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Summary We estimated component and whole-ecosystem CO_2 efflux (R_{ECO}) in a *Pinus canariensis* Chr. Sm. ex DC stand in Tenerife, Canary Islands, an ecotone with strong seasonal changes in soil water availability. From November 2006 to February 2008, we measured foliage, stem and soil CO_2 efflux by chamber techniques. Site-specific CO_2 efflux models obtained from these chamber measurements were then combined with half-hourly measurements of canopy, stem and soil temperature as well as soil water potential, leaf and stem surface area data for scaling up component-specific CO_2 efflux to R_{ECO}. Integrated over an entire year, R_{ECO} was 938 g of C m^{-2} in 2007 and comprised the following component fluxes: 77% from soil, 11% from stems and 12% from foliage. Whole-ecosystem CO_2 efflux varied markedly throughout the year. During the cold and wet season, R_{ECO} generally followed the seasonal trends in temperature, and during the warm and dry summer, however, R_{ECO} was significantly reduced because of limited soil water availability in the main rooting horizon.

Keywords: ecosystem CO_2 efflux, foliage, Mediterranean climate, Pinus canariensis, soil, stem, summer drought.

Introduction

Pinus canariensis Chr. Sm. ex DC is an endemic conifer species of the western Canary Islands where it forms pure stands under widely different ecological conditions (Blanco et al. 1989). In Tenerife, the distribution limit is between 800 and 2200 m a.s.l. on north-facing slopes and from 500 to more than 2500 m a.s.l. on south-facing slopes (Fernández-Palacios and de Nicolás 1995). These pine forests supply a local forest industry and also contribute to the water balance of the island by fog interception (Aboal et al. 2000). A common feature of pine forests in Tenerife is the Mediterranean climate with strong seasonal changes in water availability and evaporative demand. In the Canary Islands, however, dry conditions are often mitigated by the influence of the northeast trade winds bringing moisture from the sea and thus increasing the relative humidity of the air.

Despite a few studies on the net carbon gain of *P. canariensis* foliage (Wieser et al. 2002, Peters et al. 2003, 2008) no studies have focused on the ecosystem CO_2 efflux (R_{ECO}) in a *P. canariensis* forest, using chamber CO_2 efflux measurements from the soil, stems and foliage. Till now integrative studies of all these major components of R_{ECO} have rarely been reported (Granier et al. 2000, Xu et al. 2001, Bolstad et al. 2004), and to our knowledge no data are available for Mediterranean forest ecosystems, although chamber-based measurements yield results comparable to flux-tower measurements (Granier et al. 2000, Bolstad et al. 2004) and provide insights into environmental limitations. It is well established that R_{ECO} and hence the carbon balance varies significantly in response to local variations in climate, soil properties, species composition and stand density (Valentini et al. 2000, Falge et al. 2002). In addition, we also monitored environmental variables and expressed our chamber measurements on the basis of stem or leaf surface area to facilitate upscaling of these measurements to space (ecosystem) and time (throughout the year) (cf. Waring and Running 1998, Larcher 2001, Xu and Baldocchi 2004). Our specific goals were to quantify R_{ECO}, to describe spatial and temporal variations in the contributions of its component (soil, stems and foliage) carbon fluxes and to examine the effects of temperature and soil water availability on respiratory fluxes in relation to season.

Materials and methods

Study site

The study was carried out in an open 50-year-old
P. canariensis forest at 1650 m a.s.l. growing on the north-
ern slope of the Cordillera Dorsal (Morro de Isarda, El
Gaitero, 28°35′ N and 27°15′ W) in the mountains of La
Victoria, about 20 km southwest of La Laguna, Tenerife,
Canary Islands. The area was reforested in 1950 and the
canopy height averaged 21.5 m in 2007, with a stand den-
sity of 829 trees ha^{-1}, a basal stem area of 53.8 m^2 ha^{-1},
two needle age classes (current-year and 1-year-old needles)
and a leaf area index of 3.4 (Luis et al. 2005) with almost no
understory plants. Tree diameter distribution at breast
height (DBH) at the study site is shown in Figure 1. From
these data combined with stem height data, we computed
the projected stem surface area as 0.76 m^2 per square meter
of ground surface area.

According to the World Base for Soil Resources (FAO
1998), the soil at the study site is classified as an andosol.
There is a shallow layer of 3–5 cm of needle litter on the
top of the minerals A (0–50 cm depth) and C (> 50 cm)
horizons. The A horizon is enriched with 10% of organic
matter and the soil texture is dominated by the sand
(64–67%) and the silt factions (30–33%), with varying clay
content (2–4%). The water-holding capacity at field satura-
tion at 5–50 cm soil depth averaged 0.55 ± 0.05 m^3 m^{-3}
(Wieser et al. 2002). Rooting depth estimated at a ditch
close to the study site was 15 m (Luis et al. 2005).

The field site is characterized by a Mediterranean climate
with a mean annual temperature of 12.6 °C, a minimum of
−4.2 °C and a maximum of 31.2 °C. Annual precipitation
ranges from 460 (Aboal et al. 2000) to 930 mm (Peters et al.
2003). In contrast to the typical Mediterranean climate,
summer drought is often mitigated by a high relative
humidity of the air and a high frequency of clouds due to
the northeast trade winds, with the relative humidity of
the air averaging 48% and 70% during the warm and dry
and the cold and wet seasons, respectively. Further details
about the stand and climatic conditions are reported by
Luis et al. (2005) and Peters et al. (2008).

