Biogeosciences Discuss., doi:10.5194/bg-2016-291, 2016
Manuscript under review for journal Biogeosciences
Published: 8 August 2016

Soil CO_2 efflux from two mountain forests in the Eastern Himalayas Bhutan: components and controls

Norbu Wangdi[1,2], Mani Prasad Nirola[1,4], Mathias Mayer[1], Norbu Zangmo[2], Karma Orong[2], Iftekhar Uddin Ahmed[1], Andras Darabant[1], Robert Jandl [3], Georg Gratzer[1], Andreas Schindlbacher[3]

[1]Institute of Forest Ecology, University of Natural Resources and Life Sciences, 1180 Peter Jordan Strasse, Vienna, Austria
[2] Ugyen Wangchuck Institute for Conservation and Environmental Research, Department of Forests and Park Services Lamai Goempa, Bumthang, Bhutan
[3]Federal Research and Training Centre for Forests, Natural Hazards and Landscape – BFW, A-1131 Vienna, Austria
[4]National Biodiversity Center, Ministry of Agriculture and Forests, Thimphu, Bhutan

Correspondence to: Norbu Wangdi (norwangs@gmail.com)

Abstract

The biogeochemistry of mountain forests in the Hindu Kush-Himalaya range is poorly studied although climate change is expected to disproportionally affect the region. We measured the soil CO_2 efflux (Rs) at a high elevation (3260 m) coniferous, and a lower elevation (2460 m) broadleaved forest in Bhutan, eastern Himalayas, during 2014 and 2015. Both sites experienced typical monsoon weather (cold-dry winters, warm-wet summers) during the study. Trenching was applied to estimate the contribution of autotrophic (Ra) and heterotrophic (Rh) soil respiration. The temperature (Q_{10}) and the moisture sensitivities of Rh were determined under controlled laboratory conditions and were used to model Rh in the field. The higher elevation coniferous forest had a higher standing tree stock, reflected in higher soil C stocks and basal soil respiration (R_{10}). Rs was similar between the two forests (2015: 14.5 ± 1.2 t C yr^{-1} broadleaved; 12.8 ± 1.0 t C yr^{-1} coniferous). Modelled annual contribution of Ra was ~ 45% at both forests with a low autotrophic contribution during winter and high contribution during the monsoon season. Ra, estimated from trenching, was lower and highly variable, indicating that trenching poorly performed at these forests/soils. Rs neatly followed the annual course of soil temperature (field Q_{10} between 4 and 5) at both sites. Co-variation between soil temperature and moisture likely was the main cause for the high Q_{10} obtained from field Rs. Temperature sensitivity of Rh was lower (Q_{10} ~ 2.3 at both sites). Under the preceding weather conditions, a simple temperature-driven model was able to explain more than 90% of the temporal variation in Rs. To predict and understand how Rs responds to infrequently occurring extreme climate conditions such as monsoon failures, however, longer Rs time series are required for a better integration of interactions between soil temperature, moisture, Ra and Rh.

Keywords: Himalaya, soil CO_2 efflux, autotrophic soil respiration, heterotrophic soil respiration, incubation, temperature sensitivity, moisture sensitivity

Biogeosciences Discuss., doi:10.5194/bg-2016-291, 2016
Manuscript under review for journal Biogeosciences
Published: 8 August 2016

1 Introduction

Carbon dioxide (CO_2) efflux from soil (= soil respiration; Rs) is one of the major fluxes in the global C cycle, affects atmospheric CO_2 concentrations and feeds back on global climate change (Schlesinger and Andrews, 2000; Reichstein et al., 2003; Hashimoto et al., 2015). Counteracting to C uptake via photosynthesis, Rs primarily determines whether forest ecosystems serve as C sink or source to the atmosphere (Dixon et al., 1994; Schlesinger and Andrews, 2000; Bolstad et al., 2004). The current function of forests as global C sink (Janssens et al., 2003; Stocker, 2014) could weaken or even turn into the opposite if climate change disproportionally accelerates respiratory processes such as Rs (Cox et al., 2000). Rs consists of an autotrophic component (Ra; root and rhizosphere respiration), which is closely linked to C gain by photosynthesis and a heterotrophic component (Rh), which is the respiratory product of soil organic matter (SOM) decomposition. While the source of Ra is recently assimilated CO_2, Rh can release stored soil C to the atmosphere. For better prediction of the response of forest C cycling to climate change, it is crucial to understand how Rs and its components are affected by changing environmental parameters such as temperature and moisture (Davidson and Janssens, 2006). Rates and climate sensitivity of Rs, Ra and Rh can vary among forest ecosystem type and climatic region (Hashimoto et al., 2015). So far, research has primarily focused on the temperate and boreal areas of the northern hemisphere and 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 (Ohsawa, 1991; Wangda and Ohsawa, 2006a; Pandey et al., 2010; Sharma et al., 2010b; Verma et al., 2012; Sundarapandian and Dar, 2013; Dorji et al., 2014b; Tashi et al., 2016). It extends over 4.3 million km^2 across eight countries with an average forest cover of approximately 20 % (Schild, 2008), ranging from lowland tropical forest to high altitudinal forests up to ~ 4900 m (Schickhoff, 2005; Liang et al., 2016). Situated in the south-eastern range of the Himalayas, Bhutan shows 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 (Sharma and Rai, 2007; Dorji et al., 2014a) and serve as an important regional C sink (FAO, 2010). As climate change is expected to intensify in the Himalaya region (Xu et al., 2009; Tsering et al., 2010; Singh, 2011; Shrestha et al., 2012; Xu and Grumbine, 2014), 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 of the eastern Himalayas, we studied Rs, its components (Ra, Rh), as well as the effects of environmental drivers such as temperature and moisture at a high altitude cool temperate conifer forest and a lower altitude cool broadleaved forest in Bhutan. We hypothesized that (I) overall rates of Rs were higher at the lower elevation and correspondingly warmer broadleaved forest site. As precipitation was expected to be non-limiting during the growing season (~ monsoon season), we further hypothesized that (II) the seasonal course of Rs was mainly driven by soil temperature. The contribution of Ra was expected to be lowest during the cold and dry winter and to significantly increase during the growing season. We further expected that water logged soil showed decreased Rs during peak monsoon.

