LONG TERM EFFECTS OF NITROGEN AND WATER SUPPLY ON CONFERED VIGOUR AND YIELD BY SO4 AND RIPARIA GLOIRE DE MONTPELLIER ROOTSTOCKS

J.-P. TANDONNET, J.-P. SOYER, J.-P. GAUDILLÈRE, S. DECROOCQ,
L. BORDENAVE and Nathalie OLLAT*

Institut des Sciences de la Vigne et du Vin
UMR Écophysiologie et Génomique Fonctionnelle de la Vigne, INRA,
University of Bordeaux 2, University of Bordeaux 1, ENITA, Villenave d'Ornon, France
INRA, Domaine de la Grande Ferrade, BP 81, 33883 Villenave d'Ornon, France

Abstract

Aims: the present study was designed to test the hypothesis according to which rootstock effects on scion growth and yield are related to fundamental physiological traits which are expressed consistently and independently of environmental conditions.

Methods and results: Pruning weights and yield components from two independent rootstock experiments are reported. In the first experiment, the effect of two levels (30 and 70 kgN/ha/year) was studied during 15 years on Cabernet-Sauvignon vines grafted onto SO4 and Riparia Gloire de Montpellier (RGM). In the second one, Cabernet-Sauvignon and Merlot vines grafted on SO4 and RGM were submitted to two levels of soil fertility shortly after plantation: control and high (100 kgN/ha/year + irrigation) and data from the plantation to year 6 were recorded. In both experiments, vine vigour and yield were significantly affected by rootstocks and fertilisation/irrigation treatments. No interaction was recorded. The devigorating effect of RGM in comparison to SO4 was observed in both experiments, regardless of other parameters. Cabernet-Sauvignon was more affected by rootstock than Merlot.

Conclusion: Rootstock effects on vine vegetative and reproductive development were consistently expressed, indicating that scion-rootstock interactions are governed not only by adaptative, but also by specific physiological traits.

Significance and impact of study: This work provides information on scion-rootstock interactions which may be useful in rootstock breeding programs and may help to better choose the rootstock according to the scion and the environment.

Key words: grapevine, rootstock, soil fertility, interaction, growth

Résumé

Objectif : Le but de cette étude est vérifier l'hypothèse selon laquelle les effets des porte-greffes sur la croissance et les rendements sont liés à des caractères physiologiques fondamentaux, indépendants des conditions environnementales.

Méthodes et résultats : Cet article présente les résultats des pesées de bois de taille et des rendements de deux essais porte-greffe. Dans la première expérimentation, les effets de deux niveaux d'apport azoté (30 et 70 kg N/ha/an) sont étudiés pendant 15 ans sur du Cabernet-Sauvignon greffé sur SO4 ou sur Riparia gloire de Montpellier (RGM). Dans la deuxième, des plants de Cabernet-Sauvignon et de Merlot greffés sur SO4 ou sur RGM ont été soumis à deux niveaux de fertilité du sol : un témoin et l'autre sans contrainte hydrique ou azoté (100 kg N/Ha/an et irrigation). Dans ces deux dispositifs expérimentaux, la vigueur des souches et les niveaux de rendement sont significativement influencés par les porte-greffes et les traitements fertilisation/irrigation. Aucune interaction entre ces deux paramètres n'a été observée. L'effet dévigorisant du RGM par rapport au SO4 est maintenu dans les deux dispositifs quels que soient les traitements. Le cépage Cabernet-Sauvignon est plus influencé par les effets porte-greffe que le Merlot.

Conclusion : Le maintien de l'effet porte-greffe sur le développement végétatif et reproducteur du greffon montre que les interactions porte-greffe/greffon ne sont pas dépendantes de l'adaptation aux conditions environnementales, mais sont liées à des caractères physiologiques spécifiques.

Signification et impact de l'étude : Ce travail fournit des informations sur les interactions porte-greffe/greffon nécessaires aux programmes d'amélioration et au choix raisonné du porte-greffe en fonction du cépage et des conditions du milieu.

Mots clés : vigne, porte-greffe, fertilité du sol, interaction, croissance

manuscript received: 31 January 2008 - revised manuscript received: 8 April 2008

*Corresponding author: ollat@bordeaux.inra.fr

INTRODUCTION

Viticulture is currently facing several changes, including environmental and economic ones. Adaptations of cultural practices to these changes must be made in a sustainable way in order to protect the environment, human working conditions and economical health of the property. Rootstocks represent one of the most effective long-term uses of a biological control mechanism for an agricultural pest. Moreover they participate to environmental condition adaptation and may contribute, to some extent, to the control of vine vigour and yield.

Assuming that 100 % of vines are grafted in Europe and an average of 70 % for the rest of the world, it can be estimated that 80 to 85 % of the world vineyards are using rootstocks (SMITH, 2004).

In France, 30 rootstocks are allowed for plantation in any vineyard. Some of them have been used for a long time. Their general characteristics are well described (CORDEAU, 1998). SO4 (*Vitis berlandieri* x *Vitis riparia*) is the most common. Vines grafted onto this rootstock are characterized by medium to high vigour and yield. *Vitis riparia* cv « Gloire de Montpellier » (RGM) is restricted to few premium quality vineyards where water supply is not a limiting factor. This rootstock is considered to induce low vigour and moderate yield.

Even if rootstocks are widely used in viticulture and for fruit tree production, the underlying mechanisms which control plant size and scion-rootstock interactions are poorly understood (JENSEN *et al.*, 2003; OLLAT *et al.*, 2003). Many trials have provided contradictory information, leading to the conclusion that rootstock effects are largely unpredictable, because they results from too many interactions.

