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Research

Seasonal fluctuations in *Vitis vinifera* root respiration in the field

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Summary

• We studied the seasonal fluctuation of soil respiration (R_S), and its root-dependent (R_R) and basal (R_B) components, in a *Vitis vinifera* (Chardonnay) vineyard.

• The R_S components were estimated through independent field methods (*y*-intercept and trenching) and modeled on the basis of a Q_{10} response to soil temperature, and fine and coarse root respiration coefficients. The effect of assimilate availability on R_R was assessed through a trunk girdling treatment.

• The apparent Q_{10} for R_R was twice that of R_B (3.5 vs 1.6) and increased linearly with increasing vine root biomass. The fastest R_R of fine roots was during rapid fruit growth and the fastest R_R of coarse roots was immediately following fruit development. R_S was estimated at 32.6 kg ha^{-1} d^{-1} (69% as a result of R_R) for the hottest month and at 7.6 kg ha^{-1} d^{-1} (18% as a result of R_R) during winter dormancy. Annual R_S was low compared with other natural and cultivated ecosystems: 5.4 Mg ha^{-1} (46% as a result of R_R).

• Our estimates of annual vineyard R_S are the first for any horticultural crop and suggest that the assumption that they are similar to those of annual crops or forest trees might lead to an overestimation.

Introduction

Most of the CO_2 released from terrestrial ecosystems comes from the soil, which, after photosynthesis, constitutes the second largest carbon (C) flux of these ecosystems (Raich & Schlesinger, 1992). This observation has led to a number of studies on the quantification and understanding of the drivers and sources of soil CO_2 efflux (Kuzyakov, 2006). These studies usually estimate the annual root- and soil-dependent CO_2 efflux of natural and planted forests and grasslands, and only a few have quantified and partitioned the CO_2 efflux from soils of major annual crops (Subke *et al.*, 2006), such as maize (Rochette *et al.*, 1999; Parkin & Kaspar, 2005; Jiang *et al.*, 2010), wheat (Zhang *et al.*, 2009) and soybean (Parkin & Kaspar, 2005). With regard to woody crops, respiration has been measured on excised and intact roots and on soils of different fruit trees (Buwalda *et al.*, 1992; Blanke, 1997; Bryla *et al.*, 2001; Zhang *et al.*, 2008) and cultivated *Vitis* species (Comas *et al.*, 2000; Morinaga *et al.*, 2003; Huang *et al.*, 2005; Volder *et al.*, 2005), but, to our knowledge, no estimates have been published of the annual soil CO_2 efflux of horticultural crops, such as vineyards (*Vitis vinifera*). Such estimates are relevant, especially for this horticultural crop that covers 7.55 Mha worldwide (OIV, 2011). In the particular case of Chile, *V. vinifera* is the main horticultural crop with 0.18 Mha dedicated to wine (70%) and table grape (30%) production (INE, 2009). These two products are mainly exported to foreign markets which increasingly consider the 'carbon footprint' of the purchased goods (Wiedmann & Minx, 2008). Therefore, for commercial and ecological reasons, the correct estimation of the C sequestration and emission of vineyards is needed.

Soil respiration (R_S) has two major components: autotrophic respiration from the roots and their microbial

symbionts (especially mycorrhizal fungi), and heterotrophic respiration from microorganisms decomposing litter and soil organic matter (SOM) (Hanson *et al.*, 2000). The partitioning of the microbial breakdown of plant residues and rhizomicrobial respiration from root respiration is a difficult task (Koerber *et al.*, 2010); therefore, we partitioned R_S into two compartments: root-dependent respiration (R_R) and basal soil respiration (R_B), as defined by Kuzyakov & Larionova (2005). Different field methods to estimate R_B have been developed (reviewed by Kuzyakov, 2006). One robust method is the *y*-intercept of a linear regression of R_S on root biomass (Kucera & Kirkham, 1971; Baggs, 2006; Kuzyakov, 2006). This method assumes that the portion of R_S dependent on living plant roots is linearly related to root biomass. The respiration rate at zero root biomass is considered to be the basal respiration R_B, or the portion of R_S not dependent on roots (Koerber *et al.*, 2010). The use of more than a single method has been recommended in order to reduce uncertainties in R_B estimations (Hanson *et al.*, 2000; Kuzyakov & Larionova, 2005; Kuzyakov, 2006). Therefore, we applied the root exclusion method, using trenches (Fisher & Gosz, 1986; Ewel *et al.*, 1987; Bowden *et al.*, 1993; Jiang *et al.*, 2005), as a second method for the estimation of R_B. In this method, R_B is measured directly in trenched plots, in which R_R is considered to be zero (Baggs, 2006; Kuzyakov, 2006). Once an accurate estimation of R_B has been reached, R_R can be estimated by subtracting R_B from R_S. These estimates provide a useful dataset for process-based C allocation models which, at present, are largely based on assumptions regarding root respiration (Génard *et al.*, 2008).

Soil temperature (T_s) is a major driver of autotrophic and heterotrophic respiration (Lloyd & Taylor, 1994; Boone *et al.*, 1998; Atkin *et al.*, 2000). A higher sensitivity to T_s of R_R than R_B has been postulated (Boone *et al.*, 1998; Zhuo *et al.*, 2010) and reported for forest soils (Boone *et al.*, 1998; Janssens & Pilegaard, 2003; Davidson *et al.*, 2006). In addition to temperature, R_S also depends on the soil moisture content (θ) (Raich & Schlesinger, 1992; Davidson *et al.*, 1998) and on C substrate availability, as has been shown in girdling experiments (Högberg *et al.*, 2001; Bhupinderpal-Singh *et al.*, 2003). Soil temperature and moisture content, and C availability in the root system, have also been shown to control the respiration of excised fruit tree roots (Buwalda *et al.*, 1992; Lakso *et al.*, 1999; Bryla *et al.*, 2001; Zhang *et al.*, 2008) and cultivated *Vitis* species (Comas *et al.*, 2000; Morinaga *et al.*, 2003; Huang *et al.*, 2005; Lakso *et al.*, 2008).

R_R depends on different physiological processes, such as the maintenance of the basic metabolism required by living tissues (maintenance respiration), the construction of new tissues during active growth periods (growth respiration), ion uptake and phloem loading and unloading (Amthor, 1984; Poorter *et al.*, 1991; Cannell & Thornley, 2000). Seasonal patterns of root growth and its relationship to above-ground growth have been studied for cultivated *Vitis* species (Bates *et al.*, 2002; Morinaga *et al.*, 2003; Comas *et al.*, 2005; Eissenstat *et al.*, 2006; Callejas *et al.*, 2009) and can be related to patterns of growth respiration. Much less is known about seasonal patterns of root respiration as a result of ion uptake and phloem loading and unloading, which are processes of key importance in a deciduous woody species such as *V. vinifera*.