2 Materials and methods

2.1 Site description

Two representative forest ecosystems for the eastern Himalayas (Wikramanayake, 2002), a cool temperate mixed coniferous forest and a cool temperate broadleaved forest, were studied at Thimphu and Wangduephodrang districts, Bhutan. The cool temperate mixed coniferous 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 broadleaved forest was situated on an east facing gentle slope along the same mountain ridge ~ 11 km eastwards (elevation 2640 m a.s.l.). Sites will be referred to as "coniferous forest" and "broadleaved forest" in the further text. The coniferous forest was dominated by *Tsuga dumosa* along with *Picea spinulosa*, *Quercus semecarpifolia*, *Abies densa*, *Acer campbelli* and *Taxus baccata*. The broadleaved forest was dominated by *Quercus lanata* and *Quercus griffithii*. Soils at the coniferous forest were Cambisols. Soils at the broadleaved 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 control and temporarily roofed areas within each forest type. For this study, we randomly distributed all our plots within the control areas (~ 1500 m^2 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. one kilometer from the sites at the same elevation. Data was 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 vapor 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 forest types covering an area of ~ 1500 m^2 each. The location, height and the diameter at breast height of all trees having 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 Paul Lawmans (1994), Forest Survey of India (1996) and Department. of Forests and Park Services, Bhutan (2005). Aboveground litter-fall was collected monthly (since December 2014) using mesh-traps (n = 10) per site, with an area of 1.0 m^2 (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 10-30 cm mineral soil layers of 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 grinded (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). Samples from the forest floor layer were collected in September 2015 and SOC contents were determined as described above.

Rs was measured regularly in the two forest types (coniferous, broadleaved) once every three weeks, from May 2014 to December 2014 and from April 2015 to December 2015. We randomly set 10 plots (n = 10) at each forest type for Rs measurements. To cover the within-plot variability, Rs was measured at four positions within each plot (total 40 positions per site). We used a portable infrared gas analyzer (EGM-4, PP-Systems, Amesbury, USA) with an attached soil respiration chamber (SRC-1, PP-Systems, Amesbury, USA) for Rs measurements. In spring 2015 we installed four 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 Rs measurements thereafter. Due to logistic reasons, collars were not available in 2014. During the 2014 season, the SRC-1 chamber was directly placed on the ground surface and slightly pressed into the soil to produce sufficient sealing during Rs measurements. Rs was estimated by a linear fit to the increasing headspace CO_2 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 any error from temporal variations in Rs.

We installed two trenching plots at each site in 2014 to estimate the relative contributions of Ra and Rh. Two additional trenching plots per site were installed in 2015 to increase replication. Trenches (1.5 x 1.5 m squares) were dug down ~ 1 m, and all the roots within the trenches were cut. The trenches were sealed with double layered plastic foil in order to restrict tree root ingrowth. Adjoining to each trenched plot, a corresponding control plot of the same size was established. Each trenched and control plot hosted three collars for Rs measurements.

Volumetric soil water content (0 - 20 cm soil depth) was measured in the center of each plot using a portable Field Scout TDR meter (Spectrum Technologies, Inc. Aurora, USA) during Rs measurements. Soil temperature at 5 cm soil depth was measured with a handheld thermometer probe (Hanna Instruments, Germany) at each Rs measurement location during 2015. For 2014 only soil temperature records from permanently installed sensors were available. Soil temperature and soil moisture were measured continuously at soil profile pits (two pits per forest type) 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 was 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 material were sampled at six random locations (n = 6) at each forest type in mid of September 2015. The mineral soil was homogenized and sieved (2 mm mesh) and stored at 4 °C, at field moisture for one week prior to transport from Bhutan to Austria for further processing. Forest floor material was not sieved. Upon arrival in Austria, samples from mineral soil were further divided into 3 sub-samples to account for potential soil heterogeneity at the individual sampling locations. Samples were filled into 200 cm^3 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 sub-samples (cylinders) for mineral soil and 12 sub-samples for the forest floor. Filled cylinders were kept at 4 °C for 5 days for equilibration before incubation. During incubation, CO_2 efflux (= Rh) was measured using a fully automated incubation system. Samples were put

Biogeosciences Discuss., doi:10.5194/bg-2016-291, 2016
Manuscript under review for journal Biogeosciences
Published: 8 August 2016

into 2 l containers and their CO_2 efflux was determined by a dynamic closed – chamber system (Pumpanen et al., 2009). For CO_2 measurements, containers were sequentially connected to an infrared gas analyzer (SBA-4, PP Systems International Inc., Amesbury, MA, USA) by means of a tubing system. In the meanwhile, disconnected containers were ventilated in order to prevent internal CO_2 enrichment. CO_2 concentration within connected containers were measured for 6 minutes with a recording interval of 10 sec. Rates of CO_2 efflux were calculated from the headspace CO_2 increase during 2 – 6 minutes, after Pumpanen et al. (2009).

Incubation proceeded in two steps. We first incubated at different soil temperatures to assess the temperature sensitivity of Rh. In a second step, we incubated under different soil moisture contents to assess the sensitivity of Rh to changes in soil moisture. In addition, we repeated the temperature-runs with wet (140 % Grav.) and dry (30 % Grav.) soil in order to test for effects of soil moisture on the temperature sensitivity of Rh.

Temperature-incubation started with mineral soil. Soil temperature was increased from 5 °C until 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 re-measured Rh at 10 °C to assess and correct for potential effects of labile C loss during the ~ 30 h incubation. The forest floor was incubated under the same procedure as mineral soil.

After the temperature-incubations, we set soil moisture of all mineral soil sub-samples to 80 % (gravimetric), incubated at constant 15 °C for 6 h and measured Rh as described above. Afterwards, the three sub-samples from each sampling location were split into (i) a sub-sample was kept at constant soil moisture (80 % Grav.), (ii) a sub-sample was allowed to dry out (60 %, 40 % and 20 % Grav.), and (iii) a sub-sample was progressively watered (100 %, 120 % and 140 % Grav.). In-between repeated incubations (all at 15 °C for 6 h) cylinders were stored at 4 °C. The whole moisture-incubation procedure lasted for 10 weeks with ~ two-weekly intervals between incubations (time limiting step was soil drying). We used Rh from the sub-samples which had been kept at constant moisture to correct for potential decreases in Rh due to a loss in labile C throughout the experiment. After finishing incubations, samples were dried and actual bulk density, as well as gravimetric and volumetric soil moisture of each sub-sample (cylinder), was calculated and their total C content was determined (TruSpec® CN, LECO Inc., Michigan, USA). Rh rates were expressed as µmol CO_2 kgC^{-1} s^{-1}.