The term vigour is widely used in viticulture to describe the vegetative growth of the vine, and the term conferred vigour commonly characterizes the potential effect of rootstock varieties on the growth of the scion (SMITH, 2004). Yield is often positively correlated to vine vigour, because shoot number and fertility increase with vigour (HUGLIN, 1958). The vigour of the vines has trophic and genetic components. According to RIVES (1971), the genetic component of vigour for a specific scion/rootstock combination is the result of the own vigour of the scion, the effect of rootstock named conferred vigour and the affinity which results from the interaction between the two specific genotypes. So far, the genetic basis of conferred vigour and affinity remain unknown.

The rootstock ensures water and mineral uptake from the soil while the scion provides carbon assimilates to the underground parts. Nitrogen and water supply are the first determinants of plant growth (KELLER, 2005). Nitrogen uptake is considered to be mainly controlled by aerial part demand and growth (ALLEWELDT and MERKT, 1993). Nevertheless, there is evidence that rootstock affects nitrogen metabolism in roots and leaves (ZERIHUN and TREEBY, 2002). Drought tolerance of the vine is controlled by the rootstock (FREGONI *et al.*, 1978; CARBONNEAU, 1985). Differences in hydraulic conductivity (PETERLUNGER, 1990; DE HERRALDE *et al.*, 2006) or abscissic acid production (SCIENZA, 1983; SOAR *et al.*, 2006) have been suggested to explain rootstock abilities to face water limitation. Root growth, distribution and structure are also major parameters (SOAR *et al.*, 2006).

Several authors consider that the genetic component linked to rootstock effect is low, especially under fertile conditions (CHAMPAGNOL, 1984; SOUTHEY, 1992). This would imply that the rootstock effect on scion growth is related only to the ability to take up nutrients and water, especially when those are limiting, i.e. to adaptation mechanisms, rather than to any specific physiological trait (SMITH, 2004). Therefore, before initiating any rootstock breeding program, it is necessary to determine the meaning of the genetic component of conferred vigour and yield.

The aim of the present study was to test the hypothesis according to which rootstock effects on scion growth and yield are related to fundamental physiological traits which are expressed consistently and independently of environmental conditions. Four rootstock/scion combinations were studied under different regimes of nitrogen and water supply.

MATERIALS AND METHODS

1 - Location, vine material and experimental set up

Rootstock x fertilisation experiment: This experimental vineyard was located in a gravely soil from Pessac Leognan Appellation in the Bordeaux area (Domaine INRA de Couhins, France). The soil was characterized by a very low fertility (table 1). It has been planted in 1980 with Cabernet-Sauvignon (clone 341) grafted onto SO4 (unknown clone number) or RGM (unknown clone number). The planting density was 5,050 vines/ha (1.1 m x 1.8 m). Trunk height was 0.4 m, shoots were vertically positioned and trimmed 1.5 m above the ground. The vines were pruned as double short canes (31 000 buds per/ha). The control vines were fertilised yearly with 30 kg N/ha, whereas the treated vines were supplied with 70 kg N/ha. In 1995, each row was sown with *Festuca rubra*. Each treatment was applied on 10 vines growing on two consecutive rows.

Scion x rootstock x nitrogen-water experiment: This experimental plot was located in a sandy-gravely soil from « Premières Côtes de Bordeaux », in the Bordeaux region

Table 1 - Main soil analytical data for the experimental plots. Soil was sampled before plantation, i.e. two years before nitrogen and irrigation application started in experiment 2.

	Experiment 1	Experiment 2			
		Low soil fertility F0		High soil fertility F100	
	0-0.4m	0-0.2m	0.2-0.4m	0-0.2m	0.2-0.4m
Fine fraction (< 2mm, %)	65	23.8	16.5	40.1	28.3
Organic matter (%)	0.7	3.7	2.8	4.4	2.8
N (%)	0.034	0.17	0.13	0.21	0.14
K_2O (%)	0.003	0.15	0.07	0.17	0.08
P_2O_5 (%) [1]	0.024	0.029	0.031	0.021	0.018
MgO (%)	0.001	0.014	0.006	0.012	0.008
Ca (%) x 10	0.026	0.0305	0.034	0.039	0.045
CEC (meq/kg)	md	9.7	8.2	10	7.6

1: Phosphorus content was determined using Dyer methodology. Md : missing data

(Domaine INRA du Grand Parc, France). The vineyard was planted in year 2000 with *Vitis vinifera* cvs. Cabernet Sauvignon (clone 191, CS) and Merlot noir (clone 181, MN) grafted onto SO4 (clone 762) or RGM (clone 186) with 40 vines per scion-rootstock combination (8 blocs of 5 vines). The planting density was 5,050 vines per ha (1.1 m x 1.8 m) with North-South row orientation. The vines were vertical shoot positioned with a trunk height of 0.6 m and a hedging height of 1.8 m above the soil. Starting from the third year after plantation, each vine was double cane pruned with 40 000 buds/ha for CS and 30 000 buds/ha for MN. For each vine, the number of buds was distributed according to pruning wood weight of the previous season, using appropriate pruning scales (RIVES, 1972; figure 1).

After two years of plantation, considering the soil analyses and pruning wood weight recorded in 2000 and 2001, the plot was divided into two « soil fertility » parts (Table 1). A split-plot design was then used to vary the fertility of the soil (main-plot) and rootstock and scion varieties (sub-plots). The treatments were control (F0: no fertilisation, no irrigation) or high fertility (F100). The F0 and F100 treatments were located in the sub-plots were the soil fertility was already considered lower and higher respectively. The F100 treatment consisted in 100 kg N/ha/year (ammonium nitrate) at bud burst and irrigation from flowering to veraison (60 % ETP). Irrigation was supplied weekly. Within the main plots for soil fertility treatment, scion varieties were distributed between rows and rootstock sub-plots were randomised for each scion variety. This experimental design resulted in 4 blocks of 5 vines per scion x rootstock x fertility combination.