Environmental measurements

Global radiation (EMS11 EMS Brno CZ), air temperature,
relative humidity (EMS33 EMS Brno CZ) and precipita-
tion (MetOne370/676, EMS Brno CZ) were monitored
20 m aboveground on top of a scaffolding. Three gypsum
blocks were used to monitor soil water potential at a soil
depth of 30 cm, where most of the organic matter is con-
centrated (Wieser et al. 2002). All these parameters were
measured by an automatic weather station (Mini 32, Unilog
EMS Brno CZ). In addition, custom-built 1-mm-thick
type-T thermocouple sensors were connected to a data log-
ger (Delta-T, Cambridge, UK) for monitoring canopy tem-
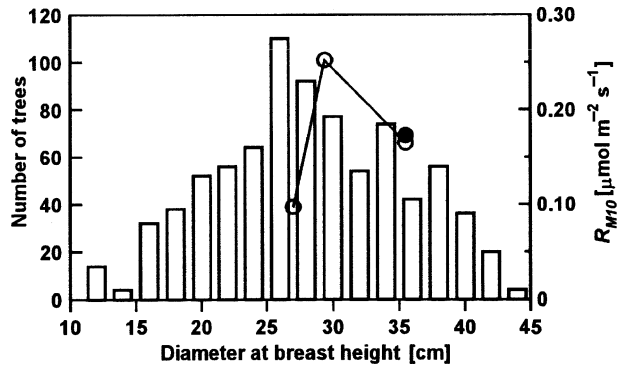perature 17 m aboveground, stem temperature at the

Figure 1. Distribution of tree diameter at breast height (DBH)
at the study site (open bars) and the relationship between stem-
surface-area-based maintenance respiration normalized to 10 °C
(R_{m10}) and DBH in south-facing (open circles) and north-facing
(solid circle) stem sections of *P. canariensis* trees.

cambial surface at breast height on the north and south
sides of one tree and soil temperature at 10-cm soil depth,
respectively. Both data loggers were programmed to record
30-min mean values of environmental measurements taken
every minute from November 11, 2006 to February 5, 2008.

Gas exchange measurements

We measured CO_2 efflux with several portable gas
exchange systems (CIRAS 1, EGM-3, PP Systems, Hitchin,
Hertfordshire, UK; LCA-4, ADC, Hoddesdon, UK) at
monthly to bimonthly intervals between November 2006
and February 2008. All the instruments were cross-
calibrated against each other during three field campaigns
that were carried out at the end of November 2006, during
mid-August and at the end of September 2007.

In November 2006, foliar nighttime CO_2 efflux (R_F) was
measured in situ with a portable gas exchange system oper-
ating in differential mode (CIRAS 1) and equipped with a
climate controlled PLC6 leaf chamber (PP Systems, Hit-
chin, Hertfordshire, UK). Measurements were made on fas-
cicles (10 needles) of fully expanded current-year needles at
different heights within the crowns of three trees. We
expressed R_F, which was calculated according to the
method described by von Caemmerer and Farquhar
(1981), on a projected leaf area basis (cf. Peters et al. 2008).

Stem CO_2 efflux (R_W, sensu Teskey et al. 2008) was mea-
sured with chambers made of clear Perspex attached per-
manently to the stem at breast height (Linder and Troeng
1981, Benecke 1985, Carey et al. 1997, Wieser and Bahn
2004). To ensure a gas-tight seal between the chambers
and the bark, the chambers were sealed on the stems with
putty (Terostat, Teroson, Ludwigsburg, Germany) and
non-hardening insulating foam. One chamber was installed
on the south side of the stem of each of the three trees hav-
ing a DBH of 27.0, 29.4 and 35.5 cm, respectively, and one
additional chamber was installed on the north side of the
third tree. We measured R_W five to six times between sun-
rise and sunset on 21 days between November 20, 2006 and

November 27, 2007. To assess R_W, air from the inlet and the outlet ports of the chambers was measured alternately with an infrared gas analyzer (EGM-3 or LCA-4). The corresponding flow rates ($0.3\,l\,min^{-1}$) were maintained by internal pumps and the data were recorded when the CO_2 concentration of the corresponding airstream had stabilized, commonly within 10–15 min. We calculated R_W from the difference in CO_2 concentration between the air entering and leaving the chambers and the flow rate. During the periods when measurements were not being made, glass wool was inserted in the inlet and the outlet tubing of the chambers to prevent insects entering the chamber while allowing adequate gas exchange (Vose and Ryan 2002). We expressed R_W on the basis of the stem surface area enclosed in each chamber.

Soil surface CO_2 efflux (R_S), which is the sum of respiration from plant roots and associated microorganisms (sensu Moyano et al. 2009), was measured with either a 1177.5-cm³ SRC-1 soil respiration chamber (PP Systems, Hitchin, Hertfordshire, UK) or a custom-made chamber (cf. Wieser 2004) connected to an EGM-3 or an LCA-4 infrared gas analyzer for data collection and storage. The soil respiration chamber was placed directly on the soil surface. A 0.5-cm sharp steel collar mounted directly on the chamber was gently pushed onto the soil to provide air tightness at five to eight marked positions covering the range of conditions that were expected to reflect the spatial variability of soil CO_2 efflux at the study site. Soil CO_2 efflux was measured between 09:00 and 12:00 h beginning on November 20, 2006 and ending on January 18, 2008. All measurements after CO_2 evolution into the chamber had stabilized, which was usually 2 min after the chamber had been positioned.

