EFFECTS OF WATER STRESS ON DRY MATTER CONTENT AND PARTITIONING IN FOUR GRAPEVINE CULTIVARS (VITIS VINIFERA L.)

EFFETS DE LA CONTRAINTE HYDRIQUE SUR LA QUANTITÉ ET LA DISTRIBUTION DE LA MATIÈRE SÈCHE DE QUATRE CÉPAGES (VITIS VINIFERA L.)

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Summary : Three-year-old grapevines of four cultivars (Garnacha tinta (Grenache noir), Tempranillo, Chardonnay and Airén) were grown on 35 L container under full irrigation and restricted irrigation conditions in order to determine the effect of water stress on carbohydrate allocation. Total grapevine dry matter was measured at pruning, fruitset, veraison and harvest. Roots, wood, shoots, leaves and clusters were dried separately. Shoots were the most affected organs by water stress, while wood was the least affected. Vines under water stress partitioned more dry matter to wood and roots to the detriment of fruits and shoots. The period from fruitset to veraison was the most active for dry matter accumulation under conditions of stress, whereas non-water stressed vines accumulated more dry matter from veraison to harvest. Under both irrigation treatments, fruits competed with roots for dry matter partitioning. Irrigation treatment and cultivar determined fruit size. Fruit size determined dry matter partitioning between organs and the dry matter accumulation pattern.

Résumé : Quatre cépages (Grenache noir, Tempranillo, Chardonnay et Airén) greffés sur 1103 Paulsen ont été cultivés dans des conditions d'irrigation normale et sous contrainte hydrique. L'objectif du travail est de comprendre le rôle de l'eau en relation avec l'allocation du carbone dans les différents organes de la plante. Les bilans de matière sèche totale ont été réalisés en hiver (au moment de la taille), durant la croissance herbacée des fruits, à la véraison et à la maturité vendange. Les racines, le tronc, les sarments, les feuilles et les fruits ont été déshydratés séparément. Les vignes ont été cultivées en containers de 35 litres (l) dans un substrat homogène. Nous avons pu observer une différence importante de la répartition de la matière sèche entre les plants. L'effet de la contrainte hydrique sur l'allocation du carbone dépend du cépage. Les rameaux en croissance ont subi plus fortement la contrainte hydrique comparés aux parties pérennes aériennes. Les vignes sous contrainte hydrique ont réparti plus de matière sèche dans les organes pérennes au détriment des fruits et des bourgeons . Les vignes ayant subi une contrainte hydrique présentent une dynamique différente de répartition de la matière sèche. La période entre la nouaison et la véraison s'est avérée la plus active pour l'accumulation de la matière sèche en condition de contrainte hydrique, alors que les vignes sans contrainte hydrique ont accumulé plus de matière sèche dans les racines entre la véraison et la maturité vendange. Pour les vignes soumises aux deux types d'irrigation, les fruits ont fait concurrence aux racines pour la distribution de la matière sèche. La croissance du fruit dépend de la quantité d'eau apportée l'état hydrique de la plante et du cépage. L'allocation du carbone entre les organes dépend à la fois du niveau de la contrainte hydrique et du cépage.

Key words : *Vitis vinifera* L., carbohydrate allocation, plant water content, grapevine organs.

Mots clés : *Vitis vinifera* L., contrainte hydrique, allocation du carbone, organes de la vigne.

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INTRODUCTION

Annual production of vine dry matter depends on both photosynthetic rates and the reserves accumulated in the previous season, primarily starch and saccharose, nitrogen and potassium (MULLINS *et al.*, 1992). Leaves are the main organ for photosynthesis, although shoot photosynthesis could compensate for respiratory requirements before ripening, and grapes could compensate for 10-90 % of these requirements before véraison (WILLIAMS, 1996). Reserves seem to be provided by mature wood, because root reserves are used for their own growth (ARAUJO and WILLIAMS, 1988). Very low values of non-structural carbohydrates have been found at budbreak (MULLINS *et al.*, 1992), because respiratory requirements during the dormant period are supported by reserves stored in structural organs. Once shoot growth has begun, increases in dry matter have a linear relationship with GDDs (Growing Degree Days, base 10 ºC) until fruitset. Afterwards, a decrease or stabilisation in growth has been observed (GUTIERREZ *et al.*, 1985; WILLIAMS, 1987). At the beginning of the season, growth is supported by reserves until photosynthetic activity fulfils vine demand. The lowest values of carbohydrate reserves have been recorded in anthesis (WILLIAMS, 1996). Between budbreak and bloom, little dry matter is produced by vines in pots (MILLER *et al.*, 1996b). After anthesis, dry matter in roots and trunks increases throughout the rest of the season (WILLIAMS, 1996). This means that, at any time near anthesis, photoassimilates should satisfy vine requirements. Root growth begins very slowly after budbreak. A peak in root development has been observed at anthesis and fruitset (FREEMAN and SMART, 1976). A second root growth phase occurs after harvest in warm areas where vegetative growth is long (CONRADIE, 1980, 1990 and 1991). Secondary growth and thickening of roots take place throughout the season (MULLINS *et al.*, 1992). After fruitset, clusters are an important carbohydrate sink in grapes (MULLINS *et al.*, 1992). At that time, shoot and root growth decrease (MULLINS *et al.*, 1992; WILLIAMS and MATHEWS, 1990). The accumulation of dry matter in clusters has been shown to have a linear relationship with GDDs (GUTIÉRREZ *et al.*, 1985; WILLIAMS, 1987; WILLIAMS *et al.*, 1985). Dry matter accumulation is greatest in fruits after veraison (COOMBE, 1992), and cluster sugar requirements are satisfied not only by photosynthesis but also by the reserves of the structural organs (CONRADIE, 1990, 1991). After harvest, plants translocate sugars to the trunk (WILLIAMS, 1996) and roots (BATES *et al.*, 2002). Before leaf fall, sugars are translocated to the structural organs (MULLINS *et al.*, 1992), but most of the nitrogen and potassium depart along with falling leaves (WILLIAMS *et al.*, 1987).