2. Data collections

For each experiment, pruning wood weight per vine and yield components, i.e. number of clusters per vine and yield per vine, were determined. In the scion x rootstock x fertility treatment, the pruning wood weight and yield components were recorded from 2000 to 2006 and from 2002 to 2006, respectively.

N content in petiole was determined at veraison in 2002, 2003, 2004, 2007 according to DELAS (2000). Fourty petioles were pooled for each combination. The analyses were performed by LCA 33 laboratory (Blanquefort, Gironde, France).

Statistical analysis

For experiment 1, data analysis was performed using MANOVA procedures of Statistica 7.0 (Statsoft). The studied parameters were rootstock and nitrogen.

For experiment 2, petiole nitrogen content data were analysed using non parametric Kruskal-Wallis test procedure of Statistica 7.0 (Statsoft). Data analysis was performed using MANOVA procedures of Statistica 7.0

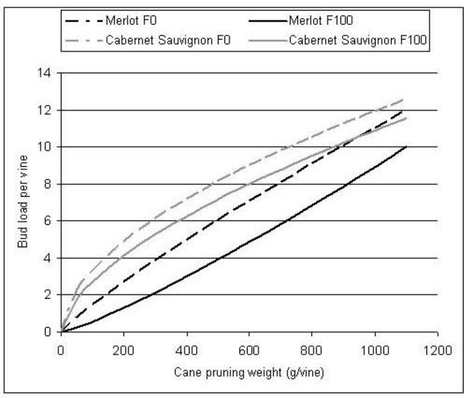

Fig. 1 - Mathematical relationships between pruning weight for year 2003 and bud load in 2004 used to determine bud load for individual vines for the different treatments in 2003.
Bud load was 40 000 buds/ha for Cabernet-Sauvignon and 35 000 buds/ha for Merlot.

Table 2 - N content (g/kg of DW) in petioles collected at veraison at different stages of this long term experiment for the different scion x rootstock x soil fertility combinations.

	year	2002	2003	2004	2007
Merlot	RGM F0	6.3	4.8	5.6	6.5
	SO4 F0	6.6	5.0	5.8	9.1
	RGM F100	9.8	5.4	7.7	8.5
	SO4 F100	10.4	5.7	9.4	10.1
Cabernet	RGM F0	7.6	5.0	5.8	5.1
	SO4 F0	7.5	4.7	5.9	6.2
	RGM F100	8.35	5.3	6.6	6.5
	SO4 F100	8.7	6.1	7.5	7.0
RT		NS	NS	NS	NS
SF		*	*	**	NS

Statistical significance of rootstocks (RT) and soil fertility (SF) was given according to the results of Kruskal-Wallis non parametric test. Significance: **$p<0.01$; *$p<0.05$; NS not significant.

(Statsoft) independently for each scion variety and each year. The studied parameters were rootstock and soil fertility. The effect of year was not studied because the period of interest was covering the first seasons after plantation and the vines had not reached equilibrium yet. Because of the experimental design, interactions between parameters were not tested. Data of experiment 2 were also submitted to Principal Component Analysis using Statistica 7.0 (Statsoft)

RESULTS

Experiment 1: Rootstock x fertilisation experiment

The yearly variations of pruning wood weights per vine have been plotted for the four rootstock-nitrogen combinations (Figure 2a). Over the 15 years of the experiment, rootstock effect on pruning wood weight per vine was always significant, with vines grafted to SO4 having a greater cane pruning weight than vines grafted to RGM. Applied N affected significantly pruning weight from 1985 to 1988. At these early stages of the experiment, the interaction between both parameters was never significant. Then nitrogen effect was no more significant until grass was sown. After 1995, nitrogen effect resumed. However there was a highly significant interaction between nitrogen and rootstock. The effect of nitrogen was highly significant for SO4, and not significant for RGM. For all treatments, pruning weight decreased after grass was sown. Nevertheless after 5 years, cane pruning weight reached more or less the same level than before sodding.

Over the 15 years of the experiment, yield was not recorded from 1990 to 1992. Yield per vine was characterized by large year to year variations, regardless of the rootstock (Figure 2b). It was significantly affected by rootstock each year, excepted in 1988, 1993 and 1996. As expected, vines grafted to SO4 presented a higher yield than those grafted to RGM. Applied N affected significantly yields of vines in 1986, 1988, 1996, 1999 and 2000. The interaction between both parameters was never significant.

Experiment 2: Scion x rootstock x nitrogen-water experiment

Nitrogen content in petiole was determined at different stages of the experiment in order to evaluate long term effects of the different studied parameters. It was significantly increased by soil fertility and nitrogen supply

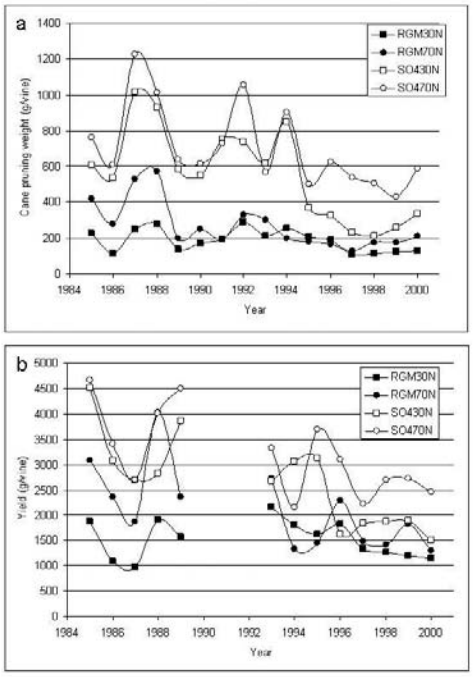

Fig. 2 - Evolution of cane pruning weight per vine (a) and yield per vine (b) during 15 years for the two rootstock combinations CS/RGM and CS/SO4 submitted to two levels of nitrogen application (30 and 70 kgN/ha/year).

Grass was sown between the rows since 1994.

