Physiological tools for irrigation scheduling in grapevine (Vitis vinifera L.)
An open gate to improve water-use efficiency?

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Abstract

Grapevine is a traditionally non-irrigated crop that occupies quite an extensive agricultural area in dry lands and semi-arid regions. Recently, irrigation was introduced to increase the low land yield, but a good compromise between grape quality and yield is of major importance for the achievement of high-quality products as wine. Therefore, water-use-efficient irrigation and regulated deficit irrigation programs need to be developed to improve water-use efficiency, crop productivity and quality in semi-arid crops.

In the present review, current knowledge on grapevine responses to water stress is summarised. Based on this knowledge, the usefulness of different physiological parameters is discussed, and current knowledge on their applicability for water stress detection and irrigation management in grapevines is reviewed. Partial root drying (PRD) and regulated deficit irrigation (RDI) programs are proposed as the most promising tools for such purpose. Among RDI programs, several parameters are proposed as putative indicators of irrigation convenience and dosage. These are sap flow (measured by sap flow meters), trunk growth variations (measured by linear transducers of displacement, LTDs), canopy temperature (assessed by infrared thermometry), reflectance indices (measured by spectroradiometers or specifically designed instruments) and chlorophyll fluorescence (measured by either active or passive fluorometers). Advantages and disadvantages of all these tools are discussed.

Keywords: Grapevines; Water stress; Water-use efficiency; Irrigation scheduling; Physiological indicators; Sap flow; Remote sensing; Reflectance indices; Chlorophyll fluorescence; Infrared thermometry; Linear transducers of displacement

1. Introduction

Water is the most limiting resource in the Mediterranean region. Rainfall is scarce and irregularly distributed along the year, and climate change models predict even more arid conditions for the near future (Ragab and Prudhomme, 2002). Therefore, increasing water-use efficiency (WUE) should be a key issue for research (Al-Kaisi and Yin, 2003) and it is currently a priority for the United Nations policy, what is called the 'Blue Revolution' and summarised as 'more crop per drop' (Annan, 2000).
Grapevine (*Vitis vinifera* L.) is a traditionally non-irrigated crop that occupies quite an extensive agricultural area in dry lands and semi-arid regions. Recently, irrigation was introduced to increase the low land yield. Grapevine is cultivated to obtain table grape, raisins or wine. In the latter case at least, a good compromise between grape quality and yield is of major importance for the achievement of high-quality premium wines. In the case of producing grapevines, even when a certain variability in the water-use efficiency is present (Bota et al., 2001), the wine-market-oriented production is restricted for the necessity of the highest grape quality standards as well as for certain regional authorised varieties, which commonly offer the tipicity of wine characteristics (‘Denominaciones de Origen’, ‘Appellations d’Origine Contrôlées’, etc.). Therefore, for grapevine as for other extensive crops irrigation remains up to now the most likely way to reduce drought impacts on yield. Hence, water-use-efficient irrigation or regulated deficit irrigation (RDI) programs would still be one of the most desirable tools to improve water-use efficiency and crop productivity in semi-arid areas (Boyer, 1996).

The recent generalisation of vine irrigation in countries with dry summer has lead to some controversy, due to the not fully understood relationships between grapevine photosynthesis and fruit yield and quality. Irrigation substantially increases photosynthesis, and grape yield is increased by 1.5–4-fold, depending on the irrigation timing, the amount of water applied, the cultivar, the environmental conditions and other cultural practices (Bravdo et al., 1985; Hepner et al., 1985; Matthews et al., 1987; Schultz, 1996; Williams, 1996; Escalona et al., 2003). On the other hand, it seems that, up to a certain amount of added water, no effects are observed on grape and wine quality, even when grape yield is increased (Bravdo et al., 1985; Hepner et al., 1985; Medrano et al., 2003; Escalona and Medrano, personal communication). However, larger amounts of water, although further increasing grape yield, have a negative effect on quality, mainly due to colour losses, low sugar content and acidity imbalances (Bravdo et al., 1985; Hepner et al., 1985; Matthews et al., 1990; Cacho et al., 1992; Esteban et al., 1999, 2001). Therefore, a deep knowledge of the mechanisms that regulate plant carbon assimilation and partitioning under different water regimes is of great interest in the frame of precision agriculture, since these mechanisms play an important role in the regulation of the fragile balance between grape yield and quality. Eventually, this will lead to the description of physiologically based criteria for irrigation scheduling.

