Plant Soil (2011) 342:195–206
DOI 10.1007/s11104-010-0684-8

REGULAR ARTICLE

Spatial and temporal effects of soil temperature and moisture and the relation to fine root density on root and soil respiration in a mature apple orchard

Christian Ceccon · Pietro Panzacchi · Francesca Scandellari · Luca Prandi · Maurizio Ventura · Barbara Russo · Peter Millard · Massimo Tagliavini

Received: 3 August 2010 / Accepted: 3 December 2010 / Published online: 29 December 2010

Abstract We identified the role of various soil parameters and root density as drivers of soil respiration (R_s) in an apple orchard, measured during different periods of the year and at a range of distances from trees, in plots with a different history of nutrient supply. R_s was measured in April, May, August and December and studied in relation to soil temperature and moisture, total soil C and N, as well as to fine root density and medium-, and large-sized root density and root N concentration. The study also aimed to partition R_s by applying the root regression technique. R_s ranged from 0.06 in December to 1.49 g CO_2 m^{-2} h^{-1} in August. Average soil temperature alone explained up to 71% of the annual variability of R_s, while soil water content was negatively correlated to R_s. Fertilization, soil C and N concentration and root N had negligible effects on R_s. Fine root density, but not medium- and large-sized root density, contributed to explaining part of the yearly variability of R_s and proved to be a good predictor in December, when the statistical significance of the regression made it possible to estimate the autotrophic component of R_s as being about 35% of total soil respiration.

Keywords Apple trees · Root density · Root respiration · Soil respiration · Soil temperature · Soil water content

Responsible Editor: Elizabeth M. Baggs.

C. Ceccon · P. Panzacchi · F. Scandellari · L. Prandi · M. Ventura
Department of Fruit Tree and Woody Plant Sciences,
Bologna University,
Viale Fanin 46,
40127 Bologna, Italy

C. Ceccon
e-mail: christian.ceccon2@unibz.it

B. Russo
Faculty of Computer Science,
Free University of Bolzano/Bozen,
Piazza Università 1,
39100 Bolzano, Italy

P. Millard
The Macaulay Land Use Research Institute,
Aberdeen AB15 8QJ, UK

C. Ceccon · M. Tagliavini (✉)
Faculty of Science and Technology,
Free University of Bolzano/Bozen,
Piazza Università 5,
39100 Bolzano, Italy
e-mail: massimo.tagliavini@unibz.it

F. Scandellari
CSRC, University of New Hampshire,
39 College Rd,
Durham, NH 03824, USA

Introduction

There is interest in understanding the drivers of the terrestrial carbon (C) budget on the global scale because of the effects of the increase of carbon dioxide (CO_2) concentration in the atmosphere on global warming. Soil represents the major sink for C in terrestrial ecosystems, and the rate at which the soil C accumulates depends on the balance between C inputs from vegetation (directly through root exudates or indirectly through root turnover, leaf litter, etc.) and C losses due to CO_2 efflux from the soil surface as a consequence of both autotrophic and heterotrophic respiration. In contrast to forest and grassland systems, agricultural systems are often regarded as a net source of atmospheric C (Schulze et al. 2010) for both direct causes (such as soil tillage and high partitioning of assimilated C to harvest products) and indirect causes (such as consequences of land use change and indirect CO_2 emissions associated with land management). Soil respiration (R_s) represents a significant fraction of the carbon leaving terrestrial ecosystems, as a result of both root-derived (R_a) and microbial (R_h) respiration. In spite of a relatively extensive literature about respiration of aboveground organs, little attention has been devoted to the study of root respiration in orchards.

Various environmental conditions have been found to affect seasonal variability of R_s, of which soil temperature and moisture are often the most important (Tedeschi et al. 2006; Cook and Orchard 2008): both factors affect the rate at which soil organic matter (SOM) is decomposed by microbes, root growth and root metabolism. SOM quality and soil N availability may also control R_s by affecting the microbial growth and activity, while soil N may affect tree and root metabolism through an indirect effect on the partitioning of photosynthates and a direct effect on root respiration.

A range of methods have been used to partition the soil surface CO_2 efflux into autotrophic (R_a) and heterotrophic (R_h) components (e.g., Hanson et al. 2000; Kuzyakov 2006; Subke et al. 2006), each one having specific applications. Trenching and girdling are probably the most common methods used, but their results are difficult to interpret due to the significant disturbance they introduce into the system (Kuzyakov 2006). Isotopic approaches making use of ^{13}C natural abundance discrimination (Rochette and Flanagan 1997; Fu and Cheng 2002; Millard et al. 2008) cause no disturbance, relying on the different isotopic composition of C_3 and C_4 plants due to their different photosynthetic pathways. In the absence of a C_3:C_4 comparison, this method has only been used once (Millard et al. 2010). An alternative approach to trenching or girdling is the root regression technique (Kuzyakov 2006; Rodeghiero and Cescatti 2006). This relies upon differing root densities in the soil, allowing soil surface efflux rate to be correlated with root density. A simple estimation of heterotrophic respiration can be obtained analytically as the y-intercept of the linear regression between soil-surface CO_2 efflux and root biomass. Extrapolation back to a zero root density should, in theory, give an estimate of R_h, which can be achieved without the disturbance caused by most other methods. Drip-irrigated apple orchards potentially provide an excellent system in which to use this approach, as root density varies a great deal over short distances (Sokalska et al. 2009).

The aim of this experiment was to identify the role of environmental parameters and root density on soil respiration rates in an apple orchard. In doing so, we have exploited variability in soil and tree conditions by measuring soil respiration in different periods of the year, positions and orchard plots with a different history of soil nutrient supply. The study also aimed to apply the root regression technique to partition R_s into R_a and R_h.