The effects of water deficit on grapevines are great and complex due to the interaction of individual responses (SMART and COOMBE, 1983) and very little information is available concerning the effects of water stress on total dry matter partitioning in grapevines.

The goal target of this study was to evaluate the effect of water stress and grapevine genotypes on vine dry matter production and vine carbohydrate partitioning in order to elucidate any possible modifications in source-sink relationships on the vine throughout the season.

MATERIALS AND METHODS

This experiment was carried out at the Universidad Politécnica de Madrid in Spain. Three-year-old grapevines were grown in 35 L pot weighing lysimeters with a mixture of peat, sand and organic soil (63:25:12) and covered with a plastic film to eliminate evaporation and the infiltration of rainfall. Drainage was collected in a second container and measured. Each vine was restricted to two shoots. This experiment was completely randomised with eleven single vine repetitions. Two factors were analysed: cultivar and irrigation. The cultivars used were Garnacha tinta (Grenache noir), Tempranillo, Chardonnay and Airén grafted onto 1103 Paulsen. The irrigation treatments were water stress (S) and no water stress (NS).

In the NS irrigation treatment the potting culture medium was kept close to field capacity by applying each week the amount of water that the vines had consumed the previous week. Water consumption was determined gravimetrically with allowances for drainage. The S irrigation treatment consisted in applying 50 % of the water consumed by NS vines for each cultivar with corrections for differences in leaf area between treatments, calculated using the following formula:

$$W_S = 0.5 \cdot W_{NS} \cdot LA_S \cdot LA_{NS}^{-1}$$

In which W_S = water applied to stressed vines, W_{NS} = water applied to non-stressed vines, LA_S = leaf area of stressed vines and LA_{NS} = leaf area of non-stressed vines.

According with grapevine water status based on predawn leaf water potential (CARBONNEAU, 1998), NS and S treatment correspond to mild or absent of water stress and mild to moderate water stress respectively.

Bi-weekly leaf area measurements were collected using the non-destructive method of CARBONNEAU (1976). Leaf area was estimated by developing a second order polynomial equation, relating main vein lenght to leaf area for each cultivar.

The growth cycle was divided into three phases for the study of dry matter production: 1) Phase PF, from pru-

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ning to fruitset (14 June, day of the year-DOY- 165); 2) Phase FV, from fruitset to veraison (26 July, DOY day 207) and; 3) Phase VH, from veraison to harvest (30 August, DOY 242). Evaporative potential (ETo), calculated by Class A pan method, was 267, 203, and 162 mm for phases PF, FV and VH respectively. Accumulated growing degree-days (GDD), calculated using a base temperature of 10ºC, were 437, 566 and 489 for each phase respectively.

The dry weight of the organs remaining on the vines after pruning was determined using 5 replicates per cultivar x irrigation treatment combination. Dry matter at fruitset and veraison was measured on three vines for each treatment combination. At harvest, dry matter was determined on the five remaining vines for each treatment combination. Roots, wood, shoots (growth of the year), leaves and fruits were dried separately. Total vine dry matter was determined after the tissue was dried in an oven at 80ºC and constant weight was recorded. Dry matter produced or loosened during each period was calculated.

Variance analyses were carried out using the software package MSTAT-C (University of Michigan).

