Soil CO$_2$ efflux in an old-growth southern conifer forest (*Agathis australis*) – magnitude, components, and controls

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Abstract

Total soil CO_2 efflux and its component fluxes, autotrophic and heterotrophic respiration, were measured in a native forest in northern Aotearoa-New Zealand. The forest is dominated by *Agathis australis* (kauri) and is on an acidic, clay rich soil. Soil CO_2 efflux, volumetric soil water content and soil temperature were measured bi-weekly to monthly at 42 sampling points over 18 months. Trenching and regression analysis was used to partition total soil CO_2 efflux into heterotrophic and autotrophic respiration. The effect of tree structure was investigated by calculating an index of local contribution (I_c, based on tree size and distance to the measurement location) followed by correlation analysis between I_c and soil CO_2 efflux, root biomass, litterfall and soil characteristics. The measured mean total soil CO_2 efflux was 3.47 μmol m^{-2} s^{-1}. Autotrophic respiration accounted for 25% (trenching) or 28% (regression analysis) of total soil CO_2 efflux. Using uni- and bivariate models showed that soil temperature was a poor predictor of the temporal variation in total soil CO_2 efflux (< 20%). In contrast, a stronger temperature sensitivity was found for heterotrophic respiration (around 47%). We found significant positive relationships between kauri tree size (I_c) and total soil CO_2 efflux, root biomass and mineral soil CN ratio within 5-6 m of the sampling points. Using multiple regression analysis revealed that 97% of the spatial variability in total soil CO_2 efflux in this kauri dominated stand was explained by root biomass and soil temperature. Our findings suggest that biotic factors such as tree structure should be investigated in soil carbon related studies.

Keywords: autotrophic and heterotrophic respiration, collar insertion, organic layer, litterfall, root biomass, soil water content, soil temperature, tree structure, trenching, New Zealand

1 Introduction

Soil CO_2 efflux (soil respiration) is the largest CO_2 flux from terrestrial ecosystems into the atmosphere (Raich and Potter, 1995; Janssens et al., 2001a; Bond-Lamberty and Thomson, 2010a). Quantifying the magnitude of soil CO_2 efflux and examining the spatial and temporal heterogeneity is critical in characterising the carbon (C) dynamics in terrestrial ecosystems (Schlesinger and Andrews, 2000; Trumbore, 2006; Smith and Fang, 2010) as even a small change in soil CO_2 efflux could have a strong impact on atmospheric CO_2 concentration (Andrews et al., 1999; Rustad et al., 2000). Advancing the understanding of soil CO_2 efflux and its driving factors is also important to predict the effects of land-use conversion and climate change on the net C sink of the terrestrial biosphere (Giardina et al., 2014).

Soil CO_2 efflux varies widely in space and time according to changes in various abiotic and biotic factors. Soil temperature is often the main abiotic factor explaining the temporal variability of soil CO_2 efflux (Raich and Schlesinger, 1992; Jassal et al., 2005; Bond-Lamberty and Thomson, 2010b). Many studies show a positive correlation between soil temperature and soil CO_2 efflux (Reich and Schlesinger, 1992; Lloyd and Taylor, 1994; Rustad et al., 2000). This relationship is often expressed as a Q_{10} function (relative increase in soil CO_2 efflux rate per 10°C difference) (van't Hoff, 1898) or modified Arrhenius function (Lloyd and Taylor, 1994). However, other abiotic factors have been found to influence the temporal and spatial variation in soil CO_2 efflux. For example, several studies have shown a parabolic relationship between soil water content and soil CO_2 efflux with the highest soil CO_2 efflux occurring at an intermediate soil water content (Davidson et al., 1998, 2000; Schwendenmann et al., 2003). Other soil factors driving the variability in soil CO_2 efflux in forest ecosystems include the quality and quantity of soil organic matter (Rayment and Jarvis, 2000; Epron et al., 2004) and microbial biomass (Xu and Qi, 2001).

Biotic factors that influence rates of soil CO_2 efflux include plant and microbial components. Vegetation type and structure are important determinants of soil CO_2 efflux because they influence the quantity and quality of litter and root biomass supplied to the soil and they also mediate the soil microclimate (Fang et al., 1998; Raich and Tufekcioglu, 2000; Metcalfe et al., 2007; 2011). For example, litter addition experiments have shown that increasing litterfall enhances soil CO_2 efflux (Sulzman et al., 2005; Sayer et al., 2011). A few studies have investigated the effect of stand structure and tree size on soil CO_2 efflux in temperate (Longdoz et al., 2000; Søe and Buchmann, 2005; Ngao et al., 2012) and tropical forests

(Ohashi et al., 2008; Katayama et al., 2009; Brechet et al., 2011). Those findings demonstrate that the spatial distribution of emergent trees strongly affects the root distribution and litterfall, partly explaining the spatial variation of soil CO_2 efflux (Katayama et al., 2009; Brechet et al., 2011). Some studies show that soil CO_2 efflux at the base of emergent trees is

70   significantly higher than soil CO_2 efflux at greater distances from the trees (Katayama et al., 2009; Ohashi et al., 2008).

Soil CO_2 efflux is the result of CO_2 production by heterotrophic and autotrophic respiration and gas transport (Fang and Moncrieff, 1999; Maier et al., 2011; Maier and Schack-Kirchner 2014). Heterotrophic respiration mainly originates from microbes decomposing plant detritus

75   and soil organic matter while autotrophic (= root/rhizosphere) respiration comes from plant roots, mycorrhizal fungi and the rhizosphere (Hanson et al., 2000; Bond-Lamberty et al., 2011). The relative contribution of autotrophic respiration to total soil CO_2 efflux varies widely (10-90%) depending on the type of ecosystem studied (Hanson et al., 2000; Subke et al., 2006; Bond-Lamberty et al., 2011). Various methods (i.e. trenching, regression analysis,

80   isotopic methods) have been developed to separate heterotrophic and autotrophic respiration under both laboratory and field conditions and are described in the review papers by Hanson et al. (2000), Kuzyakov (2006) and Bond-Lamberty et al. (2011). Separating total soil CO_2 efflux into autotrophic and heterotrophic sources is important to more accurately predict C fluxes under changing environmental conditions as heterotrophic and autotrophic respiration

85   respond differently to abiotic and biotic factors (Boone et al., 1998; Davidson et al., 2006; Brüggemann et al., 2011). For example, heterotrophic respiration was found to be more susceptible to seasonal drought in a *Pinus contorta* forest (Scott-Denton et al., 2006). Other studies showed that autotrophic respiration is more temperature-sensitive than heterotrophic respiration and total soil CO_2 efflux (Boone et al., 1998; Högberg, 2010).

90   Soil CO_2 efflux has been measured in a wide range of mature and old-growth forests across the globe (Schwendenmann et al., 2003; Epron et al. 2004; Sulzman et al., 2005; Adachi et al., 2006; Bahn et al., 2010; Bond-Lamberty and Thompson, 2014). Southern conifer forests are an exception to this (but see Urrutia-Jalabert, 2015). They include kauri (*Agathis australis* D. Don Lindl. ex Loudon, Araucariaceae) forests in Aotearoa-New Zealand. Old-growth

95   kauri forests are considered to be one of the most C-dense forests worldwide (Keith et al., 2009) with up to 670 Mg C ha^{-1} in living woody biomass (Silvester and Orchard, 1999). Kauri is endemic to northern New Zealand (north of latitude 38°S) (Ecroyd, 1982) and is the

largest and longest lived tree species in the country. Kauri has significant effects on the soil environment (Whitlock, 1985; Verkaik et al., 2007) and plant community composition (Wyse et al., 2014). Phenolic compounds in kauri leaf litter (Verkaik et al., 2006) and low pH values (around 4) (Silvester, 2000; Wyse and Burns, 2013) partly explain the slow decomposition rates of kauri litter (Enright and Ogden, 1987) which result in thick organic layers in undisturbed kauri stands (Silvester and Orchard, 1999).

Organic layers (= forest floor composed of leaves, twigs and bark in various stages of decomposition above the soil surface) are important C reservoirs (Gaudinski et al., 2000) and can be a considerable source of CO_2. Organic layers can also contain a large amount of roots which may result in increased soil CO_2 efflux (Cavagnaro et al., 2012). Mature kauri trees have an extensive network of fine roots which extends from the lateral roots into the interface between organic layer and the mineral soil (Bergin and Steward, 2004; Steward and Beveridge, 2010). A recent study also showed that roots and root nodules of kauri harbour arbuscular mycorrhizal fungi (Padamsee et al., 2016). Roots colonized by mycorrhizal fungi have been found to release more CO_2 than non-mycorrhizal roots (Valentine and Kleinert, 2007; Nottingham et al., 2010).

It remains unknown, however, how much soil CO_2 is released from these C-rich southern conifer forests and which factors are driving the temporal and spatial variability in soil CO_2 efflux. It has been shown that kauri has a significant influence on soil properties but the influence of kauri tree distribution on soil carbon related ecosystem processes is untested. Quantifying the magnitude of soil C loss and identifying the controls of this significant C flux are essential for the assessment of the C balance of these C-rich and long-lived forest stands.

The aim of this study was to determine the magnitude, components and the driving factors of soil CO_2 efflux in an old-growth southern conifer forest. The specific objectives of our study were: (i) to quantify total soil CO_2 efflux, (ii) to test the effect of collar insertion depth on soil CO_2 efflux, (iii) partition total soil CO_2 efflux into autotrophic and heterotrophic respiration, (iv) to identify the factors controlling the temporal variation of total soil CO_2 efflux and its component fluxes, and (v) to test the effect of kauri tree size and distribution on total soil CO_2 efflux and soil properties. We used direct (trenching) and indirect (regression technique) approaches to partition total soil CO_2 efflux into the autotrophic and heterotrophic components. Given that old-growth kauri forests are often characterised by thick organic

layers, deep collars were deployed to assess the effect of insertion depth on total soil CO_2

130   efflux and to quantify to proportion of autotrophic and heterotrophic respiration in this layer.

2   Material and methods

2.1   Study site

The study was conducted in the University of Auckland Huapai reserve. The reserve is a 15 ha forest remnant surrounded by farmland (Thomas and Ogden, 1983) and is located approximately 25 km west of central Auckland on the northern fringe of the Waitakere Ranges (36° 47.7' S, 174° 29.5' E). Within the long-term research plot (50 x 40 m), the diameter at breast height (DBH) of all trees ≥ 2.5 cm was measured, the species were identified and their location mapped (Wunder et al., 2010) (Fig. 1). The plot is dominated by kauri (770 stems ha^{-1}) with a basal area of 75 m^2 ha^{-1}, equating to approximately 80% of the stand basal area (Wunder et al., 2010). Kauri tree size distribution differs within the plot. Four emergent kauri trees (up to 180 cm in DBH, approx. 300 year-old) are found on the upper slope of the plot. At the lower slope tree fall and removal of five large kauri trees in the 1950s created gaps which are now dominated by a cohort of younger kauri trees. Silver ferns (*Cyathea dealbata*) are also highly abundant (785 stems ha^{-1}) (Wunder et al., 2010). Less-numerous species are a mixture of podocarps and broadleaved species, including *Phyllocladus trichomanoides*, *Myrsine australis*, *Coprosma arborea* and *Geniostoma ligustrifolium*.

Total annual rainfall, measured from 2011 to 2013 at a weather station located in the vicinity of the reserve, is approximately 1200 mm with 70% occurring during austral winter (June-August). Annual mean temperature is 14°C (Macinnis-Ng and Schwendenmann, 2015). The soils are derived from andesitic tuffs and are classified as Orthic Granular Soils (New Zealand soil classification; Hewitt, 1992) or Humults (US soil classification; Soil Survey Staff, 2014). The clayey soil is fairly sticky when wet, and hard and fragile when dry (Thomas and Ogden, 1983). The thickness of the organic layer varies between 5 and 15 cm and consists mainly of partly decomposed kauri leaves and twigs.

2.2   Experimental setup

The long-term research plot was subdivided into six equal quadrats. Within each quadrant two soil CO_2 efflux sampling points (in total 12) were randomly located (Fig. 1). For each sampling point we measured the distance to the closest tree with a DBH ≥ 2.5 cm. At each of

these 12 sampling points, a cluster of measurements was made. There was one surface measurement and three inserted measurements as described below.

Total soil CO_2 efflux was measured on the surface of the forest floor by gently pressing a polyvinyl chloride (PVC) ring attached to the soil respiration chamber (see below for details) down on the forest floor during measurements to avoid cutting fine roots. The sampling points were marked with flags and kept free of vegetation. Total soil CO_2 efflux was measured over 18 months from August 2012 to January 2014 at each location. These sampling points were named Plot_Surface.

