Soil respiration and mass balance estimation of fine root production in *Fitzroya cupressoides* forests of southern Chile

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Abstract. The soil carbon dynamics of southern hemisphere temperate rainforests have rarely been studied. Here, we report for the first time soil CO_2 effluxes and their partitioning for medium-age and old-growth *Fitzroya cupressoides* forests growing under contrasting environmental conditions in the Coastal Range and Andean Cordillera of southern Chile. *Fitzroya* is a high biomass and one of the longest lived species in the world. We characterized soil respiration patterns over almost 2 yr. Annual soil respiration was slightly higher in younger forests from the Coastal Range compared with Andean forests during the first studied year (6.37–6.66 vs. 5.06–6.14 Mg C·ha^{-1}·yr^{-1}), and significantly higher during the second year mainly due to a warmer and drier summer (8.08–8.64 vs. 4.98–5.35 Mg C·ha^{-1}·yr^{-1}). Therefore, warmer and drier conditions, likely to become more common in this region under future climate change, were associated with significantly higher respiration in the shallow soils of the coast, but not in the Andes. A higher proportion of autotrophic respiration was found in the Coastal Range forest probably due to a much higher fine root biomass in this site. However, fine root productivity, an important contributor of belowground carbon fluxes, was a little lower (not significantly) in the coastal site (0.81 ± 0.60 vs. 1.50 ± 0.42 Mg C·ha^{-1}·yr^{-1}), indicating a longer root residence time in forests from this area. Soil CO_2 effluxes from these forests and their root productivity are at the lower end of values recorded for other mature and old-growth temperate wet forests worldwide. The intrinsic longevity and the particularly poor soils and rainy conditions where these forests grow may influence these facts. Interannual climate variability appears to be especially important for soil respiration in the Coastal Range due to the more Mediterranean climate influence and shallow, poor water retention soils in this area.

Key words: autotrophic and heterotrophic respiration; climate change; CO_2 efflux; fine root productivity; old-growth forests; southern South America; temperate rainforests; temperature sensitivity.

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INTRODUCTION

Soil respiration or carbon dioxide (CO_2) efflux from soils is the largest source of carbon from terrestrial ecosystems and plays a significant role in the global carbon cycle (Raich and Potter 1995, Wang et al. 2006). It frequently contributes 30–80% of total ecosystem respiration in forests (Davidson et al. 2006*a*). Soil CO_2 efflux can be a good indicator of overall ecosystem metabolism (Ryan and Law 2005), it has a crucial influence on net ecosystem C sequestration and atmospheric CO_2 concentrations (Metcalfe et al. 2011), and a better understanding of this efflux is key to

improving the prediction of net ecosystem exchange responses to climate change (Lavigne et al. 2003).

Total soil CO_2 efflux is a combination of autotrophic (R_a) and heterotrophic (R_h) effluxes. The soil autotrophic component is contributed by living plant roots and their associated mycorrhizae and is often termed rhizosphere respiration, while the heterotrophic component mainly comes from microbes responsible for detritus and soil organic matter decomposition (Butler et al. 2012). The proportion of soil respiration from autotrophic and heterotrophic components might vary largely with seasons and among ecosystems, with mean root respiration ratios (root respiration/total respiration) of ~43.7–48.6% across a range of studies (Hanson et al. 2000, Chen et al. 2011). Distinguishing between both soil respiration components allows a better interpretation and modeling of soil processes and provides a better understanding of the implications of environmental change on the climate feedback potential of soil respiration and on the carbon cycling and sequestration in forests ecosystems (Hanson et al. 2000, Subke et al. 2006, Trumbore 2006, Bond-Lamberty and Thomson 2010, Taylor et al. 2015).

Soil respiration dynamics are primarily controlled by temperature, soil moisture, and substrate properties, which influence the production and consumption of organic matter (Davidson et al. 1998, Raich and Tufekciogul 2000). The apparent annual temperature sensitivity of soil respiration is normally characterized by the Q_{10} function, but this can be affected by covariation of temperature with soil water content, root biomass, and microbial biomass (Davidson et al. 1998). Given the complexity of factors that can affect soil respiration, it is important to understand the environmental controls on soil respiration at a site level, so potential responses of ecosystems to ongoing changes can be assessed (Fenn et al. 2010).

Most studies of soil respiration have focused on northern hemisphere ecosystems. There have been no detailed field studies of soil respiration in the temperate rainforests of southern South America, the largest area of temperate forests in the southern hemisphere (Armesto et al. 2009). Although in terms of climate this region resembles the north-western coast of North America, which also hosts temperate rainforests, large differences in forest species composition, diversity, and level of endemism remain (Armesto et al. 1996). More specifically, it is not clear how ancient and carbon massive ecosystems, such as *Fitzroya cupressoides* forests, possibly the oldest rainforests in the world in terms of mean stand age (Urrutia-Jalabert et al. 2015*a*), are behaving in terms of soil emissions to the atmosphere. Similarly, there are no estimates of belowground productivity in these ecosystems, particularly of fine root productivity (NPP_{fr}), which together with mycorrhizae are important contributors to belowground fluxes in forests (Finér et al. 2011). Studying soil respiration in these ecosystems may provide more insights into the carbon cycle and general functioning of particularly old-growth rainforests.

We here investigate the soil CO_2 efflux emitted by two contrasting *Fitzroya* forests in southern Chile over almost 2 yr. The study sites were selected from the two main mountain ranges where *Fitzroya* grows and stands were representative of the widespread condition of these forests in each area: a medium-age and an old-growth forest in the Coastal Range and the Andean Cordillera, respectively. The difference in developmental stages is mainly because there are no old-growth forests in the Coastal Range due to fires and logging during past centuries. This will allow comparison of soil respiration in stands of different ages, but perhaps more interesting, in the same forest type growing under different environmental conditions. The climate in the Coastal Range has a more Mediterranean influence and soil conditions are more restrictive (shallower depths, lower water retention capacity, and lower fertility) than in the Andes (Donoso et al. 1990, Urrutia-Jalabert et al. 2015*a*, *b*, *c*).

Since summer conditions were warmer and drier during the second studied year, we specifically evaluated the sensitivity of soil respiration to soil temperature and water content considering interannual variability in each study site. This assessment is especially relevant, because southern Chile is projected to experience significant climate warming (increase in summer temperature of up to 4°C) and drying (decrease in summer precipitation of up to 50%) by the end of this century (Fuenzalida et al. 2007).

