



Soil CO₂ efflux from two mountain forests in the eastern Himalayas, Bhutan: components and controls

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Abstract. The biogeochemistry of mountain forests in the Hindu Kush Himalaya range is poorly studied, although climate change is expected to disproportionately affect the region. We measured the soil CO₂ efflux (R_s) at a high-elevation (3260 m) mixed forest and a lower-elevation (2460 m) broadleaf forest in Bhutan, eastern Himalayas, during 2015. Trenching was applied to estimate the contribution of autotrophic (R_a) and heterotrophic (R_h) soil respiration. The temperature (Q_{10}) and the moisture sensitivities of R_h were determined under controlled laboratory conditions and were used to model R_h in the field. The higher-elevation mixed forest had a higher standing tree stock, reflected in higher soil C stocks and basal soil respiration. Annual R_s was similar between the two forest sites ($14.5 \pm 1.2 \text{ t C ha}^{-1}$ for broadleaf; $12.8 \pm 1.0 \text{ t C ha}^{-1}$ for mixed). Modelled annual contribution of R_h was $\sim 65\%$ of R_s at both sites with a higher heterotrophic contribution during winter and lower contribution during the monsoon season. R_h , estimated from trenching, was in the range of modelled R_h but showed higher temporal variability. The measured temperature sensitivity of R_h was similar at the mixed and broadleaf forest sites (Q_{10} 2.2–2.3) under intermediate soil moisture but decreased (Q_{10} 1.5 at both sites) in dry soil. R_s closely followed the annual course of field soil temperature at both sites. Covariation between soil temperature and moisture (cold dry winters and warm wet summers) was likely the main cause for this close relationship. Under the prevailing weather conditions,

a simple temperature-driven model was able to explain more than 90 % of the temporal variation in R_s . A longer time series and/or experimental climate manipulations are required to understand the effects of eventually occurring climate extremes such as monsoon failures.

1 Introduction

Carbon dioxide (CO₂) efflux from soil (soil respiration; R_s) is one of the major fluxes in the global C cycle, affects atmospheric CO₂ concentrations and potentially provides feedback on global climate change (Reichstein et al., 2003; Frey et al., 2013; Wang et al., 2014; Hashimoto et al., 2015). Counteracting to C uptake via photosynthesis, R_s primarily determines whether forest ecosystems serve as C sinks or sources to the atmosphere (Bolstad et al., 2004; Dixon et al., 1994; Schlesinger and Andrews, 2000). The current function of forests as a global C sink (Stocker, 2014; Janssens et al., 2003) could weaken and they could even become a source if climate change disproportionately accelerates respiratory processes such as R_s (Cox et al., 2000). R_s consists of an autotrophic component (R_a ; root and rhizosphere respiration), which is closely linked to C gain by photosynthesis, and a heterotrophic component (R_h), which is the respiratory product of soil organic matter (SOM) decomposition. While the source of R_a is recently assimilated CO₂, R_h can

release stored soil C to the atmosphere. For a better prediction of the response of forest C cycling to climate change, it is crucial to understand how R_s and its components are affected by changing environmental parameters such as temperature and moisture (Davidson and Janssens, 2006; Sierra et al., 2015). Rates and climate sensitivity of R_s , R_a and R_h can vary among forest ecosystem type and climatic region (Hashimoto et al., 2015). So far, research has focused on the temperate and boreal areas of the Northern Hemisphere whereas remote forested areas are still largely uninvestigated (Bond-Lamberty and Thomson, 2010).

The Hindu Kush Himalaya range represents a region where research on forest biogeochemistry is gaining momentum (Pandey et al., 2010; Sundarapandian and Dar, 2013; Sharma et al., 2010b; Dorji et al., 2014b; Ohsawa, 1991; Wangda and Ohsawa, 2006a; Tashi et al., 2016; Verma et al., 2012). It extends over 4.3 million km² across eight countries with an average forest cover of approximately 20 % (Schild, 2008), ranging from lowland tropical forest to high-altitude forests of up to ~4900 m (Liang et al., 2016; Schickhoff, 2005). Situated in the eastern Himalayas, Bhutan has a forest cover of 70 % (DoFPS, 2011). Most forests in Bhutan are natural old growth (Ohsawa, 1987), store high amounts of C in biomass and soil (Dorji et al., 2014a; Sharma and Rai, 2007) and serve as an important regional C sink (FAO, 2010). As climate change is expected to intensify in the Himalayan region (Shrestha et al., 2012; Singh, 2011; Xu and Grumbine, 2014; Tsering et al., 2010; Xu et al., 2009), the effects on forest C cycling could have implications not only regionally, but also on a global scale.

With the objective of a better understanding of soil C cycling of mountain forest ecosystems, we studied R_s and its components (R_a , R_h), as well as the effects of environmental drivers such as temperature and moisture at a moderately high-altitude cool temperate mixed forest and a lower-altitude cool temperate broadleaf forest in Bhutan. These forest types cover large areas of the eastern Himalayas.

2 Materials and methods

2.1 Site description

Two representative forest ecosystems for the eastern Himalayas (Wikramanayake, 2002), a cool temperate conifer-dominated mixed forest and a cool temperate broadleaf forest, were studied at Thimphu and Wangduephodrang districts, Bhutan. The cool temperate mixed forest (Grierson and Long, 1983) was situated on a south-east-facing slope close to the top of a mountain ridge (elevation 3260 m a.s.l.). The cool temperate broadleaf forest was situated on an east-facing gentle slope along the same mountain ridge ~11 km eastwards (elevation 2640 m a.s.l.). The sites will be referred to as “mixed forest” and “broadleaf forest” hereafter. The mixed forest was dominated by *Tsuga dumosa* along with

Picea spinulosa, *Quercus semecarpifolia*, *Abies densa*, and *Taxus baccata*. The broadleaf forest was dominated by *Quercus lanata* and *Quercus griffithii*. Soils at the mixed forest were Cambisols. Soils at the broadleaf forest were Luvisols. A detailed site and soil description and the comparison are given in Table 1. The current study was aligned within a larger-scale throughfall manipulation experiment, which consisted of controlled and temporarily roofed areas within each forest type. For this study, we randomly distributed all our plots within the control areas (~1500 m² each) of the throughfall manipulation experiment.