RESULTS AND DISCUSSION

I - VARIABILITY

High standard deviation values were obtained between vines of the same cultivar under the same irrigation conditions (data not shown). In some cultivars, final vine dry matter varied by more than 65 %. Variation was higher in absolute values than in partitioning. Roots and clusters were found to be the most variable organs. Vines had lower variability in the S treatment than in the NS treatment. High variability has been observed in the trunk of vines of non-irrigated Cabernet Sauvignon in the Napa Valley (WILLIAMS and BISCAY, 1991) and in the roots of young vines (ARAUJO *et al.*, 1995) in experiments carried out under field conditions with no water stress. This inherent vine variability precluded achieving statistical significance.

II - TOTAL PRODUCTION

1) Total vine dry matter

At harvest, whole vine dry matter varied from 581 to 173 g, depending on the cultivar and irrigation treatment (figure 1). Water stress significantly reduced total vine dry matter (fable I). S treatment vines were 29, 33 and 54 % smaller than NS treatment vines at fruitset, veraison and harvest respectively. Except at fruitset, cultivar significantly modified total dry matter, as observed by BRAVDO *et al.* (1972) and MULLINS *et al.* (1992).

Other studies have shown that pot size determines vine dry matter. Similar vine sizes were obtained when rooted cuttings of different cultivars without fruit were grown in well-irrigated 10 L lysimeters (BRAVDO *et al.*, 1972). Smaller vines (105-80 g) have been reported in two-year-old vines grown in 18 L pots (MILLER *et al.*., 1996b) and much smaller Pinot noir vines were obtained in 1 L pots (CONRADIE, 1990). Under field conditions in California, two-year-old Thompson seedless vines dry matter varied from 1 670 g to 2 500 g, depending on the pruning method (ARAUJO and WILLIAMS, 1988). Thompson seedless vines accumulated from 8 850 g to 9 471 g of dry matter in three years (ARAUJO *et al.*, 1995). Total dry matter of adult vines varies according to the pruning method (CLINGELEFER, 1993), plant density (HUNTER, 2000) and rootstock (WILLIAMS and SMITH, 1991). MULLINS *et al.* (1992) found that ten-year-old Chenin blanc vines grown in California reached a size of 18 890 g. However, MILLER *et al.*, 1996a

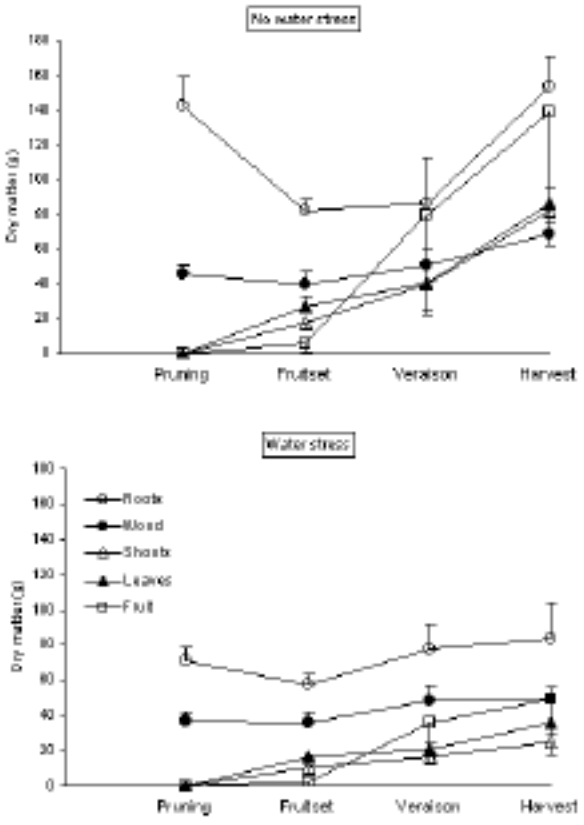


Figure 1 - Seasonal changes in dry matter in roots, wood, shoots, leaves and fruit, under non-water stress (top) and water stress conditions (bottom) for four grapevine cultivars.
Each point is the mean of the four cultivars.

Changements saisonniers de la matière sèche dans les racines, le bois, les sarments, les feuilles et les fruits sans stress hydrique (haut) et dans des conditions de stress hydrique (bas) de quatre cépages de vigne.
Chaque point représente la moyenne des quatre cépages.

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Table I.- Effect of cultivar and irrigation treatment on dry matter partitioning throughout the season in four grapevine cultivars under two irrigation treatments. Factorial analysis of variance (CUL = cultivar, IT = irrigation treatment, CUL·IT = interaction). NS : non-significant; *: P < 0.05; **: P < 0.01.

Effet de l'état hydrique de la vigne sur la distribution de la matière sèche au cours de la saison, comparaison de quatre cépages (interaction avec deux niveaux de contrainte hydrique). Analyse factorielle de la variation (CUL = cépage, IT = type d'irrigation, CUL·IT = interaction). NS : négligeable ; * : P < 0,05 ; ** : P < 0,01.