The aim of the present work is to review recent contributions on the effects of soil water availability on grapevines and to show the potential interest of some physiological indicators of grapevine water status which could better assess the irrigation schedule and dosage for a sustainable, water-use-efficient production of high-quality grapevines.

### 2. Stomatal responses of grapevines to soil water deficit

It has been known for many years that soil water deficit reduces photosynthesis (Kriedemann and Smart, 1971; Liu et al., 1978), vegetative growth (Matthews et al., 1987; Schultz and Matthews, 1988a), and reproductive growth and yield in grapevines (Kliwer et al., 1983; Bravdo et al., 1985; Hepner et al., 1985; Matthews and Anderson, 1988, 1989).

Stomatal closure is among the first processes occurring in the leaves in response to drought. A good relationship between stomatal conductance (*g*<sub>s</sub>) and leaf water potential and/or water content has been observed in some grapevine genotypes and conditions (Liu et al., 1978; Gamon and Pearcy, 1990; Rodrigues et al., 1993; Naor et al., 1994), but not in many others (Quick et al., 1992; Naor and Wample, 1994; Ponti et al., 1994; Bota et al., 2001; Flexas et al., 2002a; Medrano et al., 2002; Schultz, 2003). The latter represent a near-isohydric behaviour, which implies that the same minimum leaf water potential can be achieved at midday irrespective of soil water status. This fact makes midday leaf water potential a poor indicator of water stress, in contrast with pre-dawn leaf water potential or the stem water potential that may serve as good indicators (Schultz, 1998; Escalona et al., 1999; Choné et al., 2001). Differences between near-isohydric and anisohydric *V. vinifera* L. cultivars seem to be related to differences in hydraulic architecture (Schultz, 2003).

Whatever the regulation mechanisms of plant water relations, tight stomatal closure occur at relatively low
soil water deficit in many grapevine cultivars, leading to a rapid reduction of \( g_s \) as pre-dawn leaf water potential decreases (Fig. 1, \( r^2 = 0.50 \), see also Schultz, 2003). This fine regulation of stomatal conductance depends on some hydraulic conductance variations and on synthesis of abscisic acid (ABA) in the roots, which is transported to leaves (Lovisolo et al., 2002). Grapevines were among the first plant species in which a direct role of ABA in stomatal closure was demonstrated (Loveys and Kriedemann, 1974; Liu et al., 1978; Loveys, 1984; Loveys and Düring, 1984). More recently, Correia et al. (1995) were able to demonstrate that the maximum daily stomatal conductance (but not its diurnal fluctuation) was determined by the xylem ABA concentration in field-grown grapevines. In addition, it has been shown that partial root drying in grapevines induces stomatal closure and shoot growth reduction without modifying leaf water status, a process in which a five-fold increase in leaf ABA content is involved (Dry and Loveys, 1999; Dry et al., 2000a, 2000b; Stoll et al., 2000). On the basis of these observations, it is likely that root ABA synthesis in response to drought controls to some extent the stomatal responses in grapevines, although this could also be modulated by osmotic adjustment, xylem hydraulic conductivity, and environmental factors such as air humidity (Düring, 1987; Naor et al., 1994; Lovisolo et al., 2002).

In summary, the tight regulation of stomatal closure in grapevines in response to very mild soil water deficits makes stomatal conductance itself a more precise indicator of water stress than common water relations' parameters.

