RESPONSE OF VINE LEAF WATER POTENTIAL TO QUICK VARIATION IN CANOPY EXPOSURE. EXAMPLE OF CANOPY OPENING MANIPULATION OF MERLOT (*VITIS VINIFERA* L.)

RÉPONSE DU POTENTIEL HYDRIQUE FOLIAIRE DE LA VIGNE À DES VARIATIONS RAPIDES D'EXPOSITION DE LA VÉGÉTATION. EXEMPLE DE LA MANIPULATION DE L'OUVERTURE DE LA VÉGÉTATION DU MERLOT (*VITIS VINIFERA* L.)

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Abstract : Plants are in general subject to rapid fluctuations in the environment, particularly as regards the interception of light and therefore water regime. It is important to know the duration and the amplitude of response of the water regime (first leaf water potential) when light interception changes suddenly under natural conditions. widely planted grape variety in the world) was chosen mainly because it offers convenient possibilities of canopy manipulation, ranging from an open and exposed type architecture, to a closed and shaded configurations simply by moving inside or outside a «foldable Lyre» type trellis. Leaf water potential was measured throughout particular days corresponding to stable or variable controlled conditions. The experimental design was an Ecotron in which it is possible to control water and mineral supply and the levels of light interception by plants which have normal development and are growing under natural environmental conditions. The most significant results that emerged from this study are that leaf water potential reacts quickly to any change of light interception, and above all, that the response is almost instantaneous - occurring within few minutes - when transpiration demand decreases, and is significantly longer when the transpiration demand increases, even if the water supply corresponds to maximum transpiration conditions. This shows that the grapevine has a general regulatory system which encourages the plant to economise water even if the supply is sufficient. This could indicate the existence of an overall plant regulatory system - mediated via the water potential - which is important for the coherence of the plant's physiology and which is quite independent of the environment. From a general point of view, this would confirm the existence of biological triptych network with a superimposed regulatory element (CARBONNEAU, 1996 ; CARBONNEAU and DELOIRE, 2001).

Résumé : Les plantes sont généralement soumises à des fluctuations rapides de l'environnement, en particulier vis-à-vis de l'interception du rayonnement et donc du régime hydrique. Il est important de connaître la durée et l'amplitude de la réponse au régime hydrique (d'abord le potentiel hydrique foliaire) lorsque l'interception du rayonnement change soudainement en conditions naturelles. A cet effet, la vigne (cv. Merlot qui est le cépage le plus répandu dans le monde) a été choisie surtout parce qu' elle offre des conditions faciles de manipulation de la végétation, depuis un type d'architecture ouverte et exposée, jusqu'à des configurations fermées et ombrées, simplement en repliant ou dépliant un palissage de type «Lyre pliable». Le potentiel hydrique foliaire a été mesuré tout au long de journées particulières correspondant à des conditions d'environnement contrôlées stables ou variables. Le dispositif expérimental était un Ecotron dans lequel il est possible de contrôler l'apport hydrique et minéral, ainsi que le niveau d'interception du rayonnement par les plantes qui ont un développement normal dans des conditions naturelles.
Les résultats les plus significatifs qui ressortent de cette étude sont que le potentiel hydrique foliaire réagit très rapidement à un changement quelconque d'interception du rayonnement, et par dessus tout, qu'une telle réponse est quasiment instantanée quand la demande en transpiration diminue, alors qu'elle est significativement plus longue quand la demande en transpiration augmente, ceci même si l'apport hydrique correspond à des conditions de transpiration maximale. Ceci montre que la vigne possède un système de régulation général qui encourage la plante à économiser l'eau même si l'apport est suffisant. Cela pourrait indiquer l'existence d'un système de régulation global à la plante entière – par l'entremise du potentiel hydrique – qui est important pour assurer la cohérence de la physiologie de la plante et qui est relativement indépendant de l'environnement. D'un point de vue général, ceci confirmerait l'existence de triptyques biologiques en réseau avec un élément régulateur surimposé à l'ensemble (CARBONNEAU, 1996; CARBONNEAU et DELOIRE, 2001).