The objective of this study was to estimate the annual root respiration of *V. vinifera*, as well as its seasonal fluctuations in the field, and to analyze its dependence on soil temperature and moisture content, C substrate availability and above-ground activity. The *y*-intercept and trenching methods were used to partition R_S into R_B and R_R. The respiration rates of these components were then related to T_s and θ. The effect of C substrate availability on R_R was assessed with a tree girdling treatment. Annual R_R was estimated with a model which estimated daily R_S values on the basis of T_s, and fine and coarse root biomass.

Materials and Methods

Experimental site and plant material

Measurements were carried out in a commercial vineyard *Vitis vinifera* L. planted in 1997 in Cerrillos de Tamaya (30°35′53S, 71°11′31W) in the Coquimbo Region of Chile. The climate is arid Mediterranean, with an average annual rainfall of 120 mm that falls in winter (June–September). The soil is clay with a very low SOM. Soil analyses from six plots of the vineyard are summarized in Table 1. The vines were own-rooted Chardonnay, spaced 1 m apart along north–south-oriented rows, which were 2.5 m apart. In the plot, buds break in September, the fruits are set in October and harvested in March, and the leaves fall between April and May. The yield of the vineyard between 2009 and 2011 averaged 7.0 Mg ha^{-1} of grapes (fresh weight) per year. The vineyard was drip irrigated with one irrigation line per row, equipped with one emitter each 0.5 m, and managed following commercial standards, avoiding water stress, nutrient deficiency and damage caused by pests and diseases. Herbicides were applied in order to keep the soil completely free of weeds throughout the measurement period.

Treatments

Before the implementation of treatments, large trenches (depth, 1.0 m; length, 5.0 m) were dug along one row of the vineyard in order to assess the vine root distribution in the soil. These trenches showed that the roots grew in the first 0.6 m of soil and that root overlap was restricted to adjacent plants in a row. In the winter of 2009 (July), 15

Table 1 Vineyard soil characteristics

Soil variable	Value
Soil organic matter (SOM) content (%)	0.82 ± 0.13
Electric conductivity (dS m^{-1})	1.19 ± 0.42
pH	8.1 ± 0.1
Soluble HCO_3 (%)	4.0 ± 0.3
Clay content (%)	54.5 ± 2.6
Silt content (%)	16.5 ± 2.4
Sand content (%)	29.0 ± 2.8
Readily available moisture content (%)	18.5 ± 2.2

Mean values (n = 6) are presented ± SD.

polyvinyl chloride (PVC) collars (height, 0.12 m; diameter, 0.21 m) on which R_S was measured were installed. The collars were installed at a depth of *c.* 0.07 m in five planting rows (three collars per row), exactly in the middle between two consecutive plants (0.5 m from each plant), which were randomly selected. When needed, the irrigation line was moved in order to avoid placing the emitters inside the collars. Three different treatments were applied in each row to the vines adjacent to the collars and/or the ground between them (five replicates per treatment): control (TC), trenching (TT) and girdling (TG). In the TC treatment, soil and plants were left intact. In the TT treatment, trenches were dug to sever the roots from the shoot between the two consecutive plants using a steel knife and shovel in June 2009 (5 months before the onset of the measurements) following a 0.6 × 0.6-m horizontal frame surrounding the collars. The trenches were 0.2 m wide and 0.6 m deep (the depth of the root zone). After lining the trenches with polyethylene sheets to prevent the growth of roots into the trenched plots and to minimize disturbances, the soil was refilled into the trenches following its original soil profile distribution. The TG treatment was applied to analyze the effect of assimilate mobilization and availability on R_S by interrupting the phloem connection between roots and above-ground plant parts. This was achieved by removing the bark in a 0.5-cm-wide band with a girdling knife at the trunk base of the two plants adjacent to the collars 2 months before bud break. The *y*-intercept (TY) method was based on measurements on collars installed in six different positions of the planting frame in a layout designed to ensure the dispersion of the vine root biomass (Fig. 1).

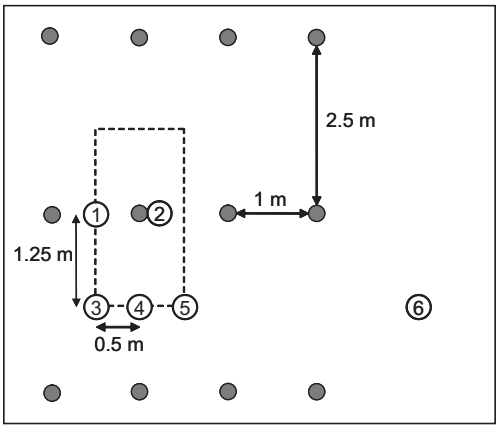

Fig. 1 Diagram representing the spatial distribution of the collars used for *Vitis vinifera* soil respiration measurements and root sampling in the *y*-intercept method. Closed circles indicate plant positions, open circles indicate collars, numbers stand for different collar positions and the dashed rectangle indicates the area occupied by a single plant. No vines were within 2 m of collar 6 and soil was kept free of other plants.

Measurements: above-ground growth

Five plants were selected (one in each row of the trial) in the winter of 2009. At fruit set, four representative fruit-bearing shoots per plant were selected, two from each side of the row. At monthly intervals (until leaf fall) the following was measured on each shoot: length and basal diameter, number of leaves, and length and width of each leaf. Fruit dimensions (bunch total length, maximum and minimum width of shoulders, and length and width of tail) were also measured at monthly intervals from fruit set to harvest. The shoot and fruit dimensions were used to estimate shoot and fruit dry mass on the basis of allometric functions, previously developed at the same site (Supporting Information Fig. S1). Final fruit dry mass and number and wood dry mass of shoots were determined at harvest and after leaf fall, respectively, in all measured plants. The dry mass data were used to estimate the seasonal accumulation of dry mass of an average fruit-bearing shoot. The above-ground growth was estimated by multiplying the shoot dry mass by the number of shoots on each plant.