Table 3 - Individual components of cane pruning weight for Merlot vines grafted onto two different rootstocks (RG and SO4) and submitted to two levels of soil fertility (F0 and F100). Mean of 20 vines per combination. Manova analysis (Rootstock RT x Soil Fertility SF) was performed for a linear model on raw data.

Merlot	Shoot number per vine				Individual shoot weight (g)			
year	2002	2003	2004	2005	2002	2003	2004	2005
RGM F0	3,05	3,7	5,45	6,35	171	95	82	82
SO4 F0	3,79	4,32	6,68	7,32	154	117	88	93
RGM F100	4	5	6,6	6,6	195	124	113	95
SO4 F100	3,72	5,94	7,39	7,56	271	152	112	116
RT	NS	*	**	*	NS	*	NS	**
SF	*	**	*	NS	**	**	**	**

Significnce: **p<0.01; *p<0.05; NS. not significant.

to the vineyard, excepted in 2007. There was no significant effect of rootstock (Table 2).

For Merlot, cane pruning weight increased sharply during the first two years after plantation. Six years after plantation, cane pruning weight had not reached a steady state and increased more or less regularly year after year. Under high fertility conditions, cane pruning weight fluctuated according to year for the vines grafted onto RGM (Figure 3a). Cane pruning weight was significantly affected by rootstock and fertility, each year. The effect of the studied parameters started to be significant shortly after plantation. After 2002 and the yearly application of nitrogen and water, the rootstock effect remained highly significant. The rootstock effect on cane pruning weight could be associated to a significant effect on shoot number and/or on individual shoot weight (Table 3) depending on the year.

For Cabernet-Sauvignon, cane pruning weight increased more or less regularly since plantation (Figure 3b). As for Merlot, it did not reach a steady state six years after plantation. Under high fertility conditions, cane pruning weight fluctuated according to year, regardless of the rootstock. Cane pruning weight was significantly affected by rootstock and fertility, excepted in 2000 and 2005 when the fertility effect was not significant. For Cabernet-Sauvignon, rootstock had a significant effect on shoot number and shoot weight (Table 4).

In order to evaluate the depressing effect of RGM in comparison to SO4 in both environmental conditions, the ratio of pruning weight of vines grafted onto RGM to the pruning weight of vines grafted onto SO4 were calculated for each fertility treatment (Figure 4). No significant differences could be recorded between fertility conditions. For Merlot, differences between rootstocks were set since the plantation. For Cabernet Sauvignon, the differences were larger during the first two years and decreased thereafter.

For Merlot, the yield per vine was significantly affected by rootstock, excepted in 2002 (Figure 5a). There was a rootstock effect on cluster number per vine and/or cluster weight, but not on shoot fertility (Table 5).

Soil fertility presented also a significant effect on yield in 2002, 2003 and 2004. The effect was no more significant during the last two seasons. In 2005, the yield

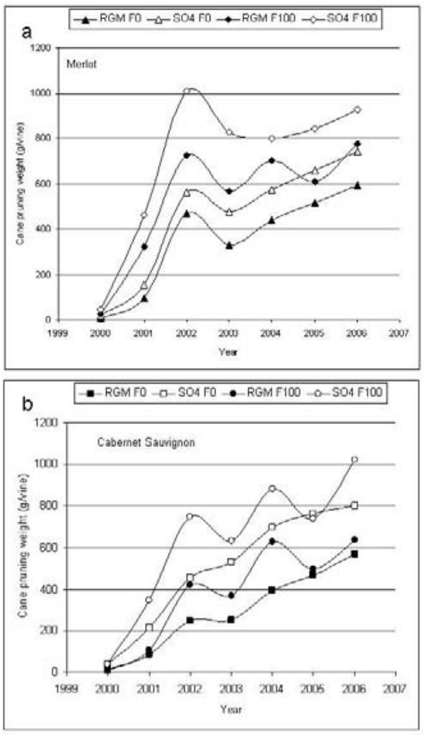

Fig. 3 - Evolution of pruning weight per vine since the plantation for the two rootstock combinations (RGM and SO4) and the two soil fertility treatments (F0 and F100) for the variety Merlot (a) and Cabernet Sauvignon (b).

Data are the mean for 20 vines. In F100 treatment, natural soil fertility was increased by the yearly application of 100 kgN/ha/year and irrigation from flowering to veraison (60 % of ETP).

Table 4 - Individual components of cane pruning weight for Cabernet Sauvignon vines grafted onto two different rootstocks (RG and SO4) and submitted to two levels of soil fertility (F0 and F100).

Cabernet	Shoot number per vine				Individual shoot weight (g)			
year	2002	2003	2004	2005	2002	2003	2004	2005
RGM F0	3,26	4,58	6,58	6,58	79	56	59	72
SO4 F0	3,8	6,6	7,55	9	125	82	93	86
RGM F100	3,37	5,21	7,37	7,21	137	78	86	70
SO4 F100	3,68	6,95	8,21	8,53	202	98	110	89
RT	*	**	**	**	*	**	**	**
SF	NS	NS	*	NS	**	*	**	NS

Mean of 20 vines per combination. Manova analysis (Rootstock RT x Soil Fertility SF) was performed for a linear model on raw data. Significance: **p<0.01; *p<0.05; NS. not significant.

of the vines grafted onto SO4 in the high soil fertility treatment was strongly decreased in comparison to 2004 and 2006.

For Cabernet Sauvignon, yield per vine was significantly affected by rootstock, regardless of the season (Figure 5b). Cluster number was significantly modified each year, whereas cluster weight was affected in 2003 and 2004 only. As for Merlot, shoot fertility was not changed by rootstock excepted during the first cropping cycle (Table 6).

The effect of soil fertility was significant in 2003, 2005 and 2006. As for Merlot, the yield of the vines grafted onto SO4 was strongly depressed in 2005, but it was true for both soil fertility conditions.