3. Downregulation of photosynthesis under drought in grapevines

A close, curvilinear correlation between stomatal conductance (\( g_s \)) and net photosynthesis (\( A_{\text{N}} \)) has been described in grapevines, as in other species (Fig. 2A, \( r^2 = 0.89 \), see also Chaves et al., 1987; Düring, 1987; Naor and Wample, 1994; Escalona et al., 1999; Flexas et al., 2002a). Due to this correlation and to the fact that stomatal closure is among the first events to occur under drought, it was assumed that the drought-induced decrease of photosynthesis was mediated by stomatal closure (Kriedemann and Smart, 1971). Under mild water stress, it is likely that grapevine photosynthesis is depressed almost exclusively by stomatal closure, as indicated by increased water-use efficiency (i.e., the ratio of photosynthesis to transpiration or stomatal conductance to water vapour, see Fig. 2B). This is presumably a general feature for most species. However, under more severe water stress situations, non-stomatal inhibition of photosynthesis has been described (Chaves, 1991; Cornic, 2000; Flexas et al., 2004).

Flexas et al. (2002a) have recently shown that drought-induced changes in many photosynthetic parameters are more related to variations in maximum daily \( g_s \) than to variations in the most commonly used water status parameters, like leaf water potential or relative water content. In fact, using \( g_s \) as an integrative parameter reflecting the severity of water stress, different grapevine cultivars (Flexas et al., 2002a) or even different C₃ species (Flexas and Medrano, 2002; Medrano et al., 2002) followed a very similar pattern of downregulation of different photosynthetic parameters in response to progressive soil
water depletion. In the case of grapevines, this observation is consistent with the above-described near-isohydric behaviour of many drought-adapted cultivars and with the suggestion that ABA-induced stomatal closure (and not decreased leaf water status) is the most immediate leaf response to drought.

Using $g_s$ as an integrative parameter for the degree of drought, three phases of photosynthesis response can be differentiated along a water stress gradient, that are shared by different grapevine cultivars (Flexas et al., 2002a; Medrano et al., 2002):

1. A phase of mild water stress is defined for a decreasing range of $g_s$ from 0.5–0.7 to 0.15 mol H$_2$O m$^{-2}$s$^{-1}$. This is characterised by a relatively small decline of $A_N$, which results in a progressive increase of intrinsic water-use efficiency ($A_N/g_s$) and a decline of sub-stomatal CO$_2$ concentration ($C_i$, Flexas et al., 2002a). As a consequence of decreased CO$_2$ availability in the mesophyll, the rate of photorespiration increases, which enables the maintenance of the thylakoid electron transport rate (ETR, Flexas et al., 1999, 2000, 2002a). At this stage, stomatal closure is probably the only limitation to photosynthesis.

2. A moderate water stress phase is characterised by intermediate $g_s$ values (0.15 > $g_s$ > 0.05 mol H$_2$O m$^{-2}$s$^{-1}$). During this phase, a further reduction in $A_N$ occurs and water-use efficiency usually increases, but it decreases in some cultivars (e.g. Naor et al., 1994). $C_i$ still decreases, but ETR and the carboxylation efficiency ($\varepsilon$; i.e., the initial slope of $A_N$–$C_i$ curve) characteristically decline during this phase (Flexas et al., 1999, 2002a). The decline of $\varepsilon$ is dominated by decreased mesophyll conductance at this stage (Flexas et al., 2002a), since the activity of photosynthetic enzymes, such as Rubisco, is mostly unaffected (Bota et al., 2004; but see Maroco et al., 2002). NPQ, a chlorophyll fluorescence parameter indicative of thermal dissipation in the antenna of photosystem II, increases under these conditions, and steady-state chlorophyll fluorescence ($F_s$) drops under high light (Flexas et al., 2000, 2002b). Therefore, in this phase, stomatal limitations seem dominant and photosynthesis is rapidly reversed upon re-watering (Flexas et al., 1999), but non-stomatal limitations are already developing (Naor et al., 1994; Flexas et al., 2002a, 2002b; Maroco et al., 2002).