To measure the effect of collar insertion depth and to quantify the proportion of autotrophic and heterotrophic respiration to total soil CO_2 efflux in the organic layer, a cluster of three 'deep' PVC collars (10 cm in diameter, 20 cm in height) was inserted next to each sampling point for surface soil CO_2 efflux measurements. Three collars per cluster were spaced evenly around the circumference of a circle 2 m in diameter, with small adjustments in the spacing to avoid large roots. Each collar was driven right through the organic layer and 1-2 cm into the mineral soil layer to cut off the roots growing in the organic layer. In order to prevent CO_2 uptake, any vegetation inside the collars was regularly removed. The thickness of the organic layer at each grid point was measured using a ruler outside each collar. The deep collars were inserted in November 2011 and left in place over the measurement period. Efflux was measured from August 2012 (9 months after insertion) to January 2014. Here after, these sampling points are known as Plot_Inserted.

We used the trenching approach to separate heterotroph and autotrophic respiration in the organic layer plus mineral soil to 30 cm depth. To avoid disturbing the long-term research plot the trenching experiment was set-up directly adjacent (upslope) to the research plot. In July 2012, six 2 x 2 m plots were trenched to 30 cm depth based on a preliminary study showing that the majority of fine roots (over 80%) are located in the organic layer and top 30 cm of the mineral soil. The trenches were double-lined with a water permeable polypropylene fabric and backfilled. During trenching, trampling and disturbance inside the 2 x 2 m plots were avoided as far as possible. Two types of measurements were conducted. First, total soil CO_2 efflux was measured at two sampling points outside each trenched plot (Outside_Trench_Surface, n=12) in the same way as the Plot_Surface samples were measured (see above). Second, two collars were randomly placed inside the trenched plot (Trench_Inserted). The collors were inserted 1-2 cm into the mineral soil layer (deep collars)

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2.3 Soil CO_2 efflux measurements

Soil CO_2 efflux was measured with a portable infrared gas analyser (EGM-4, PP Systems, Amesbury, MA, USA) equipped with a soil respiration chamber (SRC-1, PP Systems,

200 Amesbury, MA, USA). The CO_2 concentration was measured every 5 sec over 90-120 sec between 9 am and 2 pm local time and the change in CO_2 concentration over time was recorded. Diurnal soil CO_2 efflux measurements conducted in January 2013 showed that soil CO_2 efflux rates between 9 am and 2 pm were comparable as there was no siginificant diurnal trend (data not shown).

205 Soil CO_2 efflux (μmol m^{-2} s^{-1}) was calculated as follows:

$$\text{Soil } CO_2 \text{ efflux } (\mu\text{mol m}^{-2}\text{ s}^{-1}) = (\Delta CO_2/\Delta t) \text{ x } (P \text{ x } V)/(R \text{ x } T \text{ x } A) \qquad (1)$$

Where $\Delta CO_2/\Delta t$ is the change in CO_2 concentration over time (t), calculated as the slope of the linear regression (μmol mol^{-1} s^{-1} = ppm s^{-1}), P is the atmospheric pressure (Pa), V is the volume of the chamber including collar (m^3), R is the universal gas constant, 8.314 m^3 Pa K^{-1}

210 mol^{-1}), T is the temperature (K) and A is the surface area of ground covered by each chamber (0.007854 m^2).

Soil temperature (Soil temperature probe, 10 cm probe, Novel Ways Ltd, Hamilton, New Zealand) and volumentric soil water content (Hydrosense II, 12 cm probe, Campbell Scientific Inc., Logan, UT, USA) were measured at the same time next to each of the collars.

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2.4 Litterfall, root and soil characteristics

Litterfall (including leaves, twigs, fruits, flowers, cone scales, etc.) was collected from twelve litter traps (pop-up planters, 63 cm in diameter) located next to each soil CO_2 efflux cluster within the long-term research plot (Fig. 1). Litterfall was collected bi-weekly from January

220 2012-January 2014, dried at 80°C to constant mass, sorted and weighed (Macinnis-Ng and Schwendenmann, 2015).

Organic layer and mineral soil samples (0-10 cm depths) were taken next to each collar with a core sampler in November 2011 (research plot) and July 2012 (trenched locations). Samples

were ground and analysed for total C and N concentration using an elemental analyser
(TruSpec, LECO Corporation, St. Joseph, Michigan, USA). Soil (LECO Lot 1016, 1007) and
leaf (NIST SRM 1515 - Apple Leaves) standards were used for calibration. The coefficient of
variation was 0.5% for C and 1% N for plant material (45% C, 2.3% N) and 1% for C and N
for soil (2-12% C, 0.2-1% N). 10% of samples were replicated and results were within the
range of variation given for the standards.

Organic layer and mineral soil samples (0-15 cm, 15-30 cm) were collected for soil analysis
and root biomass estimation adjacent to six clusters within the plot (Fig. 1) and the trenched
plots. Organic layer samples were collected from 20 cm x 20 cm quadrats. Mineral soil
samples were taken using a 15-cm diameter steel cylinder. Samples were dried at 60°C
(forest floor) and 40°C (mineral soil). Mineral soil samples were sieved at 2 mm. pH was
measured in a 1:2.5 soil-water suspension (SensION 3 pH meter, HACH, Loveland, CO,
USA). The organic layer samples were wetted and fine roots were manually picked with
tweezers. The flotation method was used to separate roots from the clay rich mineral soil.
Roots were dried at 60°C to constant mass and weighed by size class (fine roots: < 2 mm, and
small (coarse) roots: 2-20 mm). Litterfall, root and soil data are summerized in Table 1.

2.5   Data analysis

Efflux, soil temperature and volumentric soil moisture content measured at the three
individual deep collars per cluster (Plot_Inserted) and the two samples of
Outside_Trench_Surface and Trench_Inserted were averaged before statistical analysis.
Normality of the data distribution was examined using a Kolmogorov–Smirnov test.

Descriptive statistics (minimum, maximum, mean and median values, standard error,
coefficient of variation) were used to describe soil CO_2 efflux, soil temperature and
volumetric soil water content. Differences between total soil CO_2 efflux between treatments
(Plot_Surface vs Plot_Inserted; Outside_Trench_Surface vs Trench_Inserted) and seasons
were tested using a mixed model where deep collar insertion and trenching were considered
as a fixed effect and sampling dates as a random effect.

To estimate annual total soil CO_2 efflux, a linear temperature function (see below) and
continuous half-hourly soil temperature measurements (plot center, 10 cm depth, 107
temperature probe, Campbell Scienctific, Logan, UT, USA) were used.

255   Two methods (trenching and regression-analysis) were used for partitioning of total soil CO_2 efflux. In the trenching approach, the Plot_Inserted and Trench_Inserted sampling points represents heterotrophic respiration in the organic layer and organic layer plus mineral soil to 30 cm depth, respectively. Measurements from the soil surface (Plot_Surface and Outside_Trench_Surface) represent total soil CO_2 efflux. Autotrophic respiration in the

260   organic layer and organic layer plus mineral soil to 30 cm depth was calculated as the difference between total soil CO_2 efflux and the efflux measured from the Plot_Inserted and Trench_Inserted sampling points, respectively. Heterotrophic respiration from Plot_Inserted and Trench_Inserted sampling points was not corrected for decomposing root-derived CO_2 efflux. For the regression-analysis approach (organic layer plus mineral soil to 30 cm depth),

265   the heterotrophic respiration was derived analytically as the y-intercept of the linear regression between root biomass (independent variable) and total soil CO_2 efflux (dependent variable) (Kucera and Kirkham, 1971; Kuzyakov, 2006). Autotrophic respiration was then estimated by subtracting the heterotrophic respiration from total soil CO_2 efflux.

      Univariate and bivariate models were used to investigate the relationship between total soil

270   CO_2 efflux, heterotrophic and autotrophic respiration and the abiotic factors soil temperature and volumetric soil water content. Data from within the research plot and trench sampling points were combined. The temperature response of soil CO_2 efflux was tested using a linear, exponential (Q_{10}, van't Hoff 1898) and modified Arrhenius function (Lloyd and Taylor, 1994). Linear and quadratic functions were used to assess the soil water dependence of soil

275   CO_2 efflux. The combined effect of soil temperature and soil water content on soil CO_2 efflux was tested using a polynomial function. Coefficient of determination (R^2), standard error of estimate (SEE), and Akaike Information Criterion (AIC) were used to evaluate model performance. The analysis was conducted using Sigma Plot Sigma Plot (Version 13, Systat Software Inc., Chicago, IL, USA).

280   The influence of kauri tree size and distribution on total soil CO_2 efflux, litterfall, root biomass and soil properties was tested using an index of local contribution (I_c). As described in Bréchet et al. (2011), the I_c index is a function of (1) the trunk cross section area (S, m^2) and (2) the distance (d, m) of kauri trees from the sampling points. The following functions were tested: uniform, $I_c = S$; linear, $I_c = S \times (1-d/r)$; parabolic, $I_c = S \times (1-(d/r)\char`\^2))$;

285   exponential, $I_c = S \times e\char`\^(d/r-d)$ and power, $I_c = S \times (1-(d/r)\char`\^a))$ where a is a coefficient of form and r is a fitted radius of influence (r, in m) (Brechet et al., 2011). It was assumed that all

kauri trees had the same radius of influence (r, i.e. the distance above which their contribution would become negligable). The coefficient of determination was used to assess the strength of the relationships between litterfall, root biomass or soil CO_2 efflux and the sum of the I_c.

290   The spatial variability in soil CO_2 efflux was quantified at the plot scale using the coefficient of variation. Multiple regression analysis was used to assess the spatial controls (soil temperature, soil moisture, organic layer thickness, soil C and nitrogen, root biomass) of total soil CO_2 efflux.

Statistical analyses were performed using SPSS v. 22 (IBM SPSS Statistics, IBM
295   Corporation, Chicago, IL, USA). The local contribution analysis (I_c) was conducted using R (v3.1.0 R Development Core Team, 2005). Significance for all statistical analyses was accepted at $p < 0.05$.

3   Results

3.1   Seasonal variations in soil CO₂ efflux, soil temperature and volumetric soil water content and the effect of deep collar insertion and trenching

During the study period, soil temperature and volumetric soil water content (SWC) varied with season (Fig. 2a-c). Soil temperatures peaked at about 17°C during austral summer and early autumn (January-March) while minimum temperatures of around 11°C (Fig. 2b) were measured in late winter/early spring (July-September). Annual mean soil temperature was 14.2 ± 0.1°C (Table 1). The SWC was highest during late winter/early spring (July-September) with values of 55% and soil was driest during late summer/early autumn (March-May) with around 25% (Fig. 2c). Annual average was 43.9 ± 0.9% (Table 1). Across the study period, an average of 1.9 ± 0.1 kg m^{-2} litter fell at the sampling points and the organic layer was 8.8 ± 0.9 cm thick (Table 1). Other information on soil and vegetation characteriscis is summarised in Table 1.

Total soil CO_2 efflux rates (Plot_Surface) measured at 12 sampling points within the research plot varied from 0.7-9.9 µmol CO_2 m^{-2} s^{-1} during the 18-month study period (Fig. 2a). Total soil CO_2 efflux was positively skewed with the mean larger than the median (Table 2). The mean total soil CO_2 efflux (± SE), averaged over the 12 plot sampling points and all sampling dates, was 3.6 ± 0.1 µmol CO_2 m^{-2} s^{-1}. Higher efflux rates were measured during austral summer and early autumn (December-March, 2.7-4.7 µmol CO_2 m^{-2} s^{-1}) compared to winter (June-August, 1.8 - 3.9 µmol CO_2 m^{-2} s^{-1}) (Fig. 2a). However, differences among seasons were not significant ($p > 0.05$). In contrast, soil temperature differed significantly between summer (16.5°C) and winter (11.8 °C) (Table 2). We also detected significant seasonal differences in SWC with drier conditions during summer (mean SWC = 31%) compared to winter (mean SWC = 47%) (Table 2).

Deep collar insertion (Plot_Inserted) had a significant effect on total soil CO_2 efflux but no effect on soil temperature and SWC was found (Table 2). Soil CO_2 efflux from inserted collars (3.0 ± 0.1 µmol CO_2 m^{-2} s^{-1}) was 17% lower compared to total soil CO_2 efflux (3.6 ± 0.1 µmol CO_2 m^{-2} s^{-1}) (Table 2). The overall temporal pattern of soil CO_2 efflux was similar between inserted and surface collars (Fig. 2a). However, soil CO_2 efflux from surface collars varied considerably during the dry summer in 2013 (Fig. 2a, c). Higher soil CO_2 efflux from surface collars in April 2013 coincided with rain events after a long dry period with high litter input (see Macinnis-Ng and Schwendenmann, 2015 for details).