	Structural organs				Renewable organs						
	Roots		Wood		Shoots		Leaves		Fruit		Total g
	g	%	g	%	g	g	g	%	g	%	
Pruning											
CUL	**	**	**	**							**
IT	**	NS	**	**							**
CUL·IT	**	**	NS	**							**
Fruitset											
CUL	NS	**	NS	*	**	**	*	NS	*	**	NS
IT	**	NS	NS	**	**	NS	**	NS	*	NS	**
CUL·IT	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Veraison											
CUL	**	**	**	**	**	**	**	**	**	**	**
IT	NS	**	NS	**	**	**	**	*	**	**	**
CUL-IT	NS	NS	NS	NS	**	*	*	NS	**	*	NS
Harvest											
CUL	NS	NS	**	**	**	**	*	NS	**	**	**
IT	**	**	**	**	**	**	**	**	**	NS	**
CUL-IT	**	**	NS	NS	**	**	**	**	**	**	NS

did not find significant differences in total vine dry matter were detected when crop load and shoot number were modified, indicating that the total vine dry matter production of a cultivar depends on environmental conditions nor of the number of reproductive and vegetative sinks.

2) Periodical accumulation of dry matter

Between pruning and fruitset, total vine dry matter had a mean reduction of 21 g in the NS treatment, whereas this value had a mean increase of 9 g in the S treatment (figure 2). Lower root dry matter and respiratory requirements during winter under water stress conditions could explain the differences in dry matter reduction between irrigation treatments.

During this period, dry matter in structural organs (roots and wood) decreased by 35 % and 13 % in the NS and S treatments respectively. Under both irrigation treatments roots lost more dry matter than wood. In the NS treatment dry matter decreased 43 % in roots and 13 % in wood, whereas in the S treatment dry matter decreased 18 % and 3 % in roots and wood respectively (figure 1). Other studies have also observed greater dry matter reduction in roots than in wood during winter and spring. Under field conditions, WILLIAMS (1996) quantified a 23 % and 16 % reduction in roots and wood respectively, from January until fruitset. CONRADIE (1991) also observed a reduction in root dry matter. This reduction may be due to the high proportion of fine roots that are lost in winter and the roots' use of its own reserves for growth (ARAUJO and WILLIAMS, 1988). Root carbohydrates lost in the pre-bloom period are not recovered until the end of rapid shoot development (BATES *et al.*, 2002).

Under field conditions, dry matter reduction in winter is higher. Thompson seedless vines of different ages had a 800 g reduction in dry matter from January until budbreak and a slight increase from budbreak until fruitset for a total reduction of 700 g from January until fruitset (WILLIAMS, 1996). CONRADIE (1980) observed a slight increase in dry matter between budbreak and fruitset, although the dry matter in structural organs decreased. In vines grown in 45 L pots dry matter reduction mainly took place from budbreak until fruitset (CONRADIE, 1991).

In the NS treatment 37 % of seasonal dry matter was produced between fruitset and veraison and 63 % of seasonal dry matter was produced between veraison and harvest. Under S conditions 59 and 35 % of seasonal dry matter was produced between fruitset and veraison and veraison-harvest respectively (figure 2). According to MILLER *et al.* (1996a), high dry matter production bet-

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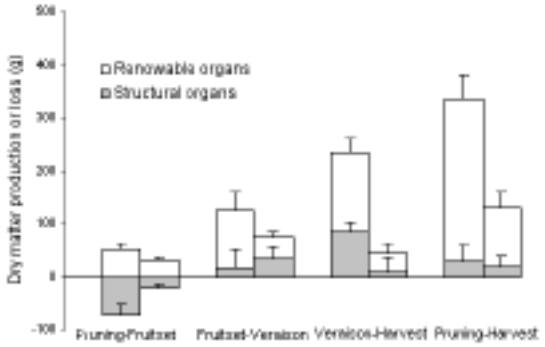


Figure 2 - Periodical and seasonal dry matter production or loss of four grapevine cultivars under non-water stress (left) and water stress (right).
Each point is the mean of the four cultivars. Bars represent standard desviation.

Production ou perte périodique et saisonnière de la matière sèche de quatre cépages sans stress hydrique (gauche) et dans des conditions de stress hydrique (droite).
Chaque point représente la moyenne des quatre cépages. Les barres représentent la déviation standard.