3 Data analysis

Effects of forest type on field Rs, soil temperature and moisture were tested by means of repeated-measures ANOVA with a mixed-effects model structure (Pinheiro and Bates, 2000) separately for each year. The significance level for this and all other analyses was set at $P < 0.05$. The relationship between field soil temperature and Rs was fitted by an exponential function (Janssens and Pilegaard, 2003):

$$R = R_{10} \times Q_{10}^{(T-10)/10} \qquad (1)$$

Biogeosciences Discuss., doi:10.5194/bg-2016-291, 2016
Manuscript under review for journal Biogeosciences
Published: 8 August 2016

Biogeosciences Discussions Open Access EGU

where R (µmol CO_2 m^{-2} s^{-1}) is the measured Rs, T (°C) is the soil temperature at 5 cm depth, R_{10} (µmol CO_2 m^{-2} s^{-1}) is the Rs rate at 10 °C and Q_{10} is the apparent temperature sensitivity (Rs change with a proportional change of 10 °C in soil temperature). Equation (1) was fitted to the individual plot data for 2014 and 2015 separately for calculating Q_{10} and R_{10}. One sampling date (2015 Jul 16) was excluded from this analysis because heavy rain occurred during measurements. The relationship between Rs and soil moisture was tested by linear regression analyses. To investigate the influence of both, soil temperature and soil moisture on Rs, and to account for a possible correlation between these variables, we used a structural equation modelling approach (Grace, 2006). To consider an exponential relation between soil temperature and Rs, the latter was log transformed prior to analysis. Data from both years were incorporated in this analysis.

Cumulative annual Rs of both sites and both years were calculated by linear interpolation of field Rs between measurement dates of each individual plot (the area beneath the curves in Fig. 1 d). In addition, model parameters of Eq. (1), together with daily field soil temperatures at 5 cm depth were used to calculate daily field Rs. To account for a spatial variation in soil temperature, continuously measured data were adjusted to discontinuously measured plot-data by linear modelling. Cumulative annual Rs rates were calculated by averaging the summed-up daily plot Rs values. Since full season Rs data and continuous soil temperature data were only available for 2015, annual Rs sums were only determined for 2015 using this approach.

Average Rh rates from laboratory incubations were calculated for each site, soil horizon (mineral soil, forest floor) and temperature step (5 – 25 °C), respectively. Equation 1 was fitted to the temperature-incubation data to determine Q_{10} and R_{10} of Rh. To determine the relationship between soil moisture and Rh, we fitted a Gaussian function to the moisture-incubation data:

$$R = \beta_0 + \beta_1 \; e^{\left(-0.5\left(\frac{VWC-\beta_2}{\beta_3}\right)^2\right)} \qquad (2)$$

where R is the measured CO_2 efflux from soil samples (Rh), βi are model coefficients and VWC is the volumetric water content of the samples. This specific function showed the best fit when compared to a set of other response functions tested.

We followed two approaches to estimate the contribution of Ra and Rh in the field. In a first approach, we used the trenching data, assuming that the CO_2 efflux from the trenched plots represented solely Rh, while the CO_2 efflux from adjacent control plots represented Rs, and accordingly, the difference between trenched and control plot CO_2 efflux represented Ra. As trenched plots lack water uptake by tree roots, they were regularly wetter than control plots. We accounted for that by correcting the soil CO_2 efflux for the difference in soil moisture by using Eq. (2).

In a second approach, we applied the response functions of Rh which we had derived during laboratory incubations together with field soil C stocks and field climate data. This allowed an alternative way to estimate the contribution of Rh in the field (Gough et al., 2007; Kutsch et al., 2010). Equation (1) and Eq. (2) of each site and soil horizon were combined:

$$R = f(T)\, f(VWC) \qquad (3)$$

Biogeosciences Discuss., doi:10.5194/bg-2016-291, 2016
Manuscript under review for journal Biogeosciences
Published: 8 August 2016

in order to account for both a Rh response to temperature (f (T)) and moisture (f (VWC)). The moisture term in Eq. (3) was rescaled to relative Rh rates between 0 and 1 (Fig. S1). For that, Eq. (2) was used to predict Rh for a moisture range between 10 – 70 Vol.%. Predicted Rh rates were then scaled to the asymptote of the curve which represents a maximum Rh rate. Since no specific moisture response function was obtained for the litter layers, we applied the same parameters as for mineral soil, combined with R_{10} and Q_{10} parameters for the litter layer. In a second step, model parameters derived from Eq. (3), together with continuously measured temperature and moisture data from 5 cm soil depth were used to model daily Rh from the litter layer and from the mineral soil in 0 – 10 cm depth respectively. Model parameters for mineral soils together with continuous measurements of soil temperature and moisture in 20 cm depth were further used to model daily Rh from the mineral soil in 10 – 30 cm depth. In the last step, predicted Rh rates (µmol CO_2 kgC^{-1}) were multiplied by the C stocks (kg C m^{-2}) of the respective soil layer, which enabled us to upscale Rh to the whole soil profile in the field (Kutsch et al., 2010).

Biogeosciences Discuss., doi:10.5194/bg-2016-291, 2016
Manuscript under review for journal Biogeosciences
Published: 8 August 2016

4. Results

Air and soil temperatures were ~ 4°C higher at the lower elevation broadleaved forest (Table 1) with a stable trend throughout both study years (Fig. 1). Air temperatures reached a maximum of 29.6 °C and 22.6 °C at the broadleaved and coniferous forest, respectively. Winter air temperatures dropped slightly below freezing at the coniferous forest which showed ephemeral snow cover. Soil temperatures remained above freezing at both sites during the full study period (Fig. 1). Precipitation was higher at the coniferous forest (coniferous 883 mm; broadleaved 688 mm) during precipitation measurements in 2014 (12th Jun – 31st Dec). Annual precipitation in 2015 was similar at both forest types (coniferous 1167 mm, broadleaved 1120 mm). Both sites received the maximum rainfall (60-75 % of annual precipitation) during the peak monsoon months (Jun, Jul and Aug). Soil moisture remained at a similar range (~ 40 Vol. %) at both sites during the summer of 2014, whereas soil moisture was significantly higher at the broadleaved forest during summer 2015 (Fig. 1). During the dry season (Nov – Apr), manually measured soil moisture decreased to < 20 Vol. % at both sites. Continuous soil moisture records indicated accelerated drying at the broadleaved forest (Fig. 1).