CO₂ efflux data analysis and scaling up to an annual budget

The temperature responses of R_F and R_W were estimated as

$$R = R_{10} \exp(\ln Q_{10}((T - 10)/T)), \qquad (1)$$

where R (either R_F or R_W) is the measured CO_2 efflux, R_{10} is the CO_2 efflux rate at a temperature of 10 °C, Q_{10} is the temperature sensitivity of CO_2 efflux and T is the temperature, corresponding to canopy (for R_F) or stem temperature (for R_W).

The mature tissue method (Amthor 1994, Sprugel et al. 1995) has been used to partition R_W into maintenance (R_m) and growth respiration (R_g). This method assumes that CO_2 efflux during the period when stem diameter growth is nil represents R_m only. Based on dendrometer readings ($n = 5$), stem growth started at the end of May (Day 150) and ceased almost completely at the beginning of November (Day 312). Thus, R_W before and after Day 150 and 312, respectively, were considered to represent R_m only. Values of R_{10} and Q_{10} obtained during this period and the annual sapwood temperature records were used in

Eq. (1) to estimate annual R_m. Annual R_g was then calculated as the difference between R_W and R_m.

To account for reduced soil respiratory fluxes at a given soil temperature during the warm and dry season when soil water potential was lower than −0.05 MPa an additional function was added to Eq. (1) that relates R_S to soil water availability in the main rooting horizon:

$$R_S = \{R_{S10} \exp(\ln Q_{10}((T_S - 10)/T_S))\}(SWA), \qquad (2)$$

where R_S is the soil surface CO_2 efflux ($\mu mol\,m^{-2}\,s^{-1}$), R_{10} is the soil CO_2 efflux rate at a temperature of 10 °C, Q_{10} is the temperature sensitivity, T_S is the soil temperature at 10-cm soil depth and SWA represents the effect of soil water potential (Ψ) at 30-cm soil depth on R_S at a given T_S. We used a linear function to describe the relationship between R_S and Ψ (cf. Rey et al. 2002, Cook and Orchard 2008) at 30-cm soil depth between −0.05 and −1.4 MPa, the latter value was chosen because the gypsum blocks were unable to measure water potentials lower than −1.4 MPa.

Values of R_F, R_W and R_S throughout the year of 2007 were estimated according to Eqs. (1) and (2) based on half-hourly measurements of canopy, stem and soil temperatures and soil water potential. Daily mean values were calculated by averaging all daily measurements (48 values per day). Preliminary gas exchange measurements on 18 shoots distributed randomly within the upper and the lower crowns of three *P. canariensis* trees carried out throughout one year (Peters 2001) failed to find significant differences in foliar CO_2 efflux between current-year ($0.28 \pm 0.15\,\mu mol\,m^{-2}\,s^{-1}$) and 1-year-old ($0.24 \pm 0.12\,\mu mol\,m^{-2}\,s^{-1}$) needles. Therefore, we assumed that the foliar CO_2 efflux rates that we estimated were representative of the entire stand. Because there was no clear correlation between R_W and DBH (Figure 1), Q_{10} and R_{10} values estimated for the four different stem sections of the three study trees were weighted equally to give a spatial mean of R_W for the site. To compare the contribution of each respiration component to R_{ECO}, we converted all CO_2 fluxes to units of $\mu mol\,CO_2\,m^{-2}$ of ground surface area. Finally, daily values were summed to obtain the annual rates of R_F, R_W, R_m, R_g, R_S and R_{ECO}.