Measurements: soil respiration and climate

R_S was measured using an Automated Soil CO_2 Flux System (LI-8100, LI-COR, Lincoln, NE, USA) and a 0.2-m-diameter accessory chamber (LI-8100-103) which fitted the collars installed in the plot. This system functions as a dynamic closed chamber, which was controlled manually using a personal digital assistant (PDA) (model Life Drive, Palm Inc., Sunnyvale, CA, USA). Measurements were as short as possible in order to keep conditions inside the chamber similar to ambient conditions. A soil temperature probe Type E (LI-COR) and a soil moisture probe (model EC-5, ECH_2O, Decagon Devices Inc., Pullman, WA, USA), attached to the soil chamber, allowed the measurement of the soil temperature (T_s) and soil water content (θ) at a depth of 5 cm, respectively. Measurements were made on the collars of each treatment at four different periods of the day (solar time: 23:00–01:00 h, 05:00–07:00 h, 11:00–13:00 h and 17:00–19:00 h). The measurements alternated treatments, such that one replicate of

each treatment was measured before passing to the next treatment; the order in which treatments were measured was randomly selected for each date. Respiration was measured at nearly monthly intervals during a whole year (October 2009–October 2010) for TT and TC, and during the growing season for TG (six dates) and TY (five dates). Only one date during winter dormancy (June 2010) was included for TG and TY.

A weather station (Vantage Pro, Davis Instruments Corp., Hayward, CA, USA), including a solar pyranometer for measurement of the solar radiation (RG), a rain collector and air temperature (T_a) and humidity (RH) probes, was positioned 500 m away from the site at 3.5 m above the ground. The weather station included a data logger that scanned measurements every minute and averaged and stored data every 15 min.

Estimation of root-dependent respiration and basal soil respiration

The R_S values at four different times of the day were used to estimate daily soil respiration from the area under the curve relating R_S to time. The integration was performed using the trapezoidal rule:

$$R_S = \sum_{t=1}^{n-1} \frac{(R_{St} + R_{St+1})}{2}(t_{t+1} - t_t) \quad \text{Eqn 1}$$

(t_t and t_{t+1}, times of two successive measurements of R_S; n, total number of time periods). In order to complete a whole day, measurements were taken from 23:00–01:00 h to 17:00–19:00 h; R_S at the end of the day (23:00–01:00 h) was assumed to be equal to the value measured at the beginning of that day during the equivalent time period. The same procedure was used to estimate daily mean T_s (T_s^d) and θ (θ^d). All further analyses were based on daily values.

A temperature correction based on the Q_{10} factor (the respiratory flux at one temperature over the flux at a temperature 10°C lower) was applied in order to remove variations caused by soil temperature fluctuations on respiration. Because Q_{10} has been shown to be different for R_B and R_R (Boone *et al.*, 1998), Q_{10} was estimated separately for each treatment, adjusting an exponential equation to all daily T_s and R_S data obtained for all measurement days:

$$R_S = \beta_0 \times e^{(\beta_1 \times T_s)} \quad \text{Eqn 2}$$

$$Q_{10} = e^{10 \times \beta_1} \quad \text{Eqn 3}$$

(β_0 and β_1, parameters). Eqn 2 was linearized through logarithmic transformation to estimate β_0 and β_1. Thereafter, the following algorithm was used to standardize all R_S measurements to 20°C according to Parkin & Kaspar (2003):

$$R_{Si}^{20} = R_{Si} \times Q_{10i}^{(20-T_s)/10} \quad \text{Eqn 4}$$

(R_{Si}^{20}, respiration rate standardized to 20°C of treatment i; R_{Si}, measured respiration at a specific hour of that treatment; Q_{10i}, Q_{10} estimated for that treatment with Eqns 2, 3).

Total soil respiration at 20°C (R_S^{20}) was estimated directly from TC. In order to ensure the validity of our estimates, basal soil respiration at 20°C (R_B^{20}) was estimated using two independent methods, TT and TY (reviewed by Kuzyakov, 2006), during the active growing period of the 2009–2010 season. In the case of TT, R_B^{20} was estimated directly from R_S measurements. In the case of TY, after respiration measurements had been performed, all roots found under the collars were sampled covering the whole root zone (i.e. cores of 0.2 m diameter and 0.6 m depth). For each new measurement date of TY, a new set of vines was chosen within the rows used for the other treatments. Roots collected in each of the six plots were separated into fine (< 2 mm diameter) and coarse (the rest) roots, and oven dried to constant weight to determine the dry mass of fine (RBM_F), coarse (RBM_C) and total ($RBM_T = RBM_F + RBM_C$) roots. For each measurement date, R_S^{20} estimates at each plot of the TY treatments were regressed against RBM_F and RBM_T, and R_B^{20} was estimated as the y-intercept of the regression lines. The R_B^{20} values estimated with each method were compared using the approach proposed by Bland & Altman (1999) for measuring agreement in method comparison studies. In order to generate a larger dataset to compare these methods, we also compared hourly R_B^{20} values. These hourly values were estimated for each date using the same Q_{10} value for both treatments, which had previously been estimated for TT from daily R_S and T_s^d values across the season.

For control and girdled plants, R_R^{20} was estimated as the difference between R_S^{20} measured in TC and TG, respectively, and R_B^{20} measured in TT. Because, for TC and TG, R_R^{20} estimations were performed on position 1 of the planting frame (Fig. 1), they were extrapolated to the complete area occupied by each plant of the vineyard, assuming that the proportion between R_R^{20} in that position and the other positions of the planting frame (positions 2–5) was the same as that measured in the same positions in TY (Fig. 1). For TC measurements during winter dormancy, this extrapolation was performed using the R_R^{20} data from the winter dormancy measurement in TY (June 2010).

Estimation of annual basal and root-dependent respirations

Annual integration of the different soil respiration components was performed on the basis of the daily estimations of R_S, R_B and R_R generated with a model relying on RBM and T_s^d. To model R_R^{20} as a function of RBM, we used R_S^{20}, RBM_F and RBM_C data obtained from TY. First, R_R^{20} for

each position and date of TY was estimated as the difference between R_S^{20} measured in TY and R_B^{20} estimated from TT (R_B^{20} was assumed to be constant for each position). Then, we used the data of each of the six positions to estimate fine (R_{RF}^{20}) and coarse (R_{RC}^{20}) root respiration rates at 20°C for each measurement date of TY by adjusting the following equation:

$$R_R^{20} = R_{RF}^{20} \times RBM_F + R_{RC}^{20} \times RBM_C \quad \text{Eqn 5}$$