2.2 Field measurements

Basic climate parameters were measured using automatic weather stations located at a distance of approx. 1 km from the sites at the same elevation. Data were recorded at 15 min intervals on a Decagon-EM50 data logger (Decagon Devices Inc., Pullman, WA, USA). The automatic weather stations recorded precipitation with an ECRN-100 rain gauge (Decagon Devices Inc., Pullman, WA, USA), and air temperature and relative humidity with a VP-3 vapour pressure, temperature and relative humidity sensor (Decagon Devices Inc., Pullman, WA, USA).

Stand and soil inventories were carried out in March and April 2014 at both sites covering an area of ~1500 m² each. The location, height and the diameter at breast height of all trees with a dbh > 10 cm were assessed. The basal area was calculated for each tree species. Standing volume was estimated based on species-specific volume equations developed by Laumans (1994), Forest Survey of India (FSI) (1996) and Department of Forests and Park Services (FRD) (2005). Aboveground litter fall was collected monthly using mesh traps ($n = 10$) at each site, with an area of 1.0 m² (100 × 100 cm). Litter was dried at 80 °C and the C content was assumed to be 50 % of the dry weight (de Wit et al., 2006). Soil samples were collected from the 0–10, 10–20 and 20–30 cm mineral soil layers from four locations at both sites in May 2014. Soil samples were sieved (2 mm) and dried (105 °C, 48 h). Soil organic C (SOC) of a ground (Pulverisette 5, Fritsch, Germany) 0.1 g subsample was measured by means of the dry combustion technique using a CN analyser (TruSpec[®] CN, LECO Inc., Michigan, USA). Soil organic C stocks (t ha⁻¹) were calculated for each horizon by multiplying the SOC concentration (%) by the bulk density (g cm⁻³) and the depth of the horizon (cm). Fine root (≤ 2 mm) biomass was estimated using the soil core method (Makkonen and Helmsaari, 1999) in spring 2014 at both sites. We used a cylindrical soil corer (7.5 cm diameter) for sampling. The extracted samples were divided into three depth sections of 0–10, 10–20 and 20–30 cm. After washing and sorting (live roots and necromass), roots were dried at 70 °C to constant mass before weighing dry biomass. The contribution of fine root C was estimated at 50 % of the plant tissue.

Table 1. Site characteristics of the two studied forests.

Parameter	Mixed forest	Broadleaf forest
Elevation (m)	3260	2460
Latitude	27°28′00″ N	28°28′51.06″ N
Longitude	89°44′30.79″ E	89°51′27.73″ E
Annual precipitation 2015 (mm)	1167	1120
Mean air temperature 2015 (°C)	7.8	12.0
Dominant overstorey species	<i>Tsuga dumosa</i> (59.5 %) <i>Quercus semecarpifolia</i> (29.3 %) <i>Picea spinulosa</i> (6.3 %) <i>Abies densa</i> (4.1 %) <i>Taxus baccata</i> (0.3 %)	<i>Quercus lanata</i> (63.5 %) <i>Quercus griffithii</i> (29.6 %)
Dominant understory species	<i>Ilex dipreyana</i> (0.2 %) <i>Rhododendron arboreum</i> (0.1 %)	<i>Symplocos</i> sp. (0.8 %) <i>Lyonia ovalifolia</i> , (2.2 %) <i>Rhododendron arboreum</i> (3.4 %)
Tree density (No. ha ⁻¹)	364 ± 50	569 ± 19
Mean tree height (m) overstorey	24.4 ± 2.1	23.6 ± 1.4
Mean tree height (m) understorey	7.8 ± 3.5	9.8 ± 0.4
Mean DBH (cm) overstorey	50.7 ± 5.8	37.8 ± 2.3
Mean DBH (cm) understorey	13.8 ± 1.4	16.1 ± 0.9
Tree basal area (m ² ha ⁻¹)	77.5 ± 4.6	39.9 ± 4.4
Standing volume (m ³ ha ⁻¹)	1066 ± 2.3	464 ± 25
Soil organic C (t ha ⁻¹) 0–30 cm	142.0 ± 25.4	90.1 ± 9.0
Soil organic C (t ha ⁻¹) 0–10 cm	61.9 ± 5.3	55.5 ± 6.9
Soil organic C (t ha ⁻¹) 10–30 cm	80.1 ± 8.0	34.6 ± 2.4
Soil N (t ha ⁻¹) 0–30 cm	7.4 ± 0.5	4.3 ± 0.4
Soil N (t ha ⁻¹) 0–10 cm	3.2 ± 0.2	2.4 ± 0.3
Soil N (t ha ⁻¹) 10–30 cm	4.2 ± 0.4	1.9 ± 0.1
pH (0–10 cm)	5.2 ± 0.1	5.0 ± 0.1
Bulk density (g cm ⁻³) 0–10 cm	0.61 ± 0.02	0.61 ± 0.01
Fine root biomass (t C ha ⁻¹) 0–30 cm	2.3 ± 0.3	3.2 ± 0.5
Litter input (t C ha ⁻¹ yr ⁻¹)	3.5 ± 0.10	3.4 ± 0.03

All stand and soil parameters are expressed as the mean ± standard error.