Total soil CO_2 efflux measured outside the trenched plots ranged from 0.6 to 6.9 µmol CO_2 m^{-2} s^{-1} with a mean of 3.1 ± 0.1 µmol CO_2 m^{-2} s^{-1} (Outside_Trench_Surface, Table 2). Soil CO_2 efflux from Trench_Inserted collars was significantly lower (25%) compared to total soil
335   CO_2 efflux (Table 2). Volumetric soil water content in the trenched plots was significantly higher (56.8%) compared to the untrenched sampling points (44%). In contrast, soil temperature was not significantly affected by trenching (Table 2).

3.2   Contribution of autotrophic respiration to total soil CO_2 efflux

340   Mean autotrophic respiration derived from the trenching approach was 0.8 ± 0.1 µmol CO_2 m^{-2} s^{-1}. The contribution of autotrophic respiration to total soil CO_2 efflux (to 30 cm depth) was 25%. Excluding the roots from the organic layer through deep collar insertion showed that roots in the organic layer contribute around 17% to total soil CO_2 efflux. The proportion of autotrophic respiration to total soil CO_2 efflux tended to be lower during summer/early
345   autumn (December-April) compared to winter (June-August). However, differences were not statistically significant due to high variability in autotrophic respiration, especially during summer (data not shown).

Mean total soil CO_2 efflux (Plot_Surface plus Outside_Trench_Surface; n = 18, mean = 3.47 µmol CO_2 m^{-2} s^{-1}; SE = 0.20 µmol CO_2 m^{-2} s^{-1}) was positively correlated with total (organic
350   layer plus mineral soil to 30 cm depth) root biomass (R^2 = 0.394, p = 0.042, intercept = 2.49 µmol CO_2 m^{-2} s^{-1}) (Fig. 3). Using the regression approach produced a autotrophic respiration estimate of 0.98 µmol CO_2 m^{-2} s^{-1}. The proportion of autotrophic respiration to total soil CO_2 efflux derived from the root biomass regression approach was 28%.

355   ## 3.3   Effect of soil temperature and volumetric soil water content on the temporal variability in total soil CO_2 efflux, heterotrophic and autotrophic respiration

Independent of the model used, soil temperature explained less than 20% of the temporal variation in total soil CO_2 efflux (Fig. 4a, Table 3). The Q_{10} values for total soil CO_2 efflux
360   was 1.6 (Table 3). A slightly stronger soil temperature response was found for heterotrophic respiration (Fig. 4b, Table 3) with a Q_{10} value of 2.2 (Table 3). However, all temperature models for heterotrophic respiration had higher AIC values compared to total soil CO_2 efflux

(Table 3) which suggests a poorer performance. No significant relationship was found between soil temperature and autotrophic respiration (Fig. 4c, Table 3).

Neither a linear nor a quadratic function resulted in a significant relationship between SWC and total soil CO_2 efflux (Fig. 4d, Table 3). Heterotrophic respiration decreased significantly with increasing SWC (Fig. 4e, Table 3). In contrast a weak, but significant quadratic relationship was found between SWC and autotrophic respiration (Fig. 4f).

Bivariate polynomial functions did not result in higher R^2 or better AIC values compared to univariate models (Table 3).

3.4 Spatial variation in total soil CO_2 efflux and environmental factors

The spatial variability of total soil CO_2 efflux between the 12 sampling points in the research plot was relatively high, with a coefficient of variation (CV) of 43% (Table 2).

We found a good relationship between the tree local contribution index (I_c) and soil CO_2 efflux (Fig. 5a). The relationship was strongest (coefficient of determination, $R^2 = 0.342$, p = 0.030, linear model) within a radius of 5 m (Fig. 5b).

The spatial variation in total root biomass (organic layer plus mineral soil to 30 cm depth, 0.9 to 8 kg m^{-2}) was very high (CV > 95%, Table 1). Similar to soil CO_2 efflux, a radius of 5 m provided also the best correlation between root biomass and I_c (Fig. 5c). The coefficient of determination was $R^2 = 0.985$ (p = 0.021, univariate model, Fig. 5d).

Compared to root biomass and soil CO_2 efflux the spatial variation in litterfall (total amount over the 18-month period, 1.1-2.2 kg m^{-2}, Table 1) was small (CV = 20%, Table 1). We did not find any significant correlations between litterfall and I_c (data not shown).

Between 8 and 29 kg C m^{-2} were stored in the 6-12 cm thick organic layer (Table 1). C:N ratio differed considerably between the organic layer (31-58) and mineral soil (13-19). Differences in pH were greater among sampling points compared to differences between organic layer and mineral soil (Table 3). Except for C:N ratio in the mineral soil ($R^2 = 0.655$, p = 0.000, linear model, Fig. 5d,e), no correlations were found between I_c and soil characteristics.

Using multiple regression analysis revealed that most of the spatial variability in total soil CO_2 efflux within the plot could be explained by soil temperature and root biomass ($R^2 = 0.977$, Adjusted $R^2 = 0.953$, $F = 41.972$, $p = 0.023$).

4 Discussion

4.1 Total soil CO₂ efflux: magnitude and temporal variation

Annual total soil CO_2 efflux (1324 ± 121 g C m^{-2} yr^{-1}; estimated using the linear temperature response function) in this kauri dominated forest was higher than mean values from mature conifer and mixed conifer-hardwood temperate rainforests along the Pacific coast of North America (500 - 2300 g C m^{-2} yr^{-1}; mean: 1100 ± 65 g C m^{-2} yr^{-1}; n = 55) (Campbell and Law, 2005; Hibbard et al., 2005; Bond-Lamberty and Tompson, 2014) and southern conifer (*Fitzroya cupressoides* forests in southern Chile (500-800 g C m^{-2} yr^{-1}; Urratia-Jalabert, 2015). Soil CO_2 emissions from the kauri stand were also higher than efflux rates measured in other New Zealand forests. For example, approximately 1000 g C m^{-2} yr^{-1} were measured in a rimu (*Dacryidium cupressinum,* conifer) dominated podocarp forest in South Westland (Hunt et al., 2008) and annual soil CO_2 efflux in *Leptospermum scoparium/Kunzea ericoides* var. *ericoides* shrublands ranged between 980 and 1030 g C m^{-2} yr^{-1} (Hedley et al., 2013). In contrast, our values are within the range of values reported for mature unmanaged tropical moist broadleaf forests (900-2000 g C m^{-2} yr^{-1}; mean: 1336 ± 70 g C m^{-2} yr^{-1}; n = 27) (Raich and Schlesinger, 1992; Schwendenmann et al., 2003; Bond-Lamberty and Tompson, 2014).

Our findings suggest that soil CO_2 efflux in a conifer dominated forest can be as high or even exceed the efflux rates from broadleaf forests. This is in contrast to previous studies which found that soil CO_2 efflux in conifer forests are lower than those in broadleaf forests (Raich and Tufekcioglu, 2000; Curiel Yuste et al., 2005a). However, these former studies were limited to temperate study sites and based on direct comparisons of sites where forest type was the principal variable differing among pairs. Mean annual soil temperature has been shown to be a good predictor of large-scale variation in total soil CO_2 efflux in non-water limited systems independent of vegetation types and biome (Bahn et al., 2010). With a mean annual temperature of 14°C, this study site was relatively warm compared to sites along the Pacific coast of North America partly explaining the high soil CO_2 efflux rates in this kauri dominated forest.

The amount of litterfall has also been associated with differences in soil CO_2 efflux at the scales of biomes (Davidson et al., 2002; Reichstein et al., 2003; Oishi et al., 2013). Annual C input via litterfall in this kauri dominated forest was 410 and 760 g C m^{-2} in 2012 and 2013, respectively (Macinnis-Ng and Schwendenmann, 2015). This litter C flux is substantially higher than those values from conifer and mixed conifer-hardwood forests in the Northern

Hemisphere (50-400 g C m^{-2} yr^{-1}; mean: 164 ± 14 g C m^{-2} yr^{-1}; n = 43; Bond-Lamberty and Tompson, 2014; Holland et al., 2015). Kauri litterfall is within the range of values (110 - 700 g C m^{-2} yr^{-1}; mean: 345 ± 30 g C m^{-2} yr^{-1}; n = 22) reported for old-growth tropical forests (Chave et al., 2010; Holland et al., 2015; Lamberty-Bond and Tompson, 2014). High litter

430   input, together with high annual temperature, can be another major factor explaining the comparatively high soil CO_2 efflux rate in this southern conifer forest. This is somewhat surprising as one would assume that organic matter mineralisation and thus soil CO_2 efflux is reduced given the slow decomposition rate of kauri litter. In four kauri forests ranging from pole to mature forests mean residence times between 9 and 78 years were estimated for 8 to

435   46 cm thick organic layers (Silvester and Orchard, 1999). According to Silvester and Orchard (1999), sites with higher litter fall were accompanied by faster breakdown and no relationship was found between litterfall and the depth of the organic layer. The organic layer in our study sites was only 5 to 15 cm thick. Possible reasons for a lack of litter accumulation and build-up of a thick organic layer are: removal and disturbance of the organic layer as a consequence

440   of tree fall and removal of five large kauri trees in the 1950s (Thomas and Ogden, 1983) and topography. The topography of the study site (moderate to steep slope) likely explains the negative correlation between organic layer thickness and elevation (r=-0.539, p=0.021). Erosive removal of the organic layer and mineral soil on steep slopes and deposition downslope have been shown to affect soil characteristics and C cycling (Vitousek et al.,

445   2003; Yoo et al., 2005; Stacy et al., 2015). For example, in a temperate forest in Japan (Nakane et al., 1994) and a tropical seasonal forest in Thailand (Takahashi et al., 2011) soil CO_2 efflux decreased with increasing slope. However, we did not find any significant correlation between elevation and total soil CO_2 efflux, root biomass, and soil moisture suggesting that forest structure (see 4.2) may have had a stronger effect on soil characteristics

450   than topography.

While mean annual soil temperature partly explains the overall high mean soil CO_2 efflux measured in this forest, soil temperature was not a very good predictor of the temporal variation in total soil CO_2 efflux. Independent of the regression model used, soil temperature explained a small proportion ($< 20\%$, Fig. 4a, Table 3) of the seasonal variation in total soil

455   CO_2 efflux. In temperate forest ecosystems in the Northern Hemisphere (Ngao et al., 2012; Bond-Lamberty and Tompson, 2014) soil temperature often explains more than 50% of the temporal variability in total soil CO_2 efflux. It is important to note that the soil temperature range in this kauri forest was narrow (around 7°C) compared to other temperate forests with a

larger seasonal soil temperature amplitude (> 10°C, Paul et al., 2004). Thus, a seasonal temperature effect may not have been visible in this kauri forest. The Q_{10} value (1.6, Table 3) was at the lower end of the range reported for mixed and evergreen forests ($Q_{10\_10\text{-}20°C}$; 0.5-5.6; Bond-Lamberty and Tompson, 2014). However, low Q_{10} values have also been reported for other conifer forest, especially at sites characterized by mild winters (Borken et al. 2002; Curiel Yuste et al., 2005b; Sulzman et al., 2005). Low Q_{10} values in evergreen forests have been explained by the lack of a distinct seasonality in photosynthesis and substrate supply (Curiel Yuste et al., 2005b).

No significant relationship was found between SWC and total soil CO_2 efflux (Fig. 4d, Table 3). However, total soil CO_2 efflux tended to decline with increasing SWC. Excess SWC may negatively affect CO_2 efflux rates by reducing soil aeration and thus CO_2 diffusivity (Janssens and Pilegaard, 2003). Further, low levels of oxygen as result of high SWC decreases activity of plant roots (Adachi et al., 2006) and the heterotrophic decomposition of soil organic matter (Linn and Doran, 1984). This may be particularly relevant in the clayey soils under study.