Materials and methods

Experimental conditions

The experiment was carried out in an apple orchard located at the Experimental Station of the Faculty of Agriculture of the University of Bologna in Northern Italy (44°33’N, 11°21’E; 32 m a.s.l.). The orchard soil was a silty clay loam (18% sand, 50% silt, 32% clay), with a pH of 7.3, organic matter content of 2.3% and with 1.2% organic C and 0.13% total N. The wilting point and the water field capacity were 0.18 and 0.41 $m^3\ m^{-3}$, respectively. Trees of cv. Gala grafted on M9 rootstocks were planted in winter 1996–1997 at 3.8 × 1.0 m spacing. The plot consisted of 30 rows, divided into blocks of six rows, each of them receiving a different nutrient supply regime since planting. For the measurements 8 tree rows were selected in 4 blocks: four rows (high fertilizer, HF) had been fertilized since 1997 with an annual application of 80 kg N/ha, 25 kg P/ha and 100 kg K/ha, while the remaining four rows (low fertilizer, LF) received half this amount of fertilizer. Nutrients were supplied through fertigation, split into several applications each year. The localized irrigation system used drippers along the tree rows (2.2 l/h) spaced every 40 cm. Soil underneath trees was kept weed-free using non-residual herbicides.

Soil respiration measurements

Measurements of R_s were taken on five separate occasions: 5 December 2006, 16 May, 7 and 27 August 2007 and 1 April 2008. Fruit harvest was carried out between 7 and 27 August 2007. Measurements were made with an EGM 4 gas exchange system (PP Systems, Amesbury, MA, USA), equipped with a soil respiration chamber (SRC-1) and a soil temperature probe (STP-1); soil water content was measured with a Theta Probe ML2x (Delta-t Devices). Soil temperature was measured at 10 cm depth, while volumetric soil water content was measured at 0–10 cm depth. In addition, over the whole experimental period, soil temperature was constantly recorded by a weather station installed in the orchard (Addcon Telemetry). One week before each measurement, plastic collars (11 cm diameter × 6 cm high) were placed into the soil (at 2 cm depth) between two adjacent trees, randomly selected in each tree row, along a line perpendicular to the tree row (Fig. 1). The central collar was placed at 30 cm from the nearest trunk along the row and the other 4 were placed at 30 and 60 cm from it, in opposite directions and perpendicular to the direction of the tree row. Leaf litter, which was only present in small amounts in December, was removed from the soil before placing the collars. The instantaneous measurement of R_s from each collar was obtained at four different times of the day, with each cycle of measurements starting at: 05:00, 10:00, 15:00 and 20:00 hours. Each cycle lasted about 2 h, during which R_s was measured on each individual collar (giving a total of 40 measurements). These instantaneous measurements of R_s from each collar were used to obtain the estimate of the daily average soil respiration. Similarly, instantaneous measurements of soil temperature and soil water content were integrated to obtain daily average values.

Soil collection and analysis

The day after each R_s measurement cycle, except for 7 August, one soil core of 40 cm depth and 53 mm diameter was collected using a soil column cylinder auger (Ejkelkamp, Netherlands) from the center of each collar (40 soil cores each period). After being

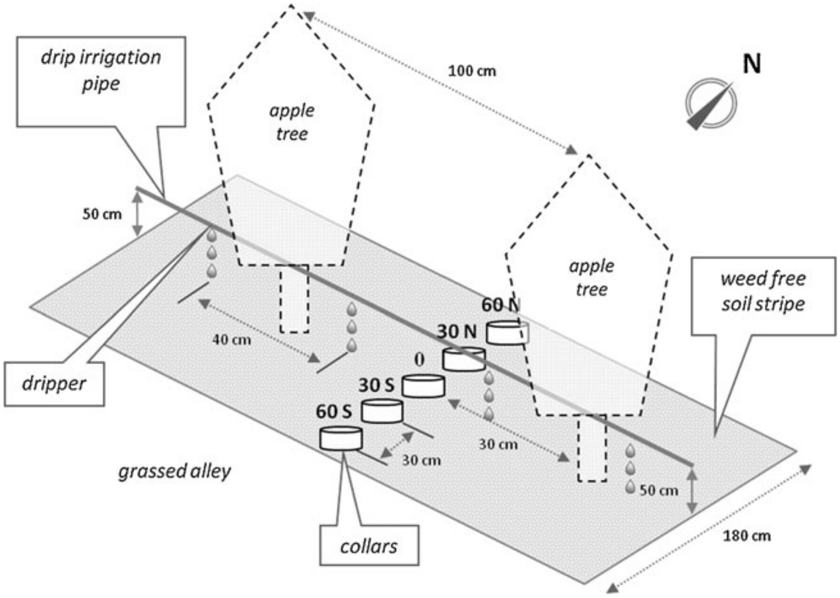

Fig. 1 Diagrammatic representation of the location of the collars where soil respiration was measured (not to scale)

removed, the core was divided into three parts according to depth: 0–5 cm, 5–20 cm, and 20–40 cm. One sample of soil of approximately 40–45 g (wet weight) was collected from each layer where no roots were visually present, for subsequent organic C, total N and soil water content determinations. The samples were immediately weighed and dried at 35°C in a ventilated oven for 24 h; a sub-sample for C and N analyses was collected and weighed. A second soil sample was weighed and fully dried at 105°C for 24 h to obtain soil water content data. Organic soil C and total soil N concentrations were determined by an elemental analyzer (elemental analyzer EA1110; Carlo Erba Instruments). Soil NH_4 and NO_3 concentrations were determined only on samples collected in May and August 2007 from central collars (position 0; Fig. 1) and were obtained through extraction in KCL (2 M) and analyzed by an autoanalyzer (AxFlow AA3; Bran + Luebbe, Norderstedt, Germany). Average values of mineral nitrogen concentrations and soil water content were calculated for the 0–40 cm soil profile underneath the collars. To quantify root density, the remaining soil from each core was separated from roots. The first two layers of soil (0–5 cm and 5–20 cm) were pooled together but kept separated from the 200–400 mm soil layer. Each sample was immersed in a Na_2CO_3 solution (2 gl^{-1}) to facilitate deflocculation, shaken for 12 h and then sieved under running water. Roots were carefully collected by tweezers and divided into three diameter classes: <2 mm (fine roots), 2–5 mm (medium roots) and >5 mm (coarse roots). Roots were dried in a ventilated oven at 65°C until constant weight was reached, and their weight was determined. Samples of roots collected under the collars present along the tree rows were ground and analyzed for C and N concentration.

