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Leaf growth rate and nitrogen content determine respiratory costs during leaf expansion in grapevines

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Respiration processes are well recognized as fundamental for the plant carbon balance, but little attention has been paid to the relationships among respiration rates, environment and genetic variability. This can be of particular interest to understand the differences in net carbon balances in crops as grapevines. Night respiration (R_n) and its associated growth (R_g) and maintenance (R_m) components were evaluated during leaf expansion in two grapevine cultivars (Tempranillo cv. and Garnacha cv.) that differ in their plant growth pattern and carbon balance. Simultaneously, leaf traits as leaf mass area, nitrogen (N) and carbon (C) content were evaluated in order to relate to the respiratory processes and the leaf growth. The results showed the differences in respiration rates associated with the leaf expansion pattern. Tempranillo developed leaves with higher leaf area and lower dry weight per leaf unit than Garnacha. Although differences between cultivars were observed in terms of growth costs in expanding leaves, the maintenance costs were similar for both cultivars. Also, a significant linear regression was found between respiration rates and N content in expanding and mature leaves. The results indicate that differences in structure and nitrogen content of expanding leaves may lead to respiratory differences between cultivars. These results also demonstrate the importance of respiratory cost components in carbon balance calculations in grapevines.

Introduction

The importance of plant respiration in the ecosystem is well known, as plant respiration releases around six to eight times more CO_2 into the atmosphere than the fossil fuels combustion, and leaf respiration represents half of the CO_2 emissions from the plant respiration (Atkin et al. 2014). Agricultural land covers 38.4% of the terrestrial land area (FAOSTAT, 2015); it is the most relevant land use in Europe, and agriculture accounts for almost half of the total land surface in Spain (INE 2015). Therefore, the study of respiration in crops is important to calculate carbon balances accurately. In grapevines, Palliotti et al. (2004) and Palliotti and Cartechini (2005) showed how most of the aerial plant respiration losses were due to leaf respiration, and the results obtained by Escalona et al. (2012) showed that leaf respiration represented around 10% of the carbon fixed by photosynthesis in an experiment with potted vines.

Respiration provides the carbon skeletons and energy needed for tissue growth and maintenance processes (Bouma 2005). The relationship between night respiration (R_n) and leaf traits (e.g. leaf structure and nitrogen content) was demonstrated by different authors (Reich et al. 1998a, Galmés et al. 2011, Laureano et al. 2013, Atkin et al. 2015). Although many studies have examined the interspecific relationship among R_n, leaf expansion and other leaf traits [i.e. leaf morphology, nitrogen (N) content, net photosynthetic capacity], more information is needed in crops, and particularly in grapevines,

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Abbreviations – LA, leaf area; RGR, relative growth rate; SGR, specific growth rate.

where the leaf growth pattern greatly differs among cultivars.

Leaf respiration can be partitioned into growth and maintenance components. Growth respiration (R_g) can be defined as the respiratory energy required to convert non-structural carbohydrates into new leaf constituents, and the maintenance respiration (R_m) as the respiratory energy associated with the energy-consuming processes that maintain cellular structure (Bouma 2005, Florez-Sarasa et al. 2007, Lambers et al. 2008). From the different methods used to estimate these respiratory components (Thornley and Cannell 2000, Lambers et al. 2008), the regression approach is one of the methods extensively used to estimate the respiratory costs of growth and maintenance. These methods require plotting respiration against relative growth rate (RGR). The slopes of the regression lines represent the specific costs for growth, and the regression line intercepts are used to estimate specific costs for maintenance (Lambers et al. 2008).

Differences in growth and maintenance costs of different organs in plants may be important to explain variations in growth rates (Lambers et al. 2008, Laureano et al. 2013). In grapevines, there are some references showing R_n rates in order to compare the performance of different cultivars in potted vines (Gómez-Del-Campo et al. 2004, Escalona et al. 2012), or under field conditions (Schultz 1991, Zufferey 2016). The interspecific variation in RGR and leaf morphology was studied by Tomás et al. (2014) among different cultivars. However, the R_g and R_m pattern and leaf traits associated during the process of leaf expansion, comparing different grapevine cultivars under realistic conditions has not been described in any of those studies. Such information is necessary for an accurate carbon balance calculation as well as to explore the possible genotype and environmental effects. In that way, the present work was addressed to quantify and qualify the production and maintenance costs of leaves in two contrasting cultivars under field growing conditions.