4.2 Forest structure and the spatial variation in soil CO_2 efflux

The spatial variability (CV = 43%) of total soil CO_2 efflux in this study is slightly higher compared to other studies with similar numbers of measurements and/or plot size (32-39%; Epron et al., 2006; Kosugi et al., 2007; Brechet et al., 2011). The higher spatial variation might be related to differences in tree size and distribution across the plot. The stand is clearly dominated by kauri trees in all size classes (Fig. 1). However, kauri occurs in clusters around the four largest and emergent kauri individuals whose neighbourhood is generally characterised by relatively few trees (see lower centre of Fig. 1). The influence of forest structure (here: kauri tree distribution and tree size, I_c) on total soil CO_2 efflux is confirmed by the significant relationships between I_c and total soil CO_2 efflux, root biomass and mineral soil C:N ratio. Previous studies have shown that kauri has significant effects on soil processes such as pH and nitrogen cycling (Silvester 2000; Jongkind et al. 2007; Verkaik et al. 2007; Wyse et al., 2014). This is the first study showing that kauri exerts a substantial influence on soil C related processes. Our results also corroborate a study by Katayama et al. (2009) suggesting that the spatial arrangement of emergent trees in a tropical forest is an important factor for generating spatial variation of soil CO_2 efflux. Studies in European beech forests

also show that the combination of root, soil and stand structure help to understand the mechanisms underlying soil CO_2 efflux and that forest structure has some influence on the spatial variability of soil CO_2 efflux (Søe and Buchmann, 2005; Ngao et al., 2012).

The relationship between soil CO_2 efflux and forest structure was strongest within a radius of 495 5 m (Fig. 5a,b). In a tropical forest, the strongest correlation between soil CO_2 efflux and forest structural parameters was within 6 m from the sampling points (Katayama et al., 2009). A radius of 5 m also provided the best correlation between root biomass and I_c. As measurements of the lateral root extension are not available for kauri, it remains unknown if this distance equals the maximum lateral extension of fine roots from the trunk or represents 500 the distance where fine root density is highest. Based on observations, large lateral roots of mature kauri trees often extent beyond the width of the crown and an extensive network of fine roots extends from the lateral roots into the interface between organic layer and the mineral soil (Bergin and Steward, 2004). The radial fine root spread in mature Northern Hemisphere conifer stands varies considerably (6-20 m) depending on site characteristics and 505 stand structure (Stone and Kalisz, 1991).

In contrast to other studies (e.g. Brechet et al., 2011; Katayama et al., 2009), we did not find a significant correlation between litterfall and forest structure. Tree size and architecture have been reported to affect the pattern of litterfall distribution on the forest floor (Ferrari and Sugita 1996; Staelens et al., 2004; Zalamea et al., 2012). However, despite a 3-fold difference 510 in tree size across the plot we did not see a significant effect of tree size on total litterfall. This is also reflected in a small within-plot variation in litterfall (CV = 20%, Table 1). This is confirmed by a litterfall study in four remnant kauri forests where a small variation in litterfall (CV=17-26%) was found across a wide range of litter trap positions (Silvester and Orchard, 1999).

515 Spatial variability in soil CO_2 efflux was largely attributed to soil temperature and the amount of fine root biomass and associated rhizosphere, with 97% of the variation explained. This implies a relationship with tree productivity which is in agreement with findings from other conifer forests (Janssens et al., 2001; Lou and Zhou 2006). Although roots accounted for less than 30% of total CO_2 efflux, recent research has shown that both recent photosynthate and 520 fine root turnover can be important sources of C for forest soil CO_2 efflux (Epron et al., 2011; Warren et al., 2012) as discussed below.

4.3 Components of total soil CO_2 efflux

Collar insertion through the organic layer into the mineral soil resulted in a 17% reduction in soil CO_2 efflux. Similar reductions were found in other ecosystems and demonstrates that collar insertion by only a few centimetres cuts off fine roots (Heinemeyer et al., 2011) and contributions by ectomycorrhizal fungal mats (Phillips et al., 2012) reducing total soil respiration. Thus, collar insertion can cause underestimation of total CO_2 efflux. This may be a particular problem in ecosystems where large amount of roots and mycorrhiza are found in the organic layer and at the interface between the organic layer and an organic rich mineral soil as in this kauri forest.

The partitioning of total soil CO_2 efflux into its main components: heterotrophic respiration (oxidation of soil organic matter) and autotrophic respiration (root and associated mycorrhiza respiration) remains technically challenging. Differences in the proportion of autotrophic or heterotrophic respiration to total soil CO_2 efflux might vary not only among species and ecosystems but also with the method used for partitioning total soil CO_2 efflux (Kuzyakov, 2006; Subke et al., 2006; Millard et al., 2010). Cutting roots through inserting deep collars and trenching increases the dead root biomass (Heinemeyer et al., 2011). As we did not correct our estimates of soil CO_2 efflux for decomposing root-derived CO_2 fluxes the heterotrophic respiration may have been slightly overestimated (Hanson et al., 2000; Kuzyakov, 2006; Ngao et al., 2012). However, both techniques used in this study, trenching and regression-analysis, showed similar results. The proportion of autotrophic respiration in this kauri was between 25% (trenching) and 28% (regression analysis) of total soil surface CO_2 efflux. The contribution of autotrophic respiration to total soil CO_2 efflux can account for as little as 10% to more than 90% worldwide (Hanson et al., 2000) but values of 45-50% are typical (Subke et al., 2006). Our estimate is at the lower end of values observed for Northern Hemisphere conifer and tropical broadleaf forests (30-70%, Epron et al., 2001; Högberg et al., 2001; Bond-Lamberty and Tompson, 2014; Taylor et al., 2015). This suggests that root/rhizosphere activity in this forest is comparatively low. However, a similar proportion of autotrophic respiration (23%) was estimated for a New Zealand old-growth beech forest (Tate et al., 1993) and an old-growth Douglas-fir site in the Cascades, Oregon (23%) (Sulzman et al., 2005). Another factor accounting for the differences in values is the depth of trenching (Hansen et al., 2000; Kuzyakov, 2006; Bond-Lamberty et al., 2011). The contribution of autotrophic respiration may have been underestimated as we only trenched to

555 30 cm depth. It is recommended to trench to a depth beyond the main rooting zone (Subke et al., 2006) and in some studies the trenched plots are dug down to the solid bedrock (Díaz-Pinés et al., 2010).

Total soil CO_2 efflux is not only directly affected by the amount of autotrophic respiration but also by the supply of C through root turnover and root exudates. The decomposition of root
560 debris has been shown to increase microbial activity and thus heterotrophic respiration (Göttlicher et al., 2006). Despite a low root/rhizosphere activity the total soil CO_2 efflux in a mycorrhizally-associated Douglas-fir forest was dominated by belowground contributions due to the large pool of rhizospheric litter with a relatively high turnover rate (Sulzman et al., 2005). In addition, root exudates containing carbohydrates, sugars and amino acids supply
565 energy for the decomposition of soil C ('priming') (Högberg et al., 2001). Further, a recent study showed that a common root exudate, oxalic acid, promotes soil C loss by releasing organic compounds from mineral-protected aggregates. This indirect mechanism has been found to result in higher C losses compared to simply increasing the supply of energetically more favourable substrates (Keiluweit et al., 2015).

570 Root activity may also affect physical soil conditions. In some studies, SWC and fine root biomass were negatively correlated (Coomes and Grubb, 2000; Ammer and Wagner, 2002). High uptake of water by kauri fine roots concentrated in the organic layer may lead to lower SWC and slightly higher soil temperatures (Verkaik et al., 2007; Verkaik and Braakhekke, 2007). The drier conditions at the base of trees might be an indicator of good soil aeration
575 that enhances the diffusivity of soil CO_2 into the air (de Jong and Schappert, 1972; Tang et al., 2003).

The soil temperature response was stronger for heterotrophic respiration (Fig. 4b, Table 3). This is in line with other studies conducted in temperate mixed forests (Kirschbaum, 1995; Boone et al., 1998; Högberg et al. 2005) and suggests a higher sensitivity of heterotrophic
580 respiration to temperature. Below 50% SWC autotrophic respiration increased with increasing water content (Fig. 4f). A positive correlation between soil water content and autotrophic respiration have also been reported for temperate and tropical forests (Zang et al., 2014; Brunner et al., 2015; Doughty et al., 2015). This is in contrast to other studies which reported that dry conditions enhanced the growth of fine roots in the surface soil resulting in
585 higher proportions of autotrophic respiration (Bhupinderpal-Singh et al., 2003; Noguchi et al., 2007).

5 Conclusion

Our study has two signifant findings for southern conifer forests. Firstly, this is the only study quantifying the amount of soil CO_2 efflux in an old-growth kauri forest. Our findings suggest that the loss of soil CO_2 (1324 ± 121 g C m^{-2} yr^{-1}) from this forest type is considerable. Although the contribution of autotrophic respiration is comparatively low ($< 30\%$), root biomass explained a high proportion of the spatial variation in soil CO_2 efflux. This suggests that, the total soil CO_2 efflux in this forest in not only directly affected by the amount of autotrophic respiration but also by the supply of C through roots and mycorrhiza. Any modification in root/rhizosphere will most likely result in long-term modifications of the soil CO_2 efflux. This is of relevance given that many kauri forests are threatened by *Phytophthora agathidicida* (Weir et al., 2015) which infects the roots and can lead to tree death (Than et al., 2013). Secondly, this study is the first to confirm that kauri not only exerts a strong control on soil pH and nitrogen cycling but also on soil carbon related processes. The effect of kauri tree size and distribution on total soil CO_2 efflux demonstrates the need to include biotic parameters for better prediction of the spatial variability in soil CO_2 efflux.

Data availability

The data will be made available through figshare.

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References

Adachi, M., Bekku, Y. S., Rashidah, W., Okuda, T. and Koizumi, H.: Differences in soil respiration between different tropical ecosystems, Appl. Soil Ecol., 34, 258-265, 2006.

Ammer, C. and Wagner, S.: Problems and options in modelling fine-root biomass of single mature Norway spruce trees at given points from stand data, Can. J. For. Res., 32, 581-590, 2002.

Andrews, J. A., Harrison, K. G., Matamala, R. and Schlesinger, W. H.: Separation of root respiration using carbon-13 labeling during free-air carbon enrichment (FACE), Soil Sci. Soc. Am. J., 63, 1429-1435, 1999.

Bahn, M., Reichstein, M., Davidson, E. A., Grünzweig, J., Jung, M., Carbone, M. S., Epron, D., Misson, L., Nouvellon, Y., Roupsard, O., Savage, K., Trumbore, S. E., Gimeno, C., Curiel Yuste, J., Tang, J., Vargas, R. and Janssens, I. A.: Soil respiration at mean annual temperature predicts annual total across vegetation types and biomes, Biogeosciences, 7, 2147-2157, 2010.

Bergin, D., and Steward, G.: Kauri: Establishment, growth and management. New Zealand Indigenous Tree Bulletin No. 2, Rotorua: New Zealand Forest Research Institute, 2004.

Bhupinderpal-Singh, Nordgren, A., Löfvenius, M. O., Högberg, M. N., Mellander, P. and Högberg, P.: Tree root and soil heterotrophic respiration as revealed by girdling of boreal Scots pine forest: Extending observations beyond the first year, Plant Cell Environ., 26, 1287-1296, 2003.

Bond-Lamberty, B., Bronson, D., Bladyka, E. and Gower, S. T.: A comparison of trenched plot techniques for partitioning soil respiration, Soil Biol. Biochem., 43, 2108-2114, 2011.

Bond-Lamberty, B. and Thomson, A.: A global database of soil respiration data, Biogeosciences, 7, 1915-1926, 2010a.

Bond-Lamberty, B. and Thomson, A.: Temperature-associated increases in the global soil respiration record, Nature, 464, 579-582, 2010b.

Bond-Lamberty, B. and Thomson, A: A Global Database of Soil Respiration Data, Version 3.0. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA http://dx.doi.org/10.3334/ORNLDAAC/1235, 2014.

Boone, R. D., Nadelhoffer, K. J., Canary, J. D. and Kaye, J. P.: Roots exert a strong influence on the temperature sensitivity of soil respiration, Nature, 396, 570-572, 1998.

Borken, W., Xu, Y. J., Davidson, E. A. and Beese, F.: Site and temporal variation of soil respiration in European beech, Norway spruce, and Scots pine forests, Global Change Biol., 8, 1205-1216, 2002.

Bréchet, L., Ponton, S., Alméras, T., Bonal, D. and Epron, D.: Does spatial distribution of tree size account for spatial variation in soil respiration in a tropical forest?, Plant Soil, 347, 293-303, 2011.

Brüggemann, N., Gessler, A., Kayler, Z., Keel, S. G., Badeck, F., Barthel, M., Boeckx, P., Buchmann, N., Brugnoli, E., Esperschütz, J., Gavrichkova, O., Ghashghaie, J., Gomez-Casanovas, N., Keitel, C., Knohl, A., Kuptz, D., Palacio, S., Salmon, Y., Uchida, Y. and

Bahn, M.: Carbon allocation and carbon isotope fluxes in the plant-soil-atmosphere continuum: A review, Biogeosciences, 8, 3457-3489, 2011.