Aboveground and below ground C stocks were markedly higher in the coniferous forest (Table 1). Standing volume was 1066 and 464 m^3 ha^{-1}, at the coniferous and broadleaved forest, respectively. Mineral soil organic C stocks down to 30 cm soil depth were 127 and 91 t ha^{-1} and leaf litter inputs (2015) were 3.5 and 3.4 t C ha^{-1} at the coniferous and broadleaved forest, respectively. Fine root biomass (0-30 cm mineral soil) was lower at the coniferous forest (2.3 t C ha^{-1}) when compared to the broadleaved forest (3.2 t C ha^{-1}).

Rs did not differ significantly among the two forest types during both years. Rs was generally higher during 2014 (mean Rs broadleaved: 6.7 ± 1.2 µmol CO_2-C m^{-2} s^{-1}, coniferous: 5.6 ± 0.9 µmol CO_2-C m^{-2} s^{-1}) than during 2015 (mean Rs broadleaved: 4.2 ± 0.7 µmol CO_2-C m^{-2} s^{-1}, coniferous: 4.0 ± 0.6 µmol CO_2-C m^{-2} s^{-1}). This difference was not explained by soil climate, nor did we observe any variations in specific above ground dynamics or in litter input during the two study years. We, therefore, attribute the higher Rs rates in 2014 to the methodological differences in Rs measurements. In 2014, Rs was measured without the use of base-collars by inserting the soil respiration chamber into the soil surface. Chamber insertion could have pumped CO_2 out of the soil thereby overestimating Rs. We therefore only refer to the cumulative annual Rs from 2015 for further site comparison. Cumulative annual (2015) Rs were 14.3 ± 0.5 t C ha^{-1} for broadleaved and 13.0 ± 0.5 t C ha^{-1} for the coniferous forest when calculated by linear interpolation between measurement dates. These values were very close to the ones obtained by the modeling approach (Eq. (1)), (14.5 ± 1.2 t C ha^{-1} for broadleaved and 12.8 ± 1.0 t C ha^{-1} for coniferous forest) and indicate that a three-week measurement interval is sufficient to explain most of the temporal variability in Rs. Rs showed a higher spatial variability at the coniferous forest (21 - 87 % CV) than at the broadleaved forest (23 - 46 % CV). Between 89 and 96 % of the annual temporal variation in measured Rs could be explained by field soil temperature (Eq. 1, Fig. 2). Q_{10} values of Rs ranged between 3.95 and 5.03 (Fig. 2). Rs showed a weak linear relationship with soil moisture at the broadleaved forest, whereas there was no significant correlation between Rs and soil moisture at the coniferous forest (Fig. 2). For both sites structural equation modelling revealed a strong influence of soil temperature on Rs, but no influence of soil moisture (Fig. 3). At both sites, soil temperature and moisture were strongly correlated with each other during both years (Fig. 3).

Laboratory incubations showed a strong positive, exponential, relationship between soil temperature and Rh (Fig. 2). Temperature sensitivity of mineral soil Rh was similar among forest types (coniferous Q_{10} = 2.32, broadleaved Q_{10} = 2.36; Fig. 2) and slightly lower for forest floor material (coniferous Q_{10} = 1.97; broadleaved Q_{10} = 2.28). Q_{10} values of dry soil (coniferous, 1.59; broadleaved, 1.60) were significantly lower than Q_{10} from the soil which had been kept at intermediate moisture content ($P < 0.05$, Table 2). Q_{10} values obtained from dry and wet soil did not differ significantly among the two forest sites (Table 2). Rh and soil moisture showed a unimodal relationship with highest rates of Rh at intermediate soil moisture (35 - 45 % Vol.) and decreasing rates at lower and higher moisture levels (Fig. 2). Soil from both forest types responded overall similarly to changes in soil moisture. Coniferous forest soil showed a slightly sharper decrease in Rh at lower and at higher soil moisture (Fig. 2).

Plots which had been trenched in spring 2014 indicated an average autotrophic contribution of 24 and 30 % at the coniferous and broadleaved forest during the 2015 season, respectively (Fig. 4). The additional plots, which had been trenched during spring 2015, did not produce any meaningful Ra values, as the trenched plots showed similar or even higher CO_2 efflux rates than the untreated control plots.

Modelled Rh (Eq. 3) was slightly lower than field Rs during the cold season (Fig. 4). The gap between Rh and Rs (measured and modelled) became larger during the growing season, implying highest contribution of Ra during the warm monsoon months at both sites (Fig. 4 and 5). The modelling approach yielded generally higher annual autotrophic contribution (Ra = 43 %, coniferous, 45 % broadleaved) when compared to the trenching experiment. At the broadleaved forest, a larger fraction of Rh was attributed to the 0-10 cm mineral soil layer, whereas all three layers (organic, 0-10, and 10-30) contributed similarly to Rh at the coniferous forest (Fig. 5). Modelled cumulative annual (2015) Rh and Ra were 7.3 and 5.5 t C ha^{-1} at the coniferous and 8.0 and 6.5 t C ha^{-1} at the broadleaved forest respectively.

5. Discussion

Our hypothesis, that Rs was higher at the lower elevation broadleaved forest site was not confirmed although soils had been consistently about 4°C warmer than at the higher elevation coniferous forest. Annual Rs was similar among both forest types (12.8 – 14.5 t C ha^{-1}) and 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); 13.7 t C ha^{-1} (Yang et al., 2007) and 14.7 t C ha^{-1} (Wang et al., 2010)). The higher altitude coniferous forest had double tree basal area and standing stock, indicating that this specific forest type is exceptionally productive (Singh et al., 1994; Wangda and Ohsawa, 2006b; Sharma et al., 2010a; Tashi et al., 2016). Soil C stocks of ~ 127 t ha^{-1} (0-30 cm depth mineral soil) indicate that these mixed coniferous forests are likely among those 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_{10}) at the coniferous forest explaining the comparatively high annual Rs rates at this cooler, higher altitude, site.