R_s was measured at both sites once every 3 weeks from April 2015 to December 2015 at 10 randomly chosen plots ($n = 10$) at each. To cover the within-plot variability, R_s was measured at four positions within each plot (total 40 positions per site). We used a portable infrared gas analyser (EGM-4, PP-Systems, Amesbury, USA) with an attached soil respiration chamber (SRC-1, PP-Systems, Amesbury, USA) for R_s measurements. Prior to measurements (March 2015), we installed permanent collars (total height 5 cm, 2–3 cm inserted into the soil, diameter 10 cm) at each plot which served as a base for R_s measurements. R_s was estimated by applying a linear fit to the increasing headspace CO₂ concentration over time (chamber closure time 90 seconds). A soil respiration measurement campaign lasted for ~5 h at each site. Measurement order among plots and collars was fully random to avoid bias from temporal variations in R_s .

We installed two trenching plots at each site in April 2014 (1 year prior soil efflux CO₂ measurements) to estimate the

relative contributions of R_a and R_h . Trenches (1.5 × 1.5 m) were dug to ~1 m depth, and all roots within the trenches were cut. The trenches were sealed with double layered plastic foil in order to restrict tree root ingrowth. Adjoined to each trenched plot was a corresponding control plot of the same size. Each trenched and control plot hosted three collars for R_s measurements. We measured soil CO₂ efflux at trenched and corresponding control plots after finishing regular R_s measurements (same day).

Volumetric soil water content (0–20 cm soil depth; (vol. %)) was measured in the centre of each plot (R_s plots, trenched plots, control plots) using a portable Field Scout TDR meter (Spectrum Technologies, Inc. Aurora, USA) during R_s measurements. Soil temperature at 5 cm soil depth was measured with a handheld thermometer probe (Hanna Instruments, Germany) at each R_s measurement location. Soil temperature and soil moisture were measured continuously at soil profile pits (two pits per site) with five combined

soil temperature–moisture sensors (TM-5; Decagon Devices, Inc., Pullman, WA, USA) at soil depths ranging from 5 to 120 cm. Data were recorded at 15 min intervals on Decagon-EM50 data loggers (Decagon Devices, Inc., Pullman, WA, USA).

2.3 Laboratory incubation

About 500 g of mineral soil (0–10 cm depth) and approximately 250 g of forest floor litter were sampled at six random locations ($n = 6$) at each site in mid-September 2015. The mineral soil was homogenised and sieved (2 mm mesh) and stored at 4 °C at field moisture for 1 week prior to transport from Bhutan to Austria for further processing. Forest floor litter was not sieved. Upon arrival in Austria, mineral soil samples were further divided into three subsamples to account for potential soil heterogeneity at individual sampling locations. Samples were filled into 200 cm³ stainless steel cylinders at approximate field bulk density (~ 0.5 g dry weight cm⁻³ for mineral soil; ~ 0.1 g dry weight cm⁻³ for forest floor). In total, we incubated 36 subsamples (cylinders) for mineral soil and 12 subsamples for the forest floor litter. Filled cylinders were kept at 4 °C for 5 days for equilibration before incubation. Soil CO₂ efflux ($= R_h$) was measured using a fully automated incubation system. During incubation, samples were put into 2 L containers and their CO₂ efflux was determined by a dynamic closed chamber system (Pumpanen et al., 2009). For CO₂ measurements, containers were sequentially connected to an infrared gas analyser (SBA-4, PP Systems International Inc., Amesbury, MA, USA) by means of a tubing system. Meanwhile, disconnected containers were ventilated by means of an air pump in order to prevent internal CO₂ enrichment. Wet tissues were put into containers to prevent samples from drying out during incubations; moisture loss was thereby negligible (< 2 vol. %). CO₂ concentration within connected containers was measured for 6 min with a recording interval of 10 s. Rates of CO₂ efflux were calculated from the headspace CO₂ increase during 2–6 min, after Pumpanen et al. (2009).

Incubations proceeded in two steps. We first incubated at different soil temperatures to assess the temperature sensitivity of R_h . In a second step, we incubated under different soil moisture contents to assess the sensitivity of R_h to changes in soil moisture. In addition, we repeated the temperature runs with wet (140 % gravimetric water content (grav. %)) and dry (30 grav. %) soil in order to test for effects of soil moisture on the temperature sensitivity of R_h . Between incubations, soil cores were stored in a cold room (+4 °C). During storage, soil moisture was kept constant by periodical water addition.

Temperature incubation started with mineral soil. Soil temperature was increased from 5 to 25 °C in 5 °C steps, with each temperature step lasting for 6 h. At each temperature step, efflux measurements were repeated three times for each cylinder. To account for a warm-up period between the individual temperature steps only a calculated mean value of the

latter two measurements was used for further analysis. After finishing the temperature run, we remeasured R_h at 10 °C to assess and correct for potential effects of labile C loss during the ~ 30 h incubation. The forest floor litter was incubated under the same procedure as mineral soil.

After the temperature incubation, we set soil moisture of all mineral soil subsamples to 80 grav. %, incubated at constant 15 °C for 6 h and measured R_h as described above. Afterwards, the three subsamples from each sampling location were split into (i) a subsample that was kept at constant soil moisture (80 grav. %), (ii) a subsample that was allowed to dry out (60 to 15 grav. %), and (iii) a subsample that was progressively watered (100 to 160 grav. %). Between repeated incubations (all at 15 °C for 6 h) cylinders were taken out from incubation containers and were stored at 4 °C. The whole moisture incubation procedure lasted for 10 weeks with ~ 2 -week intervals between incubations (time-limiting step was soil drying). We used R_h from the subsamples which had been kept at constant moisture to correct for potential decreases in R_h due to a loss in labile C throughout the experiment. After finishing all incubations, samples were dried and actual bulk density, as well as actual gravimetric (grav. %) and volumetric soil moisture (vol. %) of each subsample (cylinder), was calculated and their total C content was determined (TruSpec[®] CN, LECO Inc., Michigan, USA). R_h rates were expressed as $\mu\text{mol CO}_2 \text{ kg C}^{-1} \text{ s}^{-1}$.