660 Brunner, I., Herzog, C., Dawes, M. A., Arend, M. and Sperisen, C.: How tree roots respond to drought, Front. Plant Sci., 6, 2015.

Campbell, J. L. and Law, B. E.: Forest soil respiration across three climatically distinct chronosequences in Oregon, Biogeochemistry, 73, 109-125, 2005.

Cavagnaro, T. R., Barrios-Masias, F. H. and Jackson, L. E.: Arbuscular mycorrhizas and their
665 role in plant growth, nitrogen interception and soil gas efflux in an organic production system, Plant Soil, 353, 181-194, 2012.

Chave, J., Navarrete, D., Almeida, S., Álvarez, E., Aragão, L. E. O. C., Bonal, D., Châtelet, P., Silva-Espejo, J. E., Goret, J. -., Von Hildebrand, P., Jiménez, E., Patiño, S., Peñuela, M. C., Phillips, O. L., Stevenson, P. and Malhi, Y.: Regional and seasonal patterns of
670 litterfall in tropical South America, Biogeosciences, 7, 43-55, 2010.

Coomes, D. A. and Grubb, P. J.: Impacts of root competition in forests and woodlands: A theoretical framework and review of experiments, Ecol. Monogr., 70, 171-207, 2000.

Curiel Yuste, J., Janssens, I. A. and Ceulemans, R.: Calibration and validation of an empirical approach to model soil CO_2 efflux in a deciduous forest, Biogeochemistry, 73, 209-230,
675 2005a.

Curiel Yuste, J., Janssens, I. A., Carrara, R. and Ceulemans, R: Annual Q_{10} of soil respiration reflects plant phenological patterns as well as temperature sensitivity, Global Change Biol., 10, 161-169, 2005b.

Davidson, E. A., Belk, E. and Boone, R. D.: Soil water content and temperature as
680 independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest, Global Change Biol., 4, 217-227, 1998.

Davidson, E. A., Janssens, I. A. and Lou, Y.: On the variability of respiration in terrestrial ecosystems: Moving beyond Q10, Global Change Biol., 12, 154-164, 2006.

Davidson, E. A., Savage, K., Bolstad, P., Clark, D. A., Curtis, P. S., Ellsworth, D. S., Hanson,
685 P. J., Law, B. E., Luo, Y., Pregitzer, K. S., Randolph, J. C. and Zak, D.: Belowground carbon allocation in forests estimated from litterfall and IRGA-based soil respiration measurements, Agric. For. Meterol., 113, 39-51, 2002.

Davidson, E. A., Verchot, L. V., Henrique Cattânio, J., Ackerman, I. L. and Carvalho, J. E. M.: Effects of soil water content on soil respiration in forests and cattle pastures of
690 eastern Amazonia, Biogeochemistry, 48, 53-69, 2000.

De Jong, E. and Schappert, H. J.: Calculaton of soil respiration and activity from CO_2 profiles in the soil. Soil Science, 113, 328-333, 1972.

Díaz-Pinés, E., Schindlbacher, A., Pfever, M., Jandl, R., Zechmeister-Boltenstern, S. and Rubio, A.: Root trenching: A useful tool to estimate autotrophic soil respiration? A case
695 study in an austrian mountain forest, Eur. J. For. Res., 129, 101-109, 2010.

Doughty, C. E., Metcalfe, D. B., Girardin, C. A. J., Amézquita, F. F., Cabrera, D. G., Huasco, W. H., Silva-Espejo, J. E., Araujo-Murakami, A., Da Costa, M. C., Rocha, W., Feldpausch, T. R., Mendoza, A. L. M., Da Costa, A. C. L., Meir, P., Phillips, O. L. and Malhi, Y.: Drought impact on forest carbon dynamics and fluxes in Amazonia, Nature,
700 519, 78-82, 2015.

Ecroyd, C. E.: Biological flora of New Zealand 8. *Agathis australis* (D. Don) Lindl. (Araucariaceae) kauri, New Zealand J. Bot., 20, 17-36, 1982.

Enright, N. J. and Ogden, J.: Decomposition of litter from common woody species of kauri (*Agathis australis* Salisb.) forest in northern New Zealand., Aust. J. Ecol., 12, 109-124, 1987.

Epron D., Dantec V. L., Dufrene E. and Granier A.: Seasonal dynamics of soil carbon dioxide efflux and simulated rhizosphere respiration in a beech forest, Tree Physiol., 21, 145-152, 2001

Epron, D., Bosc, A., Bonal, D. and Freycon, V.: Spatial variation of soil respiration across a topographic gradient in a tropical rain forest in French Guiana, J. Trop. Ecol., 22, 565-574, 2006.

Epron, D., Ngao, J., Dannoura, M., Bakker, M. R., Zeller, B., Bazot, S., Bosc, A., Plain, C., Lata, J. C., Priault, P., Barthes, L. and Loustau, D.: Seasonal variations of belowground carbon transfer assessed by in situ $^{13}CO_2$ pulse labelling of trees, Biogeosciences, 8, 1153-1168, 2011.

Epron, D., Ngao, J. and Granier, A.: Interannual variation of soil respiration in a beech forest ecosystem over a six-year study, Ann. Forest Sci., 61, 499-505, 2004.

Fang, C. and Moncrieff, J. B.: A model for soil CO_2 production and transport 1: Model development, Agric. For. Meterol., 95, 225-236, 1999.

Fang, C., Moncrieff, J. B., Gholz, H. L. and Clark, K. L.: Soil CO_2 efflux and its spatial variation in a Florida slash pine plantation, Plant Soil, 205, 135-146, 1998.

Ferrari, J. B. and Sugita, S.: A spatially explicit model of leaf litter fall in hemlock-hardwood forests, Can. J. For. Res., 26, 1905-1913, 1996.

Gaudinski, J. B., Trumbore, S. E., Davidson, E. A. and Zheng, S.: Soil carbon cycling in a temperate forest: Radiocarbon-based estimates of residence times, sequestration rates and partitioning of fluxes, Biogeochemistry, 51, 33-69, 2000.

Giardina, C. P., Litton, C. M., Crow, S. E. and Asner, G. P.: Warming-related increases in soil CO_2 efflux are explained by increased below-ground carbon flux, Nat. Clim. Change, 4, 822-827, 2014.

Göttlicher, S., Knohl, A., Wanek, W., Buchmann, N. and Richter, A.: Short-term changes in carbon isotope composition of soluble carbohydrates and starch: From canopy leaves to the root system, Rapid Commun. Mass Spectrom., 20, 653-660, 2006.

Gupta, S. R. and Singh, J. S.: Soil respiration in a tropical grassland, Soil Biol. Biochem., 13, 261-268, 1981.

Hanson, P. J., Edwards, N. T., Garten, C. T. and Andrews, J. A.: Separating root and soil microbial contributions to soil respiration: A review of methods and observations, Biogeochemistry, 48, 115-146, 2000.

Hedley, C. B., Lambie, S. M. and Dando, J. L.: Edaphic and environmental controls of soil respiration and related soil processes under two contrasting manuka and kanuka shrubland stands in North Island, New Zealand, Soil Res., 51, 390-405, 2013.

Heinemeyer, A., Di Bene, C., Lloyd, A. R., Tortorella, D., Baxter, R., Huntley, B., Gelsomino, A. and Ineson, P.: Soil respiration: Implications of the plant-soil continuum

and respiration chamber collar-insertion depth on measurement and modelling of soil CO_2 efflux rates in three ecosystems, Eur. J. Soil Sci., 62, 82-94, 2011.

745   Hewitt, A. E.: Soil classification in New Zealand: legacy and lessons, Aust. J. Soil Res., 30, 843-854, 1992.

Hibbard, K. A., Law, B. E., Reichstein, M. and Sulzman, J.: An analysis of soil respiration across northern hemisphere temperate ecosystems, Biogeochemistry, 73, 29-70, 2005.

Högberg, P.: Is tree root respiration more sensitive than heterotrophic respiration to changes 750   in soil temperature?, New Phytol., 188, 9-10, 2010.

Högberg, P., Nordgren, A., Buchmann, N., Taylor, A. F. S., Ekblad, A., Högberg, M. N., Nyberg, G., Ottosson-Löfvenius, M. and Read, D. J.: Large-scale forest girdling shows that current photosynthesis drives soil respiration, Nature, 411, 789-792, 2001.

Holland, E.A., Post, W.M., Matthews, E., Sulzman, J., Staufer, R.and Krankina, O.: A Global 755   Database of Litterfall Mass and Litter Pool Carbon and Nutrients. Oak Ridge National Laboratory Distributed Active Archive Center, doi:dx.doi.org/10.3334/ORNLDAAC 1244, 2015.

Hunt, J. E., Walcroft, A. S., McSeveny, T. M., Rogers, G. N. and Whitehead, D.: Ecosystem respiration in an undisturbed, old-growth, temperate rain forest. Abstract, American 760   Geophysical Union, Fall Meeting, 2008.

Janssens, I. A., Kowalski, A. S. and Ceulemans, R.: Forest floor CO_2 fluxes estimated by eddy covariance and chamber-based model, Agric. For. Meterol., 106, 61-69, 2001a.

Janssens, I. A., Lankreijer, H., Matteucci, G., Kowalski, A. S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grünwald, T., Montagnani, L., Dore, S., 765   Rebmann, C., Moors, E. J., Grelle, A., Rannik, Ü., Morgenstern, K., Oltchev, S., Clement, R., Guomundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N. O., Vesala, T., Granier, A., Schulze, E. -., Lindroth, A., Dolman, A. J., Jarvis, P. G., Ceulemans, R. and Valentini, R.: Productivity overshadows temperature in determining soil and ecosystem respiration across European 770   forests, Global Change Biol., 7, 269-278, 2001b.

Janssens, I. A. and Pilegaard, K.: Large seasonal changes in Q10 of soil respiration in a beech forest, Global Change Biol., 9, 911-918, 2003.

Jassal, R., Black, A., Novak, M., Morgenstern, K., Nesic, Z. and Gaumont-Guay, D.: Relationship between soil CO_2 concentrations and forest-floor CO_2 effluxes, Agric. For. 775   Meterol., 130, 176-192, 2005.

Jongkind, A. G., Velthorst, E. and Buurman, P.: Soil chemical properties under kauri (Agathis australis) in The Waitakere Ranges, New Zealand, Geoderma, 141, 320-331, 2007.

Katayama, A., Kume, T., Komatsu, H., Ohashi, M., Nakagawa, M., Yamashita, M., Otsuki, 780   K., Suzuki, M. and Kumagai, T.: Effect of forest structure on the spatial variation in soil respiration in a Bornean tropical rainforest, Agric. For. Meterol., 149, 1666-1673, 2009.

Keiluweit, M., Bougoure, J. J., Nico, P. S., Pett-Ridge, J., Weber, P. K. and Kleber, M.: Mineral protection of soil carbon counteracted by root exudates, Nat. Clim. Change, 5, 588-595, 2015.

785 Keith, H., Mackey, B. G. and Lindenmayer, D. B.: Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests, Proc. Natl. Acad. Sci. U. S. A., 106, 11635-11640, 2009.

Kirschbaum, M. U. F.: The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage, Soil Biol. Biochem., 27, 753-
790 760, 1995.

Kosugi, Y., Mitani, T., Itoh, M., Noguchi, S., Tani, M., Matsuo, N., Takanashi, S., Ohkubo, S. and Rahim Nik, A.: Spatial and temporal variation in soil respiration in a Southeast Asian tropical rainforest, Agric. For. Meterol., 147, 35-47, 2007.

Kuzera, C. L. and Kirkham, D. R.: Soil respiration studies in tallgrass prarie in Missouri.
795 Ecology, 52, 912-915, 1971.

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

Linn, D. M. and Doran, J. W.: Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and nontilled soils, Soil Sci. Soc. Am. J., 48, 1267-1272, 1984.

800 Lloyd, J. and Taylor, J. A.: On the temperature dependence of soil respiration, Funct. Ecol., 8, 315-323, 1994.

Longdoz, B., Yernaux, M. and Aubinet, M.: Soil CO_2 efflux measurements in a mixed forest: Impact of chamber disturbances, spatial variability and seasonal evolution, Global Change Biol., 6, 907-917, 2000.