Results

Climatic conditions at the study site were characterized by a warm and dry period from July to October and a cold and wet period from November to June (Figure 2). Mean canopy temperature (Figure 2A) was 11.7 °C, and it varied between 27.4 °C during the warm and dry period (July 29, 2007) and 2.1 °C during the cold and wet season (February 1, 2007). Mean stem temperature (Figure 2B) was 10.4 °C and varied between 24.1 °C (July 29, 2007) and 2.6 °C (February 5, 2007). Temperature differences between the south and the north sides of the stem did not differ significantly ($P > 0.2$, *t* test) and were on average less than
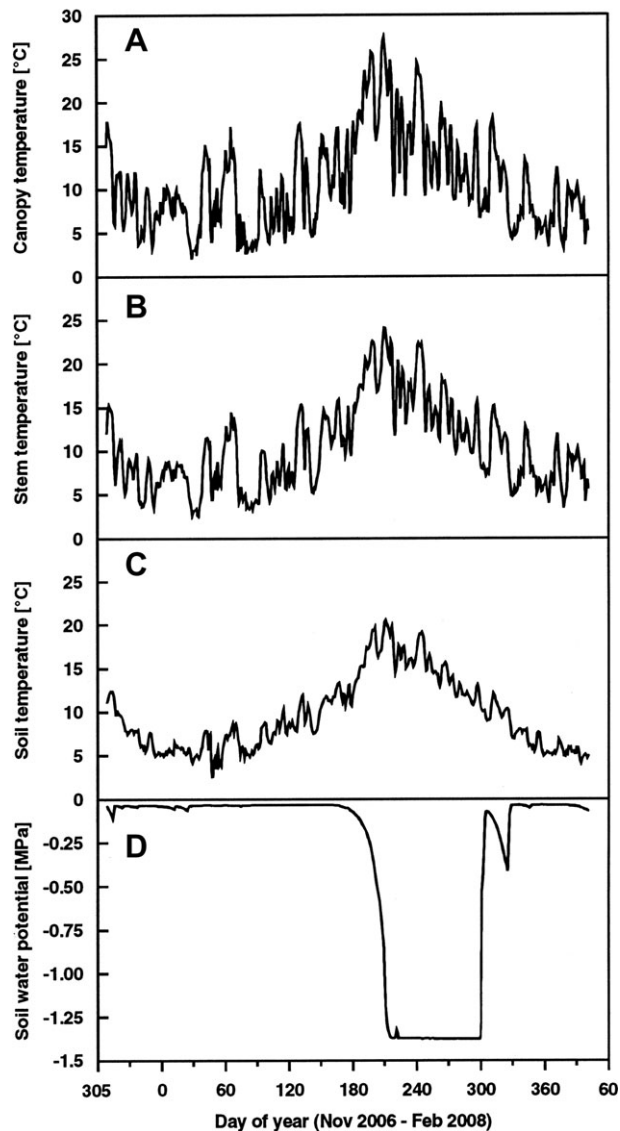
Figure 2. Time course of mean daily (A) canopy temperature 17 m aboveground, (B) stem temperature at the cambial surface 1.5 m aboveground of *P. canariensis* trees, (C) soil temperature at 10-cm soil depth and (D) soil water potential at 30-cm soil depth between November 11, 2006 and February 5, 2008.

Figure 3. Seasonal course of *P. canariensis* daily stem CO_2 efflux (R_W) per unit stem surface area. Values are mean of four chambers $\pm$ SD measured five to eight times a day.

Figure 4. Seasonal course of soil CO_2 efflux (R_S) per unit ground area. Values are mean of five to eight measurements $\pm$ SD measured five to eight times a day.

± 0.3 °C. Soil temperature at 10-cm soil depth averaged 10.4 °C. The lowest mean daily soil temperature recorded during the study was 3.3 °C on February 17, 2007 and the highest mean daily soil temperature was 20.5 °C on July 30, 2007 (Figure 2C). Daily relative humidity of the air averaged 64% and total precipitation during the study period was 650 mm with 92% falling during the cold and wet season (data not shown). Soil water potential at 30-cm soil depth always remained above -0.05 MPa (0.42 m^3 m^{-3}) during the wet and cold season, and declined progressively during July to -1.37 MPa (0.25 m^3 m^{-3}; the detection limit of the gypsum blocks) and persisted close to the wilting point (soil water potential of -1.5 MPa) throughout the warm and dry summer (Figure 2D).
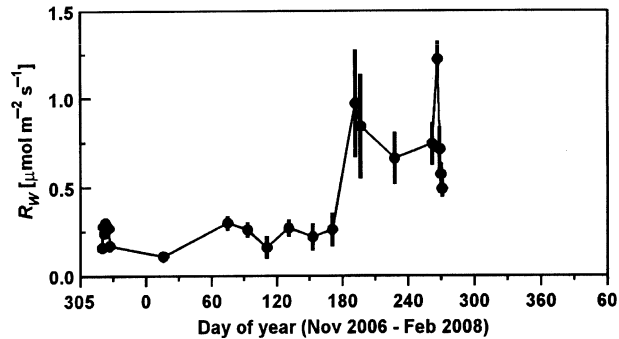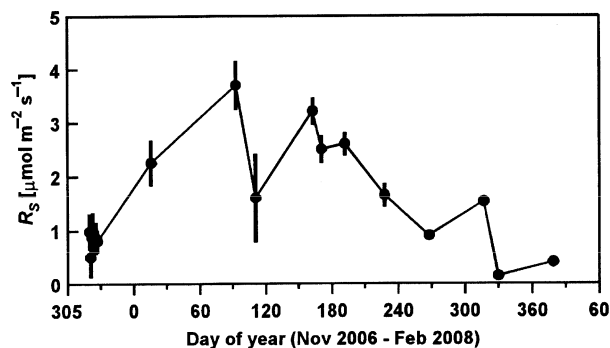
Values of R_W generally followed the seasonal trends in stem temperature (cf. Figure 2) and varied between 0.11 ± 0.02 µmol m^{-2} s^{-1} (January 16, 2007) during the cold and wet season and 1.22 ± 0.10 µmol m^{-2} s^{-1} (September 24, 2007) during the warm and dry period (Figure 3). The values of R_S increased steadily during late winter and spring following the increase in soil temperature and reached a maximum of 3.7 ± 0.44 µmol m^{-2} s^{-1} on April 4, 2007 (Figure 4). During the warm and dry period, R_S generally declined (Figure 4) and then increased again in fall as soil water availability increased (cf. Figure 2), before declining to a minimum value of 0.14 ± 0.44 µmol m^{-2} s^{-1} on November 26, 2007 (Figure 4).