2.4 Data analysis

The effects of field R_s , soil temperature and moisture on the sites were tested by means of repeated ANOVA measurements with a mixed-effects model structure (Pinheiro and Bates, 2000). The significance level for this and all other analyses was set at $P < 0.05$. The relationship between soil temperature and R_s was fitted by an exponential function (Buchmann, 2000):

$$R = \beta_0 \cdot e^{(\beta_1 \cdot T)}, \quad (1)$$

where R ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) is the measured R_s , T (°C) is the soil temperature at 5 cm depth, and b_i is the model parameters. Equation (1) was fitted to the daily averages of each site as well as to the individual plot data. Basal respiration rates at 10 °C soil temperature (R_{s10}) were subsequently calculated (using Eq. 1) for each site. One sampling date (16 July 2015) was excluded from this analysis because heavy rain occurred during the measurements. The relationship between R_s and soil moisture was tested by fitting a polynomial function obtained from lab incubation (see further below). Cumulative annual R_s of both sites and both years were calculated by linear interpolation of field R_s between measurement dates of each individual plot (the area beneath the curves in Fig. 1d). In addition, model parameters of Eq. (1), together with daily field soil temperatures at 5 cm depth were used to calculate a projected daily field R_s . To account for a spatial variation in soil temperature, continuously measured data were adjusted

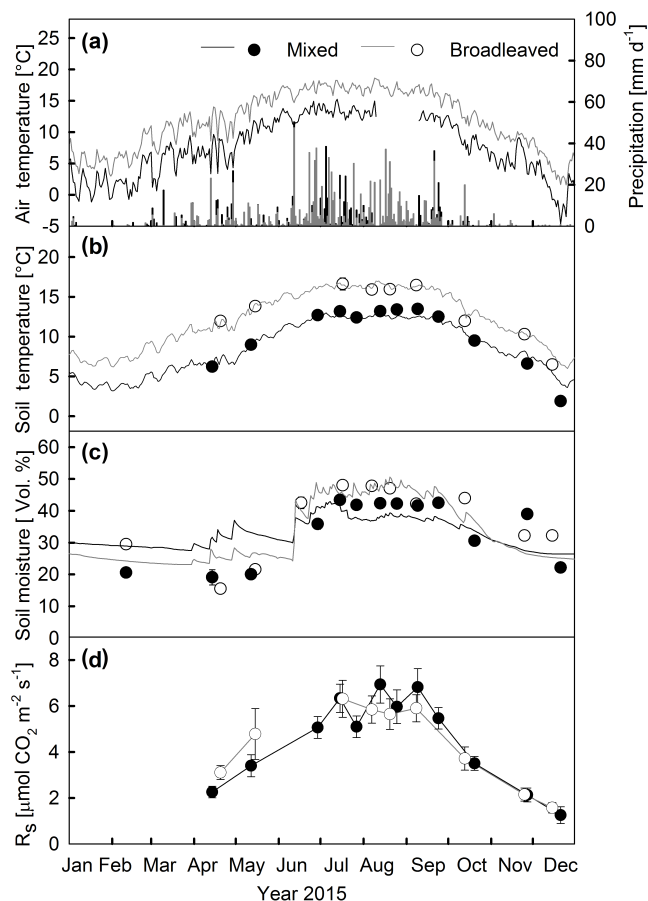


Figure 1. Seasonal course of air temperature and precipitation (a), soil temperature (b), volumetric soil water content (c) and soil respiration (d) measured at a mixed and a broadleaf forest in the Bhutan Himalayas in 2015. Circles represent daily mean values of manual measurements. Solid lines (a, b, c) represent daily mean values of continuous measurements. Error bars indicate standard error of the mean.

to discontinuously measured plot data by linear modelling. Cumulative annual R_s rates were calculated by averaging the summed-up daily plot R_s values.

Average R_h rates from laboratory incubations were calculated for each site, soil horizon (mineral soil, forest floor litter) and temperature step (5–25 °C), respectively. Equation (1) was fitted to the temperature incubation data separately for each site and soil horizon. Basal heterotrophic respiration rates at 10 °C (R_{h10}) were calculated for each site. Temperature sensitivity (Q_{10}) of R_h was calculated as follows:

$$Q_{10} = e^{(10 \cdot \beta_1)}, \quad (2)$$

where Q_{10} is the factor by which R_h changes at a temperature change of 10 °C, and β_1 is the model parameter derived from Eq. (1). To determine the relationship between soil moisture and R_h , we fitted a polynomial function to the moisture incu-

bation data:

$$R = \beta_0 + \beta_1 \cdot \text{VWC} + \beta_2 \cdot \text{VWC}^2, \quad (3)$$

where R is the measured CO₂ efflux from soil samples (R_h), β_i is the model parameters and VWC is the volumetric water content of the samples. Effects of soil moisture on Q_{10} values were tested by means of one-way ANOVA and Tukey's post-hoc tests.

We followed two approaches to estimate the contribution of R_a and R_h in the field. In a first approach, we used the trenching data, assuming that the CO₂ efflux from the trenched plots solely represented R_h , while the CO₂ efflux from adjacent control plots represented R_s and, accordingly, the difference between trenched and control plot CO₂ efflux represented R_a . As trenched plots lack water uptake by tree roots, they were regularly wetter than control plots. We accounted for that by correcting the soil CO₂ efflux for the difference in soil moisture by using Eq. (3) (see Schindlbacher et al., 2009 for details).