For the five dates of the dormant period in which TY was not measured, R_{RF}^{20} and R_{RC}^{20} were estimated using interpolated RBM_F and RBM_C data for each position and R_R^{20} data estimated previously for each position of TC. R_{RF}^{20}, R_{RC}^{20}, RBM_F and RBM_C measured and estimated for the 11 dates included in this study were then interpolated in order to estimate their daily values. These interpolated values were then used to estimate daily R_R^{20} in each of the five positions within the vineyard planting frame (Fig. 1) with Eqn 5. Then, R_R^{20} of each position was transformed to the mean R_R^{20} of the vineyard floor through a weighted average according to the area represented by each position (Fig. 1). R_B^{20} was estimated with the TT treatment for the 11 dates included in this study, which were interpolated to estimate daily R_B^{20}values. These daily estimations of R_R^{20} and R_B^{20} were transformed to respiration rates at actual soil temperature using the following equation:

$$R_i = R_i^{20} \times Q_{10i}^{(T_s^d - 20)/10} \quad \text{Eqn 6}$$

where i denotes the different components of soil respiration: basal and root dependent. The daily R_S at actual soil temperature was then estimated by adding the daily R_B and R_R values obtained with Eqn 6. T_s^d of each day was estimated by application of a multiple linear regression performed with the T_s^d data recorded during the measurement dates and using the following meteorological data as independent variables: mean solar radiation of the previous and current day and mean T_a of the current day. All the daily estimations of R_B, R_R and R_S between 26 October 2009 and 25 October 2010 were added to estimate their annual values.

Statistical analyses

One- and two-way ANOVAs were performed to compare effects of treatments and date on R_S, T_s^d, RBM and θ^d. Means were separated with Tukey's test. Pearson correlation analysis was performed to relate R_S to T_s and θ. Simple and multiple linear regressions were performed to estimate R_S from T_s and RBM. All data analysis was performed with InfoStat (Córdoba, Argentina) statistical software (InfoStat 2008).

Results

Climate

As a result of frequent cloudy days, RH and RG fluctuated widely between days throughout the year (Fig. 2). During the summer, the mean daily RH was *c.* 70%, and eventually below 60%, with daily minima that were normally between 30 and 50%. During the winter, mean RH increased to 80%, with high fluctuation in minimum daily RH

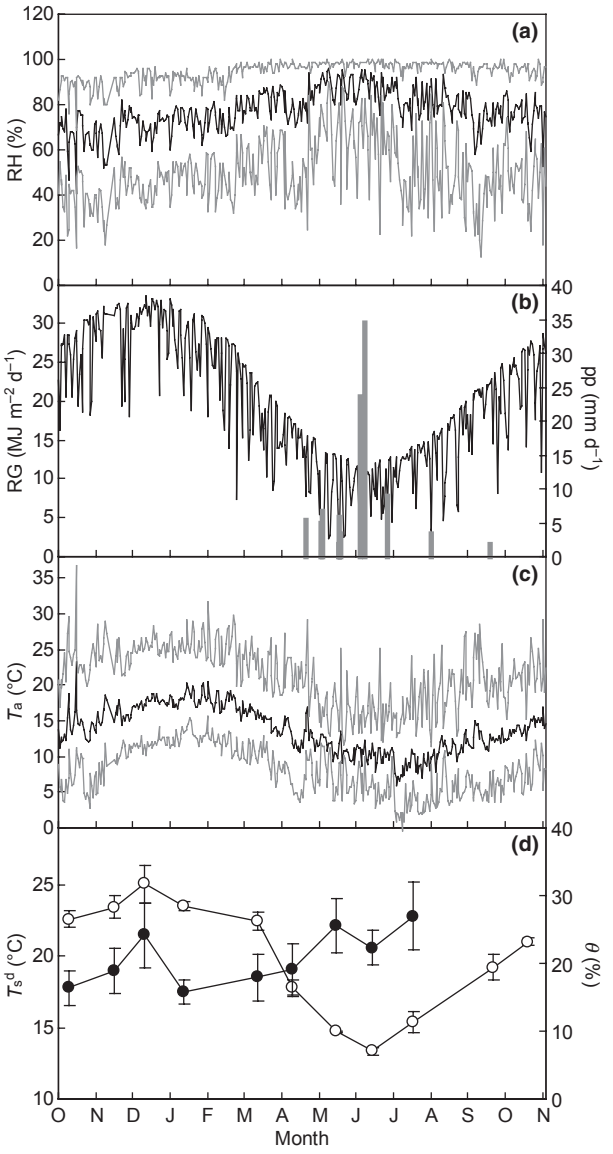

Fig. 2 Meteorological and soil variables in the vineyard over the measurement period: (a) mean (black line), minimum (lower gray line) and maximum (upper gray line) daily relative air humidity (RH); (b) global solar radiation (RG; black line) and rainfall (pp; gray columns); (c) mean (black line), minimum (lower gray line) and maximum (upper gray line) daily air temperature (T_a); (d) mean daily soil temperature (T_s^d; open symbols) and soil moisture content (θ; closed symbols); bars in (d) indicate ± 1SE (n = 5).

(30–80%; Fig. 2a). Solar radiation was highest in December and lowest in June, with averages of 30.0 and 9.1 MJ m^{-2} d^{-1}, respectively (Fig. 2b). 2010 was a normal year with regard to rainfall: 120.1 mm falling between May and September (Fig. 2b). T_a reflects the effect of proximity to the Pacific Ocean, with mild temperatures averaging 9.0°C for the coolest month of July, which exhibited an average minimum T_a of 3.8°C with only 1 d below 0°C (−0.4°C). The warmest month was January, with an average mean T_a of 18.1°C, an average maximum T_a of 25.5°C and an absolute maximum of 36.8°C (Fig. 2c). With regard to soil, T_s^d followed the same yearly pattern as T_a, but with higher annual maximum (25.1°C) and minimum (13.3°C) mean values. Soil moisture did not follow a clear pattern, with mean values ranging between 18 and 27% (Fig. 2d). The highest θ levels were registered in winter, associated with rainfall (Fig. 2b,c), and the lowest values were in October 2009 and February 2010, during the period in which plants were drip irrigated (Fig. 2d). Soil temperature and θ were not significantly affected by treatments, or by the position of the plots (Fig. 1; data not shown).

Relationship between respiration and soil temperature and moisture content

The model based on the Q_{10} factor used to estimate the temperature sensitivity of R_S was significant for all treatments (Table 2) and gave reasonable daily predictions (Fig. S2). The Q_{10} values of TC and TT were significantly different (Table 2); hence, different values of 2.5 for TC and 1.6 for TT were used across the entire year to estimate R_S^{20} (Eqn 4) in these treatments. Q_{10} was estimated to be 3.5 in the case of R_R and 1.96 for TG (Table 2). Q_{10} showed spatial variability in TY, ranging from 1.5 in position 6 to 2.7 in position 1 (Fig. 1), and was linearly related to RBM measured in these different positions (Fig. 3). No correlation between R_S and θ was found for any treatment ($R^2 < 0.1$ and $P > 0.5$ for all treatments).