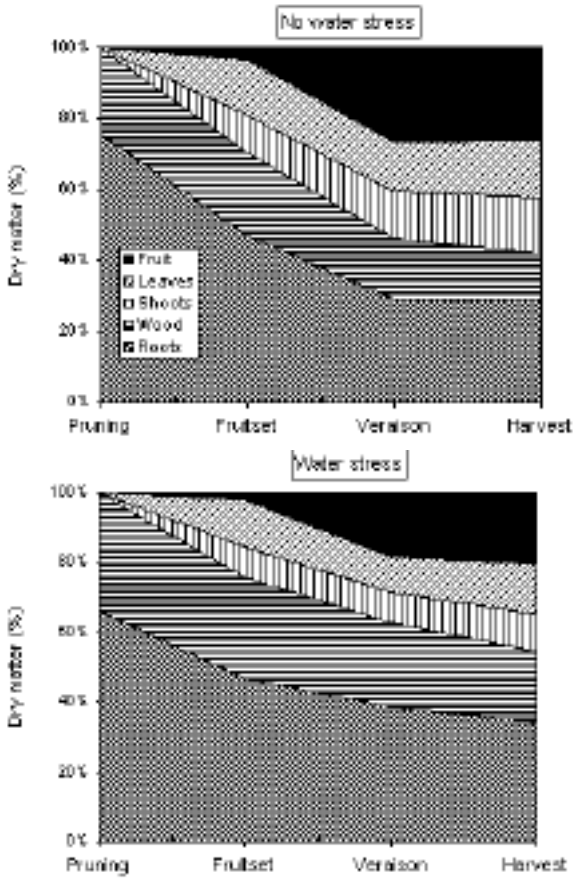


Figure 3 - Seasonal changes in dry matter partitioning in roots, wood, shoots, leaves and fruit, under non-water stress (top) and water stress conditions (bottom) for four grapevine cultivars.
Each point is the mean of the four cultivars.

Modifications saisonnières de la répartition de la matière sèche dans les racines, le bois, les sarments, les feuilles et les fruits sans stress hydrique (haut) et dans des conditions de stress hydrique (bas) de quatre cépages.
Chaque point représente la moyenne des quatre cépages.

ween veraison and harvest is due to fruit growth. A similar growth pattern has been observed in non-water stressed vines under field conditions (MULLINS *et al*., 1992).

III - DRY MATTER IN ORGANS

1) Structural Organs

Water stress determined structural organ dry matter and partitioning at harvest (table I). At harvest, irrigation treatment had a greater influence on root dry matter than on wood dry matter. Water stress caused a 45 % and 28 % reduction in root and wood dry matter respectively compared to NS treatment vines (figure 1). MULLINS *et al.* (1992) found that roots were more affected than wood when Chenin blanc was irrigated at 52 % ET, as compared to 100 % ET. Throughout the season, dry matter partitioning to permanent structures (roots and wood) was greater in the S treatment than in the NS treatment (figure 3).

Cultivar significantly influenced root and wood dry matter and partitioning, except root and wood dry matter at fruitset, and root dry matter and partitioning at harvest (table I). MULLINS *et al.* (1992) and WILLIAMS (1996) pointed out the influence of genotype on structural organs. TANDONNET *et al.* (1999) observed significant differences in trunk and shoot dry matter between cultivars. BRAVDO *et al.* (1972) observed that genotype determined root size when rooted cuttings of different cultivars were grown.The effect of cultivar genotype on root dry matter could be explained by the importance of fruits on the vine (figure4), which depends on genetic characteristics such as the number of clusters per shoot and cluster size, if these are not modified by cultural practices or environmental factors.

Roots were the main structural organ on the vine for all cultivars and irrigation treatments. Mean root dry matter content was twice that of wood (figures 1 and 3), according to CONRADIE (1980) and SAAYMAN and van HUYSSTEEN (1980). However, in other experiments wood had more dry matter than roots (WILLIAMS and SMITH, 1991; WILLIAMS and BISCAY, 1991; MULLINS *et al*., 1992; CLINGELEFFER and KRAKE, 1992; ARAUJO *et al.*, 1995; WILLIAMS, 1996; HUNTER, 2000). Vine age and wood remaining after pruning are important factors leading to these differences in results. CLINGELEFFER (1993) observed that wood was more than twice the size of roots when vines were spur pruned and nearly 3.5 times their size after minimal pruning.