Principal component analysis was performed on all the recorded data (excepted mineral analysis). The first two components explained 53.5 % of the variance, with the first one explaining 43 %. Pruning wood weights were highly correlated to this axis. The second component explained only 10 % of variance. Yield components in 2006 and 2003 were correlated to this second axis. Examination of the score-plots (PC1 vs PC2) generated from PCA analysis for both genotypes showed that the first component allowed to separate rootstocks for Cabernet-Sauvignon (Figure 6b), whereas it separated more or less soil fertility treatments for Merlot (Figure 6a). MN/SO4 and MN/RGM were not discriminated in the low soil fertility condition.

DISCUSSION

According to CHAMPAGNOL (1984), each vine is characterized by growth capacities related to its genetic background (scion/rootstock combination) and storage accumulation from the previous growing seasons. Each year, according to its growth capacities and environmental fertility, this potential lead to a certain amount of biomass accumulation, divided into vegetative (shoots, leaves, roots, perennial parts) and storage pools (fruits, starch storage). Pruning wood weight is a good indicator of the vegetative component, even if it is commonly reported as a vigour indicator (MAY, 1994). Vigour itself was originally defined as the growth rate of individual shoots and may be evaluated by the vegetative pool divided

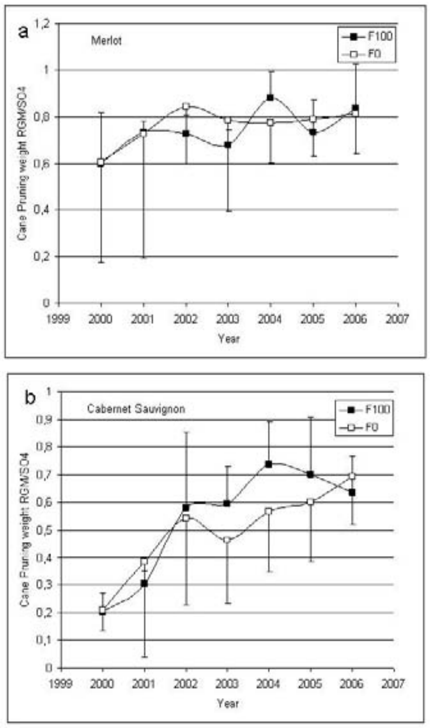

Fig. 4 - Ratio of the pruning weight of Merlot (a) or Cabernet Sauvignon (b) vines grafted onto RGM vines to the pruning weight of vines grafted onto SO4 under both fertility conditions (F0 and F100) since the plantation.

The ratio was calculated for each block. Data presented are the mean + or - standard deviation for 4 blocs.

Table 5 - Individual components of yield for Merlot vines grafted onto two different rootstocks (RG and SO4) and submitted to two levels of soil fertility (F0 and F100).

Merlot	Number of clusters per vine					Number of cluster per shoot				Individual cluster weight (g)				
year	2002	2003	2004	2005	2006	2002	2003	2004	2005	2002	2003	2004	2005	2006
RGM F0	4.3	7.6	10.7	10.7	10.7	1.48	2.12	1.97	1.7	61	142	181	186	266
SO4 F0	6.8	8.6	13.7	12.8	13	1.76	2.04	2.08	1.78	65	164	193	231	281
RGM F100	8.7	10.2	12.6	11.9	10.4	2.2	2.09	1.92	1.81	104	175	219	202	260
SO4 F100	8.9	13.3	15.3	13.3	14.8	2.35	2.31	2.05	1.75	124	212	277	240	324
RT	NS	*	**	NS	**	NS	NS	NS	NS	NS	**	*	**	**
SF	*	**	NS	NS	NS	*	NS	NS	NS	NS	**	**	NS	NS

Mean of 20 vines per combination. Manova analysis (Rootstock RT x Soil Fertility SF) was performed for a linear model on raw data. Significance: **p<0.01; *p<0.05; NS. not significant.

by the number of shoots. Bud load per vine has a limited effect on the vegetative pool, but a strong effect on shoot vigour and yield (MURISIER and ZUFFEREY, 1996; RIVES, 2000).

As expected, vegetative and storage pools were consistently affected by the genetic and environmental parameters studied in our experiments. Pruning wood weight was significantly affected by rootstock and soil fertility treatments, explained a large percentage of variability and separated efficiently the different scion/rootstock/soil fertility level combinations. Vigour, estimated as individual shoot weight, was also affected by the treatments. Nevertheless, in experiment 1, there was no nitrogen effect on pruning wood weight from 1989 to 1994 and an interaction with rootstock after grass sowing. Each year, yield per vine was modified by rootstock in both experiments. This effect was associated with differences in cluster number per vine and on individual cluster weight. However, shoot fertility was not affected. In contrast, the effect of soil fertility on yield was fluctuating from year to year. It was significant when cluster weight was affected.

Soil fertility was increased by the application of nitrogen in experiment 1 and by a large amount of nitrogen and water in experiment 2. Our results are in agreement with many reports showing the positive impact of these two factors on grapevine vegetative growth and yield. N supply before bloom stimulates shoot growth and increases yield mainly through improved fruit set, i.e. cluster weight (CONRADIE, 2005). Irrigation usually increases pruning weight and yield (MC CARTHY *et al.*, 1997). Every yield component may be affected, but berry number per cluster is the main parameter affected (MATTHEWS and ANDERSON, 1989). The fact that the yield per vine was affected by soil fertility only when cluster weight was modified may also be explained by pruning practices (RIVES, 2000). In our work, the use of two different pruning scales for the soil fertility treatments results in close bud loads per vine in both situations, despite the large range in pruning weight. Consequently the differences in yield are restricted to the direct effect of soil fertility on cluster size.