3. A phase of severe water stress takes place when $g_s$ is very low (<0.05 mol H$_2$O m$^{-2}$s$^{-1}$). In this stress phase, steeper reductions of $A_N$, $A_N/g_s$, ETR and $\varepsilon$ occur. NPQ further increases, and the excitation capture efficiency of photosystem II (Fv/Fm) is eventually reduced, especially during very hot days (Flexas et al., 2002a; Medrano et al., 2002). During this phase $A_N/g_s$ decreases (Düring, 1987) and $C_i$ steeply increases (Flexas et al., 2002a), indicating that non-stomatal limitations to photosynthesis become dominant. The rate of photorespiration is decreased, but the ratio of photorespiration to photosynthesis still increases,
maintaining ETR high relative to \( A_N \) (Düring, 1988; Flexas et al., 1999, 2002a). In this phase, photosynthesis did not recover after irrigation (Düring, 1988; Quick et al., 1992), indicating that non-stomatal inhibition is dominant. Further decreases of \( g_s \) during this phase are likely to be due to impaired Rubisco activity (Bota et al., 2002, 2004; Flexas et al., 2002a; Maroco et al., 2002). A general decline in the activity and amount of photosynthetic enzymes is observed in this phase (Maroco et al., 2002; Flexas et al., 2004).

4. Physiological tools for water stress detection and management of grapevine irrigation

As mentioned in previous sections, for water stress situations characterised by \( g_s \) values above 0.05–0.1 mol \( \text{H}_2\text{O} \text{ m}^{-2} \text{s}^{-1} \) photosynthesis is mainly limited by stomatal closure, and a complete recovery of the maximum \( A_N \) occurred just one night after irrigation (Flexas et al., 1999). For more prolonged and/or more pronounced water deficits leading to further decreases of \( g_s \), non-stomatal limitations (metabolic and/or restricted internal \( \text{CO}_2 \) diffusion) are dominant and photosynthesis did not recover rapidly after irrigation (Düring, 1988; Quick et al., 1992). Therefore, maximising WUE implies a certain reduction in crop yield. Interestingly, in grapevines (see above sections), highest crop load is linked to low grape quality. Thus, in fact, limitations to grape yield are a common practice (if not compulsory) for a market standard wine production and premium wines. Thus, being an extensive crop in drought-prone areas, irrigation would give more benefits if schedules and dosages were oriented to maximise water-use efficiency (Fereres, 2003).

Based on this knowledge, physiologically based irrigation tools may attempt to maintain the plants at a limit between water stress and excess water consumption, thus making a rational use of irrigation water. This kind of irrigation may save water with respect to empirical irrigation, improving yield as compared with rainfed grapevines, and maintaining the high fruit quality. Partial root drying (PRD) and regulated deficit irrigation (RDI) programs are currently envisaged as the most promising irrigation tools based on physiological knowledge of grapevine response to water stress.

Partial root drying (PRD) consists in drip irrigation alternating from one side of the row to the other, thus allowing that some roots of the plants are always in contact with drying soil. The aim of this technique is to control excessive vegetative vigour and save irrigation water without influencing fruit yield and quality. This treatment induces root ABA synthesis in the dried zone (Dry and Loveys, 1999; Dry et al., 2000a, 2000b), leading to partial stomatal closure without reducing leaf water status. Therefore, by adjusting the proportion of roots that are irrigated, it is possible to maintain the plants at the inflexion point of the \( A_N-g_s \) relationship, thus saving a large amount of water with only a small reduction of photosynthesis (Stoll et al., 2000). Trials in Australia with this type of irrigation have shown a significant reduction in vegetative growth while maintaining fruit yield and quality, saving in irrigation (Dry et al., 2001).

Regulated deficit irrigation (RDI) programs consist in continuously monitoring some physiological parameters indicative of vine water stress. Irrigation should be applied only when such a parameter drops below a certain threshold value. Although leaf water potential has been proposed as an indicative parameter for RDI programs in grapevines (Girona et al., 2002) and other extensive crops (Guldhammer et al., 1999), the near-isohydric behaviour of many cultivars will probably preclude its use, specially to detect mild to moderate water stress situations, in which large reductions of photosynthesis and yield occur without much effects on canopy water relations. Presently, and based on the knowledge of grapevine response to progressive water stress described in the above sections, it seems reasonable that continuously monitoring of some direct or indirect indicators of crop \( g_s \) or \( A_N \) may allow deciding when and how much water must be applied for a rational use of irrigation water. To give priority to high water-use efficiency over maximum yield, irrigation should be applied only when the indicator parameter drops below a certain threshold value, preferably corresponding to some \( g_s \) value between 0.05 and 0.15 mmol \( \text{H}_2\text{O} \text{ m}^{-2} \text{s}^{-1} \). According to current knowledge on water stress effects on grapevine photosynthesis, yield and quality, maintaining grapevines at such \( g_s \) range may, in principle, allow: (1) maximum water-use efficiency,
(2) rapid reversibility of photosynthesis upon irrigation, (3) relatively moderate yield loses as compared to intensive irrigation and (4) maintenance of optimum grape quality characters.