Mean root dry matter at harvest was 154 g and 84 g for NS and S treatment vines respectively (figure 1). A wide range of values has been measured under non-water stress conditions in other experiments. Old vine roots were larger under field conditions. Seventeen-year-old

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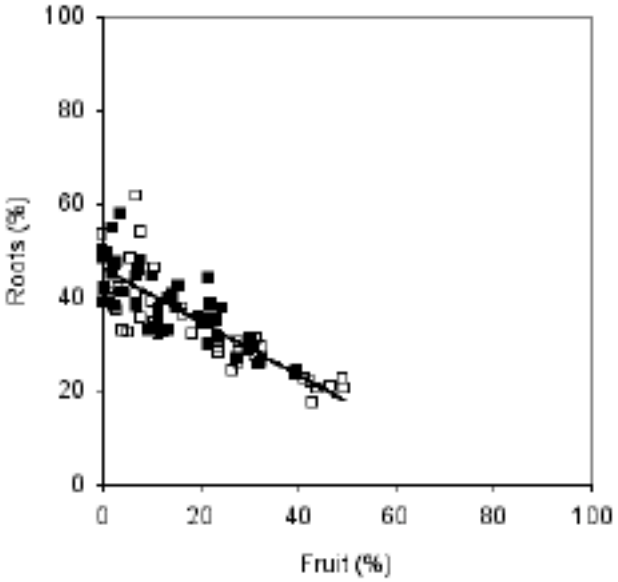


Figure 4 - Relationship between dry matter partitioning in roots and fruit at fruitset, veraison and harvest for vines of four cultivars under non-water stress (▫) and water stress conditions (▪).
Regression for pooled data is Y = 46-0.6x (R^2 = 0.69 **).

Relation entre la distribution de la matière sèche dans les racines et les fruits au moment de leur formation, de la véraison et des vendanges de quatre cépages sans (▫) ou avec (▪) stress hydrique.
L'équation de la droite de régression est Y = 46-0,6x (R^2 = 0,69 **).

Cabernet Sauvignon vines developed roots of 2515 g, as the mean of three rootstocks (WILLIAMS and SMITH, 1991). WILLIAMS (1996) measured roots of irrigated Thompson seedless grapevines of nearly 1 500 g. Our results were similar to those obtained in high plant density experiments and to those of vines grown in container. HUNTER (2000) observed roots of 62 and 345 g when fourteen-year-old Pinot noir vines were grown in 1 x 0.5 m and 3 x 3 m density treatments, respectively. At harvest, root size varied from 40 to 70 g in two-year-old Chambourcin vines grown in 19 L pots (MILLER *et al.*, 1996a), and from 115 to 139 gin young Chenin blanc grapevines grown in 45 L pots (CONRADIE, 1980 and 1991). Depending on the cultivar, rooted cuttings grown in 10 L pots had root dry matter values from 63 to 210 g at the end of the first season and from 200 to 332 g at the end of the second season (BRAVDO *et al.*, 1972).

In our experiment, a significant relationship was found between root and fruit dry matter partitioning when data at fruitset, veraison and harvest were analysed (figure 4). The slope of the regression was –0.6. This means that a 10 % increase in fruit partitioning would cause a 6 % decrease in root partitioning. The other 4 % would be used in vegetative growth. In other experiments, an inverse relationship between fruit development and roots has been found (EIBACH and ALLEWELDT 1985 ; WILLIAMS, 1996; MILLER *et al.*, 1996a ; PETRIE *et al.*, 2000 ; MORINAGA *et al*, 2003).

The seasonal pattern of root dry matter varied between water treatments. In both irrigation treatments, root dry matter decreased from pruning to fruitset (figure 1). This reduction was caused by a decrease in non-structural carbohydrates (WILLIAMS, 1996), mainly used in spring growth (MILLER *et al.*, 1996b). After fruitset, irrigation treatment determined root dry matter accumulation. In the NS treatment, root growth began after veraison, while in the S treatment the greatest root dry matter accumulation occurred during the fruitset-veraison period. This could be explained in part by cluster and leaf area development throughout the season. Between fruitset and veraison, clusters are an important carbohydrate sink (CONRADIE, 1980 and 1991; MILLER *et al.*, 1996a; MULLINS *et al.*, 1992). At this time under NS conditions, clusters seem to be a stronger sink than roots (figure 3). At veraison, leaf area reached its highest values (GÓMEZ DEL CAMPO, 1998, data not shown). After veraison, it seems that there are enough carbohydrates to satisfy cluster and root requirements, so both organs increase in dry matter. When vines are under water stress conditions, clusters do not seem to be as strong sink as under non-water stress, because roots also accumulate dry matter during the main period of cluster growth (fruitset-véraison). At véraison and harvest, S treatment vines partitioned more dry matter to roots than in the NS treatment. The seasonal pattern of root dry matter accumulation differed with that found in other experiments. These differences could be explained, in part, by carbohydrate competition between organs. In young vines grown in 45 L pots, where clusters represented 44 % of total vine dry matter at harvest, CONRADIE (1991) observed a reduction in root dry matter between veraison and harvest, as fruits are the main carbohydrate sink during this period (COOMBE, 1992). After harvest, significant dry matter accumulation was observed in roots. Nevertheless, other studies, which obtained values of dry matter partitioning to clusters similar to ours (between 26 to 20%), found that root dry matter increased progressively after budbreak (ARAUJO and WILLIAMS, 1988), or after anthesis (WILLIAMS and BISCAY, 1991) until harvest. In vines without clusters, shoots can compete with roots for carbohydrates. In a one-shoot vine, a slight increase in root dry matter was observed between an approximate date of anthesis and harvest, but in 3 to 6-shoot vines, a decrease was observed (MILLER *et al.*, 1996b).