Water and nutrients are absorbed together and strong interactions may occur. The application of nitrogen fertilizer can increase the vine's susceptibility to drought, because nitrogen favors shoot growth over root growth (KELLER, 2005). Then water limitation rather than nitrogen limitation may explain a lack of effect of nitrogen. This could be the reason why, in experiment 1, pruning

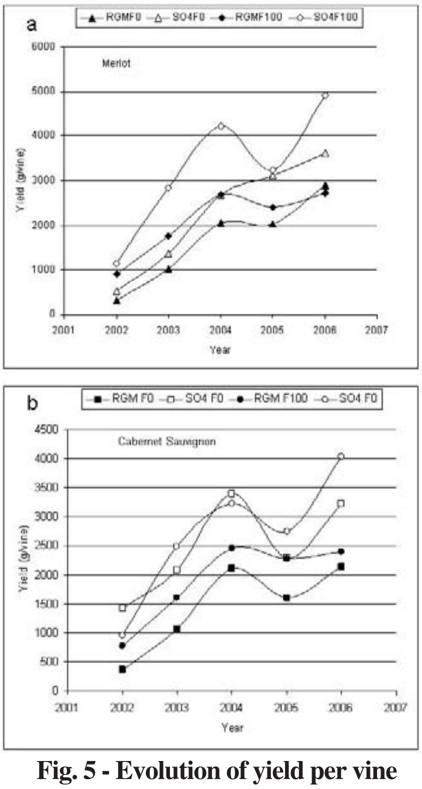

Fig. 5 - Evolution of yield per vine since the plantation for the two rootstock combinations (RGM and SO4) and the two soil fertility treatments (F0 and F100) for the variety Merlot (a) and Cabernet-Sauvignon (b).

Data are the mean for 20 vines. In F100 treatment, natural soil fertility was increased by the yearly application of 100 kgN/ha/year and irrigation from flowering to veraison (60 % of ETP).

wood weight were not significantly affected by nitrogen application from 1989 to 1994 and why RGM did not respond to nitrogen or sodding. Similarly, in experiment 2, the depressed pruning wood weight for some fertilised combinations during the fairly dry years 2003 and 2005 and the reduced yields in 2005 might result from the same phenomena.

Rootstocks are known to influence vegetative and reproductive growth. The effects of rootstocks reported here are in full agreement with the well known behaviour for RGM and SO4 (PONGRACZ, 1983; DELAS *et al.*, 1991; DELAS, 1992). RGM is considered to induce low vine vigour and productivity, SO4 to induce moderate to high vigour, mainly during the first 10 years after plantation. Moreover in our study, the differences induced by the rootstocks SO4 and RGM on growth and yield of CS and MN were not affected by nitrogen and water supplies. In comparison to SO4, the devigorating effect of RGM was the same in both soil fertility conditions. The interaction between rootstock and nitrogen supply was significant when grass was present only, SO4 responding more to nitrogen than RGM.

It has been commonly reported that rootstock effects on scion growth are more apparent in poor than in deep fertile soils (CHAMPAGNOL, 1984; DELAS, 1992; SOUTHEY, 1992). Our results show that this is not true for the rootstocks SO4 and RGM, considering nitrogen and water as two important parameters for soil fertility. It implies that rootstock/scion interactions are governed by specific physiological traits, although adaptation to environmental conditions may also be important. SMITH (2004) drew the same conclusion for the rootstock Ramsey. In fruit trees, hydraulic architecture was demonstrated to play a key role in rootstock vigour control (ATKINSON *et al.*, 2003; SOLARI and DEJONG, 2006; CLEARWATER *et al.*, 2007). However, the limiting step is not clearly identified (COHEN *et al.*, 2007).

Our results are also in agreement with many previous works dealing with nitrogen application on different rootstock / scion combinations (WOLF and POOL, 1988; DELAS *et al.*, 1991; CANDOLFI-VASCONCELOS *et al.*, 1996; KELLER *et al.*, 2001; ZERIHUN and TREEBY, 2002). In most cases, for a large range of rootstocks and different levels of nitrogen application, accumulation of whole plant biomass was highly responsive to N supply and interactions with rootstocks were rare. CANDOLFI-VASCONCELOS *et al.* (1996) and KELLER *et al.* (2001) pointed out SO4, because this rootstock induced the strongest reaction to soil N in their experiments. On the contrary, water supply seems to affect variously different scion/rootstock combinations. Interaction between rootstock and water treatment have been reported for pruning weights (SMITH, 2004; TOUMI *et al.*, 2007) and yield (MC CARTHY *et al.*, 1997). Our work did not permit to observe such interactions with water supply.

According to RIVES (1971), the genetic component of vigour is the result of three components: the own vigour of the scion, the effect of rootstock named conferred vigour and the affinity which results from the interaction between the two specific genotypes. In the present work, Cabernet-Sauvignon and Merlot did not respond exactly in the same way to rootstock and soil fertility. Considering the studied parameters (vegetative and reproductive development) al together with multivariate analysis, the rootstock effect appears clearly for Cabernet Sauvignon in any soil fertility conditions. For Merlot, the same parameters discriminate more clearly the soil fertility levels than the rootstocks. It may mean that, for Cabernet-Sauvignon, total biomass accumulation is strongly impacted by rootstock. BARBEAU *et al.* (2006) reported also differential effects of the same rootstocks for the scion varieties Chenin and Cabernet franc. It has been previously observed that