Key words : Water regime, regulation, transpiration demand, irrigation, dynamics, hysteresis, whole plant, biological triptych, leaf water potential, canopy, architecture, Ecotron, grapevine.

Mots clés : Régime hydrique, régulation, demande en transpiration, irrigation, dynamique, hystérésis, plante entière, triptyque biologique, potentiel hydrique foliaire, végétation, architecture, Ecotron, vigne.

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INTRODUCTION

Water regime is a major component of plant physiology, and the equilibrium between water potentials inside the plant (i.e. the leaf water potential) along the water gradient between the air and the soil represents the principal regulatory system of the plant as a whole. The significance of the water regime has already been demonstrated for plants in general and the grapevine in particular, by CARBONNEAU (1996) and by CARBONNEAU and DELOIRE (2001). The general concept proposed is that of a « biological triptych », an entity composed of a classical «source – sink» relationship, upon which an overall plant regulatory system is superimposed which effectively is the gradient of water potentials for plants.

This study was undertaken in order to understand how a plant reacts in terms of water regime regulation when the transpiration demand quickly increases or decreases. Variation in transpiration demand corresponds to most ecological conditions, though a lack of understanding still exists regarding the response of the plant's physiology to quickly changing environmental conditions, i.e. are the phenomena reversible or do they take the form of a hysteresis ? A sampling of literature dealing with those aspects clearly reveals a lack of knowledge on plants in general and on the grapevine in particular (AMEGLIO et ARCHER, 1996; BOYER, 1970; CHONE *et al.*,2001; DÜRING and LOVEYS, 1982; DÜRING, 1987; HSIAO, 1976; JONES, 1992; KRAMER, 1983; KRIEDEMANN and SMART, 1971; SCHULTZ and MATTHEWS, 1988; TAIZ and ZEIGER, 2002; TARDIEU and DAVIES, 1992; WINKEL and RAMBAL, 1993). Even those who studied variations in stomatal behaviour (ie: ALLEN and PEARCY, 2000) versus time and water conditions did not consider the quickness or the reversibility of the response.

The grapevine was chosen because, as a creeper, it offers convenient possibilities for manipulating the canopy (architecture), and therefore for controlling the transpiration demand without modifying the plant's natural environment. Also, the fact that the grapevine is a plant of considerable economical interest justifies the search for a better understanding of its physiology in order to optimise the application to new technologies to its cultivation.

MATERIALS AND METHODS

The genotype was 3 year old *Vitis vinifera* L. cv. Merlot which is the most commonly planted grapevine variety in the world ; the clone was n°519 and the rootstock was SO4. The plants were grown in 70 l containers, which were covered to protect them from rain which would act as a source of external water. The plants were subjected to Maximum Transpiration with permanent drainage, equipped with a drip fertirrigation system; they were supplied with an optimal nutrient solution for mineral equilibrium, and the containers were filled with a substrate « 2/3 perlite, 1/3 rough sand ». These cultural conditions allowed normal development, growth and production of entire plants.

The vines were trained in a Lyre shape (CARBONNEAU, 1980) ; the particularity being that the trellis was movable, thus allowing control of the architecture - either an open, fully exposed architecture inducing high transpiration demand in summertime (open Lyre), or a closed canopy substantially reducing the transpiration demand (closed Lyre); the change from one architecture to the other could be rapidly effected (within 1 minute). This trellis design has been called « foldable Lyre » (CARBONNEAU *et al.*, 2002).

This experimental configuration was installed under natural conditions inside the 1 ha vineyard of the AGRO Montpellier campus ; the configuration was named « Ecotron » (CARBONNEAU and de LOTH, 1985) meaning that this design allows normal development of the plant (grapevine) under controlled and natural conditions ; it allows the possibility to manipulate the canopy or the light interception (water demand), as well as the fertirrigation (water supply), simultaneously if so desired. Thus it is possible to control the differential conditions while respecting normal conditions of culture and development.