In a second approach, we applied the response functions of R_h derived during laboratory incubation together with field soil C stocks and field climate data. This allowed an alternative way of estimating the contribution of R_h in the field (Gough et al., 2007; Kutsch et al., 2010). Model parameters derived from Eq. (1), together with continuously measured temperature data from 5 cm soil depth, were used to model daily R_h from the litter and from the mineral soil at depths of 0–10 cm. Model parameters for mineral soils, together with continuous measurements of soil temperature at 20 cm depth, were further used to model daily R_h from the mineral soil at 10–30 cm depth. Predicted R_h rates ($\mu\text{mol CO}_2 \text{ kg C}^{-1}$) were multiplied by the C stocks (kg C m^{-2}) of the respective soil layer. We used the litter Q_{10} , together with continuous temperature at 5 cm soil depth, to model daily R_h from the litter layer. In order to scale to field fluxes, we used the annual litter input (Table 1) as a proxy for field litter C stocks. A first rough litter assessment in March 2015 showed that litter stocks were in a similar range to the annual litter input at both sites. This procedure enabled us to upscale R_h to the whole soil profile in the field (Kutsch et al., 2010). To account for a moisture response as well, predicted R_h rates were also corrected for soil moisture conditions in the field. For that, model parameters derived from Eq. (3) were used to calculate R_h rates at actual moisture conditions in the field (from continuous moisture data) and at initial moisture conditions of the soil samples during incubation (mixed forest: 33 vol. %, broadleaf forest: 35 vol. %, litter: 46 vol. %); their relative difference was subsequently used to correct R_h rates predicted with Eq. (1). Since litter soil moisture was not regularly measured in the field, we applied the same moisture parameters and continuous soil moisture records as for mineral soil (0–10 cm). The R code of the empirical model is provided in the Supplement.

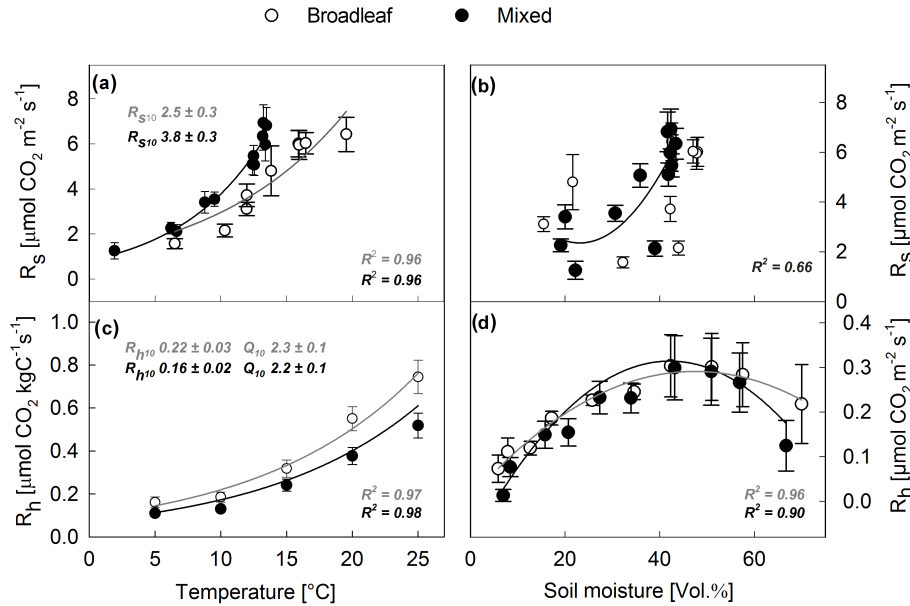


Figure 2. (a) Relationship between soil CO₂ efflux (R_S) and soil temperature, and (b) R_S and soil moisture (vol. %) at a broadleaf and a mixed forest in the Bhutan Himalayas. (c) Relationship between heterotrophic soil respiration (R_h) and soil temperature and (d) R_h and soil moisture (vol. %) as determined during a laboratory incubation. A temperature response was fitted with an exponential function (Eq. 1) and a moisture response was fitted with a polynomial function (Eq. 3). Error bars represent standard error of the mean (SE). Basal respiration rates at 10 °C (R_{S10} , R_{h10}) and temperature sensitivity of R_h (Q_{10}) are given (mean \pm SE).

Table 2. Basal respiration rates (R_{h10}) and temperature sensitivity (Q_{10}) of litter and mineral soil (0–10 cm depth) samples derived from laboratory incubations. Incubations took place initially after sampling (Incubation 1) using a set of three samples per plot (six plots per site). Subsequently, sets were split and the moisture sensitivity of R_h was tested (Fig. 2d). Subsequent to moisture incubations, the different subsets (dry, intermediate, wet) were re-incubated to test temperature sensitivities at different moisture contents (Incubation 2). The time lag between Incubation 1 and Incubation 2 was approximately 10 weeks. Different letters indicate significant differences in Q_{10} between soil moisture levels of the mineral soil samples.