Table 2 Statistical parameters for the models for the estimation of soil respiration rates measured in control (TC), trenching (TT) and girdling (TG) treatments, and estimated for roots (R_R), as a function of soil temperature (exponential model)

	Temperature model			
	Respiration measured in treatments			Respiration estimated
	TC	TT	TG	R_R
R^2	0.49	0.42	0.56	0.37
P	< 0.001	< 0.001	< 0.001	< 0.05
Q_{10}	2.50a	1.60b	1.96ab	3.50ab

Different letters in Q_{10} indicate significant differences for 95% confidence intervals.

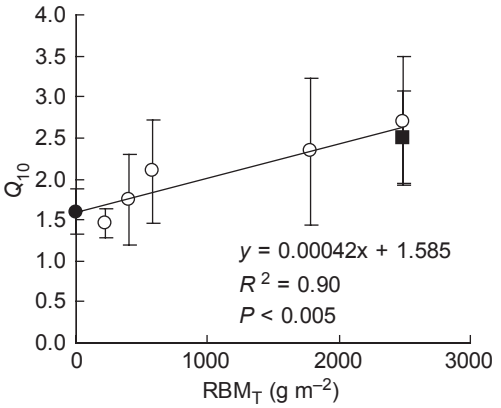

Fig. 3 Relationship between Q_{10} and the total root biomass (RBM_T) of *Vitis vinifera* measured for the different positions of the *y*-intercept treatment (open circles), and estimated for the control (square) and trenching (closed circle) treatments. Bars indicate 95% confidence intervals.

Estimation of basal soil respiration

The biomasses of fine, coarse and total roots were significantly different for the different positions in TY (Table S1). RBM was higher in the rows than in the alleys, averaging 1840 and 340 $g_{[DM]}$ m^{-2}, respectively, for RBM_C, and 2132 and 493 $g_{[DM]}$ m^{-2}, respectively, for RBM_T. RBM_F was lowest in position 6, which was significantly lower than RBM_F of row positions (293 $g_{[DM]}$ m^{-2}), with alley positions exhibiting intermediate values (153 $g_{[DM]}$ m^{-2}), not significantly different from the other positions (Fig. 1, Table S1). Although no significant differences were found, the proportion of fine roots tended to be higher in the alleys than in the rows: 36% vs 15%, respectively. Whole-plant RBM_T, RBM_F and RBM_C were not affected by the sampling date and averaged 1313, 223 and 1090 $g_{[DM]}$ m^{-2}, respectively (Table S1). The use of RBM_T to estimate R_B as the *y*-intercept of the regression line relating R_S^{20} to RBM_T (Fig. S3) gave better statistical results than the use of RBM_F (Table 3). The comparison of R_B^{20} estimated with TT and TY using RBM_T showed excellent agreement (Fig. 4), with a very low mean difference of 0.01 μmol m^{-2} s^{-1} and limits of agreement between − 0.31 and 0.29 μmol m^{-2} s^{-1}. Moreover, differences between methods did not appear to be related to their mean values (Fig. 4b). The average error deduced from 95% confidence intervals in the TY method was more than double the average standard error calculated for the TT method (Fig. 4a). Therefore, the annual estimation of R_B was based on results of the TT treatment.

Root respiration and above-ground activity

The above-ground growth rate (GR_A) followed a parabolic pattern (Fig. 5a), matching solar radiation availability and T_a (Fig. 2b,c). Three peaks of R_R^{20} were observed: one at

Table 3 Linear equations between soil respiration and fine (RBM_F) and total (RBM_T) root biomass adjusted in the *y*-intercept method

Independent variable	Date	Equation	R^2	*P*
RBM_F ($g_{[DM]}$ m^{-2})	28 Nov 2009	$y = 0.0113x + 0.440$	0.64	0.1032
	22 Dec 2009	$y = 0.0036x + 0.667$	0.41	0.1677
	23 Jan 2010	$y = 0.0052x + 0.010$	0.73	0.0296*
	23 Mar 2010	$y = 0.0088x - 0.845$	0.68	0.0877
	20 Apr 2010	$y = 0.0015x + 1.064$	0.37	0.2038
	24 Jun 2010	$y = 0.0007x + 0.893$	0.60	0.0721
RBM_T ($g_{[DM]}$ m^{-2})	28 Nov 2009	$y = 0.0011x + 0.775$	0.98	0.0013**
	22 Dec 2009	$y = 0.0001x + 0.979$	0.19	0.3895
	23 Jan 2010	$y = 0.0007x + 0.572$	0.98	0.0001***
	23 Mar 2010	$y = 0.0003x + 0.602$	0.51	0.1742
	20 Apr 2010	$y = 0.0004x + 1.040$	0.63	0.0402*
	24 Jun 2010	$y = 0.0001x + 0.926$	0.71	0.0349*

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; otherwise $P > 0.05$.

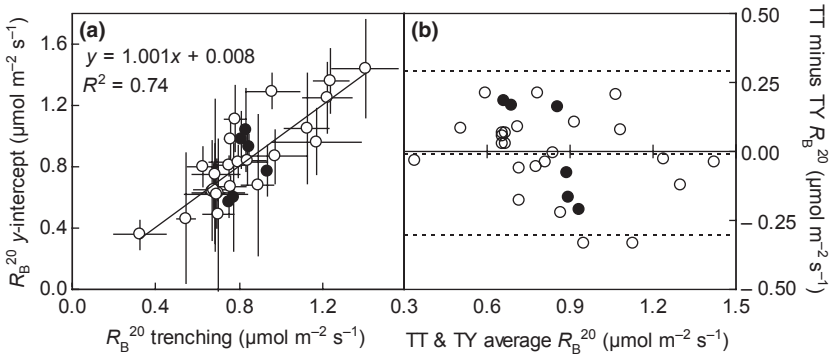

Fig. 4 (a) Basal vineyard soil respiration rate at 20°C (R_B^{20}), estimated with the *y*-intercept of the regression line relating soil respiration to total *Vitis vinifera* root dry biomass, as a function of R_B^{20} estimated with the trenching method: hourly (open circles) and daily (closed circles) estimates; the regression line was adjusted to hourly data; vertical bars indicate the 95% confidence intervals; horizontal bars indicate ± 1SE ($n = 5$). (b) Difference between R_B^{20} estimated with the trenching (TT) and *y*-intercept (TY) methods as a function of the average of these estimates: hourly (open circles) and daily (closed circles); dashed lines represent the mean of TT minus TY ± 2SD.

bud break (September), followed by the highest rate of 1.4 μmol m^{-2} s^{-1} in the middle of the summer, coinciding with the second shoot flush, and a final peak during leaf fall (April; Fig. 5b). R_R^{20} of TG, however, exhibited higher rates than TC during the first half of the growing season (October–December) and lower rates during the second half of the growing season (January–March; Fig. 5b). Although many of the present estimates of the respiration rates of fine and coarse roots showed large 95% confidence intervals, especially for dates in which interpolations were used, the main peaks of both kinds of roots showed reasonably small 95% confidence intervals (Fig. 5c). Respiration rates at 20°C were much higher in fine than coarse roots, with a highest peak in December, tightly matching the highest fruit growth rate (Fig. 5c). R_{RC}^{20}, however, peaked when the fruit growth rate slowed down. Although with larger 95% confidence intervals, both kinds of roots exhibited a peak of respiration after harvest, during leaf fall (Fig. 5c).