In consequence, the main objectives of this work were to: (1) study the leaf expansion pattern and the structural differences between cultivars; (2) analyze R_n from expanding and mature leaves and their associated growth and maintenance costs, and finally, (3) relate R_n to leaf expansion, morphological characteristics and N content of leaves from vines under field conditions.

Materials and methods

Plant material and treatments

This study was conducted in the experimental vineyard of the University of Balearic Islands (Palma, 39°38′17″N 2°38′54″E) during two consecutive years (2013 and 2014) using two *Vitis vinifera* grapevine cultivars widely cropped in Spain: Garnacha and Tempranillo. Vines were planted in 2009 in rows (distance between rows was 2.5 m and between plants 1 m) and grafted onto rootstock 110 Richter. Vines were trained to bilateral cordons and spur pruned with an average of 12 buds per vine. Soil type was a typical clay loam, maintained free of weeds by surface tillage to facilitate measurement of soil respiration.

Fig. 1. View of a shoot apex on 24 May 2013 in a Garnacha vine. A red label was set in the first expanding leaf of each shoot apex from the vines under control (around 12 shoots per vine) on 12 May 2013 and on 4 May 2014. The leaf with the red label in the picture represents one of the studied leaves in the experiment from 2013, 13 days after labeling the leaves.

For this study, the first expanded leaves from the apex of each shoot were labeled with a red marking (Fig. 1) in four plants per cultivar and treatment at the beginning of flowering stage (4 May 2013 and 12 May 2014, respectively), in order to preserve labeled leaves from the destructive measurements of leaf mass area (LMA) and N–C content. The day after the leaves were marked, the experiment was carried out across 31 days, in order to follow the expansion of the marked leaves in a period of active growth in vines. Simultaneously, a mature leaf from the same shoot was measured in order to study leaves that had completed the expansion period.

Measurements were carried out on the nights 1, 3, 7, 13, 18 and 30 after marking the leaves from the shoot apex. R_n was measured between 23:00 and 01:00, on expanding (marked) and mature leaves, using a portable gas-exchange analyzer (Li-6400, Li-Cor, Lincoln, NE). Measurements were taken until a stable respiration rate was reached. Leaf expansion was followed in the same days (six times during the 31 days of the study), in order to calculate the leaf area (LA) and dry weight (DW) increase