Throughout the study period, foliage, stem and soil CO_2 efflux rates were correlated with the corresponding canopy, stem and soil temperatures at the site. The temperature response of R_F of fully developed current-year needles had a Q_{10} of 2.44, and canopy temperature accounted for 84% of the variation in R_F (Figure 5).

Although, at a given temperature, CO_2 efflux per unit stem surface area was significantly lower during the period when radial increment had ceased than at other times during the year, Q_{10} did not vary significantly throughout the year (Figure 6). During the period of stem growth, which
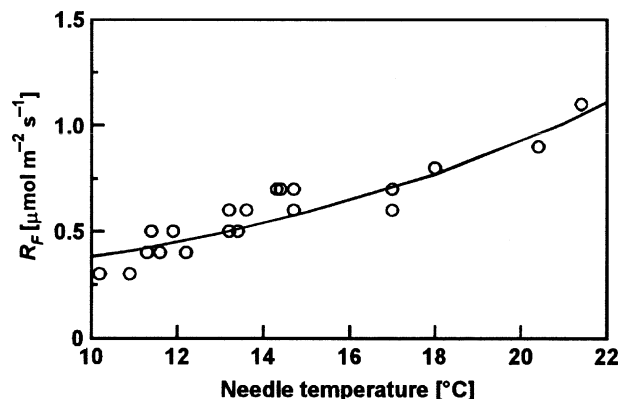
Figure 5. *Pinus canariensis* needle CO$_2$ efflux (R_F) expressed on a projected needle surface area basis as a function of canopy temperature. Values were fit by the exponential regression: $y = 0.37 \exp(\ln 2.44(T - 10)/10)$; $r^2 = 0.84$.
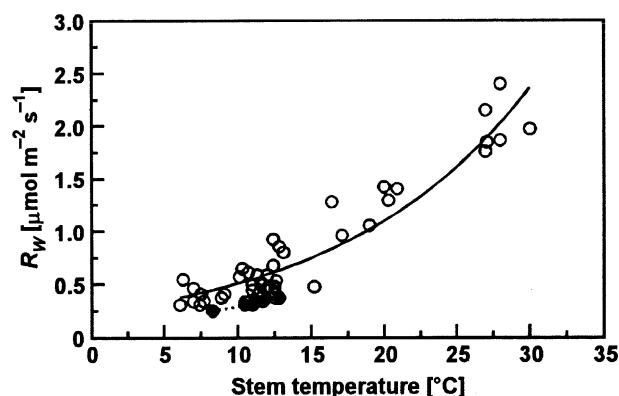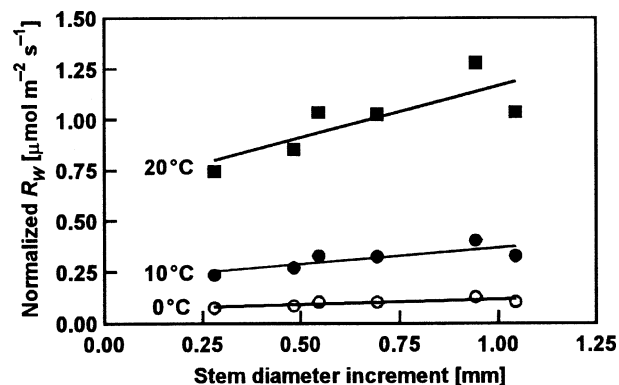

Figure 7. *Pinus canariensis* normalized stem CO$_2$ efflux (R_W) as a function of stem diameter increment during the warm and dry period. The intercept at the y-axis represents maintenance respiration only.

Table 1. *Pinus canariensis* stem surface area as a function of total woody tissue CO$_2$ efflux at 10 °C (R_{W10}) obtained during the warm and dry period and maintenance respiration at 10 °C (R_{m10}) obtained during the wet and cold season and the corresponding annual temperature sensitivity (Q_{10}). The r^2 values represent the proportion of variability in CO$_2$ efflux explained by tissue temperature.

Tree number, position	DBH (cm)	R_{W10} (μmol m^{-2} s^{-1})	R_{m10} (μmol m^{-2} s^{-1})	Q_{10}	r^2
1, South	27	0.160	0.097	3.46	0.51
2, South	29.4	0.424	0.252	2.40	0.80
3, South	35.5	0.269	0.165	3.29	0.63
3, North	5.5	0.292	0.173	3.53	0.76

Figure 6. Stem CO$_2$ efflux (R_W) expressed per unit stem surface area as a function of stem temperature at the cambial surface 1.5 m aboveground on the south side of *P. canariensis* Tree 2 during the warm and dry period (open symbols and solid line) and during the period of dormancy when radial growth had ceased completely (solid symbols and dotted line). Values were fit by exponential regressions: warm and dry period: $y = 0.424 \exp(\ln 2.39(T - 10)/10)$; $r^2 = 0.80$; dormant period: $y = 0.252 \exp(\ln 2.23(T - 10)/10)$; $r^2 = 0.80$.

started at the end of May and ceased almost completely at the beginning of November, R_W normalized to 0, 10 and 20 °C, respectively, and was positively correlated with stem diameter increment (Figure 7). Although the trees were similar in age and DBH and grew under comparable conditions, they exhibited different area-based CO$_2$ efflux characteristics and Q_{10} values (Table 1). Woody tissue temperature accounted for 51–80% of the year-round variation in surface-area-based R_W (Table 1).