At both forests, Rs followed the seasonal course of soil temperature and showed high apparent temperature sensitivities (field Q_{10} between 4 and 5). Field Q_{10} values, however, not only reflect the effects of soil temperature but manifest all interacting drivers of Rs throughout the season (Davidson and Janssens, 2006; Schindlbacher et al., 2009; Ruehr and Buchmann, 2010). Soil temperature and soil moisture co-varied during both study years with dry and cold winters and optimal soil moisture during the warm summer months. To account for this co-variation, we normalized all Rs measurements using Eq. (2), to the corresponding optimal soil moisture of the sites (39 and 43 %) and re-calculated the Q_{10} values. Moisture normalization Rs had a Q_{10} of ~ 3 at both sites which show that co-variation between soil temperature and moisture was one reason for the high apparent temperature sensitivity of Rs. The moisture normalized field Q_{10} of ~ 3 came already closer to the intrinsic temperature sensitivity of Rh (Q_{10} ~ 2.3 at both sites) which was determined under controlled lab conditions at soil temperatures from 5 to 25 °C. Since Q_{10} tend to decrease with decreasing temperatures (Leifeld and Fuhrer, 2005; Tuomi et al., 2008; Schindlbacher et al., 2010), we further calculated lab Q_{10} at temperature ranges which came closest to the soil temperature range in the field (5-15 °C coniferous, 5-20 °C broadleaved). As expected, Q_{10} were slightly higher (2.6 ± 0.5 coniferous, 2.7 ± 0.3 broadleaved) as the ones calculated over the whole 5-25 °C range, but were still below the moisture normalized field Q_{10} values. The remaining difference between lab (Rh) and field (Rs) Q_{10} can result from a higher apparent temperature sensitivity of Ra (Boone et al., 1998) driven by accelerated below ground transport of labile C during the growing season (Schindlbacher et al., 2009). Enhanced priming of SOM decomposition (Bader and Cheng, 2007; Dijkstra and Cheng, 2007; Kuzyakov, 2010; Bengtson et al., 2012) during the growing season could further add to the strong apparent temperature response of Rs.

Q_{10} of Rh was similar between sites but decreased when the soil became dry. Such dry conditions were only reached during winter, during which Rs was generally low. Our simple empirical temperature-driven Rs model explained most of the temporal variation in Rs under typical monsoon weather patterns during 2014 and 2015. However, monsoon failures and drought periods have occurred in the past and may even increase in frequency and/or severity of climate change (Cook et al., 2010; Schewe and Levermann, 2012; Menon et al., 2013; Sharmila et al., 2015). To model such drought effects, it is necessary to further develop the model by integrating potential soil moisture response of Rs (as we already did for Rh). To do so, longer Rs time series which include dry years and/or data from artificial drought experiments are needed for model parameterization and testing. It is intended to continue Rs measurements at both sites and Rs data from the ongoing throughfall manipulation experiment is in preparation for further model development. Our last hypotheses that Rs decreased during water logging at peak monsoon was not confirmed as soils at both sites were well drained and water logging did not occur even during periods of high precipitation (Fig. 1).

The two approaches to estimate the autotrophic contribution to Rs performed differently. While the trenching method showed ambivalent outcome, the modeling approach did well. Modelled Rh in the field remained slightly below Rs during the cold season. This can be expected as the contribution of Ra is generally lower during the dormant season than during the growing season (Hanson et al., 2000; Rey et al., 2002). During the growing season, the two-component model, Eq. (3) predicted an increase in the contribution of Ra. Such a pattern has frequently been observed in other forest ecosystems and reflects the higher downward allocation of labile C during the growing season. Our model estimated ~ 45 % contribution of Ra to Rs falls well within estimates from other forest sites. The modeling approach holds some uncertainty. C stocks from deeper soil layers were not accounted for and a single Q_{10} (0-10 cm depth, lab incubation) was used for the whole 10 - 30 cm mineral soil layer. Furthermore, potential effects of priming were not accounted for in our modelling approach. In contrast to our modeling approach, which was based on incubation results and soil C stocks, trenching was applied as an attempt to estimate Ra *in situ*. The trenching method, although highly invasive, can provide reasonable estimates of Ra for several forest types (Hanson et al., 2000; Subke et al., 2006) considered that all the caveats of the method were accounted for. Our trenching approach, however, largely failed at both study sites. There might be several reasons, albeit the trenching effects on soil moisture, which we had accounted for. Fine roots can maintain respiration for a comparatively long time after cutting (Lee et al., 2003) and if roots die, their decomposition adds to the soil CO_2 efflux (Hanson et al., 2000). This was likely the main reason for the absence of any effect at plots which had been trenched during spring of the same year as of subsequent Rs measurements (year 2015). Plots which had been trenched one year earlier, already showed decreased Rs, but the estimated autotrophic contribution was on average < 30 % and highly variable. Considering 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 CO_2 efflux (additional efflux ~ 1 t C ha^{-1}), the estimated contribution of Ra increased to ~ 40 % which is in the range of our modeling results.

Soil C input via aboveground litter-fall was almost similar between forest types (~ 3.5 t C ha^{-1}) although tree basal area was substantially lower at the broadleaved forest. This can be attributed to a generally higher leaf litter production in broadleaved ecosystems (Bisht et al., 2014; Tiwari and Joshi, 2015). Fine root stocks at both forest types 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. Assuming a mean fine root turnover time of one year (Brunner et al., 2013), the annual fine root litter input from 0-30 cm soil layer was ~ 2 and ~ 3 t C ha^{-1} at the coniferous and broadleaved forest, respectively. During 2015, the estimated soil C input (leaf litter and fine root litter of the top 30 cm soil) was, therefore, ~ 1.5 tons lower than the estimated annual gaseous soil C loss via Rh. This, however, is only a first rough approximation of the real soil C budget, since fine root turnover was not adequately determined and important C fluxes, such as for instance, DOC leaching, root litter production below 30 cm depth, and C input from vigorously growing herbaceous ground vegetation were not accounted for in our study, which primarily aimed at a detailed characterization of the soil CO_2 efflux.