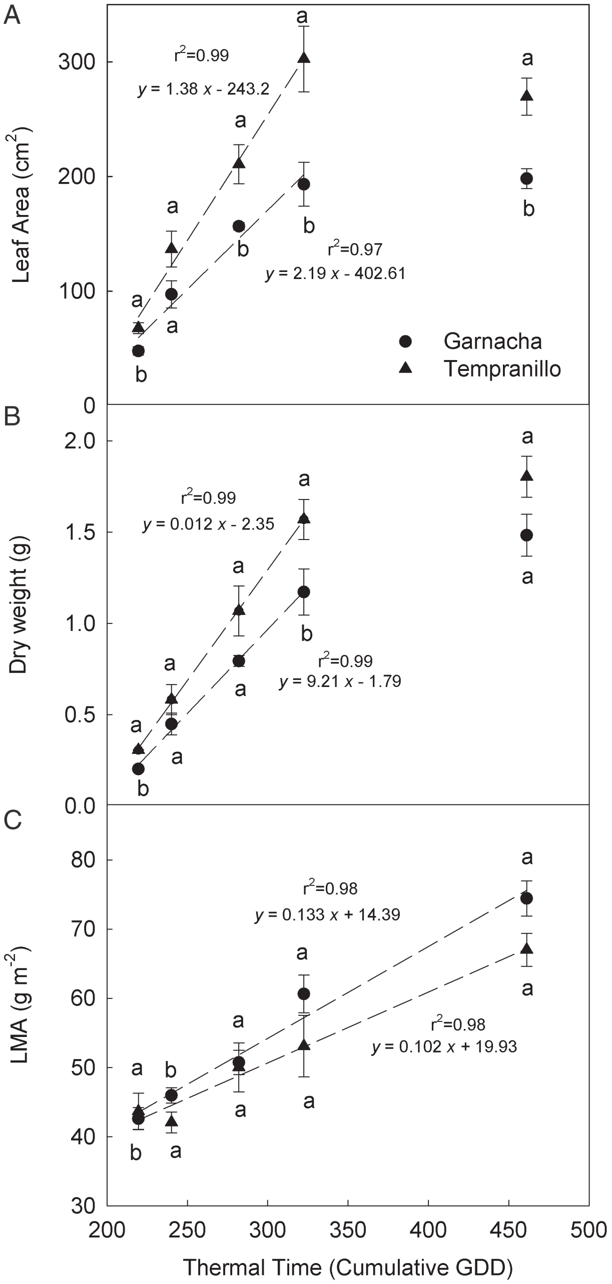


Fig. 2. Changes on (A) LA, (B) DW and (C) LMA along leaf expansion of Garnacha (circles) and Tempranillo (triangles) expanding leaves in 2013, from the leaves were unfolded until the leaf expansion was completed. Bars indicate ± SE (n = 6).

for each period. Immediately after R_n measurements, each leaf was collected and a picture was taken in order to measure the LA using the Image J software (Schneider et al. 2012). Each leaf was dried (80°C) and weight, and LMA was calculated from the division of LA into DW of each measured leaf. During 2014, LMA was calculated from two leaf discs from the sampled leaves, dried and weighed (80°C) in order to obtain the evolution of LMA of each measured leaf. The leaf expansion rate was calculated as the mass increase divided by days of growth. Also, during 2014, one leaf disc was sampled and dried from the same leaves in order to measure the total N and C content per dry mass (TruSpec CN; Leco, St Joseph, MI).

Data were presented in relation to the growing degree days (GDDs). GDDs were calculated by the sum of the 'heat units' for each calendar day of the growing season from budbreak stage, considering a base temperature of 10°C. Meteorological data were registered by a meteorological station (Meteodata 3000, Geónica S.A., Madrid, Spain).

Every 2 weeks, predawn leaf water potential (Ψ_{pd}) was measured in order to verify no water stress in plants (Ψ_{pd} under 0.3 MPa). Ψ_{pd} was measured 1 h before sunrise on mature Garnacha and Tempranillo leaves (four plants per cultivar) using a Scholander pressure chamber (Soilmoisture Equipment, Goleta, CA).

In order to estimate the growth and maintenance components of R_n in expanding leaves, a regression approach was carried out between the specific growth rate (SGR) and the R_n (Bouma 2005). The leaf mass increase from each expansion period was used to calculate the SGR as the difference in mass divided by days of growth. The R_n for each leaf was expressed per DW unit. A linear regression of R_n was performed against SGR for each cultivar. The slope (mg CO_2 g^{-1}) represents respiration associated mainly with tissue synthesis (growth respiration), while the Y intercept (mg CO_2 g^{-1} day^{-1}) represents the respiration rate at zero growth, i.e. respiration associated mainly with tissue maintenance (Bouma 2005).

Statistics

Data were processed using ANOVA procedures, and means were separated by Tukey's test. The data were analyzed using JMP 12.2.0 (SAS Institute, Cary, NC). For the estimation of R_g and R_m, R_n was regressed (linear model) against SGR. For the detection of differences in R_g and R_m, the slopes and intercepts of the regression lines for R_n vs SGR were subjected to an ANCOVA analysis.

Results

Leaf expansion pattern

The kinetics of growth and the structure of young leaves markedly changed from Garnacha to Tempranillo. No water stress was found in both cultivars along the experiment (Ψ_{pd} under 0.3 MPa, data not shown). Fig. 2 shows the growth pattern of expanding Garnacha and Tempranillo leaves, expressed as the evolution of LA and DW