Soil CO$_2$ efflux was related to soil temperature at 10-cm soil depth at soil water potentials higher than −0.05 MPa (Figure 8). Above this threshold, the soil temperature accounted for 78% of the variation in R_S and the Q_{10} was 3.89 (Figure 8). At soil water potentials lower than −0.05 MPa, R_S declined linearly with decreasing soil water

availability in the main rooting horizon by about 5% per 0.1 MPa decrease in soil water potential at 30-cm soil depth ($r^2 = 0.75$).

We used Eq. (1) to model the annual courses of R_F and R_W and Eq. (2) to model the seasonal course of R_S. In general, the modeled CO$_2$ efflux rates matched the observed CO$_2$ effluxes well showing close linear relationships with r^2 values > 0.75 for each of these ecosystem components (Table 2).

Whole-ecosystem CO$_2$ efflux varied considerably on an annual cycle (Figure 9). During the cold and wet season, R_{ECO} generally followed the seasonal trends in temperature (cf. Figure 2) and modeled R_{ECO} per unit ground surface area ranged between 1.1 on February 17, 2007 and 8.9 μmol m^{-2} s^{-1} on June 18, 2007 (Figure 9). During the warm and dry summer, when soil water availability was low (cf. Figure 2), R_{ECO} was greatly reduced and averaged 2.3 μmol m^{-2} s^{-1} (Figure 9).

Whole-ecosystem CO$_2$ efflux was largely dominated by R_S with the contribution of R_S to R_{ECO} being 85% and 60% during the cold and wet season and the warm and dry season, respectively (Figure 10). Aboveground CO$_2$ effluxes by contrast followed the seasonal trends in temperature
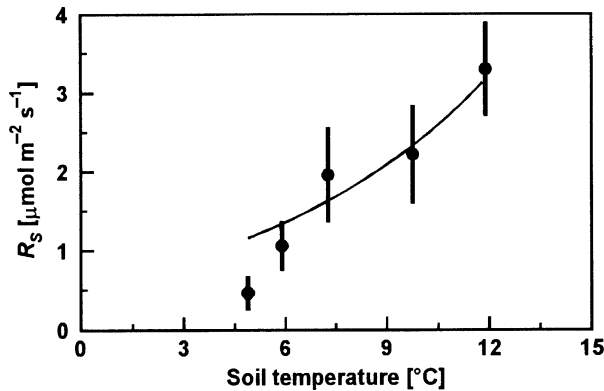
Figure 8. Soil CO_2 efflux (R_S) as a function of soil temperature at 10-cm soil depth during the wet and cold period when soil water potential was above −0.05 MPa. Values were fit by the exponential regression: $y = 2.49 \exp(\ln 3.89(T − 10)/10)$; $r^2 = 0.78$. Each value represents the mean of 10–20 values ± SD.

Table 2. Correlations between observed and modeled CO_2 efflux from *P. canariensis* foliage and stem and from soil based on the linear regression equation: modeled value (y) = observed value (x)a. Modeled values for foliage and stem CO_2 efflux were estimated with Eq. (1) and modeled values for soil CO_2 efflux were estimated with Eq. (2).

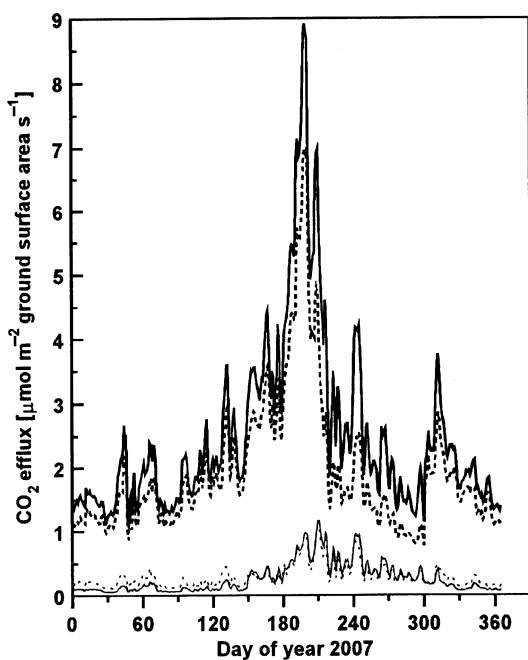| Component	Regression equation	r^2
Foliage	$y = 0.99x$	0.90
Stem	$y = 0.92x$	0.87
Soil	$y = 0.93x$	0.77