Treatment of data and statistics

Seasonal data of soil CO_2 flux, total soil organic C and N, root density, soil temperature and moisture were analyzed by two-way analysis of variance (ANOVA) with nutrient supply and collar position as factors. Data of fine root N concentration, and NO_3 and NH_4 soil concentration obtained from collars in the central position (position 0) were subjected to one-way analysis of variance with nutrient supply as the only factor. Instantaneous measurement data of CO_2-flux were analyzed by multiple regression analysis using temperature and soil water content as independent variables.

Daily average R_s data (as dependent variable) were subjected to multiple regression analysis using temperature, soil water content, average soil profile water content, fine, medium and coarse root density and soil N and C concentration as independent variables.

We analyzed the scatterplots and the correlation between R_s and all the above variables to identify the potential regressors to include in the regression analysis. Then, we performed a linear multivariate regression analysis using the stepwise regression method to determine the best fit linear model with the minimum set of independent variables. As scatterplots showed a non-linear behavior for some of the above variables, we performed a non-linear multiple regression. Finally, as some of the variables (like temperature) were influenced by the season, we also performed a multivariate linear and non-linear regression by season to understand whether the influence of the regressors on R_s applied across a year or was confined to a single season.

Results

Soil chemical and physical characteristics

Average soil temperatures differed in the four periods of measurements and ranged from 9°C in December 2006 to 28°C in August 2007 (Fig. 2a). Average temperature in May 2007 and April 2008 were 20 and 14°C, respectively. Collar position had no effect upon soil temperature in December, while in May and August 2007, collars located 30 and 60 cm south showed an average daily temperature more than 2°C higher than the others.

Soil water content (Fig. 2b) varied in the four periods of measurement and ranged from 17% (May 2007) to 33% (December 2006). Soil under collars differing for positions differed in soil water content, but this effect was not constant over the whole period: in May and August 2007, when trees were drip-irrigated, collars in position 0 showed higher soil water content values, while lowest values corresponded to collars located to the south. In December 2006 and April 2008, soil water content was uniform among soil positions.

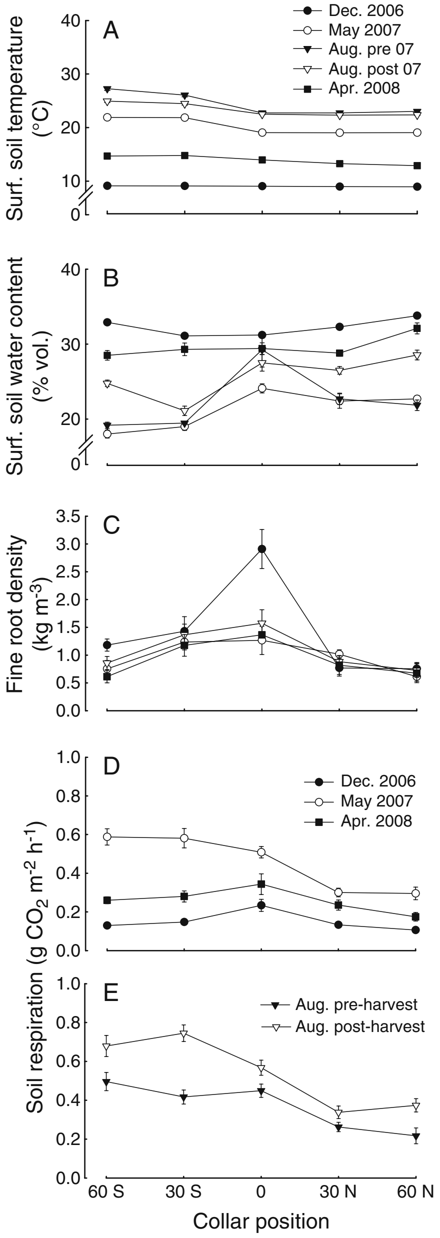

Fig. 2 Effect of collar position on the variability of **a** surface soil temperature, **b** surface soil water content, **c** fine root density and **d**, **e**) soil respiration. Values are the mean for each position (n=32, only fine root density n=8; *bars* are standard errors of the means). Data of August (**e**) refer to sampling before (*pre*) and after (*post*) harvesting of fruits. For collar positions, see Figure 1

Total soil C and N concentrations were higher in the top 0–5 cm soil layer (14.1 g kg^{-1} and 1.6 g kg^{-1}, respectively) than in the 5–40 cm layer (9.8 g kg^{-1} and 1.1 g kg^{-1}, respectively). Both soil C and N concentration were unaffected by either fertilization regime or soil position (data not shown). Soil mineral N was unaffected by the fertilization levels and increased from May (8.3 mg kg^{-1}) to August (16.4 mg kg^{-1}).

Measurements of R_s

Values of R_s were lowest in December 2006 and highest in August 2007 (Fig. 2d, e). The fertilization regime only affected R_s in December 2006 in positions 0 and 60 S, in which soil from HF collars had a 30–36% greater CO_2 efflux than LF collars (data not shown). Soil respiration differed according to the position of the collars: in December 2006 and April 2008, the highest efflux was recorded from collars in position 0 (Fig. 2d), while in May and August 2007, the highest CO_2 efflux was measured on collars located 30 cm S (Fig. 2d, e). In general, soil positions with the lowest R_s were 30 cm N and 60 cm N. Diurnal variation of R_s occurred only in April 2008, when R_s significantly increased from 10:00 to 15:00 hours (Fig. 3a), as a likely consequence of a temperature increase from 11.0 to 16.5°C (Fig. 3b). Interestling, R_s decreased again from 15:00 to 20:00 hours, even if soil temperature did not vary between these two times of the day.

Root density and root N concentration

Fertilization regime did not affect the density of roots of any size-classes (data not shown). There were significant differences in fine root density among the four measurement periods: highest values (Fig. 2c) were recorded in December 2006, while root density was similar in May and August 2007 and the April 2008 samplings (Fig. 2c). Fine root density changed according to collar position, being highest in the soil along the tree row (position 0) and in that below the collars in 30 cm S (May 2007 and April 2008). The lowest values of root density were recorded 60 cm from the center of the tree row (Fig. 2c). Fine root N concentration (Table 1) averaged 8.7 g kg^{-1} and was unaffected by the fertilization regime.