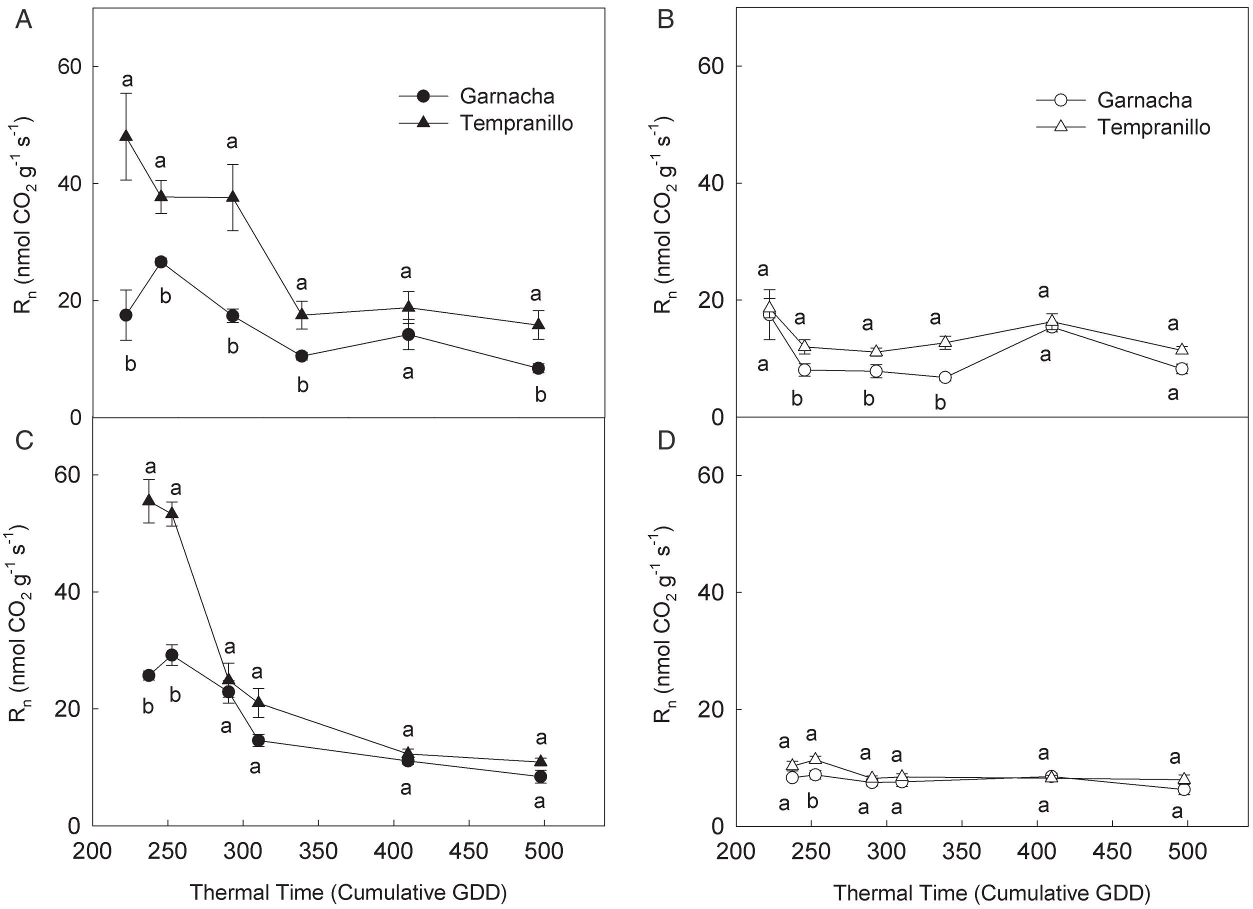


Fig. 3. Leaf respiration averages of growing (closed symbols) and mature (open symbols) leaves during leaf expansion in cv. Garnacha (circles) and Tempranillo (triangles) vines in 2013 (A, B) and 2014 (C, D) seasons. Bars indicate ± SE (n = 6–8). Different letters denote significant differences between cultivars.

per leaf unit. The LA and DW followed a logarithm function; however, the relationship between thermal time (cumulated degree day) and LA–DW was linear in the first phase of the leaf expansion (20 days) after the leaves were labeled (Fig. 2A, B; $r^2 = 0.99$ and $r^2 = 0.99$, respectively). Fig. 2C shows the relationship between thermal time and LMA, following a linear function. An ANCOVA analysis was made in order to analyze the slopes of the linear regressions from Garnacha and Tempranillo (Fig. 2A–C). Differences in slope were found between both cultivars in terms of LA and DW, reflecting that the growth rates of Tempranillo were greater than the Garnacha ones during the first phase of the leaf expansion. On the other hand, in terms of LMA, no differences in slope were found between cultivars, despite the fact that Garnacha displayed greater LMA in every sample date. After 20 days of expansion, the LA, DW of leaf unit and LMA increase slowdown to rich the maximum when the leaf maturation was completed. Final LA largely differed between cultivars, and Tempranillo registered the highest LA values and the fastest leaf expansion, from the first stages of the leaf expansion until the leaf expansion was completed. Final LA of a fully expanded leaf varied from around 200 cm^2 for Garnacha to around 300 cm^2 for Tempranillo.