Figure 1 shows the foldable Lyre trellis and the Ecotron design . Leaf water potential was measured using a pressure « Scholander » chamber supplied by the PMS Instrument Company. In addition, general ecophysiological observations were made (stem and leaf growth, leaf exposure and temperature, stomatal conductance, photosynthesis, fertility, development and maturation) proving that the plants were physiologically normal in relation to the characteristics of the vineyard.

Results are concentrated on leaf water potential (predawn and daily values) between August 13-15 and August 21-23, which were typical summer days with constant and sunny climate conditions. The exterior and interior leaves of the canopy are distinguished during daily measurements. It should be noted that the stem water potential measured on covered leaves was not taken into account in the experiment, because the experimental design revealed that it artificially reduced the water deficit particularly in the afternoon (DELOIRE *et al.*, 2003). All the following figures show

Figure 1 - General view of the Ecotron in AGRO Montpellier campus.
Left: «closed Lyre» canopy architecture and containers;
Right: «open Lyre» canopy architecture.

Vue générale de l'Ecotron au campus de l'AGRO Montpellier.
A gauche : Architecture en «Lyre fermée» avec les vases de végétation ;
A droite : Architecture en «Lyre ouverte».

mean values of leaf water potential associated with the confidence interval at 5 % risk.

RESULTS

Figure 2 shows the results of leaf water potential on the « open Lyre ‡ closed Lyre ‡ open Lyre » manipulation during the period August 13-15 (first manipulation); figure 2a presents the predawn leaf water potentials ; figure 2b the shows daily leaf water potential; these values taken immediately before and following the canopy change.

Figure 3 shows the results of leaf water potential on the « closed Lyre ‡open Lyre ‡ closed Lyre » manipulation (second manipulation) during the period August 21-23 ; figure 3a presents predawn leaf water potentials ; figure 3b daily leaf water potentials; again these values were noted immediately before and following the canopy change.

It may be observed from figures 2a and 3a, that the predawn leaf water potentials are all high (-0.15 to –0.20 Mpa) attesting that the vines were perfectly hydrated and not subject to a water deficit (CARBONNEAU, 1998).

1) First manipulation

Figure 2a indicates that the leaves in open Lyre are slightly less hydrated than the closed Lyre at the end of the night. Even if the difference in predawn leaf water potential is small, this is a significant indication that high transpiration conditions during the previous day lead to a slight limitation of reservoir recovery, even under Maximum Transpiration conditions.

Figure 2b shows that the « open Lyre to closed Lyre » manoeuvre induces rapid evolution of leaf water potential around midday which occurs almost fully within 10 minutes; leaf water potential increases significantly - particularly for leaves near the interior of the plant which are subject to considerable reduction of light exposure after canopy manipulation. Nevertheless, it can be observed that the outer leaves follow the same pattern, but to a lesser extent, even if they are still exposed (in fact, slightly more so) after closure of the canopy. This indicates that individual leaves are influenced by the general hydric status of the whole plant, the effect of which is superimposed on the influence of the particular micro-environment of the leaf.

Figure 2b also shows that the second change, a day later, « closed Lyre to open Lyre » causes the plant to react (in terms of leaf water potential) in a manner which is the mirror-image of that observed in the previous experiment, i.e., in this case, the leaf water potential decreases, particularly for the inner leaves; but the recovery to the previous level of leaf water potential requires at least one day. Therefore, the leaves respond slowly when the transpiration demand increases, whereas they respond quickly - within few minutes - if the transpiration demand decreases.

2) Second manipulation

This manipulation is the mirror-image of the first manipulation. Figure 3a confirms the observations shown figure 2a.