Annual respiration

The multiple linear model for the estimation of T_s^d from T_a and RG and the use of Eqns 5, 6 to estimate R_B, R_R and R_S gave satisfactory statistical results (Table 4, Fig. 6). R_R and R_S showed peaks of *c.* 23 and 32 $kg_{[C]}$ ha^{-1} d^{-1} during the hottest summer month (January), when the above-ground growth rates and T_s^d also peaked, whereas R_B remained relatively stable throughout the year, averaging *c.* 8.6 $kg_{[C]}$ ha^{-1} d^{-1} (Fig. 6, Table 5). The lowest rates for all R_S components were estimated for the coldest winter month (July), during vegetative rest (Table 5). Daily estimates showed a high variability of R_S between days, with R_B, R_R and R_S exhibiting an annual mean day-to-day difference in the respiration rate equivalent to 25, 20 and 21% of the maximum annual difference in daily respiration rates, respectively (Fig. 6b). The annual vineyard soil respiration was estimated at a total rate of 5.4 $Mg_{[C]}$ ha^{-1} yr^{-1}, 46% of which was dependent on roots (Table 5). The highest R_S was estimated for the

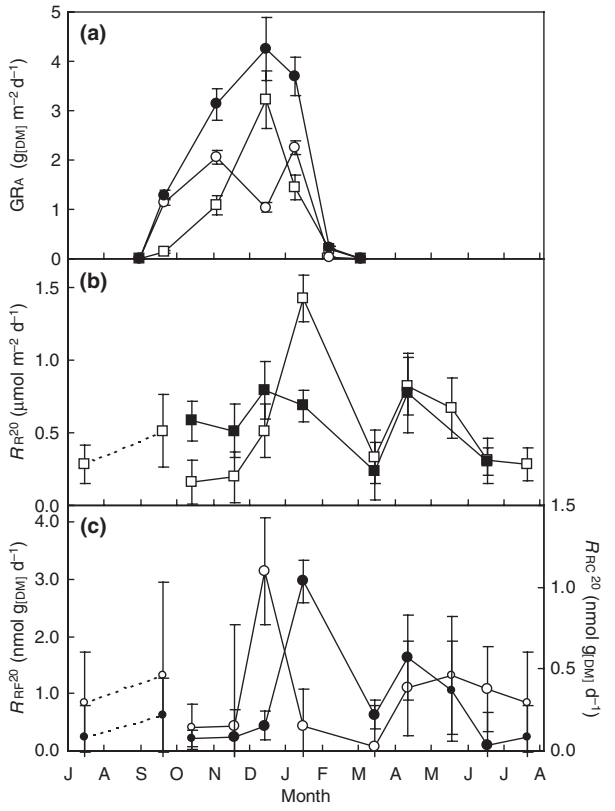

Fig. 5 Seasonal rates of *Vitis vinifera* biomass production of fruit (open squares), shoot (open circles) and total (closed circles) above-ground growth rate (GR_A) (a), root respiration rate at 20°C (R_R^{20}) estimated for intact (open squares) and girdled (closed squares) plants (b), and respiration rate of fine (R_{RF}^{20}; open circles) and coarse (R_{RC}^{20}; closed circles) roots at 20°C (c). Bars indicate ± 1SE (n = 5) in (a) and (b) and 95% confidence intervals in (c); points connected with the dashed lines in (b) and (c) correspond to measurements in 2010 that were plotted 365 d before the actual measurement date to facilitate comparison with GR_A; smaller circles in (c) indicate data that were estimated from interpolated data.

hottest month (January) and the lowest during the coldest month (July; Table 5). R_R contributed to 52% of R_S during the growing season and to 30% of R_S during the dormant period. The contribution of R_R to R_S was highest in January (69%) and lowest during July (18%) (Table 5).

Discussion

Relationship between respiration and soil temperature

The lack of correlation of R_S with θ in all treatments indicates an absence of significant water limitation to R_B and R_R, which can be attributed to irrigation during the dry season and rain in winter (Fig. 2d). Although Q_{10} = 2 is often used to model the temperature dependence of respiration, from soil to ecosystem scale (Ryan, 1991; Koerber *et al.*, 2010), the present Q_{10} fluctuated between 1.6 in TT and 2.7 in TC. Such fluctuations in Q_{10} of R_S have been reported previously for several forest ecosystems (Buchmann, 2000; Janssens & Pilegaard, 2003; Davidson *et al.*, 2006). Q_{10} of 3.5 for R_R (Table 2) is slightly higher than the maximum of *c.* 3.0 obtained by Huang *et al.* (2005) from direct respiration measurements on bare roots of potted *Vitis labruscana*. We found that Q_{10} increased linearly with RBM_T (Fig. 3), in line with the hypothesis of a higher sensitivity to T_s of tree roots than heterotrophic respiration (Boone *et al.*, 1998; Zhuo *et al.*, 2010). However, recent studies have shown that seasonal plant C allocation to the roots is positively correlated with soil temperature (Subke & Bahn, 2010). Therefore, the present higher temperature sensitivity of R_R than R_B may be a result of the fact that Q_{10} was estimated by regressing data obtained over the entire year. The C availability in the roots may also explain the lower Q_{10} of girdled plants (Table 2) as a result of a negative effect of C shortage on apparent Q_{10} (Högberg, 2010; Subke & Bahn, 2010), caused by the interruption of the transport of photoassimilates from leaves to roots.