Night respiration rates during leaf expansion

The R_n pattern of expanding and mature leaves during the flowering stage of 2013 and 2014 is shown in Fig. 3. The evolution of R_n was studied from the earliest development stages of each labeled leaf (Fig. 1), and throughout the leaf growth, until the leaf expansion was completed. Also, R_n of a fully expanded and mature leaf was measured at the same time to study the R_m. For the expanding leaves (Fig. 3A, C), the trend of R_n was the same in both cultivars and seasons, and no relationship was found between the night respiration rates and the night temperatures registered in each day (Table S1). However, significant differences between cultivars were

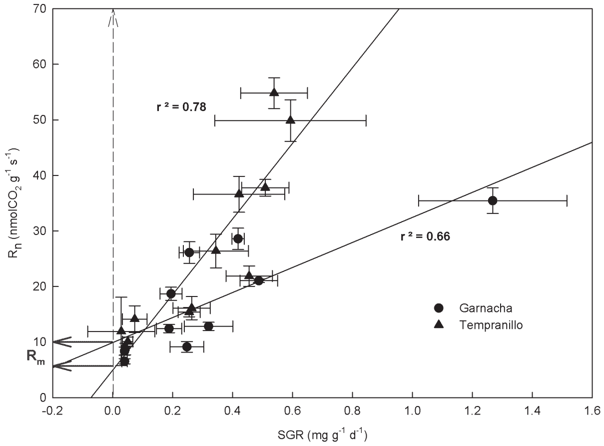


Fig. 4. Relationship between the specific respiration rate and night leaf respiration per DW (means ± SE, n = 6–8) for expanding leaves in Garnacha (circles) and Tempranillo (triangles) cultivars (2013 and 2014 years). The intercept of each line regressions represents the maintenance respiration (Rm).

found in the first stages of the leaf growth in 2013 and 2014 seasons, and the expanding leaves of Tempranillo registered higher values of R_n expressed by DW unit (35–40 nmol CO$_2$ g^{-1} s^{-1}) than Garnacha (25–35 nmol CO$_2$ g^{-1} s^{-1}). R_n per DW unit was significantly higher in growing leaves than in mature leaves during the first days of its expansion. After this period, respiration rates were similar in both types of leaves. Moreover, for the mature leaves (Fig. 3B, D), no significant differences between cultivars were observed, maintaining R_m rate around 10 nmol CO$_2$ g^{-1} s^{-1} all along the experiment.

Plant growth is associated with respiration, but this relationship varies among species and cultivars. In Fig. 4, a significant positive correlation was found in young Tempranillo ($r^2 = 0.79$, $P < 0.0005$) and Garnacha ($r^2 = 0.72$, $P < 0.0005$) leaves between the SGR and the R_n. Separate slopes analyses were made to test whether the slopes of the linear functions varied between cultivars. Based on this ANCOVA analysis, it was found that there were significant differences in slope (R_g) between both cultivars; thus, R_g per unit mass in Tempranillo expanding leaves was greater than in Garnacha. Also, R_m of expanding leaves was estimated as the intercept of the regression lines (Fig. 4). R_m was significantly higher ($P < 0.05$) in Garnacha growing leaves ($R_m = 9.25$ nmol CO$_2$ g^{-1} s^{-1}) than in Tempranillo ones ($R_m = 6.24$ nmol CO$_2$ g^{-1} s^{-1}).

Leaf N and C content: effect on night respiration

The leaf N and C content was measured in order to study the differences between cultivars. The evolution of the relationship between N–C content and R_n in expanding and mature leaves is shown in Fig. 5. The Tempranillo expanded leaves showed a significantly higher ($P < 0.05$, 0.046 g C g^{-1} DW) N concentration than the Garnacha ones at the first stages of expansion, from where it began to descend gradually to equal the N concentration of the mature leaves. As for the total C content per DW, no significant differences were found between growing and mature leaves, nor between cultivars, maintaining around 0.48 g C g^{-1} DW all along the experiment.