Wood dry matter accumulation pattern differed from that of roots (figures 1 and 3). In both irrigation treatments, a slight reduction in wood dry matter was quantified between pruning and fruitset. Wood dry matter may have decreased between pruning and a few days before anthesis, and then may have begun accumulating, as observed

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by WILLIAMS (1996) and CONRADIE (1980). In the NS treatment, wood dry matter increased progressively after fruitset as observed by WILLIAMS (1996) and CONRADIE (1980). After harvest MILLER *et al.* (1996a) found an increased trunk dry matter increased considerably. Nevertheless, wood dry matter accumulation in the S treatment mainly occurred between fruitset and harvest. No significant differences were found in wood dry matter accumulation patterns between treatments until harvest (table I). When climatic conditions were optimal, the post-harvest period seemed to be the most important in wood dry matter accumulation (WILLIAMS, 1996), ending with leaf fall (CONRADIE, 1980). A small increase in wood dry matter was detected after harvest by MILLER *et al.* (1996b), perhaps because only 60 GDDs accumulated between harvest and dormancy. The trunk did not compete for carbon once berries became a strong sink, as observed by WILLIAMS (1996).

2) Fruits

Fruits were one of the organs most affected by water stress. Fruit dry matter accumulation was 65 % lower in the S than in the NS treatment throughout the season (figure 1). Depending on the level of water stress, this reduction could be due to fruitset reduction, lower sugar concentration and smaller bunches (SMART and COOMBE, 1983; WILLIAMS *et al*., 1994). Cell division has not been shown to be reduced by water stress but water stress modified berry growth (cell enlargement) from fruitset to veraison and from veraison to harvest (OJEDA *et al.*, 2001). Under Mediterranean conditions and depending on the soil water content, vines suffer water stress after stage I because previous requirements are satisfied by spring rainfall and water availability. Berry sugar accumulation mainly depends on vine water status and photosynthesis (WANG *et al*., 2003). Similar differences in fruit dry matter accumulation patterns have been observed when fruit number is modified. After veraison, fruit dry matter increased progressively on vines with more clusters, but slowed down after veraison on vines with less fruit (MILLER *et al.*, 1996a), no direct relation has been found between berry volume and sugar concentration for a single berry (DELOIRE *et al.*, 2004). Although differences in fruit dry matter content were found between irrigation treatments, fruit dry matter partitioning was only significantly lower in the S treatment at veraison (table I). The berry sugar loading is in relation with the vine photosynthesis activity which depends mainly on plant water content (WANG *et al.*, 2003; DELOIRE *et al.*, 2004).

Fruits at harvest represented 26 % and 20 % of vine dry matter content in the NS and S treatment, respectively (figure 3). Fruit dry matter partitioning may vary under different experimental conditions. In young vines grown in 45 L pots, clusters at harvest represented nearly 44 % of total dry matter (CONRADIE, 1990 and 1991). In spite of different berry growth pattern between seedlees and seeded cultivars, similar values were obtained in young Thompson seedless grapevines under field conditions (ARAUJO *et al.*, 1995). However, in other experiments mature vines partitioned smaller values of dry matter under field conditions. Measurements of 30 %, 20-30 %, 18 % and 8 % were obtained by WILLIAMS (1996), ARAUJO and WILLIAMS (1988), WILLIAMS and BISCAY (1991) and WILLIAMS and SMITH (1991), respectively.

Fruit dry matter accumulation and partitioning were significantly influenced by cultivar in all measurements. Dry matter accumulation and partitioning in renewable organs showed significant interaction between irrigation treatment and cultivar at veraison and harvest (table I), indicating that the influence of water stress on renewable organs depends on the cultivar.

The seasonal pattern of fruit dry matter accumulation differed according to the irrigation treatment (figure 1). After veraison, fruit dry matter increased steadily in the NS treatment as in other experiments (GUTIÉRREZ *et al*., 1985; WILLIAMS, 1987; WILLIAMS *et al*., 1985; CONRADIE, 1990 and 1991; COOMBE, 1992). Nevertheless, fruit growth was greatest from fruitset to veraison in the S treatment (figure 1). Fruit dry matter increased after veraison depending on the importance of fruit as a sink (GUTIERREZ *et al*, 1985). The pattern of fruit dry matter partitioning differed from the pattern of fruit dry matter content. Fruit dry matter partitioning increased steadily from fruitset to veraison, but increased only slightly after veraison in the S treatment. No increase was observed in dry matter partitioning in the NS treatment (figure 3). This could indicate that after veraison clusters are not the only priority sink in the vine, and carbone is distributed between the different vine organs.