6. Conclusion

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 coniferous forest in our study. The high-temperature sensitivity of Rs (Q_{10} 4-5) suggests that soil C cycling could react particularly vulnerable to global warming. Deeper analyses, however, showed that Rh had similar temperature sensitivities as other forest soils (Q_{10} 2-3) and that co-variation of soil moisture and Ra led to the high field Q_{10}. At both forests studied, a simple temperature-driven model was sufficient to explain most of the temporal variation in Rs during the two study years. Both study years had 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 Rs in these forest ecosystems.

7. Author contribution

N. Wangdi carried out the research and data analysis and drafted the manuscript. M P. Nirola carried out the incubation experiment and analysed the data. N. Zangmo and K. Orong collected the data and continuously monitored the research sites. I.U Ahmed carried out the root and the soil sampling study within our research sites. M. Mayer performed modelling and contributed to writing the manuscript. A. Darabant, R. Jandl, G. Gratzer designed the experiment and provided feedback on the manuscript. A. Schindlbacher supervised the overall work, designed the experiment and critically revised the manuscript.

8. Acknowledgements

We are highly grateful to the all the staff of Renewable Natural Resources Research and Development Centre, Yusipang for all the support for the field work. We also thank the management and staff of the Ugyen Wangchuck Institute for Conservation and Environment, Bumthang for providing additional support for the study. This study was part of the work package I of the BC-CAP project (Climate Change Adaptation potentials of forests in Bhutan – Building human capacities and knowledge base) jointly implemented by the Department of Forest and Park Services, Bhutan and University of Natural Resources and Applied Life Sciences (BOKU), Austria with funding from Government of Austria, through the Ministry of Agriculture, Forestry, Environment and Water Management.

Biogeosciences Discuss., doi:10.5194/bg-2016-291, 2016
Manuscript under review for journal Biogeosciences
Published: 8 August 2016

9. Disclaimer

The views and opinions expressed in this article are those of the authors and do not necessarily reflect the views of any institutions of the Royal Government of Bhutan or the Government of Austria.

Biogeosciences Discuss., doi:10.5194/bg-2016-291, 2016
Manuscript under review for journal Biogeosciences
Published: 8 August 2016

References

Adhikari, B., Rawat, Y., and Singh, S.: Structure and function of high altitude forests of central Himalaya I. Dry matter dynamics, Ann. Bot., 75, 237-248, 1995.

Bader, N. E. and Cheng, W.: Rhizosphere priming effect of *Populus fremontii* obscures the temperature sensitivity of soil organic carbon respiration, Soil Biol. Biochem., 39, 600-606, 2007.

Bengtson, P., Barker, J., and Grayston, S. J.: Evidence of a strong coupling between root exudation, C and N availability, and stimulated SOM decomposition caused by rhizosphere priming effects, Ecology and Evolution, 2, 1843-1852, 2012.

Bisht, V. K., Nautiyal, B. P., Kuniyal, C. P., Prasad, P., and Sundriyal, R. C.: Litter Production, Decomposition, and Nutrient Release in Subalpine Forest Communities of the Northwest Himalaya, J. Ecosyst., 2014, 2014.

Bolstad, P., Davis, K., Martin, J., Cook, B., and Wang, W.: Component and whole-system respiration fluxes in northern deciduous forests, Tree Physiol., 24, 493-504, 2004.

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

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.

Brunner, I., Bakker, M. R., Björk, R. G., Hirano, Y., Lukac, M., Aranda, X., Børja, I., Eldhuset, T. D., Helmisaari, H. S., Jourdan, C., Konôpka, B., López, B. C., Miguel Pérez, C., Persson, H., and Ostonen, I.: Fine-root turnover rates of European forests revisited: an analysis of data from sequential coring and ingrowth cores, Plant and Soil, 362, 357-372, 2013.

Cook, E. R., Anchukaitis, K. J., Buckley, B. M., D'Arrigo, R. D., Jacoby, G. C., and Wright, W. E.: Asian monsoon failure and megadrought during the last millennium, Science, 328, 486-489, 2010.

Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A., and Totterdell, I. J.: Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model, Nature, 408, 184-187, 2000.

Dar, J. A., Ganie, K. A., and Sundarapandian, S.: Soil CO2 efflux among four coniferous forest types of Kashmir Himalaya, India, Environmental monitoring and assessment, 187, 715, 2015.

Davidson, E. A. and Janssens, I. A.: Temperature sensitivity of soil carbon decomposition and feedbacks to climate change, Nature, 440, 165-173, 2006.

de Wit, H. A., Palosuo, T., Hylen, G., and Liski, J.: A carbon budget of forest biomass and soils in southeast Norway calculated using a widely applicable method, For. Ecol. Manage., 225, 15-26, 2006.

Díaz-Pinés, E., Schindlbacher, A., Pfeffer, M., Jandl, R., Zechmeister-Boltenstern, S., and Rubio, A.: Root trenching - A useful tool to estimate autotrophic soil respiration? Case study in an Austrian mountain forest, European Journal of Forest Research, 129, 101-109, 2010.

Dijkstra, F. A. and Cheng, W.: Interactions between soil and tree roots accelerate long-term soil carbon decomposition, Ecology Letters, 10, 1046-1053, 2007.

Dixon, R. K., Solomon, A., Brown, S., Houghton, R., Trexier, M., and Wisniewski, J.: Carbon pools and flux of global forest ecosystems, Science, 263, 185-190, 1994.

DoFPS: Forestry Facts, Figures & Trends. Department of Forest and Park Services,Ministry of Agricuulture and Forests,Royal Government of Bhutan, Thimphu, 2011.

Dorji, T., Odeh, I., and Field, D.: Vertical Distribution of Soil Organic Carbon Density in Relation to Land Use/Cover, Altitude and Slope Aspect in the Eastern Himalayas, Land, 3, 1232-1250, 2014a.

Dorji, T., Odeh, I. O., Field, D. J., and Baillie, I. C.: Digital soil mapping of soil organic carbon stocks under different land use and land cover types in montane ecosystems, Eastern Himalayas, For. Ecol. Manage., 318, 91-102, 2014b.

FAO: Global Forest Resources Assessment :Country Report -Bhutan, Food and Agriculture Organization of the United Nations, Rome, 56 pp., 2010.