805 Luo, Y. and Zhou, X.: Soil Respiration and the Environment, in: Soil Respiration and the Environment, 2006.

Macinnis-Ng, C. and Schwendenmann, L.: Litterfall, carbon and nitrogen cycling in a southern hemisphere conifer forest dominated by kauri (*Agathis australis*) during drought, Plant Ecol., 216, 247-262, 2015.

810 Maier, M. and Schack-Kirchner, H.: Using the gradient method to determine soil gas flux: A review, Agric. For. Meterol., 192-193, 78-95, 2014.

Maier, M., Schack-Kirchner, H., Hildebrand, E. E. and Schindler, D.: Soil CO_2 efflux vs. soil respiration: Implications for flux models, Agric. For. Meterol., 151, 1723-1730, 2011.

Metcalfe, D. B., Fisher, R. A. and Wardle, D. A.: Plant communities as drivers of soil
815 respiration: Pathways, mechanisms, and significance for global change, Biogeosciences, 8, 2047-2061, 2011.

Metcalfe, D. B., Meir, P., Aragão, L. E. O. C., Malhi, Y., da Costa, A. C. L., Braga, A., Gonçalves, P. H. L., de Athaydes, J., de Almeida, S. S. and Williams, M.: Factors controlling spatio-temporal variation in carbon dioxide efflux from surface litter, roots,
820 and soil organic matter at four rain forest sites in the eastern Amazon, J. Geophys. Res. G Biogeosci., 112, 2007.

Millard, P., Midwood, A. J., Hunt, J. E., Barbour, M. M. and Whitehead, D.: Quantifying the contribution of soil organic matter turnover to forest soil respiration, using natural abundance d13C, Soil Biol. Biochem., 42, 935-943, 2010.

825 Ngao, J., Epron, D., Delpierre, N., Bréda, N., Granier, A. and Longdoz, B.: Spatial variability of soil CO_2 efflux linked to soil parameters and ecosystem characteristics in a temperate beech forest, Agric. For. Meterol., 154-155, X136-146, 2012.

Noguchi, K., Konôpka, B., Satomura, T., Kaneko, S. and Takahashi, M.: Biomass and production of fine roots in Japanese forests. J For Res, 12,83-95, 2007

830   Nottingham, A. T., Turner, B. L., Winter, K., van der Heijden, M. G. A. and Tanner, E. V. J.: Arbuscular mycorrhizal mycelial respiration in a moist tropical forest, New Phytol., 186, 957-967, 2010.

Ohashi, M., Kumagai, T., Kume, T., Gyokusen, K., Saitoh, T. M. and Suzuki, M.: Characteristics of soil CO_2 efflux variability in an aseasonal tropical rainforest in Borneo
835   Island, Biogeochemistry, 90, 275-289, 2008.

Oishi, A. C., Palmroth, S., Butnor, J. R., Johnsen, K. H. and Oren, R.: Spatial and temporal variability of soil CO_2 efflux in three proximate temperate forest ecosystems, Agric. For. Meterol., 171-172, 256-269, 2013.

Padamsee, M., Johansen, R. B., Stuckey, S. A., Williams, S. E., Hooker, J. E., Burns, B. R.
840   and Bellgard, S. E.: The arbuscular mycorrhizal fungi colonising roots and root nodules of New Zealand kauri *Agathis australis*, Fungal Biology, 120, 807-817, 2016.

Paul, K. I., Polglase, P. J., Smethurst, P. J., Connell, A. C., Carlyle, C. L. and Khanna, P. A.: Soil temperature under forests: a simple model for predicting soil temperature under a range of forest types. Agric. For. Meterol., 121, 167–182, 2004.

845   Phillips, C. L., Kluber, L. A., Martin, J. P., Caldwell, B. A. and Bond, B. J.: Contributions of ectomycorrhizal fungal mats to forest soil respiration, Biogeosciences, 9, 2099-2110, 2012.

Quideau, S.A.: Organic matter accumulation. In: Encyclopedia of Soil Science, pp. 891-894, New York, USA, Marcel Dekker Inc, 2002

850   Raich, J. W. and Potter, C. S.: Global patterns of carbon dioxide emissions from soils, Global Biogeochem. Cycles, 9, 23-36, 1995.

Raich, J. W. and Schlesinger, W. H.: The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate, Tellus, Series B, 44 B, 81-99, 1992.

Raich, J. W. and Tufekcioglu, A.: Vegetation and soil respiration: Correlations and controls,
855   Biogeochemistry, 48, 71-90, 2000.

Rayment, M. B. and Jarvis, P. G.: Temporal and spatial variation of soil CO_2 efflux in a Canadian boreal forest, Soil Biol. Biochem., 32, 35-45, 2000.

Reichstein, M., Rey, A., Freibauer, A., Tenhunen, J., Valentini, R., Banza, J., Casals, P., Cheng, Y., Grünzweig, J. M., Irvine, J., Joffre, R., Law, B. E., Loustau, D., Miglietta, F.,
860   Oechel, W., Ourcival, J. -., Pereira, J. S., Peressotti, A., Ponti, F., Qi, Y., Rambal, S., Rayment, M., Romanya, J., Rossi, F., Tedeschi, V., Tirone, G., Xu, M. and Yakir, D.: Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices, Global Biogeochem. Cycles, 17, 15-1, 2003.

865   Rustad, L. E., Huntington, T. G. and Boone, R. D.: Controls on soil respiration: Implications for climate change, Biogeochemistry, 48, 1-6, 2000.

Sayer, E. J., Heard, M. S., Grant, H. K., Marthews, T. R. and Tanner, E. V. J.: Soil carbon release enhanced by increased tropical forest litterfall, Nat. Clim. Change, 1, 304-307, 2011.

870   Schlesinger, W. H. and Andrews, J. A.: Soil respiration and the global carbon cycle, Biogeochemistry, 48, 7-20, 2000.

Schwendenmann, L., Veldkamp, E., Brenes, T., O'Brien, J. J. and Mackensen, J.: Spatial and temporal variation in soil CO_2 efflux in an old-growth neotropical rain forest, La Selva, Costa Rica, Biogeochemistry, 64, 111-128, 2003.

875   Scott-Denton, L. E., Rosenstiel, T. N. and Monson, R. K.: Differential controls by climate and substrate over the heterotrophic and rhizospheric components of soil respiration, Global Change Biol., 12, 205-216, 2006.

Silvester, W. B.: The biology of kauri (*Agathis australis*) in New Zealand II. Nitrogen cycling in four kauri forest remnants, New Zealand J. Bot., 38, 205-220, 2000.

880   Silvester, W. B. and Orchard, T. A.: The biology of kauri (*Agathis australis*) in New Zealand. I. Production, biomass, carbon storage, and litter fall in four forest remnants, New Zealand J. Bot., 37, 553-571, 1999.

Smith, P. and Fang, C.: Carbon cycle: A warm response by soils, Nature, 464, 499-500, 2010.

Soil Survey Staff.: Keys to Soil Taxonomy, 12th ed. USDA-Natural Resources Conservation
885   Service, Washington, DC, 2014

Søe, A. R. B. and Buchmann, N.: Spatial and temporal variations in soil respiration in relation to stand structure and soil parameters in an unmanaged beech forest, Tree Physiol., 25, 1427-1436, 2005.

Stacy, E. M., Hart, S. C., Hunsaker, C. T., Johnson, D. W. and Berhe, A. A.: Soil carbon and
890   nitrogen erosion in forested catchments: implications for erosion-induced terrestrial carbon sequestration, Biogeosciences, 12, 4861-4874.

Staelens, J., Nachtergale, L. and Luyssaert, S.: Predicting the spatial distribution of leaf litterfall in a mixed deciduous forest, For. Sci., 50, 836-847, 2004.

Steward, G. A. and Beveridge, A. E.: A review of New Zealand kauri (*Agathis australis* (D.
895   Don) Lindl.): Its ecology, history, growth and potential for management for timber, New Zealand J. For. Sci., 40, 33-59, 2010.

Stone, E. L. and Kalisz, P. J.: On the maximum extent of tree roots. For. Ecol. Manage, 46, 59-102, 1991.

Subke, J., Inglima, I. and Cotrufo, M. F.: Trends and methodological impacts in soil CO_2
900   efflux partitioning: A metaanalytical review, Global Change Biol., 12, 921-943, 2006.

Sulzman, E. W., Brant, J. B., Bowden, R. D. and Lajtha, K.: Contribution of aboveground litter, belowground litter, and rhizosphere respiration to total soil CO_2 efflux in an old growth coniferous forest, Biogeochemistry, 73, 231-256, 2005.

Takahashi, M., Hirai, K., Limtong, P., Leaungvutivirog, C., Panuthai, S., Suksawang, S.,
905   Anusontpornperm, S. and Marod, D.: Topographic variation in heterotrophic and autotrophic soil respiration in a tropical seasonal forest in Thailand, Soil Sci. Plant Nutr., 57, 452-465, 2011.

Tang, J., Baldochi, D. D., Qi, Y. And Xu, L.: Assessing soil CO_2 efflux using continuous measurements of CO_2 within the soil profile with small solid-stat sensors, Agri. Forest
910   Meteorol, 118, 207-220, 2003.

Tate, K. R., Ross, D. J., O'Brien, B. J. and Kelliher, F. M.: Carbon storage and turnover, and respiratory activity, in the litter and soil of an old-growth southern beech (Nothofagus) forest, Soil Biol. Biochem., 25, 1601-1612, 1993.

915 Taylor, A. J., Lai, C., Hopkins, F. M., Wharton, S., Bible, K., Xu, X., Phillips, C., Bush, S. and Ehleringer, J. R.: Radiocarbon-based partitioning of soil respiration in an old-growth coniferous forest, Ecosystems, 18, 459-470, 2015.

Than, D. J., Hughes, K. J. D., Boonhan, N., Tomlinson, J. A., Woodhall, J. W. and Bellgard, S. E.: A TaqMan real-time PCR assay for the detection of Phytophthora 'taxon Agathis' in soil, pathogen of Kauri in New Zealand, For. Pathol., 43, 324-330, 2013.

920 Thomas, G. M. and Ogden, J.: The scientific reserves of Auckland University. I. General introduction to their history, vegetation, climate and soils, Tane, 29, 143-162, 1983.

Trumbore, S.: Carbon respired by terrestrial ecosystems - Recent progress and challenges, Global Change Biol., 12, 141-153, 2006.

Urrutia-Jalabert, R.: Primary Productivity and Soil Respiration in Fitzroya Cupressoides
925 Forests of Southern Chile and Their Environmental Controls. University of Oxford, Oxford (DPhil Thesis), 2015.

Valentine, A. J. and Kleinert, A.: Respiratory responses of arbuscular mycorrhizal roots to short-term alleviation of P deficiency, Mycorrhiza, 17, 137-143, 2007.

van't Hoff, J.H.: Lectures on Theoretical and Physical Chemistry. Part I. Chemical Dynamics
930 (translated by R. A. Lehfeldt), pp. 224-229. Edward Arnold, London, 1898.

Verkaik, E. and Braakhekke, W. G.: Kauri trees (*Agathis australis*) affect nutrient, water and light availability for their seedlings, New Zealand J. Ecol., 31, 39-46, 2007.

Verkaik, E., Gardner, R. O. and Braakhekke, W. G.: Site conditions affect seedling distribution below and outside the crown of Kauri trees (*Agathis australis*), New Zealand
935 J. Ecol., 31, 13-21, 2007.

Verkaik, E., Jongkind, A. G. and Berendse, F.: Short-term and long-term effects of tannins on nitrogen mineralisation and litter decomposition in kauri (*Agathis australis* (D. Don) Lindl.) forests, Plant Soil, 287, 337-345, 2006.

Vitousek, P., Chadwick, O. A., Matson, P., Allison, S., Derry, L., Kettley, L., Luers, A.,
940 Mecking, E., Monastra, V. and Porder S.: Erosion and the rejuvenation of weathering-derived nutrient supply in an old tropical landscape, Ecosystems, 6, 762-772, 2003.

Warren, J. M., Iversen, C. M., Garten Jr., C. T., Norby, R. J., Childs, J., Brice, D., Evans, R. M., Gu, L., Thornton, P. and Weston, D. J.: Timing and magnitude of C partitioning through a young loblolly pine (*Pinus taeda* L.) stand using ^{13}C labeling and shade
945 treatments, Tree Physiol., 32, 799-813, 2012.

Weir, B. S., Paderes, E. P., Anand, N., Uchida, J. Y., Pennycook, S. R., Bellgard, S. E. and Beever, R. E.: A taxonomic revision of phytophthora clade 5 including two new species, *Phytophthora agathidicida* and *P. cocois*, Phytotaxa, 205, 21-38, 2015.