Several contact and remote sensing approaches have been proposed as such indicators of \( g_s \). Among contact approaches, the most promising are (1) sap flow meters and (2) linear transducers of displacement (LTDs). Among the remote sensing approaches, (3) thermal imaging, (4) reflectance indices and (5) chlorophyll fluorescence have been evaluated with some success.

4.1. Sap flow meters

Sap flow measurements give reliable, direct estimates of plant or shoot water loss without disturbing the conditions of the leaf environment (Shulze et al., 1985; Ansley et al., 1994; Fernandez et al., 2001). In irrigated grapevines, sap flow measurements were shown as a good tool to estimate canopy transpiration (Yunusa et al., 2000). More recently, Escalona et al. (2002) have demonstrated a very high correlation between single leaf \( g_s \) and the instantaneous sap flow in water-stressed, potted grapevines (see also Table 1). For the total daily water consumption, the correlation was even higher \((r^2 = 0.98)\) and close to a 1:1 relationship. Net photosynthesis rate was correlated as well with sap flow values \((r^2 = 0.78)\), and this correlation increased \((r^2 = 0.91)\) when the daily balances of both parameters were compared. Ginestar et al. (1998) have already started to apply sap flow measurements to establish different irrigation coefficients to Shiraz grapevines, obtaining a gradient of grape yield and qualities. The main advantages of sap flow measurements may be: (a) the fact that they directly reflect canopy sap flow and transpiration, therefore being directly related to whole-canopy \( g_s \), and (b) the fact that they correlate with \( g_s \) at any given range of the latter, therefore allowing a continuous monitoring of \( g_s \) from full water availability to severe water depletion. The principal disadvantages are: (a) that the sensors are quite expensive, thus not allowing establishing a high number of them per field; and (b) the fact that this is a contact or intrusive technique, which may imply some interference with plant performance.

4.2. Linear transducers of displacement

LTDs were mainly introduced by Garnier and Berger (1986), and envisaged as a powerful tool for irrigation scheduling (Fereres et al., 1999; Moriana et al., 2000). They permit the continuous measurements of the stem diameter, which can be related to plant growth, water-use and status. The shrinking and swelling of the extensible plant tissues provide an indirect measure of the transpiration streams during daylight periods, and is related to changes in water content and turgor potential of their cells. In spite of its potential usefulness, little attention has been paid to this technique in grapevine studies, although Escalona et al. (2002) have recently demonstrated that diurnal stem diameter variations closely track sap flow (see also Table 1). The main advantage of this technique is that the sensors are very inexpensive, thus allowing the establishment of a high number of them per field. As remarkable disadvantages, there is the fact that this is a contact technique, which may imply some interference with plant performance, and that any possible correlation with \( g_s \) would be somewhat indirect.

4.3. Infrared thermometry

It has been long recognised that leaf or canopy temperature is highly dependent on the rate of

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**Table 1**

<table>
<thead>
<tr>
<th>Trunk growth (µm)</th>
<th>Maximum daily Sap flow (g m(^{-2}) h(^{-1}))</th>
<th>Daily Sap flow (g m(^{-2}) day(^{-1}))</th>
<th>Leaf-level ( A_N ) (µmol m(^{-2}) s(^{-1}))</th>
<th>Daily carbon gain (g m(^{-2}) day(^{-1}))</th>
<th>Leaf-level ( g_s ) (mol m(^{-2}) s(^{-1}))</th>
</tr>
</thead>
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<tr>
<td>50</td>
<td>150</td>
<td>1174</td>
<td>11.1</td>
<td>3.4</td>
<td>0.15</td>
</tr>
<tr>
<td>0</td>
<td>83</td>
<td>630</td>
<td>6.9</td>
<td>2.6</td>
<td>0.09</td>
</tr>
<tr>
<td>−50</td>
<td>36</td>
<td>320</td>
<td>3.7</td>
<td>2.1</td>
<td>0.02</td>
</tr>
</tbody>
</table>