Figure 3b confirms the observations shown figure 2b, though with slightly less of a difference when the canopy is changed from the open Lyre shape to the

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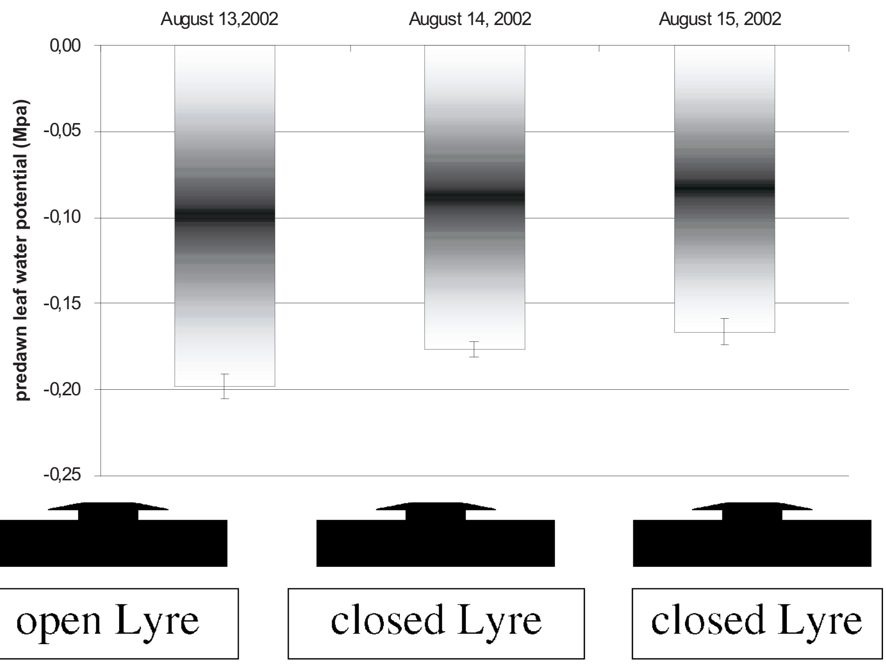

Figure 2a - Results of predawn leaf water potential in Merlot in the Ecotron.
First canopy manipulation " open Lyre ‡ closed Lyre ‡ open Lyre ".Confidence intervals at 5% risk are indicated.

Résultats de potentiel hydrique foliaire de base sur Merlot dans l'Ecotron.
Première manipulation de la végétation " Lyre ouverte ‡ Lyre fermée ‡ Lyre ouverte". Les intervalles de confiance au risque de 5% sont indiqués.

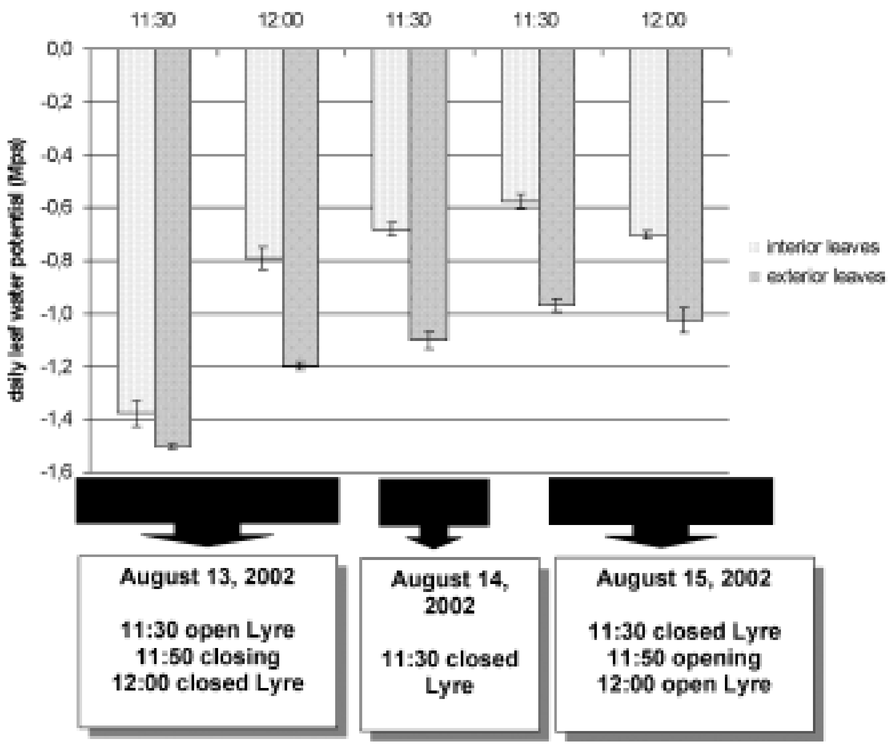

Figure 2b : Results of daily leaf water potential in Merlot in the Ecotron.
First canopy manipulation " open Lyre ‡ closed Lyre ‡ open Lyre ".
Confidence intervals at 5% risk are indicated.