Our specific objectives were to (1) examine seasonal patterns of total respiration (R_s), R_a, and R_h
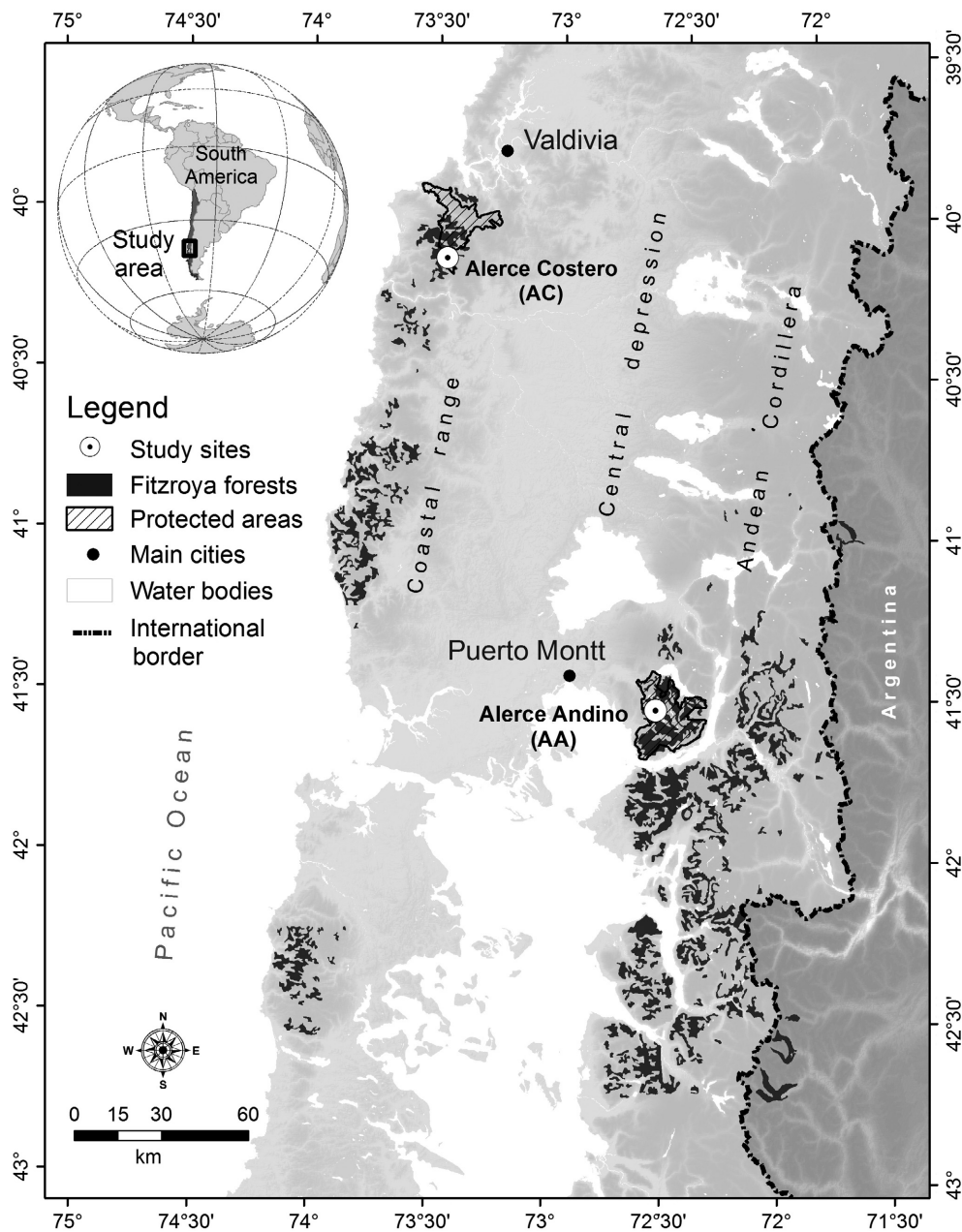
Fig. 1. Map of the study sites in the Coastal Range (AC) and Andean Cordillera (AA) of southern Chile.

in forests from both areas, (2) quantify annual fluxes of R_s, R_a, and R_h and the proportion of total respiration partitioned to these components in each site, (3) assess the soil environmental factors that might influence total respiration changes between the two studied years in each site, and (4) use a mass balance approach to estimate NPP_{fr} and compare belowground productivity in both areas.

MATERIALS AND METHODS

Study sites

Two 0.6-ha plots were installed in *Fitzroya* forests within the Alerce Costero National Park (AC) in the Coastal Range (40°10′ S, 73°26′ W) and within the Alerce Andino National Park (AA) in the Andean Cordillera (41°32′ S, 72°35′ W; Fig. 1).

Table 1. Soil features, nutrient contents, and forest stand characteristics in each study plot (Alerce Costero, AC1 and AC2; and Alerce Andino, AA1 and AA2).

Plot	EMSD† (cm)	Bulk density (g/cm³)	SOM (%)	C/N	N (%)	P (Olsen) ppm	K (ppm)	Density‡ (trees/ha)	BA§ (m²/ha)	AGB (Mg C/ha)	dbh¶ (cm)	H** (m)
AC1	63	0.75	9.57	34.5	0.17	3.1	72	1415	89	114.1	26.8	14.4
AC2	43	0.70	10.06	32.7	0.18	3.1	94.3	1408	87	112.8	26.7	14.1
AA1	72	0.16	78.70	113.2	0.40	5.2	470	782	171	447.5	132	31.8
AA2	94	0.22	59.99	83	0.43	7.2	553	722	193	517.1	141.8	30.8

Notes: Soil characteristics correspond to the surface horizons (a mix of organic and mineral soil, AC1: 23 cm, AC2: 16 cm, AA1: 18 cm, AA2: 20 cm), where most of the roots develop. SOM, soil organic matter; AGB, aboveground biomass.

† Effective mean soil depth (EMSD): soil depth where roots can potentially develop and extract water and nutrients without any apparent physical or chemical restriction.

‡ Density: Values include trees ≥10 cm diameter at breast height (dbh).

§ Basal area: Values include trees ≥10 cm dbh.

¶ Mean dbh of *Fitzroya* trees.

** Mean height of *Fitzroya* trees ≥30 cm dbh.

These plots were established with the purpose of measuring primary productivity and soil respiration in *Fitzroya* forests of different structure and origin, which were characteristic of these two ranges. Plots AC1 and AC2 were installed at 850 m a.s.l., and AA1 and AA2 at 760 m a.s.l. Weather stations were installed in open clearings at less than 1 km from the study plots in both areas. Climate in the coastal site is characterized by high annual precipitation (4860 mm during 2012), a mean annual temperature of ~7.26°C (~3.5°C and 11.9°C in winter and summer 2012, respectively), and a Mediterranean influence where most of the precipitation occurs in winter (~47% falling from June to August and ~9% from December to February, period 1999–2010; Veblen and Ashton 1982, DGA 2011). Climate in the Andes is characterized by an even higher precipitation amount (~6600 mm during 2012) and somewhat lower air annual temperatures than in AC (~6.89°C, and ~3.2°C and 10.7°C in winter and summer 2012, respectively). Summer precipitation (December–February) in AA was on average 1413 mm compared with 839 mm in AC (periods 2011–2012 and 2012–2013; Urrutia-Jalabert et al. 2015b).

Soils in the coastal site have a sandy loam texture, are derived from Pre-Cambrian to Paleozoic metamorphic rocks, and are generally thin, poor in nutrients, and severely podzolized (Veblen and Ashton 1982, Urrutia-Jalabert et al. 2015a). The soils have poor drainage conditions, but a low water retention capacity, and can get particularly dry during rainless periods (Barichivich 2005; V. Gerding, *personal communication*). Soils in the Andean site have a silty loam texture, are derived from volcanic parental material, have high C/N ratios, and contain high organic matter (Peralta et al. 1982, CONAF 1985; Urrutia-Jalabert et al. 2015a, Table 1). Soils in this site remain wet all year round.

The forest stands in AC are dense and mostly dominated by *Fitzroya* in terms of number and basal area (Table 1). These stands have been affected by fires in the past (a stand forming fire in 1681 and fire events leading to partial mortality and stand release probably in the 1800s and 1900s; Lara et al. 1999, Barichivich 2005, Urrutia-Jalabert et al. 2015c), so these slow-growing trees are not as large and old as expected for the species. The biggest trees are *Fitzroya* and reach up to ~86 cm in diameter. Other main species are *Drimys winteri* and two species from the *Nothofagus* genus (*Nothofagus nitida* and *Nothofagus betuloides*). The forest in AA is less dense in stem number and mostly dominated by *Fitzroya* in basal area and biomass (Table 1). The stand has over four times as much biomass (around 450–520 Mg C/ha); the largest *Fitzroya* trees reach up to 235 cm in diameter and the species is mainly accompanied by evergreen species where the most abundant are *N. nitida*, *Myrceugenia chrysocarpa*, and the conifer *Saxegothaea conspicua* (Urrutia-Jalabert et al. 2015a).