Whitlock, J. S.: Soil development in a kauri forest succession: Huapai scientific reserve.
950 Unpublished Master thesis. University of Auckland, 1985

Wunder, J., Perry, G. L. W. and McCloskey, S. P. J.: Structure and composition of a mature kauri (*Agathis australis*) stand at Huapai Scientific Reserve, Waitakere Range. New Zealand Tree-Ring Site Report, 33, 1-19, 2010.

955   Wyse, S. V. and Burns, B. R.: Effects of *Agathis australis* (New Zealand kauri) leaf litter on germination and seedling growth differs among plant species, New Zealand J. Ecol., 37, 178-183, 2013.

Wyse, S. V., Burns, B. R. and Wright, S. D.: Distinctive vegetation communities are associated with the long-lived conifer *Agathis australis* (New Zealand kauri, Araucariaceae) in New Zealand rainforests, Austral Ecol., 39, 388-400, 2014.

960   Xu, M. and Qi, Y.: Spatial and seasonal variations of Q_{10} determined by soil respiration measurements at a Sierra Nevadan forest. Glob. Biogeochem. Cycl., 15, 687–697, 2001.

Yoo, K., Amundson, R., Heimsath, A. M., Dietrich, W.E.: Erosion of upland hillslope soil organic carbon: Coupling field measurements with a sediment transport model. Glob. Biogeochem. Cycl., 19, GB3003, 2005.

965   Zalamea, M., Gonzalez, G. and Gould, W.: Comparing litterfall and standing vegetation: assessing the footprint of litterfall traps. pp 21 – 36. in: Sudarshana, P., Nageswara-Rao, M. and Soneji, J.R. (eds). Tropical Forests. Intech, published online at: http://www.intechopen.com/books/tropical-forests, 2012

Zang, U., Goisser, M., Häberle, K., Matyssek, R., Matzner, E. and Borken, W.: Effects of
970   drought stress on photosynthesis, rhizosphere respiration, and fine-root characteristics of beech saplings: A rhizotron field study, J. Plant Nutr. Soil Sci., 177, 168-177, 2014.

Table 1. Descriptive statistics for litter, root, and soil characteristics. Samples were taken in the vicinity of the surface soil CO_2 efflux (n = 12, except for root biomass, n = 10)

Parameter	mean	STDEV	SE	median	min-max	CV %
Litterfall						
Σ 2012 (kg m^{-2})	0.9	0.2	0.1	0.9	0.6-1.1	21.7
Σ 2013 (kg m^{-2})	1.6	0.3	0.1	1.7	1.0-1.9	21.3
Organic layer (OL)						
Thickness (cm)	8.8	2.3	0.9	8.2	6.2-12.2	26.1
Root biomass (kg m^{-2})	0.8	0.9	0.3	0.3	0.02-2.7	115.6
pH	4.85	0.57	0.23	5.06	3.88-5.51	11.8
C/N ratio	43.9	10.4	4.2	43.2	31.4-58.7	23.7
Carbon stock (kg m^{-2})	18.7	7.7	3.1	18.4	7.9-28.9	41.2
Nitrogen stock (kg m^{-2})	0.45	0.18	0.07	0.45	0.22-0.77	40.0
Mineral soil						
Root biomass, 0-15 cm (kg m^{-2})	2.2	1.6	0.5	1.6	0.7-6.3	75.1
Root biomass, 15-30 cm (kg m^{-2})	0.7	1.2	0.4	0.4	0.2-3.9	97.7
Root biomass, ΣOL+0-30 cm (kg m^{-2})	3.8	2.2	0.7	3.8	0.9-8.0	57.9
pH, 0-10 cm	4.68	0.52	0.21	4.91	3.75-5.13	11.1
C/N ratio, 0-10 cm	16.1	1.9	0.8	16.2	13.7-19	12.1
Carbon stock, 0-10 cm (kg m^{-2})	8.4	1.9	0.8	8.6	6.0-10.7	22.7
Nitrogen stock, 0-10 cm (kg m^{-2})	0.53	0.13	0.05	0.52	0.40-0.75	24.1
Soil temperature (°C)	14.2	0.2	0.1	14.2	14.0-14.5	1.4
Volumetric soil water content (%)	43.9	2.1	0.9	44.3	41.2-46.1	4.9

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	N	n	Soil CO_2 efflux ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)					Soil temperature (°C)					Volumetric soil water content (%)				
			mean	SE	med	min max	CV %	mean	SE	med	min max	CV %	mean	SE	med	min max	CV %
Plot																	
Plot_Surface	12	30	3.61a	0.09	3.37	0.65 9.96	42.6	14.2a	0.11	14.4	10.9 17.5	13.5	43.1a	0.65	44.7	15.2 66.6	27.1
Plot_Inserted	12	30	2.98b	0.07	2.72	0.69 8.02	43.6	14.1a	0.10	14.1	10.9 17.4	13.8	44.7a	0.56	46.6	15.2 62.3	23.0
Trench																	
Outside_ Trench_Surface	6	17	3.11c	0.14	2.92	0.55 6.92	43.0	13.1c	0.17	13.2	10.2 17.2	12.5	44.0c	1.27	44.2	17.4 72.5	25.2
Trench_Inserted	6	17	2.34d	0.08	2.14	0.67 5.30	41.0	12.9c	0.14	13.0	10.1 16.9	13.1	56.8d	0.74	56.4	20.2 76.5	14.8

N = number of sampling points; n = number of sampling dates between August 2012 and January 2014; SE = standard error; med = median; min = minimum; max = maximum

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Table 3. Relationships of total soil CO_2 efflux, heterotrophic and autotrophic respiration with soil temperature (T) and volumentric soil water content (W) using uni- and bivariate functions.

Model	Var	Total soil CO_2 efflux					Heterotrophic respiration					Autotrophic respiration				
		R^2	SEE	p	AIC	Q_{10}	R^2	SEE	p	AIC	Q_{10}	R^2	SEE	p	AIC	Q_{10}
Linear	T	0.168	0.747	0.0043	-22.9		0.475	0.461	<0.0001	-68.2		0.012	0.463	0.5061	-55.4	
Exponential (Q_{10})	T	0.160	0.750	0.0054	-22.5	1.6	0.475	0.461	<0.0001	-68.3	2.2	0.011	0.463	0.5229	-55.4	1.3
Mod. Arrhenius	T	0.181	0.741	0.0029	-23.7		0.471	0.463	<0.0001	-67.9		0.016	0.462	0.4493	-55.6	
Linear	W	0.015	0.799	0.4262	-16.1		0.369	0.510	<0.0001	-57.5		0.072	0.440	0.1043	-57.7	
Quadratic	W	0.123	0.763	0.0597	-19.1		0.408	0.499	<0.0001	-58.0		0.168	0.423	0.0399	-59.4	
Polynomial	T,W	0.177	0.739	0.0150	442		0.508	0.455	<0.0001	442		0.158	0.427	0.0490	345	

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Var = Variables; R^2 = coefffient of determination; SEE = standard error of estimate; AIC = Akaike Information Criterion

y = soil CO_2 efflux, heterotrophic or autotrophic respiration; x = soil temperature; z = volumetric soil water content,

1000 Functions: Linear: $y = a \times x/y + b$; Exponential: $y = a \times \exp(b \times x)$; Modified Arrhenius $y = a \times \exp(-b/(x-x_0))$; Quadratic: $y = a \times y^2 + b \times y + c$; Polynomial: $y = a + b \times x + c \times z$;

$Q_{10} = \exp(10 \times b)$, b derived from exponential function.

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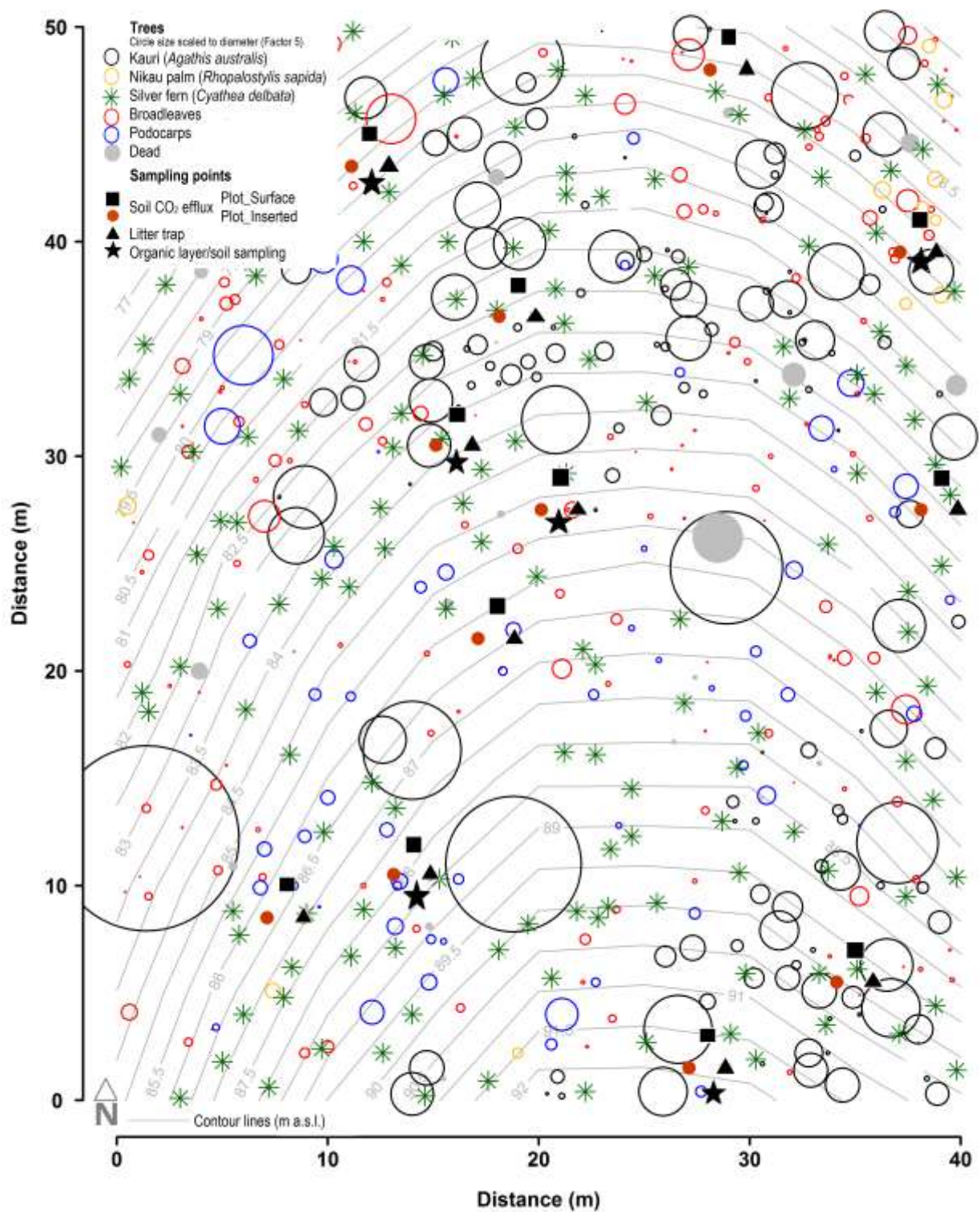
Figure 1. Overview of the research plot showing the position of all trees ≥ 2.5 cm diameter (circle size scaled to diameter – Factor 5) and sampling points for soil CO_2 efflux measurements (Plot_Surface, Plot_Inserted), litter and soil sampling. The trench plots are located adjacent (upslope) of the research plot at around 92 m a.s.l..