Values inferred from data in Escalona et al. (2002).
transpiration and can therefore be used as an indicator of stomatal opening (Sinclair et al., 1984). Accordingly, infrared thermometry has been developed as a means for irrigation scheduling (Jones, 1999; Jones et al., 2002). The main advantages of this tool are: (a) the potential amplitude of its fields of view, allowing measurements at different scales ranging from single leaves to several hectares, and (b) the fact that, in principle, thermometric signals should correlate with \( g_s \), at any given range of the latter, therefore allowing a continuous monitoring of \( g_s \) from full water availability to severe water depletion. Riou et al. (2000) have recently described a thermometric parameter sensible to water stress in grapevines, and Jones et al. (2002) have shown reasonable estimations of whole canopy \( g_s \) based on thermometric determinations. The principal disadvantages are: (a) the possibility of misleading interpretations whenever the temperature sensed is biased by, for example, bare soil in the sensor’s field of view, although recent investigations have shown that this problem can be avoided by the use of modern thermal imagers with associated image analysis software (Jones et al., 2002); and (b) the fact that scaling-up to satellite level for regional-scale purposes would be difficult due to the strong absorption of infrared radiation by the atmosphere. Despite its big potential interest, much knowledge has still to be gained prior to this tool becomes easily used for irrigation scheduling.

4.4. Canopy reflectance indices

Different parameters reflecting changes in canopy reflectance at different wavelengths have been used for monitoring plant performance. The general advantage of all these parameters or indexes is that they are not restricted by the dimension of their field of view, allowing measurements from small to large scales, including airborne and satellite detection (Gamon et al., 1990; Sellers et al., 1992; Peñuelas and Filella, 1998).

Among them, the simplest indexes, as the simple ratio \( SR = \text{NIR}/R \), i.e., the ratio between near-infrared to visible red) and the so-called normalised difference vegetation index \( \text{NDVI} = \frac{\text{NIR} - R}{\text{NIR} + R} \), correlate with the amount of green biomass over an area and with the absorbed PPFD, and they have even been shown to reflect stomatal conductance and photosynthesis in unstressed plants (Sellers et al., 1992; Peñuelas and Filella, 1998). The main disadvantage, that precludes their use for irrigation purposes, is that they are quite static, failing to follow \( g_s \) and photosynthesis changes with developing drought (Peñuelas et al., 1994; Runyon et al., 1994).

A water index has been defined \( (W1 = R900/R970) \) that closely follows leaf water content and \( g_s \) during drought (Peñuelas et al., 1993, 1994; Peñuelas and Filella, 1998). This seems a very promising tool for drought assessment, provided that it performs better at the canopy than at the leaf scale (Peñuelas et al., 1993). Its main disadvantage is that, because it involves structural changes like loss of cell wall elasticity, its variations appear only when RWC drops below 85% (Peñuelas et al., 1993). This precludes its use for mild water stress assessment or for assessment of plants, like many near-isohydric grapevine cultivars, capable of maintaining RWC within narrow ranges.

The photochemical reflectance index \( \text{PRI} = R531 - R570/R531 + R570 \) is strongly correlated to the de-epoxidation state of the xanthophyll cycle (Gamon et al., 1990; Peñuelas et al., 1994; Peñuelas and Filella, 1998). PRI has been shown to correlate with photosynthesis and \( g_s \), thus been capable to reflect drought at the leaf level in many species (Peñuelas et al., 1998; Styinski et al., 2002; Winkel et al., 2002), including grapevines (Evain et al., 2004). Its principal disadvantages are that (a) the precise PRI values as well as their relationship to \( A_N \) and \( g_s \) seem dependent on the species and/or the instrument used (Styinski et al., 2002; Winkel et al., 2002) and (b) on occasions it fails to follow drought at the canopy scale, which is probably due to leaf changes in orientation as a consequence of wilting (Gamon et al., 1990; Peñuelas et al., 1994).