Soil carbon stocks reflect the contrasting environmental and stand structure conditions between sites. Carbon stocks in the upper horizon in the Andes are almost the double than in the Coastal site (124.7 Mg/ha compared with 64.8 Mg/ha), reflecting the slower dynamics of the old-growth

stand. Table 1 presents important features of the soils and forest structure in each plot.

Soil respiration measurements

Total soil CO_2 efflux was measured in permanent collars installed at the center of fifteen 20×20 m subplots within the plots in AC and AA. An infrared gas analyzer (IRGA) with a closed static chamber (EGM-4 IRGA and SRC-1 chamber; PP Systems, Amesbury, Massachusetts, USA) was used to measure total efflux for 2 min on every collar (11 cm diameter) inserted around 3–5 cm into the litter and/or organic layer. Due to the remoteness, difficult accessibility and mobility within the forests (especially in the Andean site) measurements were mainly taken between 9:00 and 17:00 hours. The sampling frequency was once a month mostly from August 2011 to August 2013 in AC and from October 2011 to May 2013 in AA. Measurements in both sites were taken within a week of each other. There were gaps in the collected data especially during winter months in AA, where bad weather and dangerous road conditions prevented the access to the study site. In the coastal site, gaps in winter months were mostly due to instrument failure under cold conditions. Soil surface temperature (12-cm temperature probe; Electronic Temperature Instruments, West Sussex, UK) and volumetric water content (12-cm Hydrosense probe; Campbell Scientific, Loughborough, UK) were measured at the same time as respiration at a distance of less than 50 cm from each collar. The height of the collar was recorded after each measurement.

The partitioning of autotrophic and heterotrophic respiration was estimated using tubes installed at the four corners of each 0.6-ha plot. A long (40 cm) PVC collar was inserted at least 30 cm into the soil where roots were previously removed in order to measure heterotrophic respiration. Roots were manually removed and the root free soil was carefully reinstalled back within the collar without mixing the horizons nor compacting the soil. Soil respiration measurements started from 1 day (one plot in the Andes) to 2 weeks after installation. We did not observe high fluxes in the collars 1 day after installation in the Andean site, so we decided to keep these measurements. A short collar inserted 3–5 cm into the soil was installed next to each long collar to measure total respiration. The difference between the effluxes coming from these two collars was considered an estimate of autotrophic respiration. This partitioning method has a limitation regarding the potential waterlogging caused by the deliberate removal of roots, which may suppress heterotrophic respiration. We address this limitation further below. Soil temperature and water content were also monitored during each respiration measurement. These partitioning measurements were less continuous than those of total respiration, ranging from October 2011 to August 2013 in AC and from November 2011 to May 2013 in AA, but with a longer gap during winter 2012.

Annual soil respiration estimates

Soil respiration fluxes per collar (μmol $CO_2 \cdot$ m$^{-2} \cdot$s^{-1}) were calculated from the rate of CO_2 concentration increase within the closed static chamber for a known period of time, following the procedures and formula presented in Marthews et al. (2012; gem.tropicalforests.ox.ac.uk). A diurnal temperature correction was applied afterward to convert spot measurements into estimates of daily mean respiration. Hourly soil respiration was calculated using hourly soil temperature measurements and the widely used Van't Hoff's formula (Davidson et al. 2006*b*):

$$R_2 = R_1 \exp^{b(T_2 - T_1)}$$

where R_2 corresponds to the hourly soil respiration after the temperature correction, R_1 to the soil respiration flux in each collar, T_2 to the hourly soil temperature record, and T_1 to the soil temperature at the time of measurement, and b is the regression coefficient for temperature sensitivity. We assumed a temperature coefficient $Q_{10} = 2$ for diurnal scale variation, which was considered appropriate at a short-time scale in a cold climate ecosystem (Lavigne et al. 2003). As $b = \ln(Q_{10})/10$, this corresponds to $b = 0.069$. The diurnal correction was very small, because of the small diurnal amplitude of soil temperature variations, reaching at the most 1°C during the warmest month in AA.

Mean respiration rates per plot (μmol $CO_2 \cdot$ m$^{-2} \cdot$s^{-1}) were obtained for the period November–May (spring to fall), when the four plots had almost complete measurements. Annual carbon budgets (in Mg C$\cdot$ha$^{-1} \cdot$yr^{-1}) were calculated by linear interpolation of fluxes between

measurement days. The annual periods considered were from the first measurement made in August 2011 to August 2012 (year 1) and from August 2012 to August 2013 (year 2). Gaps in spring months in AA2 were filled using values from AA1. Furthermore, values for the two gaps in the Andes at the beginning (August–September 2011) and end of the measurement period (June–August 2013) were assumed to be equal to values measured in October 2011 and May 2013, respectively. Fluxes in winter and early spring were particularly low, so gap filling assumptions did not have much influence on annual respiration budgets. Annual soil respiration was calculated separately for each of the 15 collars, and sampling uncertainty was estimated as the standard error of the mean across these 15 collars.

Due to the low number of measurement points for respiration partitioning, both plots from the same site were analyzed together (a total of eight long and short collars per site). As pointed out above, some long collars suffered waterlogging and their measurements had to be discarded (two collars from AC that were too close to the basal schist and were observed to have almost permanent standing water were not considered for further analysis). In the other collars that had no visual standing water, we saw no evidence of suppressed fluxes at high soil moisture content to warrant their exclusion. To estimate autotrophic and heterotrophic respiration for each site, the partitioning fractions determined from the experiment were multiplied by the total soil respiration obtained from the wider grid of soil respiration collars; that is, the partitioning data were only used to determine the proportion of total soil respiration assigned to R_h and R_a.

Error propagation was carried out for the partitioning components using standard rules of quadrature, assuming that uncertainties are independent and normally distributed (e.g., Malhi et al. 2014).

Relationship between CO_2 efflux and soil environmental conditions

Mid-summer (January and February) climate conditions in 2013 were particularly warmer and drier than conditions during the same period in 2012. Rainfall was 41% and 31% lower in AC and AA, respectively, and mean temperature was 1.98°C and 2.63°C warmer in AC and AA,

respectively. At a broader scale, maximum and minimum temperatures in southern Chile were above the climatological mean during January and February 2013; maximum temperatures during January in Valdivia (a lowland site close to AC) were up to 4.9°C warmer than the climatological mean (Quintana and Aceituno 2013). Due to these conditions, and since future climate is expected to be warmer and drier in the study areas (Fuenzalida et al. 2007), it was particularly interesting to assess any changes in soil respiration between these 2 yr.

To analyze total respiration responses to interannual changes in temperature and moisture in each site, the differences in soil temperature and water content between the same collar and month in both years (year 2 − year 1) were used as independent variables in a model to explain changes in the ratio of monthly respiration between both years (resp. year 2/resp. year 1) for each site. We did this to factor out the seasonal cycle of soil respiration, because seasonal patterns in phenology and microbial populations are likely to be uncorrelated with interannual and long-term relationships between environmental variables and respiration (Fenn et al. 2010). We applied a linear mixed model considering differences in temperature ($T_2 − T_1$), soil water content ($H_2 − H_1$), and plot, as well as their interactions as fixed terms and "month" as a random effect. Logarithmic transformation was applied to soil respiration ratios to achieve linearity. We used the protocol for model selection proposed by Zuur et al. (2009), and the chosen model was evaluated for normality and homoscedasticity in the residuals. Goodness of fit of the models was assessed using the marginal and conditional R^2, specially developed for generalized linear mixed effects models by Nakagawa and Schielzeth (2013). Marginal R^2 (R^2_{mar}) corresponds to the variance explained by fixed factors and conditional R^2 (R^2_{con}) to the variance explained by both random and fixed effects (Nakagawa and Schielzeth 2013). Relationships were calculated considering all the months as well as just the period November–May in each study site. To test the relationship between soil respiration and temperature and to compare with the wider literature, the Q_{10} coefficient was calculated for the studied period.