Figure 9. Seasonal trends in total ecosystem (thick solid line), soil (thick dotted line), stem (thin solid line) and needle nighttime CO_2 efflux (thin dotted line) estimated from chamber-based measurements for the entire year of 2007.
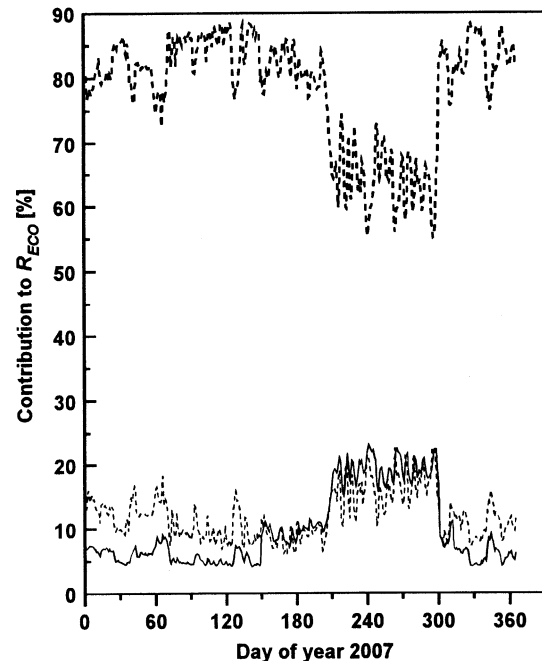

Figure 10. Seasonal trends in the contribution of soil (thick dotted line), stem (thin solid line) and needle nighttime CO_2 efflux (thin dotted line) to total ecosystem CO_2 efflux (R_{ECO}) throughout the entire year of 2007.

Table 3. Whole-ecosystem and component CO_2 efflux rates estimated for 2007. Values are mean ± SD derived from our component models.

CO_2 efflux component	g C m^{-2} (surface area) year^{-1}	%
Soil	726	77
Stem	100	11
Foliage	111	12
Total	937	100

(cf. Figure 2) and were the highest during the warm and dry season (Figure 9). During the cold and wet season, R_W was reduced to the rate of R_m (Figure 9). The contribution of R_W to R_{ECO} averaged 5% during the cold and wet season and 20% during the period of stem growth in summer (Figure 10). The corresponding mean seasonal values for R_F were 15% and 20% (Figure 10). Cumulative R_{ECO} estimated from summed chamber and modeled values for 2007 was 937 g C m^{-2} year^{-1} (Table 3). The annual contribution of C efflux from the soil, stems and foliage was 77%, 11% and 12%, respectively (Table 3).

Discussion

We focused on the seasonal variations in ecosystem CO_2 efflux and its components in a 50-year-old *P. canariensis*

forest growing on a north-facing slope at 1650 m a.s.l. in Tenerife, Canary Islands. Although the study site is characterized by a Mediterranean climate with cold and wet seasons alternating with a warm and dry period when soil water availability is low, summer drought at the site is often mitigated by the influence of the northeast trade winds, bringing moisture from the sea and thus increasing the relative humidity of the air (Peters et al. 2003, 2008, Luis et al. 2005). In addition, at our study site, *P. canariensis* develops 15-m deep roots enabling the trees to access groundwater sources (Luis et al. 2005), thus the needles are able to maintain a positive carbon gain throughout the year (Peters et al. 2003, 2008).

Our cumulative R_{ECO} of 937 g C m^{-2} year^{-1} is within the range of tower-based eddy covariance assessments reported for other Mediterranean forests (600–1600 g C m^{-2} year^{-1}; Granier et al. 2000, Falge et al. 2002, Chiesi et al. 2005, Medlyn et al. 2005, Pereira et al. 2007, Allard et al. 2008) and savanna ecosystems (890–1360 C m^{-2} year^{-1}; Ma et al. 2007). The annual contributions of C efflux from the soil (77%), stems (11%) and foliage (12%) were similar to the values reported in other studies (Xu et al. 2001, Bolstad et al. 2004), although no data from Mediterranean forest ecosystems are available. Raich and Schlesinger (1992) estimated soil CO$_2$ efflux to be 48–71% of R_{ECO}. Our value of 77% (726 g C m^{-2} surface area year^{-1}) matches the upper end of this range and is comparable to the value of 900 g C m^{-2} surface area year^{-1} reported for an Italian oak forest (Rey et al. 2002).

In Mediterranean-type climates, the dominant factors controlling the seasonal course of R_{ECO} are temperature and soil water availability. At our study site, R_{ECO} generally followed the seasonal trends in temperature during the cold and wet season. During the warm and dry summer, however, R_{ECO} was mainly controlled by soil water availability, which is a common feature of Mediterranean forest (Law et al. 2000, Medlyn et al. 2005, Ma et al. 2007, Pereira et al. 2007, Allard et al. 2008) and grassland ecosystems (Xu and Baldocchi 2004).

We found that R_{ECO} was largely dominated by R_S (i.e., the sum of respiration from plant roots and associated microorganisms (sensu Moyano et al. 2009)). At our study site, soil organic matter is mainly concentrated in the upper 30 cm of the soil profile (Wieser et al. 2002), whereas roots can reach to a depth of 15 m (Luis et al. 2005). Consequently, R_S was largely determined by temperature and water availability of the top soil, and hence also by the microbial decomposition of organic matter and belowground litter, as also observed in a Mediterranean *Quercus ilex* L. forest in southern France by Allard et al. (2008). The latter being a major component of total carbon efflux from Mediterranean forest soils (Rey et al. 2002).