In order to study the relationship between the leaf N content and R_n, a correlation between both factors was carried out (Fig. 6). Significant linear regressions were found for both mature ($R^2 = 0.44$) and growing ($R^2 = 0.7$) leaves. The slope of the expanding leaves regression was significantly different from the mature one. Thus, mass-based R_n showed a greater dependence on the N content in the expanding leaves than in the mature leaves.

The respiration rate per unit of N or C gives us information about N or C use efficiency during the leaf growth. In this sense, the leaves in the first stages of expansion in Tempranillo recorded greater R_n rates per unit of N and C than Garnacha (Fig. 7A, C). However, in mature leaves, no significant differences were found between both cultivars.

Discussion

Respiration is an important plant process to be taken into account when calculating carbon balances in plants (Amthor 1984, 1989, Thornley and Cannell 2000). Nowadays, the interest of increasing the knowledge on respiration processes in crops is growing because of a recognized paucity of data on respiration rates and the relevance of this process to understand different physiological responses, such as the whole-plant carbon balance. Therefore, the study of grapevine respiratory activity to better understand the genetic and environmental effects is gaining interest and importance (Franck et al. 2011, Zufferey 2016, Hernández-Montes et al. 2017). Inside this frame work, this study analyses the respiration rate activity during the leaf expansion in order to evaluate the growth and maintenance components of grapevine leaves. LA is an important part of the grapevine vegetative growth and results in a development of 2–6 m^2 of new leaves per plant during the first weeks of the vines growth cycle (Gómez-Del-Campo et al. 2004), thus this respiratory cost results in an important sink for grapevines during the spring.

The study of the leaf growth pattern showed a slower LA expansion coupled to a faster DW and thickness increase in Garnacha than in Tempranillo, which

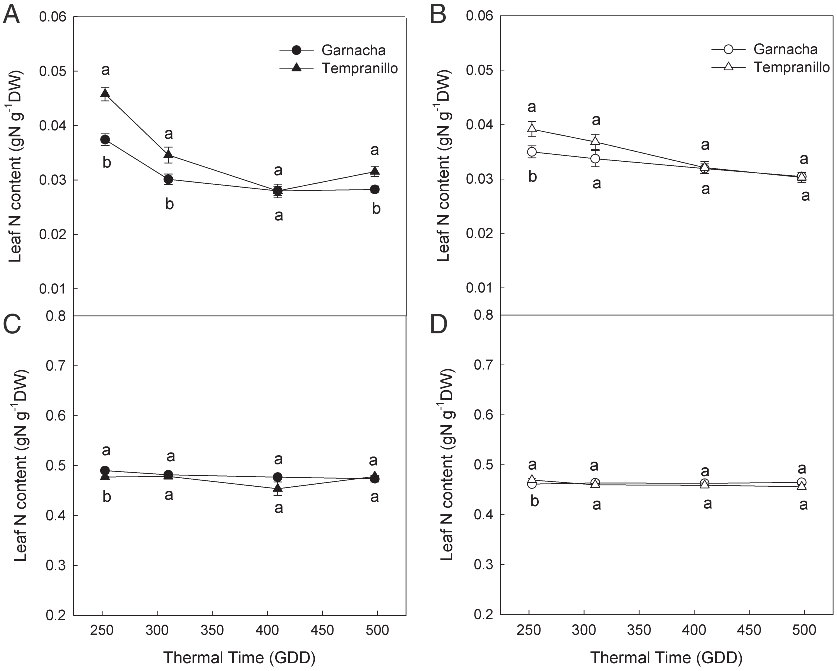


Fig. 5. Mean values (±SE, n = 8) of nitrogen (A, B) and carbon (C, D) content per DW unit in growing (A, C; closed symbols) and mature (B, D; open symbols) leaves for Garnacha (circles) and Tempranillo (triangles) during the leaf expansion experiment of 2014. Different letters represent significant differences from ANOVA analysis, $P < 0.05$.