The Van't Hoff relationship (equation above) was used to calculate the interannual temperature

sensitivity, where b is the slope of the relationship of $\ln(R_2/R_1)$ against $(T_2 - T_1)$, and $Q_{10} = \exp^{10b}$. A linear mixed model with month as a random effect was also applied in this case.

Mass balance estimation of root productivity

This study formed part of a broader research program that quantified the productivity and carbon cycle of *Fitzroya* forests in these two sites (Urrutia-Jalabert et al. 2015a). Given the availability of heterotrophic respiration measurements and carbon inputs to the soil, a mass balance approach could be applied to estimate fine root production. Carbon (C) inputs to the soil (root mortality and litterfall) are assumed to correspond with belowground outputs (R_h, and dissolved organic C in water, DOC), including any alteration in soil C stocks (Malhi et al. 2009, Fenn et al. 2015). We recognize there are a number of assumptions and uncertainties in these calculations and apply conservative uncertainty estimates around each assumed parameter.

In this analysis, the period November 2011–October 2012 was used, since R_h/R_a respiration measurements started this month in both sites and more reliable estimates can be obtained with less gaps in the annual data. We assumed quasi-equilibrium conditions on an annual timescale, that is, no net accumulation or loss of belowground carbon. The use of only 1 year of data was mainly because we cannot assume multiyear steady state conditions in the coastal site, due to different amounts of litterfall in the two studied years (Urrutia-Jalabert et al. 2015a), and warmer and drier conditions during the second summer. NPP_{fr} (Mg C·ha^{-1}·yr^{-1}) in each study site was estimated as follows:

$$NPP_{fr} = R_h - \text{Litterfall} - (\text{Mort}_{AG} + NPP_{bf}) \\ \times F_{cwd} - \text{Mort}_{BG} + F_{DOC} + \Delta C$$

where R_h is the soil heterotrophic respiration for the period November 2011–October 2012 in AC or AA. Litterfall corresponds to the mean annual amount of litterfall collected in both plots from each site. Mort_{AG} corresponds to the mean aboveground mortality and NPP_{bf} to the mean productivity associated with branchfall in both plots from each site. Litterfall, Mort_{AG}, and NPP_{bf} were obtained from Urrutia-Jalabert et al. (2015a) and are listed in Appendix S1: Table S1. F_{cwd}

corresponds to the fraction of coarse woody debris (CWD) entering the soil (not lost through in situ respiration). Mort_{BG} is the belowground mortality which enters the soil and was determined as 6.9% of aboveground mortality (equivalent to the coarse root/aboveground biomass ratio found in *Fitzroya* forests from Chiloé Island; Battles et al. 2002). We applied a conservative uncertainty estimate for this parameter (±75%), that is, $\text{Mort}_{BG} = 0.069 \pm 0.052$. Finally, we assumed that aqueous carbon leakage (F_{DOC}) and the net change in carbon stocks (ΔC) were zero or insignificant terms on an annual basis.

F_{cwd} has been rarely measured. Malhi et al. (2009) estimated F_{cwd} to be 0.24 ± 0.15 in lowland Amazon rainforests and Fenn et al. (2015) assumed a value of 0.25 ± 0.25 in a temperate broad-leaved woodland in the UK, with a large (100%) uncertainty. Given the lack of information, in our study we assumed the value adopted by Fenn et al. (2015), and since material derived from CWD is not a very large component in our plots, this assumption would not have important effects in the final estimations. We applied a rigorous uncertainty propagation procedure throughout using uncertainty propagation by quadrature, as in Malhi et al. (2009, 2014).

Additionally, mean fine root biomass (≤2 mm diameter) was estimated from five cores (11 × 30 cm) extracted from the four corners and center of each plot in August–November 2011. Live and dead roots were manually removed from the soil in six 10-min time steps, washed as soon as possible, oven-dried for 48 h (at 60°C), and weighed. Calculation of the total biomass was made following a method that fits a curve to the cumulative dry root mass in order to estimate the amount of unsampled roots (Metcalfe et al. 2007).

Fine root residence time was calculated dividing fine root biomass by productivity and fine root carbon use efficiency was calculated as the ratio between fine root productivity and the sum of this productivity plus belowground autotrophic respiration.

Statistical analyses

The significance of the difference in total soil respiration between sites was tested for each year considering a nested design, with plots nested within sites. A linear mixed model with sites as fixed and plots as random effects was used.

This allows accounting for the soil respiration measurements within plots as possible pseudo-replicates. The same approach was employed to detect differences in R_s and soil temperature and water content between both summers (end of December to end of February, where the highest fluxes were recorded). A paired t test was used to assess differences in soil heterotrophic and autotrophic respiration between both sites during each year. All statistical analyses were performed using the R statistical environment (R Development Core Team 2014), and the "lme" function from the "nlme" package was used to perform the linear mixed models (Pinheiro et al. 2014).

RESULTS

Seasonal patterns in soil respiration

Seasonal variation in soil respiration showed the expected pattern of higher values during summer months in both study sites. There is not much information for winter months in the Andean site, but it is possible to observe that R_s values during these months were much lower than during the rest of the year (Fig. 2). These patterns broadly correspond with soil temperature variations, with higher R_s values occurring when higher soil temperatures were recorded. Moreover, high R_s values in AC corresponded with periods of particularly lower soil water content, especially during January 2013, when the highest R_s value ($\sim$4.8 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) coincided with the highest soil temperature ($\sim$14.7°C) and the lowest soil water content recorded during the studied period ($\sim$24%; Fig. 2). In the Andean plots, higher R_s during both summers was also associated with higher temperatures and lower soil water contents (Fig. 2). It is noticeable how soil conditions from the end of December 2012 to February 2013 were significantly different (warmer and drier) than the previous summer in the coastal site ($P < 0.05$), leading to particularly high respiration values during this period. Soil respiration was significantly different between both summers in AC ($P < 0.05$), a pattern that was not reproduced in the Andes ($P > 0.05$).

Despite similar elevations at the two sites, summer soil temperatures were higher in the coastal site (10.9–12.7°C during 2011–2012 and 2012–2013, respectively) compared with the Andes (10–9.8°C during 2011–2012 and 2012–2013, respectively) and soil water contents were much lower in the former site along the studied period (monthly means of 24–43% in AC compared to 44–61% in AA; Fig. 2).

Autotrophic and heterotrophic respiration showed the same pattern as total respiration with higher values during summer in both sites, and especially during the second growing season in AC (2012–2013; Fig. 3). Monthly R_a was higher than R_h respiration for most of the studied period in AC, and this was especially the case for summer 2012–2013. The opposite was true in AA, where monthly heterotrophic respiration was higher than root respiration for most of the recorded period (Fig. 3).