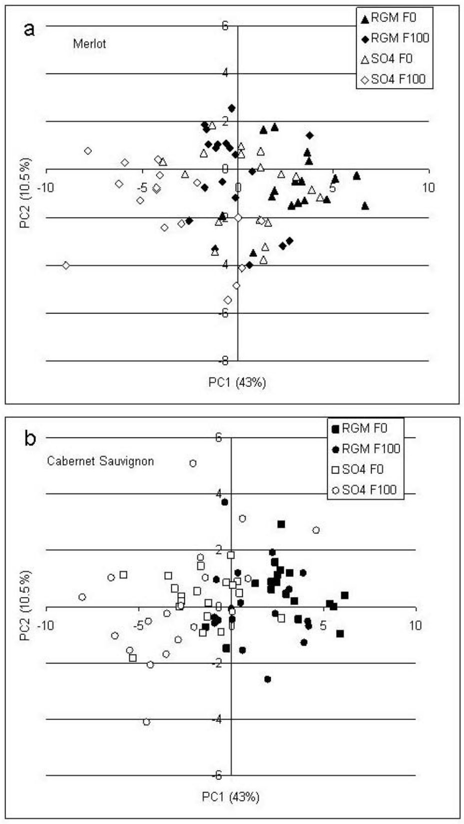

Fig. 6 - Score plots (PC1 versus PC2) resulting from the principal component analysis performed on all the data collected on single vines for Merlot (a) and Cabernet-Sauvignon (b) grafted onto RGM or SO4 under two soil fertility treatments (F0 and F100).
The number in bracket indicates the percentage of variability explained per each component.

Cabernet Sauvignon and Merlot noir grafted on the same rootstock did not respond in the same way to three different water supplies, with regard to vegetative versus reproductive growth (TANDONNET *et al.*, 1999). The present work can not conclude whether the different behaviours are related to the scion by itself or to the affinity between scions and rootstocks. Nevertheless, these interactions can not be neglected when rootstock effects are considered in relation with environmental fertility (LEFORT and LÉGLISE, 1977).

CONCLUSION

Our results provide evidence that, although soil fertility is a major parameter for vine vigour and productivity, the rootstock effect on vine growth and production is maintained for RGM and SO4 under high soil fertility conditions. These effects are probably related to fundamental physiological traits which are expressed consistently and independently of environmental conditions. Interactions with scion have to be taken into account. Indeed Cabernet-Sauvignon and Merlot appear to interact differently with these two rootstocks. The present results are very important for the investigations about rootstock-scion interactions and before initiating a rootstock breeding program for such traits. According to these results, new rootstocks could be evaluated for this kind of properties on young vines growing in fertile soils. A responsive scion variety, as Cabernet Sauvignon should be preferred. Nevertheless, the specific rootstock effect may be not so strong for all rootstocks, explaining why more complex interactions with environmental parameters are observed under some circumstances. Other nutrients could also be more important than nitrogen and further studies should be undertaken in that direction.

Acknowledgements : The authors would like to thank the Aquitaine Region and the Conseil Interprofessionnel des Vins de Bordeaux which supported financially this work. They acknowledge the staff of Experimental Vineyard Unit from INRA-Bordeaux for taking care of the experimental vineyards. They want also to express their recognition to the technicians involved in data collection.

REFERENCES

ALLEWELDT G. and MERKT N., 1993. The nitrogen output of the root and the nitrogenous compounds in the xylem exudate. Part 2: The influence of grafting. *Vitic. Enol. Sci.*, **48**, 55-60.

ATKINSON C.J., ELSE M.A., TAYLOR L. and DOVER C.J., 2003. Root and stem hydraulic conductivity as determinants of growth potential in grafted trees of apple (*Malus pumila* Mill.). *J. Exp. Bot.*, **54**, 1221-1229.

BARBEAU G.E., GOULET E., AMILLON D.R., RIOUX D., BLIN A., ARSAULT J.M. and PANNEAU J.-P., 2006. Effets de l'interaction porte-greffe / enherbement sur la réponse agronomique de la vigne (*Vitis vinifera* L., cvs Cabernet franc et Chenin). *Prog. Agric. Vitic.*, **123**, 80-86.

CANDOLFI-VASCONCELOS M.C., KUMMER M., KELLER M., BASLER P. and KOBLET W., 1996. Nitrogen response of *Vitis vinifera* Müller-Thurgau grafted on six different rootstocks: canopy characteristics and leaf gas exchange. *In 4th International Symposium on Cool Climate Viticulture and Enology*, Vol III, Rochester NY, p 32-36.

CARBONNEAU A., 1985. The early selection of grapevine rootstocks for resistance to drought conditions. *American Society for Enology and Viticulture*, **36**, 195-198.

CHAMPAGNOL F., 1984. *Éléments de physiologie de la vigne et de viticulture générale*. Imp. Duhan, Montpellier.

CLEARWATER M.J., BLATTMANN, P., LUO Z. and LOWE R.G., 2007. Control of scion vigour by kiwifruit rootstocks is correlated with spring pressure phenology. *J. Exp Bot.*, **58**, 1741-1751.

COHEN S., NAOR A., BENNINCK J., GRAVA A. and TYREE M., 2007. Hydraulic resistance components of mature apple trees on rootstocks of different vigours. *J. Exp. Bot.*, **58**, 4213-4224.

CONRADIE W.J., 2005. Partitioning of mineral nutrients and timing of fertilizer applications for optimum efficiency. *In Soil Environment and Vine Mineral Symposium*. P. Christensen, D.R. Smart eds, Davis, CA, p 69-81.

CORDEAU J., 1998. *Création d'un vignoble. Greffage de la vigne et porte-greffes. Élimination des maladies à virus*. Ed. Féret, Bordeaux.

DE HERRALDE F., DEL MAR ALSINA M., ARANDA X., SAVE R. and BIEL C., 2006. Effects of rootstocks and irrigation regime on hydraulic architecture of *Vitis vinifera* L. cv. Tempranillo. *J. Sci.Vigne Vin*, **40**, 133-139.

DELAS J., 1992. Criteria used for rootstock selection in France. *In Rootstock Seminar: a worldwide perspectiv*e. American Society for Enology and Viticulture, S.A. Fike ed., Reno, Nevada, USA, p 1-14.

DELAS J., 2000. *Fertilisation de la vigne*, Ed. Féret, Bordeaux.