In agreement with other studies carried out in Mediterranean climates (Fang et al. 1998, Epron et al. 1999, Conant et al. 2000, Xu and Qi 2001, Rey et al. 2002), R_S in the Canary Islands pine forest followed soil temperature only during the cold and wet season when soil water potential

was higher than −0.05 MPa. Our Q_{10} for R_S (3.89) is higher than the global mean of 2.4 (Raich and Schlesinger 1992, Kirschbaum 1995), but within the range of 2.0–6.3 reported for European (Janssens et al. 2003) and North American forest ecosystems (Davidson et al. 1998). During the warm and dry summer, however, low soil water availability limited the response of R_S to temperature whenever soil water potential was lower than −0.05 MPa (≈ 25 m^3 m^{-3}). Similar threshold values for soil-water-induced controls over R_S have also been observed in a *Pinus ponderosa* Dougl. Ex Laws. plantation in California (Xu and Qi 2001) and in a Mediterranean mixed oak forest in Italy (Rey et al. 2002). This drought-induced restriction on R_S at our study site became clearly evident when R_S increased sharply immediately after a 15-mm precipitation pulse that resulted in a significant short-term increase in soil water content in the upper 2 cm of the soil layer (Bahn et al. unpublished) and a quick recovery in soil microbial activity (Birch 1958, Anderson 1973, Joffre et al. 2003, Jarvis et al. 2007). Thus, the frequency and intensity of summer rains may be a critical factor in determining the annual total soil CO$_2$ efflux, and therefore the overall carbon balance of Mediterranean ecosystems (cf. Rey et al. 2002). At our study site, where summer rain contributed < 8% of annual precipitation, the overall effect of the short-term soil CO$_2$ outbursts occurring in response to summer rain episodes on the annual total R_S, and hence on R_{ECO}, was < 1% (Bahn et al. unpublished observations).

In contrast to R_S, aboveground CO$_2$ effluxes followed seasonal trends in temperature (Figure 2) and were the highest during the warm and dry season, and R_F and R_S were hardly affected by soil water availability of the top soil, probably because the trees used groundwater sources to maintain a favorable water status (Dawson 1994, Villar-Salvador et al. 1997, Luis et al. 2005).

Values of R_W were significantly lower during the cold and wet season than during the warm and dry period, and the close linear correlation between normalized R_W and DBH increment reflects an enhanced metabolic activity in the cambial region during the period of stem increment (Havranek 1981, Lavigne et al. 2004). The Q_{10} values, however, did not vary significantly in relation to season. Similar small inter-annual changes in the temperature sensitivity of R_W have been reported for *Pinus cembra* L. at the alpine timberline (Wieser and Bahn 2004) and for *Pinus sylvestris* L. under boreal conditions (Zha et al. 2004), and our Q_{10} values of 2.40–3.53 were within the range of 1.0–3.9 reported for other conifer species (Ryan 1990, Sprugel 1990, Ryan et al. 1994, Lavigne 1996, Lavigne et al. 1996, Carey et al. 1997, Lavigne and Ryan 1997, Wieser and Bahn 2004). Furthermore, normalized R_W expressed on a stem surface area basis varied significantly within the study trees, as was also found within the even-aged *Abies amabilis* (Dougl.) trees in a stand (Sprugel 1990), and this can probably be attributed because CO$_2$ can be transported in the xylem and released from parts of the tree other than where

it was produced (for a review see Teskey et al. 2008). These within-tree differences in stem-surface-area-based R_W may cause errors when scaling up R_W to the stand level; however, the effects of this error on stand-level R_{ECO} estimates were probably small because R_W was only a small component (11%) of total year-round R_{ECO}.

Because we were unable to assess the response of R_F to temperature repeatedly throughout the study period, scaling-up year-round R_F was based on several assumptions. First, nighttime foliar CO_2 efflux rates of fully developed current-year needles in the upper canopy were similar in summer and in winter (Peters et al. 2003). Second, frequent measurements of R_F made between January 1999 and March 2000 showed that R_F normalized to 10 °C (R_{F10}) in fully developed current-year and 1-year-old needles, did not vary significantly throughout a year and averaged 0.33 ± 0.06 μmol m^{-2} s^{-1} irrespective of the canopy position (Peters, unpublished observations), equivalent to the R_{F10} of 0.37 μmol m^{-2} s^{-1} that we obtained in November 2006. Thus, seasonal changes in R_F were expected to be influenced more by canopy temperature than by other factors. Therefore, based on these assumptions, we considered that about 12% of the annual total R_{ECO} was respired by the foliage which is within the range of values 5–20% reported for other forest ecosystems at high elevations or high latitudes (Xu et al. 2001, Bolstad et al. 2004, Wieser and Stöhr 2005).

In conclusion, we observed strong seasonal variations in R_{ECO} in a *P. canariensis* forest in Tenerife and found that R_{ECO} was mainly controlled by soil water availability. Our component measurements indicated that R_{ECO} was largely dominated by R_S which contributed 85% and 60% to R_{ECO} during the cold and wet season and the warm and dry season, respectively. In contrast, as a result of access to deep soil water reserves and because the dryness of the air at the site is often mitigated by the northeast trade winds bringing moisture from the sea, R_W and R_F were significantly higher during the warm and dry season than during the cold and wet season. Under predicted scenarios of increasing aridity in Mediterranean regions (IPCC 2007), it is likely that there will be a shift in the contribution of these components to R_{ECO} from predominantly belowground to increasingly aboveground. This shift should be accounted for when evaluating the possible future response of *P. canariensis* forests to a changing climate.

Acknowledgments

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