Total soil, autotrophic, and heterotrophic respiration

Annual R_s values were lower in AA (5.06–6.14 Mg C·ha^{-1}·yr^{-1}) than in AC plots (6.37–6.66 Mg C·ha^{-1}·yr^{-1}) during the 2011–2012 period and significantly lower (4.98–5.35 Mg C·ha^{-1}·yr^{-1} compared with 8.08–8.64 Mg C·ha^{-1}·yr^{-1}, $P < 0.05$) during the 2012–2013 period, when the AC values rose dramatically (Table 2). Mean respiration values obtained for November–May were not significantly different between the two sites for the period 2011–2012, but they were significantly different during the following year (2.59–2.79 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ in AC compared to 1.63–1.79 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ in AA, $P < 0.05$; Table 2). We estimated that respiration during November–May represented 68–70% and 71–74% of total annual soil respiration during 2011–2012 in AC and AA, respectively. For 2012–2013, these proportions were 71% and 71–73% in AC and AA, respectively. Annual R_a was lower in AA (2.68 ± 0.36 Mg C·ha^{-1}·yr^{-1}) than in AC (3.38 ± 0.64 Mg C·ha^{-1}·yr^{-1}, difference not significant) during 2011–2012 and significantly lower during 2012–2013 (2.09 ± 0.29 compared with 4.68 ± 0.63 Mg C·ha^{-1}·yr^{-1}, $P < 0.05$; Table 2). Heterotrophic respiration was similar during the first year in both sites ($\sim$3.14 Mg C·ha^{-1}·yr^{-1}) and a little lower in AA (3.13 ± 0.33 Mg C·ha^{-1}·yr^{-1}) than in AC (3.65 ± 0.54 Mg C·ha^{-1}·yr^{-1}) during the second period, although values were not significantly different ($P > 0.05$). Finally, the proportion R_a/R_s was higher in AC (51.8–56.2%) than in AA (46.1–39.9%; Table 2) for the two studied years.
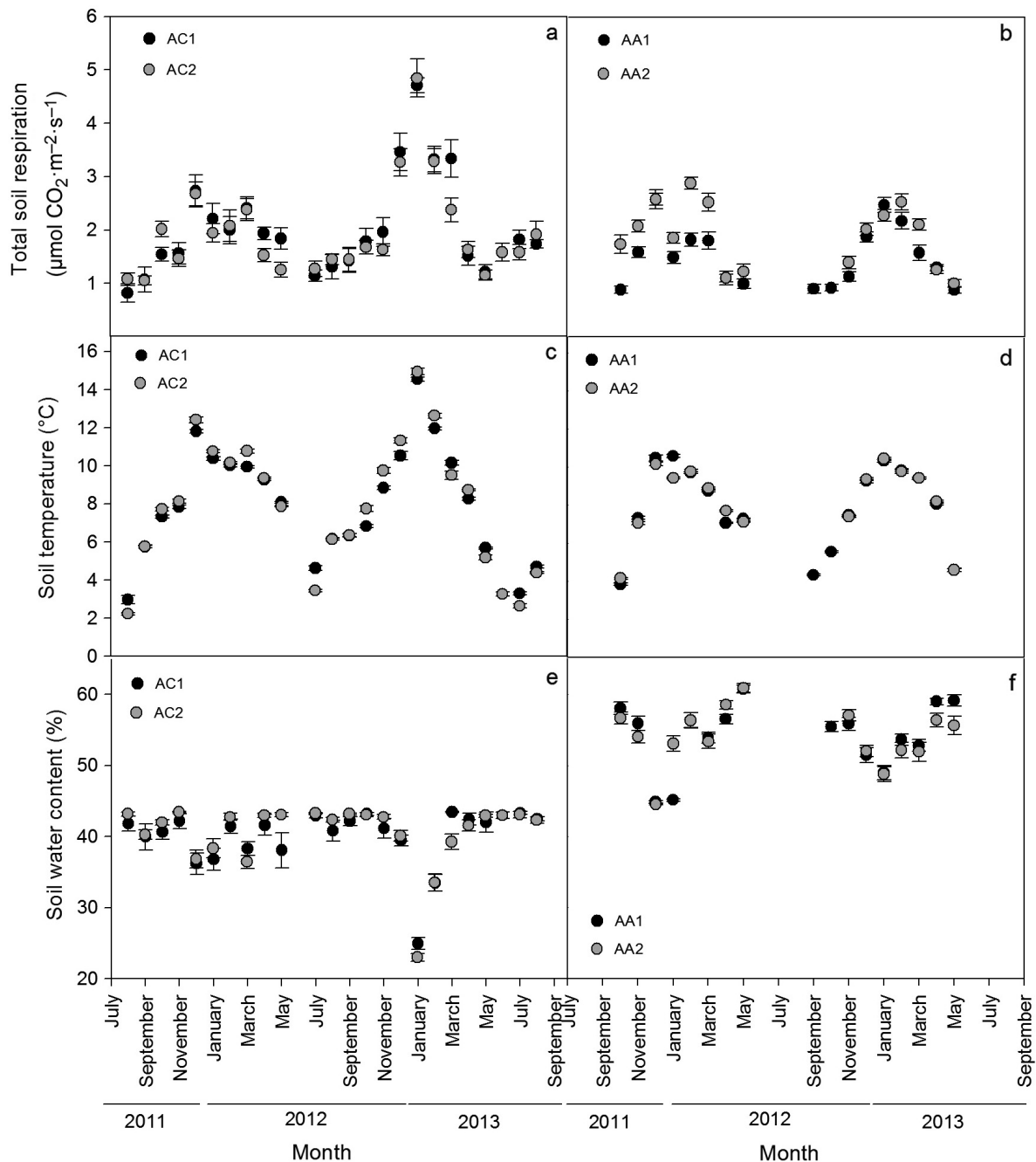
Fig. 2. (a) Total soil respiration discrete measurements in Alerce Costero plots (AC1, AC2) and (b) Alerce Andino plots (AA1, AA2) mainly from August 2011 to August 2013. (c, d) Soil temperatures measured at the same time as soil respiration, and (e, f) soil water content also monitored during each respiration measurement.

Sensitivity of soil respiration to soil temperature and water content

The outputs from the linear mixed model in AC included both the difference in soil temperature ($T_2 - T_1$) and water content ($H_2 - H_1$), as well as the interaction between both terms as variables significantly explaining the ratio of monthly soil respiration between both years (Table 3). The
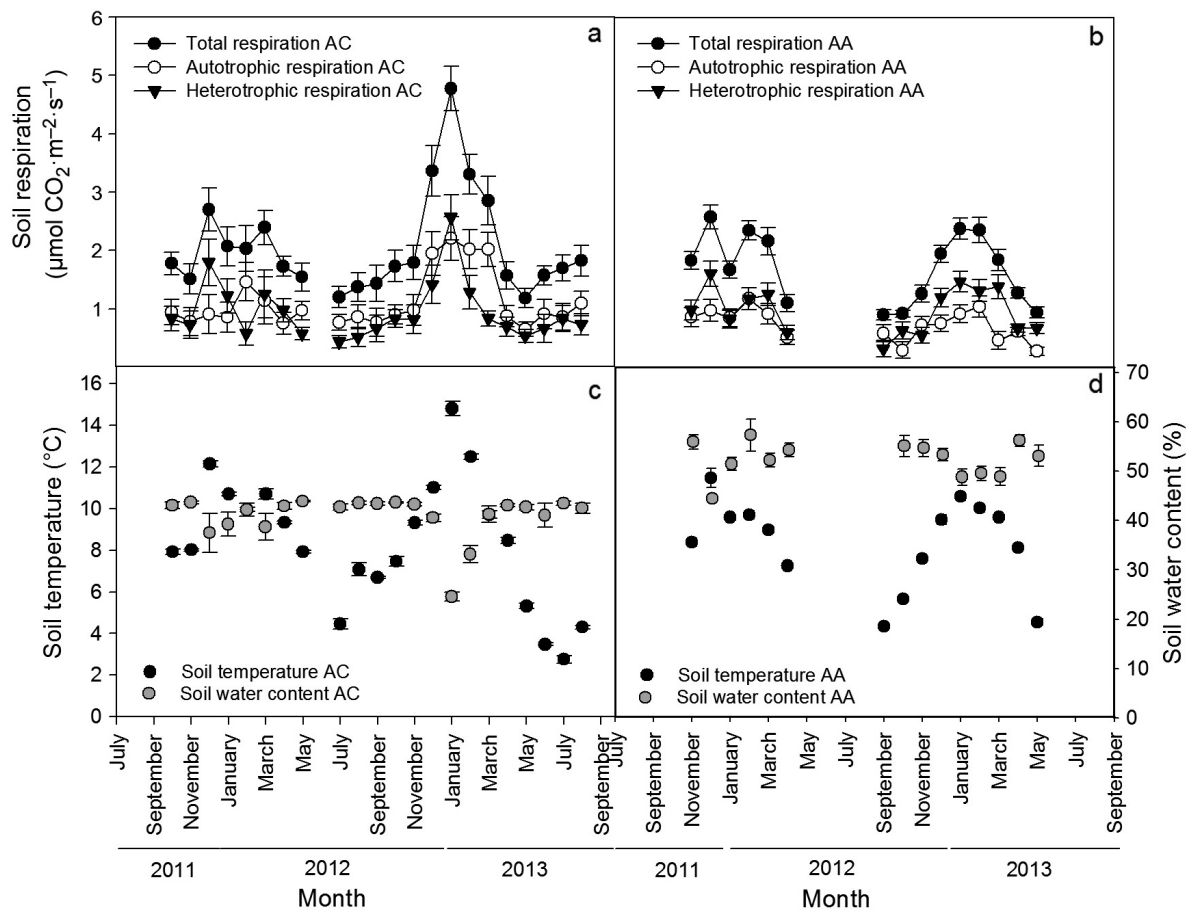
Fig. 3. (a) Total (R_s), heterotrophic (R_h), and autotrophic (R_a, total minus heterotrophic) respiration in Alerce Costero (AC) and (b) Alerce Andino (AA) covering the period October/November 2011 to May/August 2013. (c) Soil temperature and water content measured at the same points and time as soil respiration in AC; (d) the same as (c), but for AA.