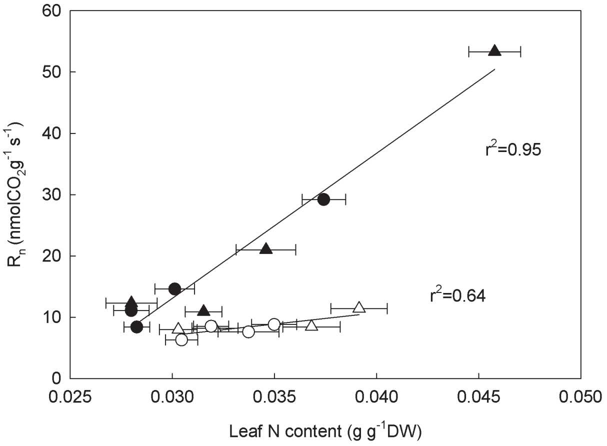
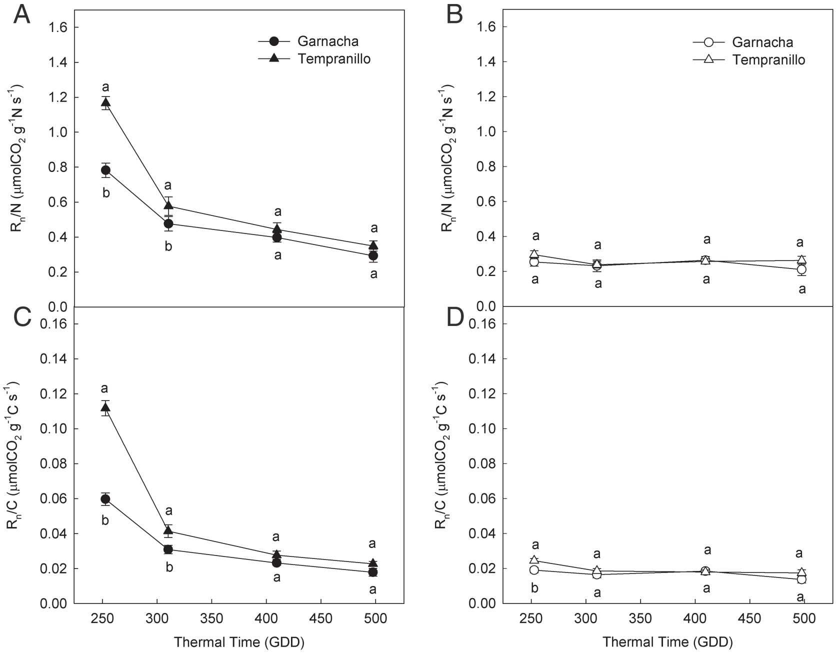


Fig. 6. Relationship between leaf nitrogen content per DW and night leaf respiration per DW (means ± SE, n = 8) for expanding (closed symbols) and mature (open symbols) leaves, in Garnacha (circles) and Tempranillo (triangles) vines.

resulted in LMA values around 10% higher in mature leaves for Garnacha than for Tempranillo. Previous results in a wider range of species showed that high values of LMA are commonly associated with high thickening of cuticle and epidermis (Niinemets and Sack 2006), consistent with a recent study by Tomás et al. (2014) in potted vines. Effectively, Tomás et al. (2014) showed that mature leaves of Garnacha have thicker leaves (mesophyll and epidermis) than Tempranillo, highly due to a greater epidermal cell thickness (upper and lower epidermis). According to Kutschera (1992), outer cell layers constrain the extension of internal tissues and thus limit organ elongation. These greater epidermal cell thickness observed in Garnacha could be linked to a higher limitation of the internal leaf tissues growth, probably due to a lower deformation of epidermal cell walls (leaf tissue less plastic), limiting the leaf expansion. Moreover, several authors reported a link between the leaf expansion rate and the cell-wall deformation properties, via the activities of enzymes under the control of chemical signals such as ABA (Dodd and Davies 1996, Salah and Tardieu 1997, Tardieu et al. 2010). In fact, Martorell et al. (2015) reported higher values of ABA in Garnacha than in Tempranillo in an experiment with grapevines under field conditions. These facts all together could contribute to explain the differences in leaf expansion between cultivars in this study.