Layer	Incubation	Moisture (vol.%)	R_{h10} ($\mu\text{mol CO}_2 \text{ kg C}^{-1} \text{ s}^{-1}$)	Q_{10}
Broadleaf				
Litter	1	46 \pm 1	0.58 \pm 0.04	2.22 \pm 0.09
Mineral	1	35 \pm 2	0.22 \pm 0.03	2.31 \pm 0.06
Mixed				
Litter	1	46 \pm 2	1.05 \pm 0.24	1.93 \pm 0.06
Mineral	1	33 \pm 1	0.16 \pm 0.02	2.25 \pm 0.06
Mineral	2	dry (10 \pm 1)	0.10 \pm 0.01	1.54 \pm 0.11a
Mineral	2	interm. (33 \pm 1)	0.14 \pm 0.02	2.39 \pm 0.22b
Mineral	2	wet (56 \pm 1)	0.18 \pm 0.03	2.12 \pm 0.25ab
Mineral	2	dry (9 \pm 1)	0.08 \pm 0.01	1.55 \pm 0.18a
Mineral	2	interm. (29 \pm 1)	0.10 \pm 0.01	2.63 \pm 0.39b
Mineral	2	wet (51 \pm 1)	0.13 \pm 0.01	2.06 \pm 0.10ab

3 Results

Air and soil temperatures were ~ 4 °C higher at the lower-elevation broadleaf forest (Table 1) with a stable trend throughout both study years (Fig. 1a). Air temperatures

reached maximums of 29.6 and 22.6 °C at the broadleaf and mixed forests, respectively. Winter air temperatures dropped slightly below freezing at the mixed forest, which showed ephemeral snow cover. Soil temperatures remained above freezing at both sites during the full study period

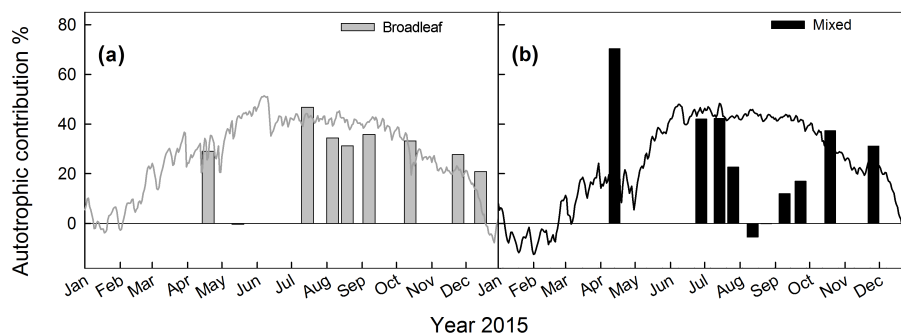


Figure 3. Contribution of autotrophic soil respiration (R_a) to total soil CO₂ efflux (R_s) at a (a) broadleaf and (b) mixed forest in Bhutan Himalayas. Autotrophic contribution was derived from the differences between R_s measured at control and trenched plots (bars) and from the differences between modelled R_s and heterotrophic soil respiration rates (lines), respectively.

(Fig. 1b). Annual precipitation in 2015 was similar at the sites (1167 mm at the mixed forest, 1120 mm at the broadleaf forest). Both sites received maximum rainfall (60–75 % of annual precipitation) during the peak monsoon months (June, July and August). Soil moisture was significantly higher at the broadleaf forest during summer (Fig. 1c). During the dry season (November–April), manually measured soil moisture decreased to <20 vol. % at both sites. Continuous soil moisture records indicated accelerated drying at the broadleaf forest (Fig. 1c).

Aboveground and belowground C stocks were markedly higher in the mixed forest (Table 1). Standing volumes were 1066 and 464 m³ ha⁻¹, at the mixed and broadleaf forests. Mineral soil organic C stocks down to 30 cm soil depth were 142 and 90 t ha⁻¹ and leaf litter inputs (2015) were 3.5 and 3.4 t C ha⁻¹ at the mixed and broadleaf forests. Fine root biomass (0–30 cm mineral soil) was lower at the mixed forest (2.3 t C ha⁻¹) compared to the broadleaf forest (3.2 t C ha⁻¹).

R_s did not differ significantly between the two sites (mean R_s broadleaf: $4.2 \pm 0.7 \mu\text{mol CO}_2\text{-C m}^{-2} \text{s}^{-1}$, mixed: $4.0 \pm 0.6 \mu\text{mol CO}_2\text{-C m}^{-2} \text{s}^{-1}$) but basal respiration rates (R_{s10}) were higher at the mixed forest (Fig. 2a). Cumulative annual R_s were $14.3 \pm 0.5 \text{ t C ha}^{-1}$ for the broadleaf forest and $13.0 \pm 0.5 \text{ t C ha}^{-1}$ for the mixed forest when calculated by linear interpolation between measurement dates. These values were very close to the ones obtained by the modelling approach (Eq. 1): $14.5 \pm 1.2 \text{ t C ha}^{-1}$ for broadleaf and $12.8 \pm 1.0 \text{ t C ha}^{-1}$ for mixed. R_s showed a higher spatial variability at the mixed forest (21–87 % coefficient of variation, CV) than at the broadleaf forest (23–46 % CV). Between 89 and 96 % of the annual temporal variation in measured R_s was explained by field soil temperature (Eq. 1, Fig. 2a). R_s showed a weak relationship with soil moisture at the broadleaf forest site, whereas there was no significant correlation between R_s and soil moisture at the mixed forest site (Fig. 2b).

Laboratory incubations showed a strong positive, exponential relationship between soil temperature and R_h (Fig. 2c). Temperature sensitivity of mineral soil R_h was sim-

ilar between sites (mixed $Q_{10} = 2.2$, broadleaf $Q_{10} = 2.3$; Fig. 2c, Table 2) and slightly lower for forest floor litter (mixed $Q_{10} = 1.9$; broadleaf $Q_{10} = 2.2$; Table 2). Q_{10} values of dry soil (mixed $Q_{10} = 1.6$; broadleaf $Q_{10} = 1.5$) were significantly lower than Q_{10} from the soil which remained at intermediate moisture content ($P < 0.05$, Table 2). Q_{10} values obtained from dry and wet soil did not differ significantly (Table 2). R_h and soil moisture showed a unimodal relationship with the highest rates of R_h at intermediate soil moisture (40–50 vol. %) and decreasing rates at lower and higher moisture levels (Fig. 2d). Overall, soil from both sites responded similarly to changes in soil moisture. Mixed forest soil showed a slightly sharper decrease in R_h at lower and higher soil moisture (Fig. 2d).