goodness of fit of this model was $R^2_{mar} = 0.28$ and $R^2_{con} = 0.36$ and was much higher when just considering the period November–May which mainly excludes winter in the analysis ($R^2_{mar} = 0.42$ and $R^2_{con} = 0.47$; Table 3). The interaction term mainly

indicates that low soil humidity conditions during year 2 intensified the effect of warmer temperatures on higher respiration rates. If the ratio of respiration between years was ascribed to temperature alone, R^2_{mar} values were much lower than

Table 2. Total annual and mean November–May soil respiration (R_s) in each plot for the two studied periods. Annual autotrophic respiration (R_a) and heterotrophic respiration (R_h) are also presented for each site (Alerce Costero [AC] and Alerce Andino [AA]) and the proportion of autotrophic to total soil respiration.

Plot/ period†	Annual R_s (Mg C·ha^{-1}·yr^{-1})		Mean November–May R_s (µmol CO$_2$·m^{-2}·s^{-1})		Annual R_a (Mg C·ha^{-1}·yr^{-1})		Annual R_h (Mg C·ha^{-1}·yr^{-1})		Proportion R_a/R_s (%)	
	1	2	1	2	1	2	1	2	1	2
AC1	6.66 ± 0.58	8.64 ± 0.73	2.09 ± 0.23	2.79 ± 0.25	3.38 ± 0.64	4.68 ± 0.63	3.14 ± 0.54	3.65 ± 0.54	51.8 ± 10.7	56.2 ± 8.70
AC2	6.37 ± 0.47	8.08 ± 0.54	1.89 ± 0.20	2.59 ± 0.22						
AA1	5.06 ± 0.33	4.98 ± 0.29	1.62 ± 0.13	1.63 ± 0.11	2.68 ± 0.36	2.09 ± 0.29	3.14 ± 0.37	3.13 ± 0.33	46.1 ± 6.73	39.9 ± 5.92
AA2	6.14 ± 0.31	5.35 ± 0.25	2.03 ± 0.13	1.79 ± 0.11						

† Period 1 corresponds to 2011–2012 and period 2 to 2012–2013.

Table 3. Models of total soil respiration (monthly ratio between year 2 and year 1, R_2/R_1) in relation to the difference in soil temperature and water content between both years for Alerce Costero (AC).

Site	N	a	b	c	d	Residual variance	Random intercept variance	Q_{10}	R^2_{mar}/R^2_{con}
AC	287	0.130	0.116	0.019	−0.009	0.194	0.024	...	0.28/0.36
AC$_{Nov–May}$	186	0.101	0.132	0.015	−0.008	0.171	0.018	...	0.42/0.47
AC	290	...	0.125	...	...	0.203	0.057	3.49	0.20/0.38
AC$_{Nov–May}$	189	...	0.148	...	...	0.178	0.049	4.39	0.32/0.47

Notes: Models including all data available from August 2011 to August 2013 and just including the period November–May are shown in the upper two rows. Models only including the difference in temperature as an independent variable, in order to calculate a Q_{10} value, are presented in the bottom two rows. N (number of data points), the residual variance, random intercept variance, Q_{10} and marginal and conditional R^2 (R^2_{mar} and R^2_{con}) are included. a, b, c, and d correspond to the intercept, and coefficients for the difference in temperature ($T_2 − T_1$), soil water content ($H_2 − H_1$), and the interaction between them ($T_2 − T_1$) ($H_2 − H_1$), respectively.

when also considering soil water content effects (0.20 and 0.32 for the whole year and the period November–May, respectively; Table 3). In addition, the Q_{10} values were 3.49 ± 1.01 and 4.39 ± 1.40 considering either all months or the period November–May only, respectively (Table 3). In AA, none of the environmental terms significantly explained soil respiration, so results are not presented. Warmer soil temperatures and lower soil water contents during the second year produced significantly higher respiration rates in the coastal site, but not in the Andes where soil conditions were not particularly different between both summers and pronounced changes in respiration were not observed (Fig. 4).

Fine root production estimation

Our mass balance-based estimates of NPP$_{fr}$ in AC and AA for the period November 2011–October 2012 were 0.81 ± 0.60 and 1.50 ± 0.42 Mg C·ha^{-1}·yr^{-1} in AC and AA, respectively (Table 4). Due to the relatively large error term, calculated differences between sites are not significant.

The estimates of fine root biomass were almost the double in the Coastal Range site than in the Andes (~21–22 vs. 10–12 Mg C/ha, respectively; Table 4). Therefore, mean estimates of fine root residence times are much larger in AC than in AA (Table 4). The low productivity but high fine root biomass suggests very long fine root lifetimes in these forests, especially in the Coastal Range site.

DISCUSSION

In this paper, we have assessed seasonal patterns and annual fluxes of total soil respiration

and its autotrophic and heterotrophic components in two *Fitzroya* stands from southern Chile. We have assessed the soil environmental variables that were mostly related to total respiration and have employed a mass balance approach that uses heterotrophic respiration and soil carbon inputs, to estimate fine root productivity in each study site.

Seasonal and annual CO_2 effluxes in total respiration and its partitioning

Seasonal variability in soil respiration in both sites was characteristic of patterns observed in other temperate systems, where higher respiration rates correspond with warmer summer conditions (Curiel Yuste et al. 2004, Sulzman et al. 2005, Fenn et al. 2010, Ngao et al. 2012).

General weather conditions were warmer and drier during summer 2012–2013 than in the previous year, but this translated into significantly warmer soil temperatures and lower soil water contents only in AC. There was a notable increase in soil respiration in AC over the warm and dry summer, probably due to the increased diffusion and contact surface for oxygen in pore spaces in these usually wet soils, increasing the rates of aerobic respiration (Davidson et al. 1998). Sites such as AC that are normally wet, but that occasionally dry considerably during summer, can experience a large increase in microbial and autotrophic respiration (Davidson et al. 1998). Moreover, the increase in CO_2 effluxes under drier conditions in this site could also be reflecting a higher diffusion rate (Schwendenmann et al. 2003, Wood et al. 2013).