Basal and root-dependent respiration

Although a large number of replicates is recommended (Kuzyakov, 2006) and used (Jia *et al.*, 2006; Wang *et al.*,

Table 4 Statistical parameters of the models for the estimation of the daily soil temperature (T_s^d) from daily global radiation and air temperature; basal soil respiration (R_B) from soil temperature; root-dependent respiration (R_R) from soil temperature and fine and coarse root biomass; and total soil respiration (R_S) from estimated R_B and R_R

	T_s^d (°C)	R_B ($kg_{[C]}$ ha^{-1} d^{-1})	R_R	R_S
n	11	11	11	11
Mean	19.9 (13.4–25.1)	8.6 (7.1–32.2)	7.2 (6.2–11.5)	14.5 (0.9–23.0)
SE	1.01	0.43	0.86	0.96
RMSE	0.92	0.40	0.86	0.97
R^2	0.94	0.95	0.98	0.98
Eq. est–obs	$y = 0.97x + 0.6$	$y = 0.95x + 0.5$	$y = 0.96x + 0.1$	$y = 0.94x + 0.8$
P	< 0.001	< 0.001	< 0.001	< 0.001

Mean, minimum–maximum; SE, standard error; RMSE, root of the mean squared error; Eq. est–obs, equation of the linear regression adjusted to the relationship between estimated and observed values.

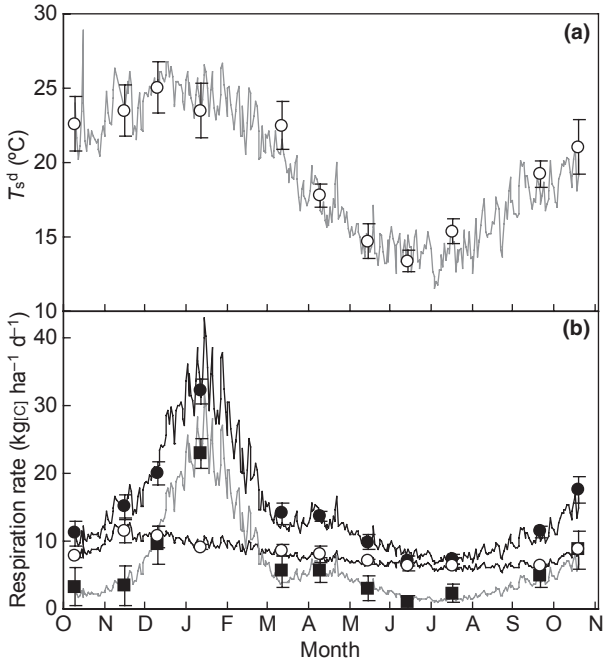

Fig. 6 (a) Seasonal evolution of measured (open circles) and modeled (gray line) daily mean soil temperature (T_s^d) and (b) vineyard soil respiration components estimated with the trenching method (symbols) and modeled at a daily time step (lines), which was partitioned into total (closed circles and upper black line), basal (open circles and lower black line) and *Vitis vinifera* root-dependent (closed squares and gray line). Bars indicate ± 1SE (n = 5).

Table 5 Basal (R_B), root-dependent (R_R) and total (R_S) soil respiration and the fraction of R_R to R_S (R_R/R_S) estimated with a model based on soil temperature and root biomass: annual integration and daily averages for the growing season, the dormant period and the hottest (January) and coldest (July) months (for which R_S exhibited the highest and lowest rates, respectively)

		Soil respiration component			
Period	Unit	R_B	R_R	R_S	$R_R : R_S$
Year	$Mg_{[C]}$ ha^{-1} yr^{-1}	2.93	2.50	5.42	0.46
Growing season	$kg_{[C]}$ ha^{-1} d^{-1}	8.98	9.57	18.55	0.52
Dormant period	$kg_{[C]}$ ha^{-1} d^{-1}	6.62	2.87	9.48	0.30
January	$kg_{[C]}$ ha^{-1} d^{-1}	10.05	22.54	32.59	0.69
July	$kg_{[C]}$ ha^{-1} d^{-1}	6.20	1.39	7.59	0.18

2008; Koerber *et al.*, 2010) for the TY method, we obtained reasonable results with only six replicates (Table 3). This result may be attributed to the following: low SOM (Table 1), which reduces noise from heterotrophic respiration; active root respiration of a single plant species growing under agronomical conditions; and the wide dispersion in RBM achieved with the sampling method, which also included collars with very low RBM, thereby avoiding errors caused by far extrapolation of the regression line (Kuzyakov, 2006). However, for two of the six dates, the regressions were not statistically significant (Table 3), but were still consistent with R_B estimates from TT (Fig. 4). This could be related to the low R_S values measured for these dates (Fig. S2b,d). The better statistical performance for the estimation of R_B from RBM_T, rather than RBM_F (Table 3), indicates that coarse roots of cultivated vines contribute significantly to total root respiration, contrary to the findings reported for much larger coarse roots of tropical forests (Behera *et al.*, 1990). Alternatively, the lack of a good result when estimating R_B from RBM_F may be attributable to the difficulty in accurately estimating RBM_F. The TT method also gave good estimates of R_B, as indicated by the good agreement with the TY method (Fig. 3). This result indicates that the increase in organic matter made available by the trenches, which can lead to a burst in heterotrophic respiration as a result of increased substrate availability (Kuzyakov, 2006), did not significantly affect R_S in the TT treatment. This may be explained by the 5-month period between the construction of the trenches and the onset of R_S measurements in TT and/or to the relatively low RBM found in the vineyard (Table S1), where canopy development was restricted to a small fraction of the land area because of row planting.

As a result of adequate water availability, the seasonal pattern of R_B paralleled that of T_s^d, and R_R mainly matched conditions favoring plant growth, such as solar energy availability and mean T_a above *c.* 10°C (Figs 2, 6), which is the base temperature for *V. vinifera* (Winkler *et al.*, 1974; Jackson & Cherry, 1988; Lebon *et al.*, 2004).

As expected, fine roots showed more active respiration than coarse roots (Fig. 5c), which is consistent with the higher proportion of nonrespiring woody tissue in coarse roots, resulting in a decrease in respiration rate with increasing root diameter (Pregitzer *et al.*, 1998; Desrochers *et al.*, 2002; Marsden *et al.*, 2008). Moreover, it has been shown that the root respiration rate decreases rapidly with fine root age in fruit trees, such as apples and oranges (Bouma *et al.*, 2001), as well as in another cultivated *Vitis* species (Comas *et al.*, 2000). Present R_{RC}^{20} values were similar to rates of excised roots of forest trees (Desrochers *et al.*, 2002; Marsden *et al.*, 2008), but R_{RF}^{20} was lower than rates reported for forest trees (Reich *et al.*, 1998; Desrochers *et al.*, 2002; Drake *et al.*, 2008; Marsden *et al.*, 2008). The respiration of fine roots at 20°C was an order of magnitude lower than that reported in cultivated woody crops such as *V. rupestris* × *V. labruscana* (Volder *et al.*, 2005), *V. labruscana* (Comas *et al.*, 2000; Huang *et al.*, 2005), *Citrus sinensis* and *Malus domestica* (Bouma *et al.*, 2001). In the present study, the low R_{RF}^{20} may be explained by the inclusion of old, dead and woody roots (which can be included with a 2-mm cut-off), which probably had much lower respiration than younger roots (Comas *et al.*, 2000;

Volder *et al.*, 2005). However, our results are in line with the average respiration rates of white and brown fine roots reported for five fruit tree species (Zhang *et al.*, 2008) and the respiration rates of excised *M. domestica* roots (Buwalda *et al.*, 1992).