Trenching plots indicated average autotrophic and heterotrophic contributions of 29 and 27 % and 71 and 73 % at the mixed and broadleaf forest sites during the whole 2015 season, respectively (Fig. 3). The contribution of R_a and R_h to R_s , obtained by trenching, showed high temporal variability and strong fluctuations between individual measurement dates at the mixed forest site (Fig. 3).

The modelling approach yielded annual heterotrophic contributions of 67 % in mixed forest and 63 % in broadleaf forest. Modelled cumulative annual R_h and R_a were 8.6 and 4.2 t C ha⁻¹ at the mixed forest and 9.5 and 5.0 t C ha⁻¹ at the broadleaf forest. Modelled R_h was in the range of field R_s during the cold season (Fig. 3). The gap between R_h and R_s became larger during the growing season, implying the highest contribution of R_a during the warm monsoon months at both sites (Figs. 3 and 4). The strong temporal fluctuation in sources (R_a , R_h) which was obtained from trenching was not confirmed by R_h model output (Fig. 3).

4 Discussion

Annual R_s of both forest sites (12.8–14.5 t C ha⁻¹) was in the range of values reported for similar ecosystems (10.1–13 t C ha⁻¹, Dar et al., 2015; 10–12 t C ha⁻¹, Li et al., 2008;

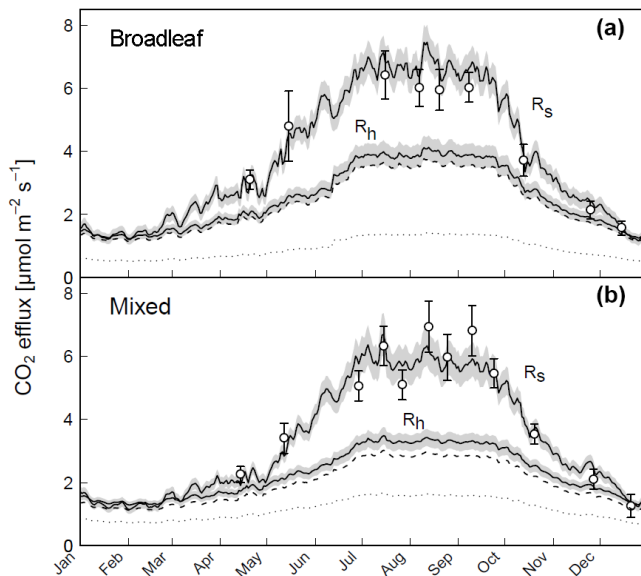


Figure 4. Seasonal course of modelled soil CO₂ efflux (R_s) and heterotrophic soil respiration rates (R_h) at a broadleaf and mixed forest in Bhutan Himalayas in 2015. Open circles are measured R_s rates. Error bars and shaded areas represent standard error of the daily mean. Dashed and dotted lines indicate the CO₂ contributions of litter and mineral soil layers to R_h . The area between the full line (total R_h) and the dashed line represents the contribution from litter, the area between dashed and dotted line represents the contribution of the topsoil (0–10 cm), and the area below the dotted line represents the contribution from the 10–30 cm mineral soil layer.

13.7 tC ha⁻¹, Yang et al., 2007 and 14.7 tC ha⁻¹, Wang et al., 2010). The higher-altitude mixed forest had a double tree basal area and standing stock, indicating that this specific site is exceptionally productive (Singh et al., 1994; Sharma et al., 2010a; Tashi et al., 2016; Wangda and Ohsawa, 2006b). Soil C stocks of ~ 140 tC ha⁻¹ (0–30 cm depth mineral soil) indicate that these mixed forests are likely among the ecosystems with the highest C storage capacity in the eastern Himalayas (Wangda and Ohsawa, 2006a; Sheikh et al., 2009; Dorji et al., 2014a; Tashi et al., 2016). High soil C contents and stocks were reflected in generally higher basal respiration (R_{s10}) at the mixed forest, explaining the comparatively high annual R_s rates at this cooler, higher-altitude site. Soil C input via aboveground litter fall was almost identical between sites (~ 3.5 tC ha⁻¹), although the tree basal area was substantially lower at the broadleaf forest. This can be attributed to a generally higher leaf litter production in broadleaf ecosystems (Tiwari and Joshi, 2015; Bisht et al., 2014). Fine root stocks at both sites fall within the upper range of estimates from other surveys in the Himalayan region (Adhikari et al., 1995; Usman et al., 1999; Garkoti, 2008; Rana et al., 2015), especially if it is considered that fine root contents in this study were estimated solely for 0–30 cm mineral soil depth.

At both forests, R_s tightly followed the seasonal course of soil temperature because soil temperature and soil moisture covaried with dry and cold winters and optimal soil moisture during the warm summer months (Figs. 1b, c; 2a, b). R_s can also be affected by labile C allocation to soil (Gu et al., 2004). During the growing season, trees tend to allocate higher amounts of labile C below ground, thereby potentially increasing the contribution of R_a and simultaneously accelerating SOM decomposition by increased availability of labile C and rhizosphere priming (Kuzyakov, 2010; Bader and Cheng, 2007; Bengtson et al., 2012; Dijkstra and Cheng, 2007; Schindlbacher et al., 2009). Such processes would further increase R_s and R_a during the warm summer months. Our modelled R_h and R_a data suggest that this was also likely the case in the studied forests (significant increase in R_a contribution during the summer months; Fig. 3).