Effects of root and environmental characteristics on R_s

Measurements of R_s were positively and linearly correlated with instantaneous measurements of soil

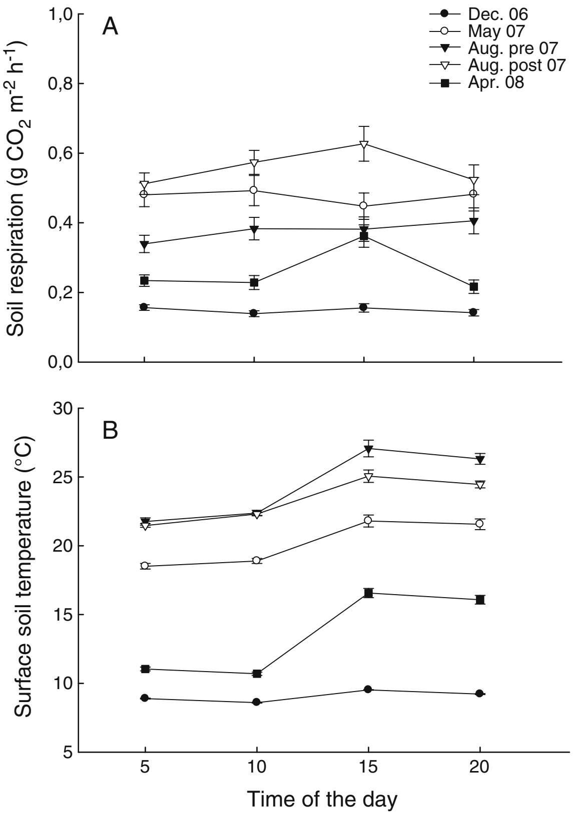

Fig. 3 Daily pattern of soil respiration (**a**) and surface soil temperature (**b**); values are mean of all collar positions for each season (n=40, except for Apr. 2008 where n=20; *bars* are standard errors of the means)

temperature and negatively and linearly correlated with soil water content (Table 2, eq. 1 and 2, respectively). R_s measurements were related to soil temperature (°C) and soil water content (% in volume) by a multiple regression analysis (Table 2, eq. 3). When non-linear regression analysis was performed, an exponential equation produced the best fitting to experimental data (Table 2, eq. 4).

The variations of daily average soil CO_2 efflux were studied in relation to environmental factors and root biomass. When multiple linear regression analysis was applied to the whole dataset of daily soil CO_2-efflux, average soil temperature alone explained 26% (Table 2, eq. 5) of the variability of CO_2 efflux data; considering fine root density in addition to average soil temperature improved the goodness of fit of the model (Table 2, eq. 6). Non-linear multiple regression analysis on the whole dataset again indicated soil temperature and fine root density as major determinants of daily average values of soil CO_2 efflux (Table 2, eq. 9).

The best fit of daily average R_s versus soil temperature using non linear regression was obtained by an exponential model (R^2=0.71; Fig. 4b). Surface soil water content also related to R_s by a second order curve (Table 2, eq. 8; Fig. 4a). As surface soil temperature data were negatively correlated with surface soil water content data with r=−0.77 (P=0.01, not reported in tables), the models to predict daily average R_s using the two variables together were discarded.

As surface soil temperature was the major environmental parameter varying among the four measurements periods, we tested whether the effect of temperature on R_s was confirmed within each period or if other factors explained more of the variability in the data. In December 2006, fine root density and soil water content explained 48% of the R_s value (Table 3). In May and August 2007, soil temperature was the only factor affecting R_s, while in April 2008 R_s depended upon soil water content (Table 3).

To assess the heterotrophic-derived component of soil respiration, R_s was related to the density of roots of different size-classes. Only fine root density was related to R_s and this relationship was only significant in December 2006 (Table 4), when the rate of R_h was estimated being 0.096 g CO_2 m^{-2} h^{-1}.

Discussion

As soil respiration determines the major fluxes of CO_2 in many terrestrial ecosystems (Law et al. 1999; Bolstad et al. 2004; Borken et al. 2006; Euskirchen et al. 2006), it is of great importance to understand to what extent R_s is affected by environmental drivers and the activity of the trees (Knorr et al. 2005). In our study, R_s was measured under a relatively high range of soil temperatures, soil water contents and an even greater range of root densities (Table 1). In contrast to other studies which have quantified R_s across a range of sites with different characteristics (e.g., Maekiranta et al. 2008; Martin et al. 2009), the variation in soil C and soil N concentration in the soil under our collars was relatively low (C.V. = 13 and 8%, respectively; Table 1).

Instantaneous R_s data showed a large temporal and spatial variation due to the interactive effects of time

Table 1 Soil and root parameters when soil CO_2 efflux was measured across the four measurement periods

Parameter	Average ± SD[a]	Min–max	CV[b] (%)	*n*
Soil respiration (g CO_2 m^{-2} h^{-1})	0.38±0.25	0.06–1.49	66	720
Surface soil temperature (°C)	18.6±6.5	8.1–37.7	35	720
Surface soil water content (% in vol) (average 0–10 cm depth)	25.9±5.4	14.1–36.1	21	720
Soil water content (% in vol) (average 0–40 cm depth)	23.9±3.6	16.5–32.2	15	140
Soil C concentration (g kg^{-1})	10.5±1.4	8.1–16.7	13	140
Soil N concentration (g kg^{-1})	1.2±0.1	0.9–1.8	8	140
Soil mineral N concentration (g kg^{-1})	0.020±0.009	0.007–0.041	45	100
Fine root density (kg m^{-3})	1.12±0.7	0.22–4.4	62	140
Medium-sized root density (kg m^{-3})	0.51±0.58	0.04–2.8	115	140
Large-sized root density (kg m^{-3})	1.46±2.81	0.054–15.2	193	140
Total root density (kg m^{-3})	3.09±3.36	0.28–17.6	109	140
Fine root N concentration[c] (g kg^{-1})	8.7±1.2	0.7–1.2	13	28

Except for surface soil temperature (recorded at 10 cm depth) and surface soil water content (average of 0–10 cm layer), the remaining parameters refer to the average of 0–40 cm soil layer, as recorded from the soil core.