DELAS J., MOLOT C. and SOYER J.P., 1991. Effects of nitrogen fertilization and grafting on the yield and quality of the crop of *Vitis vinifera* cv. Merlot. *In International Symposium on Nitrogen in Grapes and Wine*. American Society for Enology and Viticulture. J.M. Rantz ed., Seattle, Washington, USA, p 242-248.

FREGONI M., SCIENZA A. and MIRAVALLE R., 1978. Évaluation précoce de la résistance des portes-greffes à la sécheresse. *In Génétique et Amélioration de la Vign*e, INRA ed., p 287-297.

HUGLIN P., 1958. Recherches sur les bourgeons de la vigne: initiation florale et développement végétatif. *Ann. Amélior. Plantes*, **8**, 113-272.

JENSEN P.J., RYTTER J., DETWILER E.A., TRAVIS J.W. and MCNELLIS T.W., 2003. Rootstock effects on gene expression patterns in apple tree scions. *Plant Mol. Biol.*, **53**, 493-511.

KELLER M., 2005. Deficit irrigation and vine mineral nutrition. *Am. J. Enol. Vitic.*, **56**, 267-283.

KELLER M., KUMMER M. and CARMO VASCONCELOS M., 2001. Soil nitrogen utilisation for growth and gas exchange by grapevines in response to nitrogen supply and rootstock. *Aust. J. Grape Wine Res*., **7**, 2-11.

LEFORT P.L. and LÉGLISE N., 1977. Quantitative stock-scion relationships in vine. Preliminary investigations by the analysis of reciprocal graftings. *Vitis*, **16**, 149-161.

MATTHEWS M.A. and ANDERSON M.M., 1989. Reproductive development in grape (*Vitis vinifera* L.): Responses to seasonal water deficits. *Am. J. Enol. Vitic*., **40**, 52-60.

MAY P., 1994. Using grapevine rootstocks - The Australian perspective. Ed. Winetitles, Adelaïde, Australia.

MC CARTHY M.G., CIRAMI R.M. and FURKALIEV D.G., 1997. Rootstock response of Shiraz (*Vitis vinifera*) grapevines to dry and drip-irrigated conditions. *Australian J. Grape Wine Research*, **3**, 95-98.

MURISIER F. and ZUFFEREY V., 1996. Optimisation de la charge en rameaux de la vigne : essai sur Chasselas. *Revue Suisse Vitic, Arboric. Hortic.*, **28**, 131-137.

OLLAT N., TANDONNET J.-P., BORDENAVE S., DECROOCQ S., GENY L., GAUDILLÈRE J.-P., FOUQUET R., BARRIEU F. and HAMDI S., 2003. La vigueur conférée par le porte-greffe : hypothèses et pistes de recherches. *Bulletin O.I.V.*, 869-870, 581-595.

PETERLUNGER E., 1990. Conductivité hydraulique racinaire du porte-greffe. *Vignevini*, **6**, 43-46.

PONGRACZ D.P., 1983. *Rootstocks for grape-vines*. Ed. David Philip, Cape Town.

RIVES M., 1971. Principes d'étude du déterminisme de la vigueur en vue de la création de variétés nouvelles de porte-greffes de vigueur donnée. *Ann. Amélior. Plantes*, **21**, 5-13.

RIVES M., 1972. Essais de porte-greffes multicombinaisons. *Connaissance de la Vigne et du Vin*, **6**, 223-235.

RIVES M., 2000. Vigour, pruning, and cropping in the grapevine (*Vitis vinifera* L.). II. experiments on vigour, pruning and cropping. *Agronomie*, **20**, 205-213.

SCIENZA A., 1983. Adattamento genetico della vite allo stress idrico. *Vignevini*, **10**, 27-39.

SMITH J.P., 2004. Investigations into the mechanisms underlying grapevine rootstock effects on scion vigour and yield. *pHD*. Charles Sturt University, Wagga Wagga, Australia.

SOAR C.J., DRY P.R. and LOVEYS B.R., 2006. Scion photosynthesis and leaf gas exchange in *Vitis vinifera* L. cv. Shiraz : mediation of rootstock effects via xylem sap ABA. *Australian J. Agric. Research*, **12**, 82-96.

SOLARI L.I. and DEJONG T., 2006. The effect of root pressurization on water relations, shoot growth, and leaf gas exchange of peach (*Prunus persica*) trees on rootstocks with differing growth potential and hydraulic conductance. *J. Exp. Bot*., **57**, 1981-1989.

SOUTHEY J.M., 1992. Grapevine rootstock performance under diverse conditions in South Africa. *In Rootstock Seminar: A worldwide perspective*. American Society for Enology and Viticulture, S.A. Fike ed., Reno, Nevada, USA, p 27-51.

TANDONNET J.P., OLLAT N., NEVEUX M. and RENOUX J.-L., 1999. Effect of three levels of water supply on the vegetative and reproductive development of Merlot and Cabernet-Sauvignon grapevines. *In Acta Horticulturae*, J. Schmid ed., Vol 493. ISHS, Stuttgart, p 301-308.

TOUMI I., M'SEHLI W., BOURGOU S., JALLOULI N., BENSALEM-FNAYOU A., GHORBEL A. and MLIKI A., 2007. Response of ungrafted and grafted grapevine cultivars and rootsotcks (*Vitis* sp.) to water stress. *J. Int. Sci. Vigne Vin*, **41**, 85-93.

WOLF T.K. and POOL R.M., 1988. Effects of rootstock and nitrogen fertilization on the growth and yield of Chardonnay grapevines in New York. *Am. J. Enol. Vitic.*, **38**, 29-37.

ZERIHUN A. and TREEBY M.T., 2002. Biomass distribution and nitrate assimilation in response to N supply for *Vitis vinifera* L. cv. Cabernet-Sauvignon on five *Vitis* rootstock genotypes. *Australian J. Grape Wine Research*, **8**, 157-162.