FRDD: Local Volume Table, Forest Resources Development Division, Department of Forests and Park Services, Bhutan, 2005.

FSI: Volume Equations for Forests of India, Nepal and Bhutan, Ministry of Environment and Forests, Govt. of India, 1996.

Garkoti, S.: Estimates of biomass and primary productivity in a high-altitude maple forest of the west central Himalayas, Ecol. Res., 23, 41-49, 2008.

Gough, C. M., Vogel, C. S., Harrold, K. H., George, K., and Curtis, P. S.: The legacy of harvest and fire on ecosystem carbon storage in a north temperate forest, Global Change Biol., 13, 1935-1949, 2007.

Grace, J.: Structural equation modeling and natural systems, Cambridge University Press, Cambridge, UK, 2006.

Grierson, A. J. C. and Long, D. G.: Flora of Bhutan, Royal Botanical Garden Edinburgh, Edinburgh, U.K., 1983.

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

Hashimoto, S., Carvalhais, N., Ito, A., Migliavacca, M., Nishina, K., and Reichstein, M.: Global spatiotemporal distribution of soil respiration modeled using a global database, Biogeosciences, 12, 4121-4132, 2015.

Janssens, I. A., Freibauer, A., Ciais, P., Smith, P., Nabuurs, G.-J., Folberth, G., Schlamadinger, B., Hutjes, R. W., Ceulemans, R., and Schulze, E.-D.: Europe's terrestrial biosphere absorbs 7 to 12% of European anthropogenic CO2 emissions, Science, 300, 1538-1542, 2003.

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

Kutsch, W. L., Persson, T., Schrumpf, M., Moyano, F. E., Mund, M., Andersson, S., and Schulze, E.-D.: Heterotrophic soil respiration and soil carbon dynamics in the deciduous Hainich forest obtained by three approaches, Biogeochemistry, 100, 167-183, 2010.

Kuzyakov, Y.: Priming effects: Interactions between living and dead organic matter, Soil Biology and Biochemistry, 42, 1363-1371, 2010.

Laumans, P.: Height -Diameter Functions form a Country Level Site classification and Local Volume Table Selection., UNDP/FAO Forest Resources Management and Institutional Development Project Thimphu, Bhutan, 1994.

Biogeosciences Discuss., doi:10.5194/bg-2016-291, 2016
Manuscript under review for journal Biogeosciences
Published: 8 August 2016

Lee, M.-s., Nakane, K., Nakatsubo, T., and Koizumi, H.: Seasonal changes in the contribution of root respiration to total soil respiration in a cool-temperate deciduous forest. In: Roots: The Dynamic Interface between Plants and the Earth: The 6th Symposium of the International Society of Root Research, 11–15 November 2001, Nagoya, Japan, Abe, J. (Ed.), Springer Netherlands, Dordrecht, 2003.

Leifeld, J. and Fuhrer, J.: The temperature response of CO_2 production from bulk soils and soil fractions is related to soil organic matter quality, Biogeochemistry, 75, 433-453, 2005.

Li, H.-j., Yan, J.-x., Yue, X.-f., and Wang, M.-b.: Significance of soil temperature and moisture for soil respiration in a Chinese mountain area, Agric. For. Meteorol., 148, 490-503, 2008.

Liang, E., Wang, Y., Piao, S., Lu, X., Camarero, J. J., Zhu, H., Zhu, L., Ellison, A. M., Ciais, P., and Peñuelas, J.: Species interactions slow warming-induced upward shifts of treelines on the Tibetan Plateau, Proceedings of the National Academy of Sciences, 113, 4380-4385, 2016.

Menon, A., Levermann, A., Schewe, J., Lehmann, J., and Frieler, K.: Consistent increase in Indian monsoon rainfall and its variability across CMIP-5 models, Earth Syst. Dynam. Discuss., 4, 1-24, 2013.

Ohsawa, M. (Ed.): Life zone ecology of the Bhutan Himalaya, Chiba University, Chiba, Japan, 1987.

Ohsawa, M. (Ed.): Life Zone ecology of the Bhutan Himalaya, Chiba University, Chiba, 1991.

Pandey, R., Sharma, G., Singh, T., and Tripathi, S.: Factors influencing soi l CO2 efflux in a north eastern Indian oak forest and plantation, Afr. J. Plant Sci., 4, 280-289, 2010.

Pinheiro, J. C. and Bates, D. M.: Mixed-Effects Models in S and S-Plus, Springer - Verlag, New York Berlin Heidelberg, 2000.

Pumpanen, J., Longdoz, B., and Kutsch, W.: Field measurements of soil respiration: principles and constraints, potentials and limitations of different methods. In: Soil Carbon Dynamics - An Integrated Methodology, Kutsch, W., Bahn, M., and Heinemeyer, A. (Eds.), Cambridge University Press, Cambridge, 2009.

Rana, S., Bargali, K., and Bargali, S.: Assessment of plant diversity, regeneration status, biomass and carbon stock in a Central Himalayan cypress forest, Int. J. Biodivers. Conserv., 7, 321-329, 2015.

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., Oechel, W., Ourcival, J. M., 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.: Modelling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices, Global Biogeochemical Cycles, 17, 1104, 2003.

Rey, A., Pegoraro, E., Tedeschi, V., De Parri, I., Jarvis, P. G., and Valentini, R.: Annual variation in soil respiration and its components in a coppice oak forest in Central Italy, Global Change Biol., 8, 851-866, 2002.

Ruehr, N. K. and Buchmann, N.: Soil respiration fluxes in a temperate mixed forest: seasonality and temperature sensitivities differ among microbial and root–rhizosphere respiration, Tree Physiology, 30, 165-176, 2010.

Schewe, J. and Levermann, A.: A statistically predictive model for future monsoon failure in India, Environ. Res. Lett., 7, 044023, 2012.

Schickhoff, U.: The upper timberline in the Himalayas, Hindu Kush and Karakorum: a review of geographical and ecological aspects. In: Mountain Ecosystems, Springer, 2005.

Schild, A.: ICIMOD's Position on Climate Change and Mountain Systems, Mountain Research and Development, 28, 328-331, 2008.