3) Shoots and Leaves

Shoot and leaf dry matter accumulation and partitioning were significantly higher in the NS than in the S treatment throughout the season (table I, figures 1 and 3), with the exception of leaf partitioning at fruitset. Water stress modified dry matter partitioning in shoots and leaves. In the NS treatment, both shoots and leaves partitioned 16 % of all vine dry matter, but in the S treatment shoots partitioned 10 % and leaves partitioned 15 %. The effect of water stress on vegetative organs has been observed by MERIAUX *et al.* (1974), BRAVDO *et al.* (1972) and GUTIERREZ *et al.* (1985). Interaction between cultivar and irrigation treatment in dry matter partitioning in shoots and leaves was significant in all measurements except at fruitset. Thus, the response of shoots and leaves to water stress differed according to genotype. Shoots were the

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organ on the vine most affected by water stress according to other authors (WILLIAMS and MATTHEWS, 1990 ; WILLIAMS *et al.*, 1994; EIBACH and ALLEWELDT, 1985).

At harvest, shoot dry matter content was 70 % lower in the S than in the NS treatment (figure 1). At harvest shoot dry matter was 82 g and 25 g for the NS and S treatments respectively and leaf dry matter was 87 g and 36 g for the NS and S treatments respectively (figure 1). Shoot dry matter depends on many factors: the vineyard (WILLIAMS *et al.*, 1985), shoot positioning and pruning method (WILLIAMS, 1996), number of shoots per vine (CLINGELEFFER and KRAKE, 1992), shoot orientation (KLIEWER *et al*., 1989), training system (CARBONNEAU*et al*., 2001).

- Shoot and leaf dry matter accumulation pattern.

Shoot and leaf dry matter increased progressively from budbreak to harvest (figure 1). The increase in leaf dry matter during veraison to harvest was the result of an increase in weight per unit leaf area, as leaf area did not increase significantly (GÓMEZ DEL CAMPO, 1998, data not shown). In both irrigation treatments, dry matter partitioned to leaves and shoots increased from budbreak to fruitset. After fruitset, values remained nearly stable (figures 1 and 3). The importance of leaves and shoots as a sink increased from budbreak to fruitset under both irrigation treatments. Water stress did not change shoot and leaf dry matter accumulation patterns, but a significant increase in shoot and leaf dry matter accumulation was detected from veraison to harvest in the NS treatment (figure 1). This pattern has also been observed in young grapes (ARAUJO and WILLIAMS, 1988) and in Cabernet-Sauvignon vines in the Napa Valley (WILLIAMS and BISCAY, 1991). In other experiments, shoot and leaf dry matter increased until veraison depending on the cultivar, and subsequent shoot growth diminished, levelled off or continued during pre- and post-harvest periods (GUTIERREZ *et al*., 1985). CONRADIE (1990) observed that shoot dry matter accumulation ceased between veraison and harvest and continued after harvest until leaf fall. Dry matter accumulation of over 40 % in fruits may compete with shoot growth. MILLER *et al.* (1996a) observed a decrease in shoot and leaf dry matter from veraison to harvest. The carbohydrates produced may have accumulated in the fruit due to low temperatures (200 GDDs accumulated). WILLIAMS (1987) and CONRADIE (1980) found that weight per unit leaf area increased throughout the season. A significant increase in dry matter has been detected in shoots from harvest to leaf fall (CONRADIE, 1991; MILLER *et al.*, 1996a).

CONCLUSIONS

Plant water status determined dry matter production (i.e. photosynthesis) and its partitioning between the different organs of the vine. Dry matter partitioning to permanent structures was greater under water stress than under non-water stress conditions. However, the effect of water stress on dry matter content and partitioning should not be generalised for all vine genotypes. Both cultivar and its interaction with irrigation were found to have a significant effect on most of the measurements taken in this experiment.

Water stress modified the periodical accumulation of dry matter. Total vine dry matter was reduced between pruning and fruitset under non water stress conditions but increased slightly under water stress conditions. Total vine dry matter accumulation was greatest in the phase from fruitset to veraison under water stress conditions, whereas under non water stress conditions dry matter accumulation was greater in the phase from veraison to harvest.

Fruits and roots together represent more than half of total vine dry matter. Fruits competed with roots for dry matter partitioning under both irrigation treatments. Plant water status and cultivar determined yield which, in turn, determined the dry matter accumulation pattern and dry matter partitioning between organs.

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