[a] *SD* standard deviation

[b] *CV* coefficient of variation

[c] Data refer only to collars in position 0

of the day, the period of the year and the position of the collars in the soil, ranging from 0.06 g CO_2 m^{-2} h^{-1} in December 2006 to 1.49 g CO_2 m^{-2} h^{-1} in the south-exposed soil areas in August 2007 (data not shown). The fact that R_s was generally slower in the north exposed rings was probably due to their lower fine root density, cooler soil temperature and higher soil water content (Fig. 2a–c). Our minimum values fall in the range reported by Davidson et al. (1998) for temperate mixed hardwood forest and by Law et al. (1999) for a ponderosa pine plantation. For apple trees, the only available data refer to the studies by

Table 2 Relationships between soil respiration (g CO_2 m^{-2} h^{-1}) and measured parameters

Type of analysis	Dependent variable (y)	Independent variable(s)	R^2	Equation	*n*	Equation number
Simple linear regression	Hourly CO_2 flux (g CO_2 m^{-2} h^{-1})	Soil temperature (x, °C)	0.32***	$y=-0.031+0.022x$	720	1
		Soil water content (z, % in volume)	0.25***	$y=0.981-0.023z$	720	2
Multiple linear regression (stepwise)	Hourly CO_2 flux (g CO_2 m^{-2} h^{-1})	Soil temperature (x, °C) and soil water content (z, % in volume)	0.34***	$y=0.32+0.016x-0.010z$	720	3
Non-linear simple regression	Hourly CO_2 flux (g CO_2 m^{-2} h^{-1})	Soil temperature(x, °C)	0.29***	$y=0.135e^{0.052x}$	720	4
Multiple linear regression (stepwise)	Daily CO_2 flux (g CO_2 m^{-2} h^{-1})	Soil temperature (x, °C)	0.26***	$y=-0.4771+0.0444x$	140	5
		Soil temperature (x, °C) and fine root density (z, kg m^{-3})	0.32***	$y=-0.503+0.0415x+0.083z$	140	6
Non-linear simple regression	Daily CO_2 flux (g CO_2 m^{-2} h^{-1})	Soil temperature (x, °C)	0.71***	$y=0.0629e^{0.09x}$	140	7
		Soil water content (z, % in volume)	0.50 ***	$y=-0.0846+0.0675z-0.0183z^2$	140	8
Non-linear multiple regression	Daily CO_2 flux (g CO_2 m^{-2} h^{-1})	Soil temperature (x, °C) and fine root density (z, kg m^{-3})	0.67 ***	$y=-0.147+0.114e^{0.074x}+0.083z-0.00000071z^2$	140	9

*** significant at 0.1% level of probability

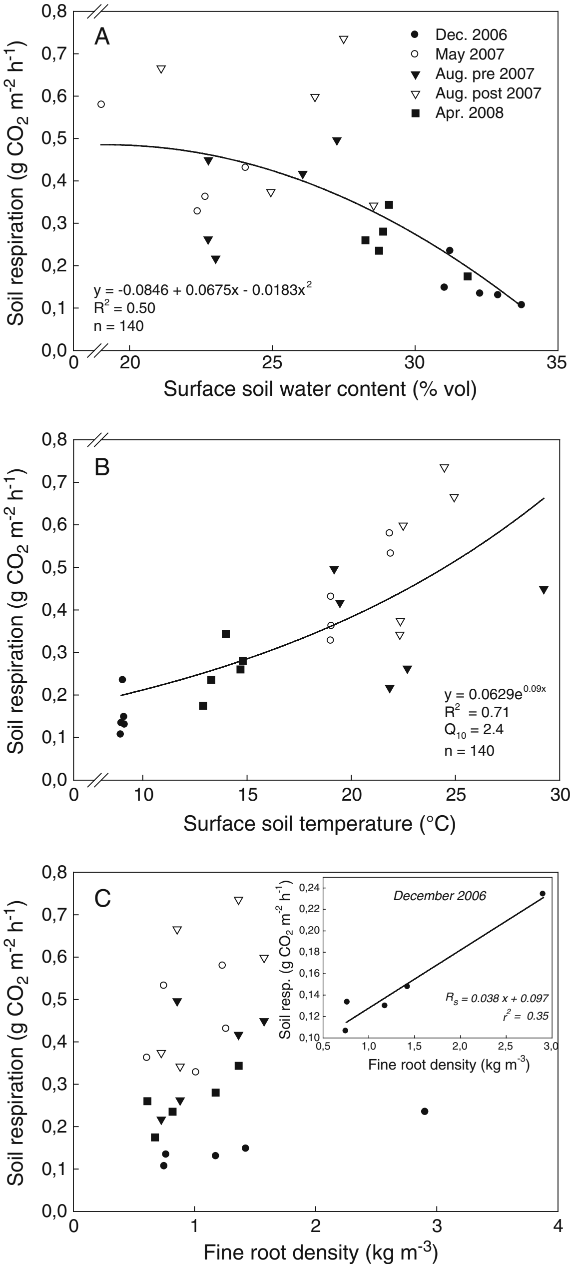

Fig. 4 Soil respiration in relation to **a** surface soil water content, **b** surface soil temperature and **c** fine root density. Each point represents the mean value for each position (*n*=32, except for April 2008 when *n*=16)

Blanke (1996, 1998) who measured soil respiration in the weed-free strip underneath apple trees and concluded that maximum soil respiration can reach values as high as 3.8 g CO_2 m^{-2} h^{-1}, which, he concluded, exceed values of leaf photosynthesis in the corresponding periods.

The regression analysis applied to the whole dataset revealed that soil temperature was the environmental parameter accounting for most of the variance in R_s, with instantaneous measurements less well correlated to soil temperature than were daily average values. This effect was likely explained by diurnal variation of soil temperatures, resulting in similar temperatures being recorded at different periods of the year at different times of the day. Temperature affects almost all aspects of respiration processes (Luo and Zhou 2006) being either root-dependent or caused by the activity of heterotrophic soil organisms. Exponential models better explain the variation of soil respiration to soil temperature. As shown in Fig. 4a, b, Q_{10} of 2.4 for soil respiration was found in our experiment, which is slightly higher than that reported in a pine plantation under a similar range of temperature (Q_{10}=1.8), lower than the value of 3.1 reported by Boone et al. (1998), but equal to the estimated global median value reported by Raich and Schlesinger (1992). To estimate yearly soil CO_2 flux, we used its exponential relationship with soil temperature obtained by the weather station, which from 2006 to 2008 averaged 17.6°C. Simulation indicated a total flux of 2.5 kg CO_2 m^{-2} $year^{-1}$, a value slightly higher than that reported by Liguori et al. (2009) in a citrus orchard soil. Scaling up our data to the orchard soil area underneath the weed-free strips in the centre of tree rows, where most apple roots resides, suggests that some 3.2 t C ha^{-1} were lost by soil respiration annually; this value is lower than that of aboveground primary productivity of apple trees measured in the same experimental orchard in its sixth year after planting (Scandellari et al. 2010).