Most studies in temperate forests report lower respiration rates when drier conditions occur, due to slower nutrient transport and reduced
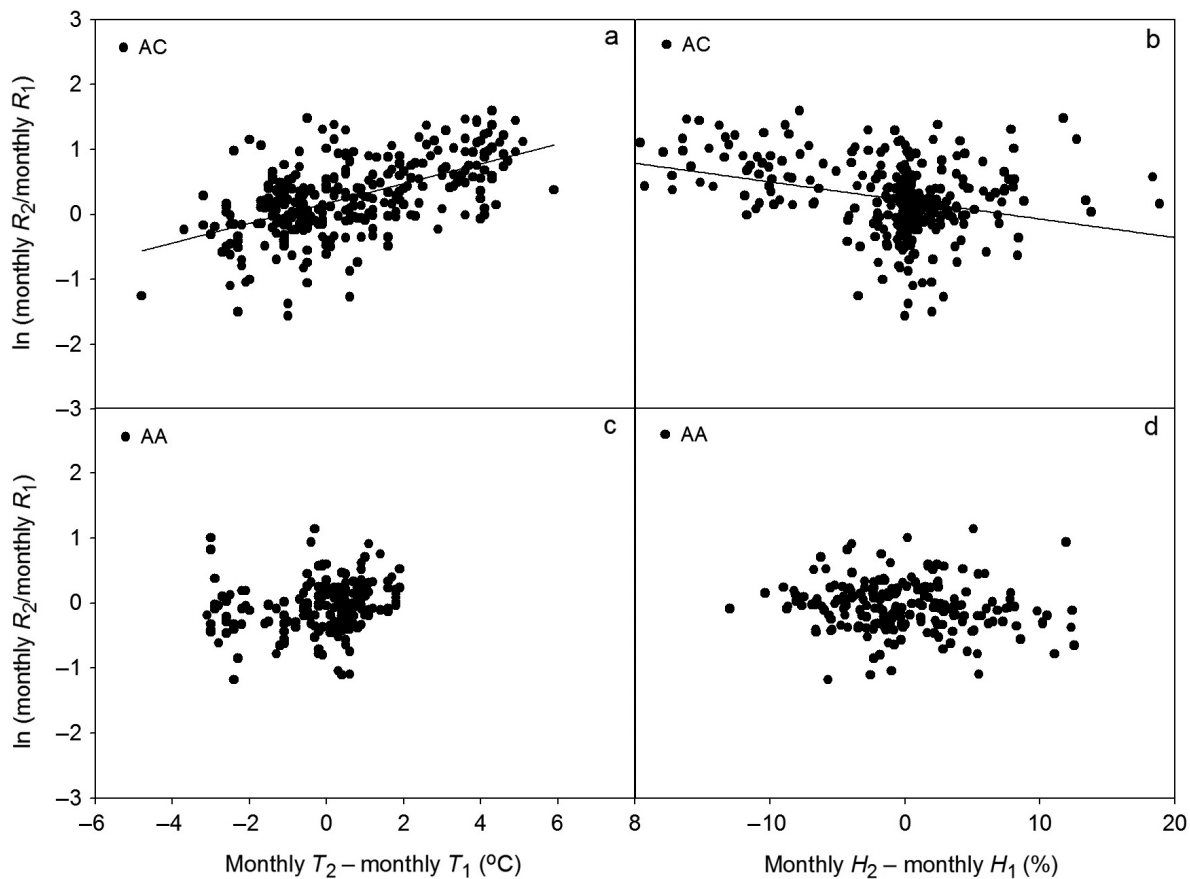
Fig. 4. (a, c) Relationship between soil temperature ($T_2 - T_1$) and soil respiration (ln (R_2/R_1)) in Alerce Costero (AC) and Alerce Andino (AA), respectively. (b, d) Relationship between soil water content ($H_2 - H_1$) and soil respiration (ln (R_2/R_1)) in AC and AA, respectively. R_2 and R_1 correspond to soil respiration recorded in each collar during each month in years 2 and 1, respectively, and the same applies to temperature (T_2 and T_1) and soil water content (H_2 and H_1). The straight lines reflect the direction of the relationship between the environmental variables and the natural logarithm (ln) of (R_2/R_1). The statistics of the combined effect of ($T_2 - T_1$) and ($H_2 - H_1$) on ln (R_2/R_1) are presented in Table 3.

and less active microbial populations (Singh and Gupta 1977, Davidson et al. 1998, Savage and Davidson 2001, Irvine and Law 2002, Lavigne et al. 2004, Fekete et al. 2014). However, soil water contents along the year never dropped below 24% and 44% in the Coastal and Andean sites, respectively. These values are well above the 12–15% threshold below which a positive response of soil respiration to water content has been reported for temperate forests in the United States and Europe (Davidson et al. 1998, Ruehr et al. 2010). This would indicate that in these

Table 4. Fine root biomass, fine root productivity (NPP_fr), and fine root mean residence time in each of the study sites (Alerce Costero, AC; and Alerce Andino, AA).

Site	Fine root biomass (Mg C/ha)	NPP_fr (Mg C·ha^{-1}·yr^{-1})	Fine root residence time (yr)
AC	21.3 ± 1.1; 22.2 ± 1.6	0.81 ± 0.60	26.4 ± 19.6; 27.4 ± 20.4
AA	10.1 ± 1.4; 12.1 ± 2.2	1.5 ± 0.42	6.7 ± 2.1; 8.04 ± 2.7

Note: The two values shown for biomass and residence times correspond to the two plots per site.

normally wet *Fitzroya* sites (more than 4800 mm of annual rainfall), water content probably rarely falls below a threshold that would negatively influence soil respiration even during summers.

Annual total soil respiration estimates during the first year in both sites (5.06–6.66 Mg C·ha^{-1}·yr^{-1}) were lower than the values reported for an old-growth coniferous forest in Oregon (7.27–8.41 Mg C·ha^{-1}·yr^{-1}; Sulzman et al. 2005), lower than the mean value recorded for evergreen (mostly coniferous) forests along an altitudinal gradient in Europe (7.72 Mg C·ha^{-1}·yr^{-1}; Rodeghiero and Cescatti 2006), and similar to fluxes modeled for an old-growth Ponderosa Pine forest in the drier eastern Cascades, Oregon (4.83–5.97 Mg C·ha^{-1}·yr^{-1}; Irvine and Law 2002). Values during both years were within the broad range of values reported for temperate coniferous forests from the northern hemisphere (4.27–18.05 Mg C·ha^{-1}·yr^{-1}; Hibbard et al. 2005) and much lower than the values reported for high biomass and old-growth stands in temperate rainforests of western Oregon (10.8–20.7 Mg C·ha^{-1}·yr^{-1}; Campbell and Law 2005).

Higher annual respiration amounts in AC than in AA were primarily due to higher R_a in the coastal site than in the Andes (significantly higher during the second year). This is consistent with differences in root biomass between sites, since positive correlations have been reported between R_a and root biomass in temperate forests (Wang and Yang 2007).

R_h was generally higher than R_a in the Andes and there were no significant differences with the coastal site in the two studied years. The accumulation of organic matter inputs throughout time due to larger and older trees and higher rates of mortality in the Andean forests could result in relatively higher heterotrophic respiration in this site (Saiz et al. 2006, Urrutia-Jalabert et al. 2015*a*).

Limitations in total respiration estimates and its partitioning

One possible bias to consider is that total soil respiration in these sites may have been overestimated in the short term (after a few weeks) due to root mortality and decomposition (Keller et al. 2000) or underestimated in the long term because of collar insertion cutting roots and reducing root biomass and autotrophic respiration (Heinemeyer et al. 2011). However, roots were not cut with a knife in our setup, and are likely to just have been displaced downward rather than cut with collar insertion. Most soil respiration studies with which we compare our results apply a similar methodology and do not correct for this effect, so relative comparisons are still valid.