Résultats de potentiel hydrique foliaire au cours de la journée sur Merlot dans l'Ecotron.
Première manipulation de la végétation " Lyre ouverte ‡ Lyre fermée ‡ Lyre ouverte".
Les intervalles de confiance à 5% sont indiqués.

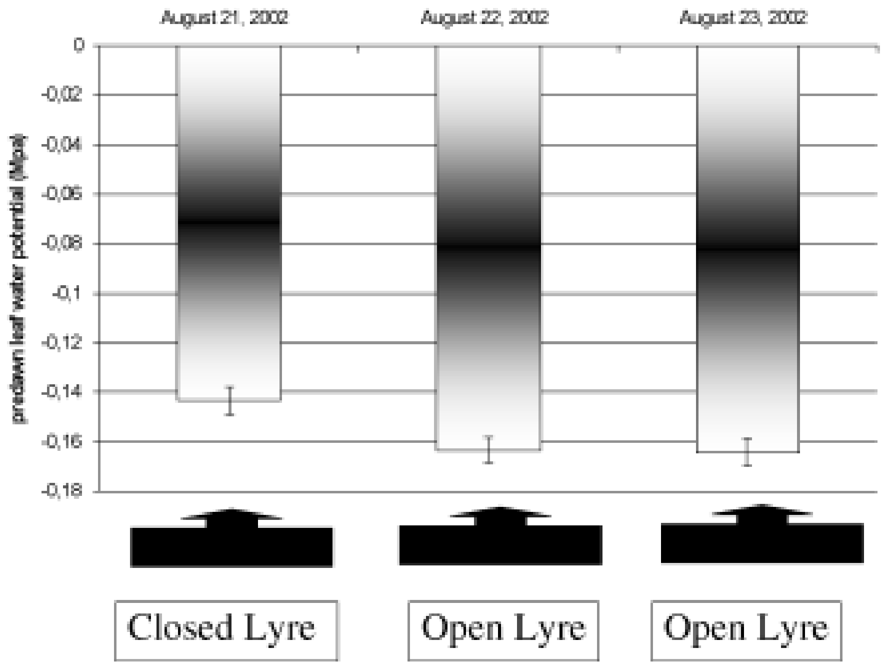

Figure 3a - Results of predawn leaf water potential in Merlot in the Ecotron.

Second canopy manipulation " closed Lyre ‡ open Lyre ‡ closed Lyre ".

Confidence intervals at 5% risk are indicated.

Résultats de potentiel hydrique foliaire de base sur Merlot dans l'Ecotron.

Seconde manipulation de la végétation " Lyre fermée ‡ Lyre ouverte ‡ Lyre fermée". Les intervalles de confiance à 5% sont indiqués.