As a predictor, fine root density significantly improved the goodness of the prediction, when associated to temperature in non-linear models, but did not improve the linear model (Table 2). The other parameters measured (medium- and large-sized root density, soil nitrogen concentration and the average of soil water content over the 0–40 cm profile) had no significant effect on R_s.

Soil water content negatively correlated to instantaneous values of R_s (Table 2, eq. 2) and, when associated to soil temperature, it increased the ability to predict soil respiration under multiple linear regression analysis compared to soil temperature

Table 3 Multiple linear regression analysis applied to daily average soil CO_2 flux (g CO_2 m^{-2} h^{-1}) within each measurement period

Period	R^2	Equation	*n*
Dec 2006	0.48***	y=0.742+0.0417 (fine roots, kg m^{-3}) − 0.0196 (soil water content, % vol)	40
May 2007	0.22**	y=−0.4594+0.0447 (soil temperature, °C)	40
Aug 2007	0.38***	y=−1.8566+0.1028 (soil temperature, °C)	40
Apr 2008	0.23*	y=0.8977 − 0.0217 (soil water content, % vol)	20

*, ** and *** Significant at 5%, 1% and 0.1% level of probability, respectively

alone. Xu and Qi (2001) have shown that the relationship between R_s and soil temperature is affected by soil water content, being significantly lower under soil water limitation. In our experiment, water limitations rarely occurred because the orchard was irrigated (Table 1). When we analyzed the factors affecting soil respiration within each single period of the year (Table 3), we found that soil temperature represented a significant predictor in May and August 2007. In contrast, in December 2006, fine roots and soil water content, together, explained almost half of the variability of soil respiration, while in April 2008, only soil water content related to soil respiration. In December and April, soil temperature was relatively cool and showed limited variations among collars (Fig. 2a). The inverse correlation between surface soil temperature and surface soil water content using the whole dataset might suggest that the negative effect of soil water content on R_s was largely due to the positive effect of temperature. As the effects of soil water content were significant in periods when soil temperature showed a limited variation across the soil positions (Table 3; Fig. 2a), the data suggest that soil water content effects were independent from soil temperature. Soil respiration often increases with soil water content from values at wilting point until values of approximately 50–60% of water-filled pore space are reached (Bryla et al. 2001), after which R_s decreases if the soil becomes wetter, due to a limitation in soil aeration and a depression of microbial activity (Linn and Doran 1984; Mielnick and Dugas 2000). Data in Fig. 4a are in line with those reported by Mielnick and Dugas (2000) who found a negative trend of R_s at soil water content data above 25% of volumetric soil water content. Low R_s values in dry soils are likely associated with reduced root growth (Espeleta and Eissenstat 1998) and reduced ion-uptake (Eissenstat et al. 1999).

On an annual scale, the inability to use fine root density to predict R_s is likely because fine root metabolism varies during the season, possibly as a function of their N concentration. Bouma et al. (2001) have shown that fine roots reach their maximum respiration rates in their early developmental phases, which soon declines. The periods of more intense production of new fine roots have been studied using minirhizotrons, but even in the same location data are not very consistent, showing either spring or summer peaks (Psarras et al. 2000; Eissenstat et al. 2006). The highest fine root density, at least from positions 60 cm S and 0, were measured at the end of autumn (Fig. 2c), suggesting a cumulative root production over the season.

The history of nutrient supply to the orchard soil had a small effect on soil respiration only in December 2006. Previous studies carried out in the same experimental orchard indicated that nutrient supply stimulated tree growth and enhanced tree N status when the trees were young (Rombolà et al. 2000). However, when the trees reached the adult phase, different nutrient supplies only slightly affected leaf N concentration (averaging 2.5 and 2.3% in HF and LF trees, respectively) and had no effect on

Table 4 Coefficients of determination, significance and equations for the linear regression analysis of data of daily average soil CO_2 flux (y in g CO_2 m^{-2} h^{-1}) versus fine root density (x in kg m^{-3}), in soil cores excavated at the center of the collar after respiration measurements

Period	R^2	Equation	*n*
Dec 2006	0.35***	y=0.0965+0.0375x	40
May 2007	$0.05^{n.s.}$	y=0.3682+0.075x	40
Aug 2007	$0.09^{n.s.}$	y=0.4129+0.104x	40
Apr 2008	$0.05^{n.s.}$	y=0.2186+0.0417x	20

n.s. Not significant effect

***Significant at 0.1% level of probability leaf P and K, fruit yield and vegetative growth (Malaguti et al. 2006). Total soil N might not really reflect the N availability for root uptake, but it is also possible that several years of localized application of two levels of N did not markedly modify either total soil N or soil mineral nitrogen. The literature on the effect of soil and root N availability on R_s draws different scenarios, depending on the time scale of the observations. In the short period after N addition, an initial increase of R_s, due to a priming effect on the microbial component and a consequent enhanced litter decomposition can be expected (Söderström et al. 1983; Fog 1988; Berg and Matzner 1997; Bowden et al. 2004), while increased long-term N availability tends to cause a decline in R_s due to both, the increase of recalcitrant soil organic matter compounds and the reduction of microbial activity (Fog 1988; Berg and Matzner 1997; Bowden et al. 2004; Burton et al. 2004). In a recent paper, Migliavacca et al. (2010) suggested that on the whole an increased total N deposition in forests as well as in any anthropogenic managed ecosystem tends to reduce soil respiration. This tendency has also been observed by others (Bowden et al. 2004) and can in part be explained by a reduction in mycorrhizal colonization and fungal development under nutrient-rich soil conditions (Bryla and Eissenstat 2005). In trees, the long-term effect of soil N availability usually leads to a reduction in C allocation to the belowground plant organs in favor of aboveground organs (Vogt et al. 1990; Haynes and Gower 1995), but not necessarily to a reduction of total amount of photosynthates allocated to the roots. Roots with higher N availability usually show higher specific respiration rates (Burton et al. 1996, 2002; Ryan et al. 1996).

