimental to reproductive growth. The origin of the strength of the vegetative sink should be further investigated. It could be determined during the previous season. Data from HUGLIN, 1958 for example suggest that the number of pre-formed leaves could be different between varieties. A higher number of pre-formed leaves could induce a higher vegetative sink. Other hypothesis such as variations in the number of cells in the leaves primordia should also be tested.

For both varieties, fruit set was not modified by the leaf/fruit ratio of the preceding year. Variations in the number of berries are related to the number of flowers but not to the fecundation process. A covariance analysis shows that the number of berries depends on the number of flowers but also on growth parameters (table IX). Coefficients are all positive which means that for an equivalent number of flowers, the number of berries would have been higher in the R+ treatment where growth conditions were more favourable. This result is consistent with positive relationships between growth and berry formation already reported (COOMBE, 1962; CASPARI *et al.*, 1998). Although fruit set was correct for both Gewurztraminer treatments, it is known that competitions among vegetative and reproductive growth can reduce fruit set (COOMBE, 1962; KOBLET, 1966; SMITHYMAN *et al.*, 1998; VASCONCELOS and CASTAGNOLI, 2000). A high vegetative demand associated with a lack of assimilate supply, mainly coming from photosynthesis around flowering, could induce detrimental competitions for assimilates between the reproductive and vegetative sinks and hence prevent correct fruit set for Gewurztraminer.

CONCLUSION

Our data clearly showed that the leaf/fruit ratio can modify reserve levels, affect growth as well as yield components in the following season but fruit set was not affected. The two varieties studied exhibited different behaviours. Yield variability is a characteristic of a variety and could be related to the priority between vegetative and reproductive growth when over-wintering reserves are limited. The high vegetative growth observed for Gewurztraminer could also be an explanation for its susceptibility to poor fruit set in some circumstances.

These results suggest that management of ripening conditions and hence of reserves constitution can be considered as a tool for yield control through the number of flowers. Specific mechanisms of flowers formation, especially the respective influence of budbreak conditions compared to floral initiation conditions, as well as the basic components of the vegetative sink strength would need to be further investigated.

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