The bias associated with the potential waterlogging in the partitioning experiment was a concern especially in Alerce Costero due to the shallow soils on top of schist. We tried to minimize the effect of waterlogged soils on R_h estimates by not considering the points that had water build-up within the collars. It is still possible that other collars were waterlogged below the soil surface; however, we did not monitor soil moisture within individual collars. While recognizing this as a potential bias, we note that our R_a/R_h ratio estimate in both sites of around 1:1 is typical of the range found in other temperate forests (Epron et al. 2001, Irvine and Law 2002, Lavigne et al. 2003, Ruehr and Buchmann 2010).

Finally, it is possible that soil disturbance caused by root removal at the setup of the partitioning experiment would cause increased fluxes immediately after installation, followed by a gradual decline (Hanson et al. 2000). Two days has been reported to be enough for CO_2 rates to stabilize after root removal in larger soil volumes than the ones used in our experiment (Edwards 1991). However, we did not observe high fluxes 1 day after collar installation, and when analyzing trajectories in R_h over the 2 yr, we found no evidence of such a pattern in the flux data (Appendix S1: Fig. S1).

Sensitivity of soil respiration to soil temperature and water content

Our study allowed the assessment of differences between sites in their soil respiration response to drier and warmer weather conditions, which are expected to increase in frequency under climate change. The soil respiration ratio between both years (R_2/R_1) was sensitive to soil temperature differences, as well as to soil water content differences and the interaction between them in AC. A strong influence of differences in temperature was expected, because most biological processes correlate with soil temperature in moist temperate ecosystems (Wang and Yang 2007). The strong decline in soil water content in AC during

summer (covarying with a sharp increase in temperature) led to a strong increase in respiration and a high apparent Q_{10}. The apparent Q_{10} values found in AC (3.49–4.39) were higher than the values reported for other coniferous forests growing under milder conditions (1.49–3.0; Campbell and Law 2005, Sulzman et al. 2005), but they were within the range of values reported for temperate forests in a global database (2.1–6.3; Bahn et al. 2010). Occasional drier conditions in usually wet sites can lead to higher Q_{10} values (Davidson et al. 1998). This is because in wet ecosystems substrate availability can increase at warmer temperatures when drier soils have a larger effect on redox conditions rather than on the diffusion of substrates (Davidson et al. 2006b). It is important to note that Q_{10} values in this study are approximations, since they were calculated with interannual temperature variations much lower than 10°C and relationships can change when considering larger temperature ranges.

In contrast to the Coastal Range site, at the Andean site interannual changes in soil temperature and water content were not large enough to cause a significant response in soil respiration. This suggests that this site seems more resilient to climate change due to the larger amounts of annual and summer precipitation, the reduced transpiration under frequent cloudy conditions, and the greater retention properties of the soils.

Soil respiration, root biomass, and root productivity

Our mean fine root biomass estimates (22.2 ± 1.6 and 21.3 ± 1.1 Mg C/ha in AC1 and AC2 and 10.1 ± 1.4 and 12.1 ± 2.2 Mg C/ha in AA1 and AA2) are higher than the mean recorded for temperate coniferous forests in a global study (8.2 Mg/ha; Jackson et al. 1997). These values are also higher or, in the case of the Andean site, in the range of indirect biomass estimates for old-growth wet forests from the Pacific Northwest (5.2–12.6 Mg C/ha; Smithwick et al. 2002). High fine root biomass values in AC are probably associated with the predominantly low nutrient conditions and poor water retention properties of the soils (Table 1), which is consistent with the widely reported negative correlation between root biomass and soil fertility conditions (Yuan and Chen 2010). Given the higher fine root biomass and the lower (or somewhat similar) root

productivity in the coastal site compared with the Andes, the fine root residence time appears much longer in the younger forests from the Coastal Range. Long-lived fine roots in *Fitzroya* are supported by a number of studies that report fine roots to present decadal turnover timescales in temperate forests (Gaudinski et al. 2001, 2010, Riley et al. 2009).

Fine root production estimates in both sites are below the mean reported for temperate forests in a global study (~2.14 Mg C·ha^{-1}·yr^{-1}; Finér et al. 2011), and these low values are consistent with the overall low estimates of aboveground productivity reported for these forests (3.35–3.36 and 2.22–2.54 Mg C·ha^{-1}·yr^{-1} in AC and AA, respectively; Urrutia-Jalabert et al. 2015a). Fine root production may be low due to the high exchangeable aluminum content in both sites that can prevent cell division and root elongation (Lambers et al. 2008, Urrutia-Jalabert et al. 2015a).

Fine root production was also well below total belowground carbon allocation (TBCA) as defined by Raich and Nadelhoffer (1989), suggesting that fine root production was considerably lower than root respiration. Fine root carbon use efficiencies reached 0.19 and 0.36 in AC and AA, respectively. The Andean value is close to the fine root production/TBCA ratio obtained for some deciduous and coniferous forests in the United States (0.33; Nadelhoffer and Raich 1992), and both estimates are much lower than the mean belowground carbon use efficiency (including fine and coarse roots) found for mature forests (0.47; Chen et al. 2011) and for forests in a temperature gradient worldwide (0.5; Litton and Giardina 2008). A likely explanation for the low fine root carbon use efficiency particularly in the coastal site could be the high fine root biomass found in these forests, which could cause higher rates of maintenance respiration per unit ground area (McDowell et al. 2001, Chen et al. 2011). The apparent extraordinary longevity of the fine roots, particularly in the AC site, may also require greater investment in root maintenance and defense against herbivores and pathogens, rather than investment in growth. It is also possible that if there was any underestimate of R_h (caused by non-apparent waterlogging, for example), this would lead to an underestimate of fine root productivity and thereby of fine root carbon use efficiency.

How much is our difference between sites affected by forest age and stand structure rather than by environmental conditions? Litter inputs to soil were higher and fine root production was lower in the younger than in the old studied forest, as would be expected if this aggrading forest is allocating more carbon aboveground due to more intense competition for available light (Urrutia-Jalabert et al. 2015*a*). Mortality (in terms of stem number or biomass) was higher in the older forest, mainly because the *Nothofagus*-dominated "sub-canopy" is closer to a dynamic equilibrium, where mortality balances growth, while the younger forest has not reached this stage (Urrutia-Jalabert et al. 2015*a*). Hence, it is likely that stand age effects partially explain differences in soil carbon dynamics between sites. However, we suspect the large environmental differences between sites (i.e., AC forests growing in an occasionally water-stressed climate with infertile, shallow soils with poor water retention properties) are probably the major reason for differences in soil carbon dynamics between sites.

CONCLUSIONS

To our knowledge, there have been no other medium-term (more than a year) field studies on the soil carbon fluxes in temperate ecosystems of southern South America. Therefore, this study contributes to understanding how these particularly humid ecosystems may in principle respond to interannual variability. Our study points out the potential for strong interannual variability in the CO_2 effluxes emitted especially by medium-age *Fitzroya* forests growing in the Coastal Range of southern Chile, but less variability in the more humid climate and soils of the Andean Range. Warmer and drier weather conditions significantly influence the soil environment at the Coastal Range and lead to higher respiration rates in this wet site. However, much stronger drying under the projected climate change scenario could cause the opposite effect (Davidson et al. 1998).

Our measured CO_2 effluxes in *Fitzroya* forests are at the lower end of values reported for other mature and old-growth wet temperate forests in the world. *Fitzroya* forests also show slower fine root dynamics. These features could be due to the longevity of the dominant trees as well as the very rainy and poor soil conditions where these forests grow. There seems not to be a significant difference in soil respiration between forests of different ages growing under different environmental conditions, but differences appear when climate changes and the site with more restrictive conditions increases CO_2 effluxes. Therefore, the underlying environment is a key factor to consider when evaluating forests responses to a changing climate.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1640/full