Assessing the relative contribution of the heterotrophic and autotrophic components of soil respiration is an important goal in ecological studies as each one can differentially respond to soil climate, nutrient availability and management practices (Maekiranta et al. 2008). With the exception of December 2006 and, to a less extent, of April 2008, daily average soil temperature varied among soil collars (Fig. 2a). Considering that temperature has a major effect on root activity and its respiration, it is not surprising that we could only detect a significant linear relationship between fine root density and R_s in December, when soil temperature values were relatively constant. Several other studies have used a regression between R_s and fine root biomass to estimate R_h, by calculating the y-intercept. In a ponderosa pine plantation, Xu et al. (2001) estimated that R_h contributed 53% of R_s during the growing season; while in tropical deciduous forest, Behera et al. (1990) calculated that R_h contributed 49% of R_s. In another study, Rodeghiero and Cescatti (2006) estimated that R_h accounted for 42–84% of annual R_s in a range of evergreen forests. When we applied the root regression technique to our December 2006 data (Fig. 4c) to assess the contribution of R_h, we found that it contributed to some 65% of total R_s, the remaining 35% being attributed to R_a. Root regression has been critically evaluated as an approach to measure R_h. Kuzyakov (2006) pointed out that, compared with other techniques, high numbers of replicates are needed; there can be overestimation of root-derived CO_2 when big and old roots are present, and that frequently there is a poor correlation between root amount and total CO_2 with R_h estimates being biased by considerable extrapolation of the regression line. A clear limitation of the present study was our inability to estimate R_h when the trees were actively growing, when the overall contribution of R_h to R_s would likely have been smaller.

The increase of R_s values in August 2007 in the post-harvest period, as compared to the pre-harvest period, is likely associated to fruit removal (Fig. 2e), as surface soil temperature and surface soil water content were respectively lower and higher in post-harvest compared to pre-harvest (Fig. 2a, b). Fruits are a major sink for carbohydrates (Wardlaw 1990), and their removal results in a shift of carbohydrate allocation to the root system. This has been already reported in a study by Glenn and Welker (1993), who observed new fine root production immediately after fruit removal in mature peach trees. This suggests that the increase in CO_2 efflux after fruit removal is to assign to the autotrophic, rather than the heterotrophic, component of R_s.

In conclusion, our study demonstrated that, on an annual scale, surface soil temperature was the most important environmental factor affecting respiration of the orchard soil. Surface soil water content showed an adverse effect on soil respiration and controlled a great part of the variability of soil respiration measured in December and April. The history of soil fertilization, soil C and N concentration, as well as root N and soil mineral N had negligible or no effect on soil respiration. Fine root density, but not medium-and large-sized root density, contributed to explain part of the yearly variability of soil respiration, and proved to be a good predictor of soil respiration in December; in this period only, autotrophic component of soil respiration could be estimated by the root regression technique and represented roughly 35% of total soil respiration.

Acknowledgements The research was funded by the Italian Ministry of University and Research through the National Project "PRIN 2008, CARBON CYCLE IN MANAGED TREE ECOSYSTEMS" and by internal funds of the Free University of Bolzano/Bozen to M.T. We thank the two anonymous reviewers for their constructive comments on the manuscript.

References

Behera N, Joshi SK, Pati DP (1990) Root contribution to total soil metabolism in a tropical forest soil from Orissa, India. For Ecol Manag 36:125–134

Berg B, Matzner E (1997) Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. Environ Rev 5:1–25

Blanke MM (1996) Soil respiration in an apple orchard. Environ Exp Bot 36:339–348

Blanke MM (1998) Seasonal variation in soil respiration of a fruit orchard. J Appl Bot Angew Bot 72:153–156

Bolstad PV, Davis KJ, Martin J et al (2004) Component and whole-system respiration fluxes in northern deciduous forests. Tree Physiol 24:493–504

Boone RD, Nadelhoffer KJ, Canary JD, Kaye JP (1998) Roots exert a strong influence on the temperature sensitivity of soil respiration. Nature 396:570–572

Borken W, Savage K, Davidson EA, Trumbore SE (2006) Effects of experimental drought on soil respiration and radiocarbon efflux from a temperate forest soil. Global Change Biol 12:177–193

Bouma TJ, Eissenstat DM, Yanai RD et al (2001) Estimating age-dependent costs and benefits of roots with contrasting lifespan: comparing apples and oranges. New Phytol 150:685–695

Bowden RD, Davidson E, Savage K et al (2004) Chronic nitrogen additions reduce total soil respiration and microbial respiration in temperate forest soils at the Harvard forest. For Ecol Manag 196:43–56

Bryla DR, Eissenstat DM (2005) Respiratory costs of mycorrhizal associations. Adv Photosyn Resp 18:207–224

Bryla DR, Bouma TJ, Hartmond U, Eissenstat DM (2001) Influence of temperature and soil drying on respiration of individual roots in citrus: integrating greenhouse observations into a predictive model for the field. Plant Cell Environ 24:781–790

Burton AJ, Pregitzer KS, Zogg GP, Zak DR (1996) Latitudinal variation in sugar maple fine root respiration. Can J For Res 26:1761–1768

Burton AJ, Pregitzer KS, Ruess RW et al (2002) Root respiration in North American forests: effects of nitrogen concentration and temperature across biomes. Oecol ogia 131:559–568

Burton AJ, Pregitzer KS, Crawford JN et al (2004) Simulated chronic NO_3^- deposition reduces soil respiration in northern hardwood forests. Global Change Biol 10:1080–1091

Cook FJ, Orchard VA (2008) Relationships between soil respiration and soil moisture. Soil Biol Biochem 40:1013–1018

Davidson EA, Belk E, Boone RD (1998) Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Global Change Biol 4:217–227

Eissenstat DM, Waley E, Volder A, Wells C (1999) Recovery of citrus roots following prolonged exposure to dry soil. J Exp Bot 50:1845–1854