R_n is one of the important processes to be taken into account when calculating carbon balances in crops (Amthor 1984, Thornley and Cannell 2000), and this study is among few in the literature providing direct R_n measurements in field growing grapevines. In this experiment, the recorded R_n values agreed with previous reports for grapevines in different experimental locations (Schultz 1991, Gómez-Del-Campo et al. 2004, Escalona et al. 2012, Zufferey 2016) showing high R_n rates associated with leaf expansion rates, followed by a deep decline when the leaf expansion finished. Focusing on this general response, the present results showed an important genotype effect on R_n rates, showing consistently higher respiratory losses in Tempranillo

Fig. 7. Mean values (±SE, n = 8) of R_n per N and C units of expanding (A, C; closed symbols) and mature (B, D; open symbols) leaves in cv. Garnacha (circles) and Tempranillo (triangles). Different letters represent significant differences between cultivars from ANOVA analysis, $P < 0.05$.



than in Garnacha. According to the reported differences between cultivars in R_n rates, as well as the higher drought tolerance of Garnacha than Tempranillo, a deeper study on the leaf characteristics and leaf respiration can provide an interesting insight on the effects of leaf morphological characteristics on the respiratory cost of leaves. The results support that the growth costs of expanding leaves were associated with leaf morphology and growth rates (Fig. 4). In this sense, the construction costs for a gram of leaf tissue was higher in Tempranillo than in Garnacha, since the photosynthesis rates are similar for both cultivars in this phenological stage (data not shown). This corresponds with a faster leaf expansion (high LA and low DW), and a higher leaf N concentration in Tempranillo than Garnacha expanding leaves. Tomás et al. (2014) showed a higher mesophyll porosity and number of cell layers (spongy and palisade cells) in Tempranillo than other six grapevine cultivars. Therefore, the particular growth cost of LA unit could be linked to the type of mesophyll structure, as recently reported by Ronzhina and Ivanov (2014). In addition, the higher N content observed on the Tempranillo expanding leaves could contribute to a higher metabolic machinery and consequently, to a higher growth costs of young leaves construction. However, the absence of a significant difference in maintenance costs of leaves between the two compared cultivars agrees with the absence of differences in N content in mature leaves. The relationship between foliar R_n and N concentrations has also been widely reported across different species and climates (Reich et al. 1998a, Atkin et al. 2015), and within varieties of a certain species (Bouma et al. 1992, Galmés et al. 2011, Laureano et al. 2013). It is well established that the relationships between tissue N and leaf CO_2 exchange rates are fundamental in plants due to the biochemical role of proteins in photosynthesis and respiration (Reich et al. 1998a). In this study, N content in young and mature leaves showed a significant correlation with R_n. Particularly in expanding leaves, the leaf N content expressed by DW explained most of the variability on R_n. These differences between cultivars in R_n along the leaf expansion will clearly account for the cost of canopy growth and maintenance in those varieties.

In conclusion, the correlation among leaf growth, leaf morphology and CO_2 exchange reported among different species (Reich et al. 1998b), seem to be present among different cultivars in grapevine: some cultivars (as Tempranillo) produce expanding leaves with lower LMA, higher N content per DW unit and greater respiration rates than some others (as Garnacha), that have a higher LMA, less N content and lower respiration rates. In general, data from this study are consistent with the hypothesis that fast-growing cultivars have high tissue metabolic rates relative to characteristic of slow-growing ones. Tempranillo displayed high leaf growth rates (LA) and associated traits, such as high respiration rates and N content, as well as leaf morphology (i.e. low LMA) associated with enhanced resource acquisition (i.e. high LA). These results reinforce the close coupling of tissue structural, chemical and metabolic characteristics within leaves that, in combination, are strongly associated with differences in growth rates. The type of leaf expansion (rapid or slow, Fig. 2) seemed to play an important role in the leaf structure and as a consequence, in the respiratory rates and resources use efficiency (C and N) throughout the leaf expansion.

Author contributions

E.H.M. conducted the experiment, wrote the body of the paper, and carried out sample preparations and laboratory and data analyses. M.T. set the experimental design, conducted the experiment and analyzed data. J.M.E. contributed to treatment planning, data discussion and manuscript corrections. J.B. conducted the field experiment and discussed data. H.M. coordinated the project, supported the experimental planning, data discussion and manuscript corrections.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Mean values (±SE, n = 4) of night temperature (from 22:00 to 01:00) during the sample days of 2013 and 2014. Different letters denote a significant difference according to Tukey's test ($P < 0.05$).

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