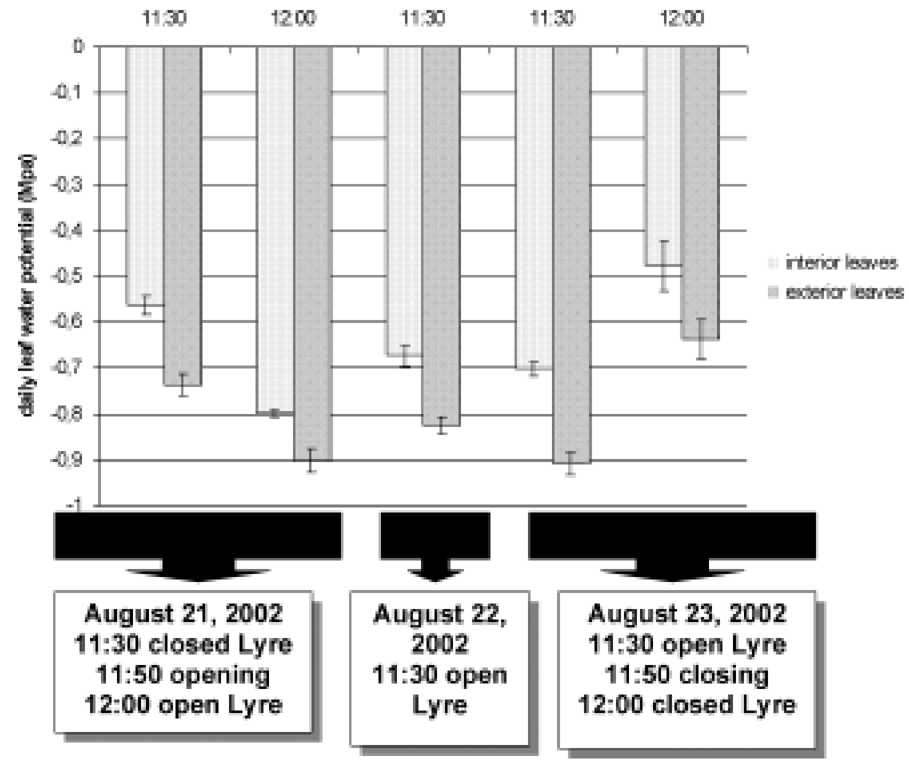

Figure 3b - Results of daily leaf water potential in Merlot in the Ecotron.

Second canopy manipulation « closed Lyre ‡ open Lyre ‡ closed Lyre ».

Confidence intervals at 5% risk are indicated.

Résultats de potentiel hydrique foliaire au cours de la journée sur Merlot dans l'Ecotron.

Seconde manipulation de la végétation « Lyre fermée ‡ Lyre ouverte ‡ Lyre fermée ».

Les intervalles de confiance à 5 % sont indiqués.

closed Lyre shape. This difference is explained by the general evapotranspiration conditions which were slightly lower for the period August 21-23 than for the period August 13-15.

DISCUSSION

The general evolution of leaf water potential as a function of changes in light interception produced

by canopy manipulation is as what would be expected according to general plant physiology, and 7 corresponds to earlier observations from other related experiments on the

The new aspects of this particular study are :

- the difficulty of the plant to become fully rehydrated at the end of the night under Maximum Transpiration conditions after having been previously subjected to a high transpiration demand (This concurs to some extent with the phenomenon of late rehydratation shown by CARBONNEAU and OLLAT, 1991) ;

- the presence of a global regulating effect covering the whole plant which is superimposed on the individual regulation of the leaf, the outer leaf water potential is modified when the plant water regime is changed due to other leaves, even if their micro-environment is much the same ; such a superimposed regulatory system fits the theory of the biological triptych proposed by CARBONNEAU (1996, 2001) ;

- the existence of a differential or a « hysteresis » phenomenon, corresponding to a facile adaptation - within few minutes - of the leaf water potential when the transpiration demand decreases, with a more difficult and longer adaptation to an increase in the transpiration demand; this seems to show that the grapevine is more adapted to save water than to consume it, even if the water supply is optimal. In addition, this phenomenon occurs whatever the previous hydric status of the plant, indicating that structural effects are probably not involved and that this regulatory process relies on a chemical mediator (possibly abscissic acid).

CONCLUSION

Canopy manipulation of the grapevine inside an Ecotron design is an interesting tool or method for the in-depth study of Ecophysiology in relation to plant water regime. This study has lead to the verification of some general theories such as the biological triptych and to a better understanding how the plant adapts to quickly changing environmental conditions, which occur naturally in agriculture or in viticulture.

A particular application to canopy management, or training system design, is the foldable Lyre which permits, by a simple and convenient manoeuvre, the benefits of the open Lyre architecture which is the optimum for grape berry quality, while at the end of a dry season, the closed Lyre architecture may be used to save enough water to avoid significant stress. (CARBONNEAU *et al.*, 2002). These results confirm the practical interest of this new training system. Further investigations are being developed in order to characterise the hydric architecture of the grapevine and the whole plant regulation.

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