4.5. Chlorophyll fluorescence indices

Chlorophyll fluorescence indices have been proposed as well as irrigation tools. With current instrumentation, chlorophyll fluorescence can be measured at short distances, of several meters, with laser-based fluorometers (Flexas et al., 2000; Onis et al., 2001), and from airborne using sun-induced chlorophyll fluorescence (Moya et al., 1998). However, satellite detection is theoretically possible if
Fig. 3. (A) The relationship between net CO₂ assimilation ($A_N$) and stomatal conductance. (B) The relationship between intrinsic water-use efficiency ($A_N/g_w$) and stomatal conductance. (C) The relationship between $F_{s}/F_{0}$ and stomatal conductance. (D) The relationship between $F_{s}/F_{0}$ and net CO₂ assimilation ($A_N$). Data are from grapevines (V. vinifera L.) growing in a commercial vineyard in 1999 in Mallorca, and submitted to different water supply, as described by Flexas et al. (2002a, 2002b). Circles correspond to Tempranillo, and triangles to Mantó Negro. Closed symbols are from irrigated plants, and empty symbols from non-irrigated. All data are average values of 6–8 replicates.

fluorescence is measured within the $H_0$ Fraunhofer band, or even within the oxygen bands, i.e. at certain wavelengths not present in the solar spectrum due to attenuation by the sun atmosphere (Moya et al., 1998). Instruments are currently envisaged for this purpose (Moya et al., 2004).

Among all chlorophyll fluorescence parameters, steady-state chlorophyll fluorescence ($F_s$) normalised to its dark-adapted state ($F_0$) is especially remarkable, because it can be measured by remote sensing without depending on measuring fluorescence during saturating flashes. Passive detection is inexpensive and non-necessary. In addition, because of its remote measurements, this technique causes no interference with plant performance (Flexas et al., 2000; Moya et al., 2004). Moreover, like reflectance indices, the measurement of $F_s/F_0$ is not restricted by the dimension of the target or by the instrument field of view, allowing measurements from small to large scales. All together makes the continuous remote recording of $F_s/F_0$ a promising tool for plant management.

The diurnal response of $F_s/F_0$ to light intensity could be a sensitive indicator of water deficit. A positive correlation is observed between $F_s/F_0$ and PPFD under irrigation, but an inverse correlation develops as drought progresses, which is a characteristic signal of water stress that can be related to a strong increase of the non-photochemical quenching (Cerovic et al., 1996; Flexas et al., 1999, 2000). In addition, Flexas et al. (2002b) have shown that, at saturating light intensity (a condition often met in vineyards in summer), $F_s/F_0$ directly correlates with $g_s$ and photosynthesis in different $C_3$ species. In grapevines, the relationship between $F_s/F_0$ and $g_s$ is curvilinear ($r^2=0.52$) (Fig. 3C, see also Flexas et al., 2002b). Thus, proper monitoring of $F_s$ would be a useful tool to irrigate plants only when $g_s$ drops below the inflexion point between predominant stomatal and non-stomatal limitations to photosynthesis, which is close to the inflexion point of the $A_N$–$g_s$ relationship.
water-use-efficient irrigation programs. Partial root drying (PRD) and regulated deficit irrigation (RDI) programs are such tools. Among RDI programs, several indicator parameters seem promising. These are sap flow, trunk growth variations, canopy temperature, photochemical reflectance index (PRI) and steady-state chlorophyll fluorescence. All these tools have yielded promising results at the ecophysiological level. A combination of PRD and RDI techniques has not been tested, and could yield even more promising results. In addition, it would be time now to conduct a number of studies at the agronomical level to confirm the usefulness of these approaches, prior to their extension as common, practical tools, for vineyard management and irrigation.

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References


5. Conclusions

In summary, current knowledge on physiological responses of grapevines to water stress allows envisaging physiologically based irrigation tools for


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