Relationship between root respiration and above-ground activity

The high dependence of R_R on substrate availability (Yoshida & Eguchi, 1992; Hansen *et al.*, 1997; Högberg *et al.*, 2001; Högberg, 2010) has been confirmed previously for *V. labruscana* (Comas *et al.*, 2000). Therefore, the higher R_R^{20} of girdled plants during the early growing season (Fig. 5a,b) can be explained by a higher availability of C reserves in the roots, which could not be mobilized to sustain initial above-ground growth (Zapata *et al.*, 2004; Weyand & Schultz, 2006). Indeed, the concentration and content of root C reserves have been shown to be higher during dormancy than in any other phenological stage in *Vitis* species (Bates *et al.*, 2002; Zapata *et al.*, 2004), and support the early shoot growth in the spring (Scholefield *et al.*, 1978). However, as fuits are highly competitive with root growth in *V. vinifera* (Rodríguez-Lovelle & Gaudillère, 2002), C becomes available to the latter plant part towards the final fruit ripening stage, when fruit growth declines, as observed in several deciduous woody crops (Buwalda & Smith, 1987; Palmer, 1992; Morinaga *et al.*, 2003; Eissenstat *et al.*, 2006; Weyand & Schultz, 2006). Therefore, the lower R_R^{20} observed in the girdled plants of TG as fruit growth declines (Fig. 5a,b) is probably the result of the shortage of C in the roots, caused by the interruption of the C supply from leaf photosynthesis (Palmer, 1992; Comas *et al.*, 2005; Génard *et al.*, 2008).

The standardization of respiration to 20°C (R_R^{20}) reduces the fluctuations in maintenance respiration, which is highly dependent on temperature (Amthor, 1984; Sprugel & Benecke, 1991). Thus, this standardization enables us to assess the respiration required for growth, ion uptake and phloem loading and unloading (Amthor, 1984; Poorter *et al.*, 1991; Cannell & Thornley, 2000). The three peaks observed in R_R^{20} (Fig. 5b) closely match the pattern of new root intersections observed in a rhizotron study of *V. vinifera* cv Thompson seedless, undertaken in Chile by Callejas *et al.* (2009) under drier climatic conditions. The same parallels between patterns of root growth and respiration can be established when comparing present R_{RF}^{20} and the fine root elongation rate described for *V. vinifera* cv Merlot grown in California (Eissenstat *et al.*, 2006). These similar patterns indicate that R_{RF}^{20} is tightly related to active root growth. The main R_{RF}^{20} peak in midsummer was much more pronounced than the peaks of root growth observed in the above-mentioned studies in *V. vinifera* (Eissenstat *et al.*, 2006; Callejas *et al.*, 2009). The coincidence of this peak in R_{RF}^{20} with the highest fruit growth rate (Fig. 5a,c) indicates that, in addition to growth, respiration during this period was devoted to active nutrient uptake and transport to supply the high fruit demand (Cannell & Thornley, 2000; Bates *et al.*, 2002). R_{RC}^{20}, however, was highest when fruit demand decreased (Fig. 5a,c), probably resulting from C storage activities related to the import of surplus C from leaf photosynthesis, not consumed by fruits (Bates *et al.*, 2002; Comas *et al.*, 2005; Génard *et al.*, 2008).

Annual CO_2 efflux from the vineyard's soil

The present annual R_S of 5.4 $Mg_{[C]}$ ha^{-1} yr^{-1} (Table 5) is in the low range of soil CO_2 efflux of different biomes reviewed by Subke *et al.* (2006), which ranged from 0.44 in arctic scrublands to 24.0 in tropical forests and pastures (Trumbore *et al.*, 1995). This low R_S may be partly explained by the low yearly R_B (Table 5), which was 30–50% of R_B values reported for a range of agricultural soils in the UK (Koerber *et al.*, 2010) and maize fields in Ottawa (Rochette *et al.*, 1999). The present low R_B can be attributed to the extremely low SOM (Table 1). R_R during the growing season was similar to that of a maize field in Ottawa (Rochette *et al.*, 1999), but *c.* 10% of maize and *c.* one-third of soybean fields in Iowa (Parkin & Kaspar, 2005), and one-half of the value estimated for 17 annual crop farms in the UK (Koerber *et al.*, 2010). However, the present R_R was triple that estimated in a Concord grape process-based plant C balance model (Lakso *et al.*, 2008). Although the present annual contribution of R_R to R_S was comparable with the results obtained for several forest biomes (Subke *et al.*, 2006), it was much higher than the results obtained for other cropping systems, such as winter wheat fields (Zhang *et al.*, 2009) and a range of annual crops (Koerber *et al.*, 2010). This high contribution of R_R to R_S, when compared with other agricultural soils, was mainly attributable to low R_B (Fig. 6).

The low annual R_R presently estimated for a vineyard, as compared with forest trees and annual crops, may be explained by the lower canopy cover as a result of row planting, and is in line with low root respiration previously modeled for other fruit crops (Grossman & DeJong, 1994; Lakso *et al.*, 2008, 1999). This indicates that the use of values obtained for forest trees or annual crops would result in an over-estimation of root-dependent respiration of vineyards and, probably, other fruit trees.

The present estimates of annual soil and root respiration are, to our knowledge, the first to be published for any horticultural crop, and can be used for the modeling of C balance at the plant and ecosystem level and for a more accurate estimation of the 'carbon footprint' of the wine industry.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Fruit dry mass estimated separately from fruit dimensions (length, shoulder width and tail width) for different dates as a function of measured fruit dry mass, and shoot dry mass estimated from shoot dimensions (basal cross-sectional area, shoot length and number of leaves) as a function of measured shoot dry mass.

Fig. S2 Daily soil respiration rates estimated with Q_{10} values adjusted separately to the control, trenching and girdling treatments as a function of the measured R_S values.

Fig. S3 Relationship between soil respiration and total root dry biomass measured at different times of the day and daily integrations obtained for six different measurement dates.

Table S1 Distribution of fine, coarse and total root biomass for different soil positions and dates

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