Eissenstat DM, Lakso AN, Neilsen D et al (2006) Seasonal patterns of root growth in relation to shoot phenology in grape and apple. Acta Hort 721:21–26

Espeleta JF, Eissenstat DM (1998) Response of citrus fine roots to localized soil drying: a comparison of seedlings with adult fruiting trees. Tree Physiol 18:113–119

Euskirchen ES, Pregitzer KS and Chen JQ (2006) Carbon fluxes in a young, naturally regenerating jack pine ecosystem. J Geophys Res Atmos 111 (D1):D01101

Fog K (1988) The effect of added nitrogen on the rate of decomposition of organic matter. Biol Rev 63:433–462

Fu SL, Cheng WX (2002) Rhizosphere priming effects on the decomposition of soil organic matter in C_4 and C_3 grassland soils. Plant Soil 238:289–294

Glenn DM, Welker WV (1993) Root development patterns in field grown peach trees. J Am Soc Hortic Sci 118:362–365

Hanson PJ, Edwards NT, Garten CT Jr, Andrews JA (2000) Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry 48:15–146

Haynes BE, Gower ST (1995) Belowground carbon allocation in unfertilized and fertilized plantations in northern Wisconsin. Tree Physiol 15:317–325

Knorr W, Prentice IC, House JI, Holland EA (2005) Long-term sensitivity of soil carbon turnover to warming. Nature 433:298–301

Kuzyakov Y (2006) Sources of CO_2 efflux from soil and review of partitioning methods. Soil Biol Biochem 38:425–448

Law BE, Ryan MG, Anthoni PM (1999) Seasonal and annual respiration of a ponderosa pine ecosystem. Global Change Biol 5:169–182

Liguori G, Gugliuzza G, Inglese P (2009) Evaluating carbon fluxes in orange orchards in relation to planting density. J Agric Sci 147:637–645

Linn DM, Doran JW (1984) Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and non-tilled soils. Soil Sci Soc Am J 48:1267–1272

Luo Y, Zhou X (2006) Soil respiration and the environment. Elsevier, Burlington

Maekiranta P, Minkkinen K, Hytonen J, Laine J (2008) Factors causing temporal and spatial variation in heterotrophic and rhizospheric components of soil respiration in afforested organic soil croplands in Finland. Soil Biol Biochem 40:1592–1600

Malaguti D, Rombolà AD, Quartieri M et al (2006) Effects of the rate of nutrients by fertigation and broadcast application in Gala and Fuji apples. Acta Hortic 721:165–172

Martin JG, Bolstad PV, Ryu SR, Chen JQ (2009) Modeling soil respiration based on carbon, nitrogen, and root mass across diverse great lake forests. Agric For Meteorol 149:1722–1729

Mielnick PC, Dugas WA (2000) Soil CO_2 flux in a tallgrass prairie. Soil Biol Biochem 32:221–228

Migliavacca M, Reichstein M, Richardson AD et al (2010) Semiempirical modeling of abiotic and biotic factors controlling ecosystem respiration across eddy covariance sites. Global Change Biol. doi:10.1111/j.1365-2486.2010.02243

Millard P, Midwood AJ, Hunt JE et al (2008) Partitioning soil surface CO_2 efflux into autotrophic and heterotrophic components, using natural gradients in soil $\delta^{13}C$ in an undisturbed savannah soil. Soil Biol Biochem 40:1575–1583

Millard P, Midwood AJ, Hunt JE et al (2010) Quantifying the contribution of soil organic matter turnover to forest soil respiration, using natural abundance $\delta^{13}C$. Soil Biol Biochem 42:935–943

Psarras G, Merwin IA, Lakso AN, Ray JA (2000) Root growth phenology, root longevity, and rhizosphere respiration of field grown "Mutsu" apple trees on "Malling 9" rootstock. J Am Soc Hortic Sci 125:596–602

Raich JW, Schlesinger WH (1992) The global carbon-dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus Ser B Chem Phys Meteorol 44:81–99

Rochette P, Flanagan LB (1997) Quantifying rhizosphere respiration in a corn crop under field conditions. Soil Sci Soc Am J 61:466–474

Rodeghiero M, Cescatti A (2006) Indirect partitioning of soil respiration in a series of evergreen forest ecosystems. Plant Soil 284:7–22

Rombolà AD, Zavalloni C, Scudellari D et al (2000) La fertirrigazione del meleto nella fase d'allevamento: effetti di dose e nutrienti. Riv Frutticoltura 6:67–74

Ryan MG, Hubbard RM, Pongracic S et al (1996) Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. Tree Physiol 16:333–343

Scandellari F, Ventura M, Ceccon C et al (2010) Net primary productivity and partitioning of absorbed nutrients in field-grown apple trees. Acta Hortic 868 (in press)

Schulze ED, Luyssaert S, Ciais P et al (2010) Importance of methane and nitrous oxide for Europe's terrestrial greenhouse-gas balance. Nature Geosci 2:842–850

Söderström B, Bååth E, Lundgren B (1983) Decrease in soil microbial activity and biomass owing to nitrogen amendments. Can J Micro 29:1500–1506

Sokalska DI, Hamanb DZ, Szewczukc A et al (2009) Spatial root distribution of mature apple trees under drip irrigation system. Agric Water Manag 96:917–926

Subke JA, Inglima I, Cotrufo MF (2006) Trends and methodological impacts in soil CO_2 efflux partitioning: a metaanalytical review. Global Change Biol 12:921–943

Tedeschi V, Rey A, Manca G et al (2006) Soil respiration in a Mediterranean oak forest at different developmental stages after coppicing. Global Change Biol 12:110–121

Vogt KA, Vogt DJ, Gower ST and Grier CC (1990) Carbon and nitrogen interactions for forest ecosystems. In: Above and belowground interactions in forest trees in acidified soils. Commission of the European Communities, Belgium, pp 203–235

Wardlaw IF (1990) The control of carbon partitioning in plants. New Phytol 116:341–381

Xu M, Qi Y (2001) Soil-surface CO_2 efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California. Global Change Biol 7:667–677

Xu M, DeBaise TA, Qi Y et al (2001) Ecosystem respiration in a young ponderosa pine plantation in the Sierra Nevada Mountains, California. Tree Physiol 21:309–318