Our model-generated wintertime R_h fluxes were in the range of, or slightly below, R_s fluxes (Fig. 4). During frost periods, downward C-flux from the tree canopy is limited and the contribution of R_a to R_s is considered low during winter (Rey et al., 2002; Hanson et al., 2000). Our modelled wintertime (and overall) R_h therefore lay in a realistic range. However, there is evidence that the contribution of R_a can be significant even during cold winters (Schindlbacher et al., 2007; Tucker et al., 2014). Roots in deeper and warmer soil layers can remain active and add to the soil CO₂ efflux. Accordingly, modelled R_h rather represents the upper edge of potential R_h at our site. Our modelling approach was based on a relatively simple set of soil C stocks combined with temperature and moisture sensitivities, and holds corresponding uncertainty with regard to quantity of R_h and its temporal dynamics. C stocks from deeper soil layers (> 30 cm depth) were not accounted for and a single Q_{10} (obtained from 0–10 cm depth) was used for the whole mineral soil layer. Stabilisation of SOC usually increases with soil depth (Fontaine et al., 2007). Our R_h predictions for deeper layers (10–30 cm) might therefore overestimate the real rate. Using annual litter input as proxy for litter C stocks is a further source of uncertainty. Litter input has temporal patterns and therefore affects litter decomposition dynamics. Such temporal patterns in litter input/decomposition were not reflected in our model. The modelled contribution of the litter layer to total soil R_h was, however, small (Fig. 4) and, therefore, the uncertainty related to temporal litter layer dynamics can also be considered small. We further used a constant Q_{10} throughout the year, although the Q_{10} may vary with season due to changes in substrate supply and quality (Davidson and Janssens, 2006; Gu et al., 2004) and/or interactions with soil moisture (Sierra et al., 2015). We showed that soil moisture affected the temperature sensitivity of R_h by significantly lowering Q_{10} under dry conditions (lab incubation, Table 2). Such dry conditions were, however, not observed in the field. We therefore assume that ignoring potential moisture effects on Q_{10} in our model only had minimal effects on the R_h estimate. Rhizosphere priming could have affected R_h dynamics as well, but

we were not able to account for that in our model. Moreover, soil sieving could have positively affected R_h rates during incubation by releasing physically protected SOM and/or providing additional C sources via disrupted fungal hyphae and fine root fragments (Datta et al., 2014). Nevertheless, the modelled annual $\sim 65\%$ contribution of R_h falls well within estimates from similar forests (Lee et al., 2010). Even if we overestimated the real contribution of R_h , we are confident that the model relatively robustly reflected the temporal dynamics of R_h / R_a throughout the year.

In contrast to the modelling approach, trenching was applied as an attempt to estimate R_a in situ. The trenching method, although highly invasive, was shown to provide reasonable estimates of R_a for several forest types (Hanson et al., 2000; Subke et al., 2006). Trenching suggested slightly higher contributions of R_h at both sites (average 72% both sites) but showed much stronger temporal variations in R_h / R_a , especially at the mixed forest (Fig. 3). Trenching has several drawbacks. Soil moisture is usually higher in trenched plots because water uptake by roots is interrupted. This bias was accounted for as we used the moisture response function (Eq. 3) for correction. However, trenched fine roots can maintain respiration for a comparatively long time after cutting (Lee et al., 2003) and, when fine roots finally die, their decomposition can add to the soil CO₂ efflux from the trenched plots (Hanson et al., 2000). Assuming a dead fine root mass loss of roughly one-third during the second year after trenching (Díaz-Pinés et al., 2010) and accounting for the corresponding effects on soil CO₂ efflux (additional efflux $\sim 1 \text{ t C ha}^{-1}$), the estimated annual contribution of R_h decreases to $\sim 65\%$ of R_s , which is in the range of our modelling results. Potential effects of root decomposition, however, do not explain the atypically strong temporal variation in R_a at the mixed forest site. Soil CO₂ efflux from trenched plots was similar or even higher than from corresponding control plots, suggesting a steep decrease in R_a between July and September (Fig. 3). We do not have a straightforward explanation for this pattern. We probably did not trench deep enough and missed a larger proportion of roots, which added to the summertime CO₂ efflux from trenched plots. A further explanation could be an altered availability of nutrients to decomposers in the trenched plots. In trenched plot soil, roots do not compete for nutrients, potentially increasing nutrient availability to decomposers. This could accelerate SOM decomposition and soil CO₂ efflux. In summary, trenching showed a less clear outcome at the two study sites when compared to other forests. Therefore, other methods, such as girdling or isotope labelling might be alternatively applied to the studied forest types.

Our simple empirical temperature-driven R_s model explained most of the temporal variation in R_s under the typical monsoon weather patterns during 2015. However, monsoon failures and drought periods have occurred in the past and may even increase in frequency and/or severity of climate change (Schewe and Levermann, 2012; Menon et al., 2013;

Cook et al., 2010; Sharmila et al., 2015). To model drought effects, it is necessary to further develop the model by integrating potential soil moisture response of R_s . To do so, longer R_s time series, including dry years and/or data from artificial drought experiments, are needed for model parameterisation and testing.

5 Conclusions

The monsoon climate allows for highly productive mountain forests in the eastern Himalayas. Such forests can store high amounts of C in plant biomass and soil, which was particularly evident in the high-altitude mixed forest in our study. At both forests, a simple temperature-driven model was sufficient to explain most of the temporal variation in R_s during the study year. The sites experienced a typical monsoon climate with dry and cold winters and monsoon rain during the warm season. Further research and model development is, however, warranted to better understand how infrequent/extreme events such as monsoon failure and drought affect soil/ecosystem C cycling and R_s in these forest ecosystems.

6 Data availability

All relevant soil respiration, soil moisture and soil temperature data from the field and the laboratory incubations are freely available from the open source figshare repository (<https://figshare.com>) via doi:10.6084/m9.figshare.4239122.

The Supplement related to this article is available online at doi:10.5194/bg-14-99-2017-supplement.

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