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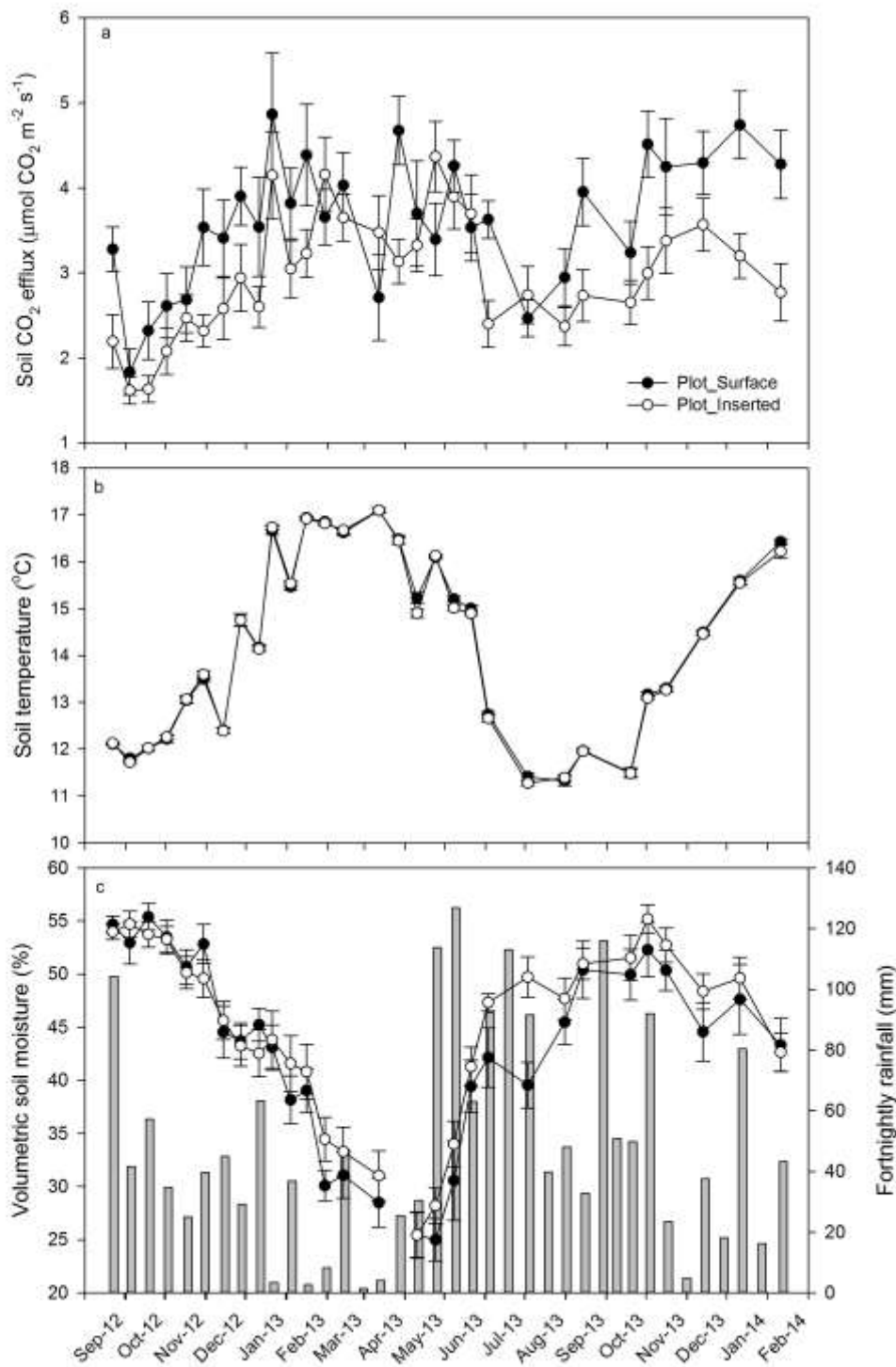
Figure 2. Soil CO_2 efflux (a), soil temperature (b) and volumetric soil water content (c) measured in the research plot from August 2012 to January 2014. Values show mean ± standard error of the Plot_Surface (n=12) and Plot_Inserted (deep collar, n=12) sampling points, respectively.Volumetric soil water content was not measured in March 2013 due to
1015 equipment failure. Fortnightly rainfall (c) was measured in a paddock in the vicinity of the research plot.

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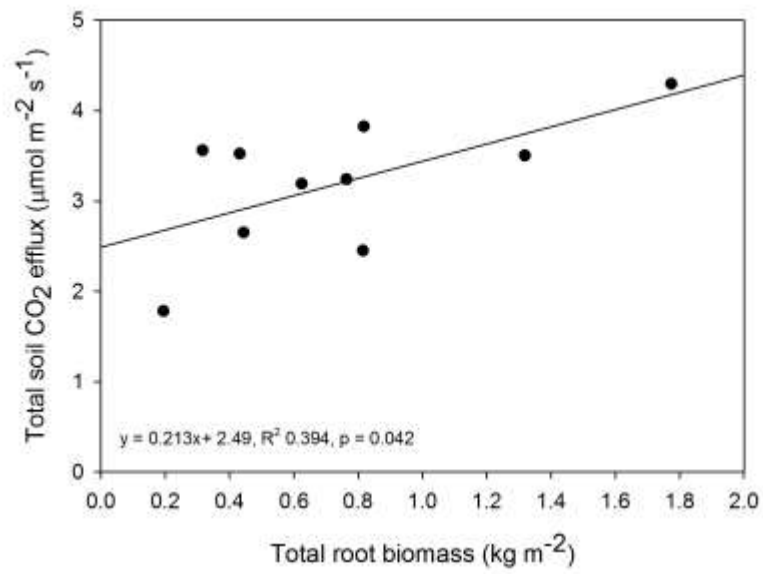
Figure 3. Regression of total root biomass (fine and coarse roots, organic layer plus mineral soil to 30 cm depth) vs total soil CO_2 efflux.

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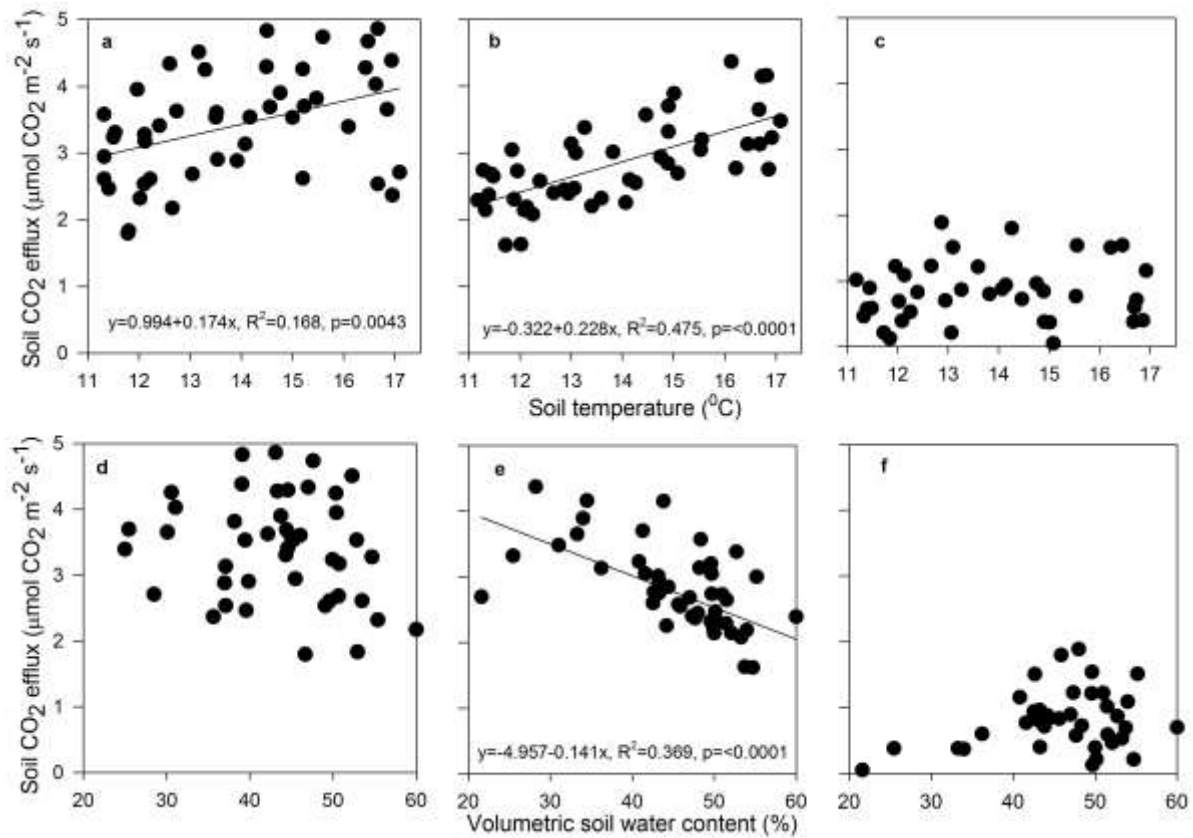
Figure 4. Upper panels. Relationship between soil temperature and total soil CO_2 efflux (a), heterotrophic respiration (b) and autotrophic respiration (c). Lower panels: Relationship between soil volumetric water content and total soil CO_2 efflux (d), heterotrophic respiration (e) and autotrophic respiration (f). Regression lines are only displayed for significant linear

1040   relationships. The results for other uni- and bivariate functions are shown in Table 3.
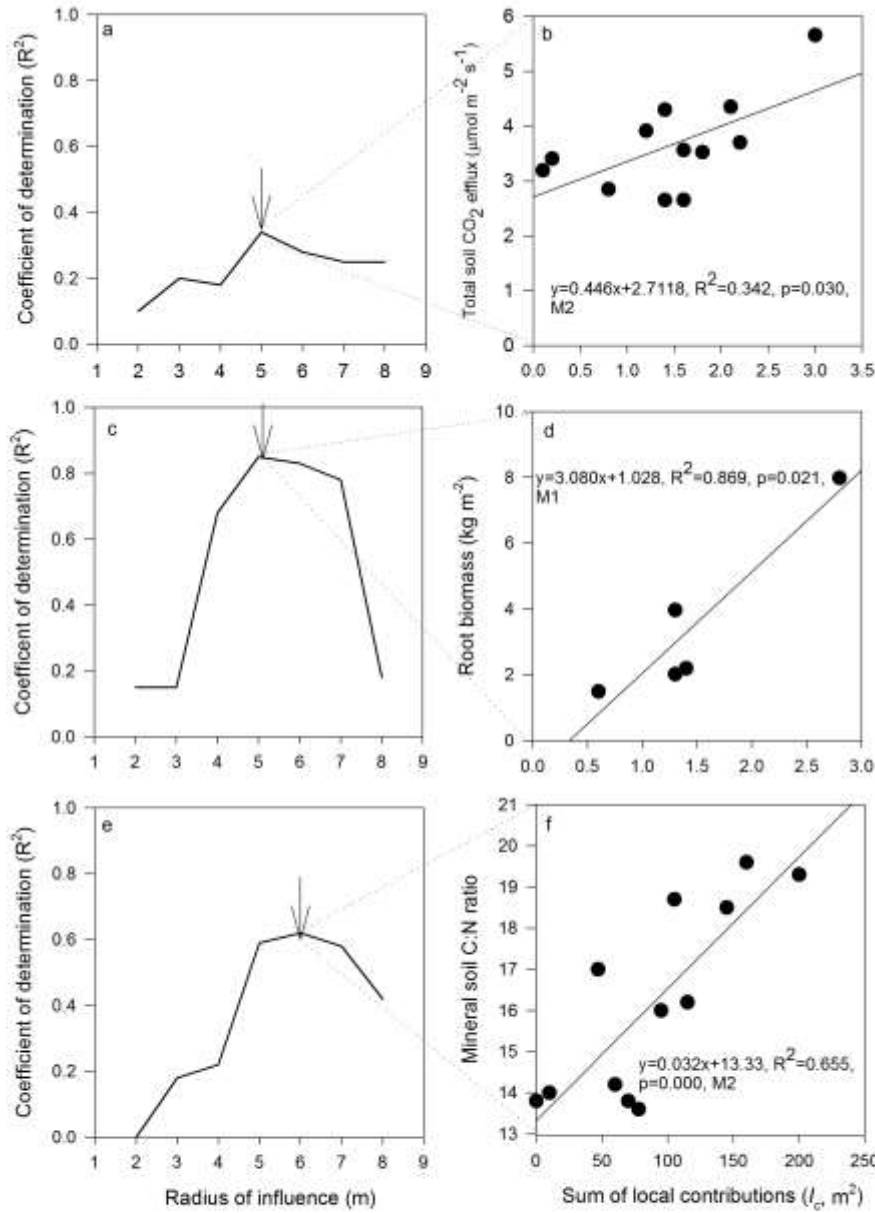
Figure 5. Relationships between the sum of local contribution indices of surrounding trees within the fitted radius of influence and total soil CO_2 efflux (5.a,b), root biomass (5c,d) and mineral soil CN ratio (5e,f). The arrows in panel a, c and e indicate the best coefficients of variation (highest R^2 value) with models shown in panel b, d and f.

M1 = univariate model (I_c = S); M2 = linear model (I_c = S x (1-d/r)) where S = trunk cross section area (S, m²), d = distance between the trees and the measurement point (d, m), r = fitted radius of influence (r, m).