Biogeosciences Discuss., doi:10.5194/bg-2016-291, 2016
Manuscript under review for journal Biogeosciences
Published: 8 August 2016

Biogeosciences
Discussions
Open Access
EGU

Schindlbacher, A., De Gonzalo, C., Díaz-Pinés, E., Gorría, P., Matthews, B., Inclán, R., Zechmeister-Boltenstern, S., Rubio, A., and Jandl, R.: Temperature sensitivity of forest soil organic matter decomposition along two elevation gradients, Journal of Geophysical Research, 115, G03018, 2010.

Schindlbacher, A., Zechmeister-Boltenstern, S., and Jandl, R.: Carbon losses due to soil warming: Do autotrophic and heterotrophic soil respiration respond equally?, Global Change Biol., 15, 901-913, 2009.

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

Sharma, C. M., Baduni, N. P., Gairola, S., Ghildiyal, S. K., and Suyal, S.: Tree diversity and carbon stocks of some major forest types of Garhwal Himalaya, India, For. Ecol. Manage., 260, 2170-2179, 2010a.

Sharma, E., Chettri, N., and Oli, K. P.: Mountain biodiversity conservation and management: a paradigm shift in policies and practices in the Hindu Kush-Himalayas, Ecol. Res., 25, 909-923, 2010b.

Sharma, P. and Rai, S. C.: Carbon sequestration with land-use cover change in a Himalayan watershed, Geoderma, 139, 371-378, 2007.

Sharmila, S., Joseph, S., Sahai, A. K., Abhilash, S., and Chattopadhyay, R.: Future projection of Indian summer monsoon variability under climate change scenario: An assessment from CMIP5 climate models, Global Planet. Change, 124, 62-78, 2015.

Sheikh, M. A., Kumar, M., and Bussmann, R. W.: Altitudinal variation in soil organic carbon stock in coniferous subtropical and broadleaf temperate forests in Garhwal Himalaya, Carbon balance and management, 4, 1-6, 2009.

Shrestha, U. B., Gautam, S., and Bawa, K. S.: Widespread climate change in the Himalayas and associated changes in local ecosystems, PLoS One, 7, e36741, 2012.

Singh, S. B. K., Isabella; Singh Karky, Bhaskar; Sharma, Eklabya: Climate change in the Hindu Kush-Himalayas: the state of current knowledge, ICIMOD, 2011. 88 2011.

Singh, S. P., Adhikari, B. S., and Zobel, D. B.: Biomass, productivity, leaf longevity, and forest structure in the central Himalaya, Ecol. Monogr., 1994. 401-421, 1994.

Stocker, T. F.: Climate change 2013: the physical science basis: Working Group I contribution to the Fifth assessment report of the Intergovernmental Panel on Climate Change, Cambridge University Press, 2014.

Subke, J.-A., Inglima, I., and Francesca Cotrufo, M.: Trends and methodological impacts in soil CO2 efflux partitioning: A metaanalytical review, Global Change Biology, 12, 921-943, 2006.

Sundarapandian, S. and Dar, J.: Variation in Soil CO2 Efflux in Pinus Wallichiana and Abies Pindrow Temperate Forests of Western Himalayas, India. Forest Res, 3, 2, 2013.

Tashi, S., Singh, B., Keitel, C., and Adams, M.: Soil carbon and nitrogen stocks in forests along an altitudinal gradient in the eastern Himalayas and a meta-analysis of global data, Global Change Biol., 2016. 2016.

Tiwari, S. and Joshi, R.: Litter-fall production in cool-temperate forests of the Nanda Devi Biosphere Reserve, Uttarakhand Himalaya, India, Braz. J. Biolo. Sci., 2, 147-154, 2015.

Tsering, K., Sharma, E., Chettri, N., and Shrestha, A.: Climate Change Impact and Vulnerability in the Eastern Himalayas – Synthesis Report. ICIMOD, Kathmandu,Nepal2010, 110.

Tuomi, M., Vanhala, P., Karhu, K., Fritze, H., and Liski, J.: Heterotrophic soil respiration - Comparison of different models describing its temperature dependence, Ecological Modelling, 211, 182-190, 2008.

Biogeosciences Discuss., doi:10.5194/bg-2016-291, 2016
Manuscript under review for journal Biogeosciences
Published: 8 August 2016

Usman, S., Singh, S., and Rawat, Y.: Fine root productivity and turnover in two evergreen central Himalayan forests, Ann. Bot., 84, 87-94, 1999.

Verma, A., Tewari, A., and Shah, S.: Carbon storage capacity of high altitudeQuercus semecarpifolia, forests of Central Himalayan region, Scand. J. For. Res., 27, 609-618, 2012.

Wang, X., Jiang, Y., Jia, B., Wang, F., and Zhou, G.: Comparison of soil respiration among three temperate forests in Changbai Mountains, China, Can. J. For. Res, 40, 788-795, 2010.

Wangda, P. and Ohsawa, M.: Gradational forest change along the climatically dry valley slopes of Bhutan in the midst of humid eastern Himalaya, Plant Ecology, 186, 109-128, 2006a.

Wangda, P. and Ohsawa, M.: Structure and regeneration dynamics of dominant tree species along altitudinal gradient in a dry valley slopes of the Bhutan Himalaya, For. Ecol. Manage., 230, 136-150, 2006b.

Wikramanayake, E. D.: Terrestrial ecoregions of the Indo-Pacific: a conservation assessment, Island Press, 2002.

Xu, J. and Grumbine, R. E.: Building ecosystem resilience for climate change adaptation in the Asian highlands, Wiley Interdisciplinary Reviews: Climate Change, 5, 709-718, 2014.

Xu, J., Grumbine, R. E., Shrestha, A., Eriksson, M., Yang, X., Wang, Y., and Wilkes, A.: The melting Himalayas: cascading effects of climate change on water, biodiversity, and livelihoods, Conserv. Biol., 23, 2009.

Yang, Y.-S., Chen, G.-S., Guo, J.-F., Xie, J.-S., and Wang, X.-G.: Soil respiration and carbon balance in a subtropical native forest and two managed plantations, Plant Ecol., 193, 71-84, 2007.

Table 1 Site characteristics of the two studied forests types

Parameter	Coniferous forest	Broadleaved 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	*Tsuga dumosa (59.5%)* *Quercus semecarpifolia (29.3%)* *Picea spinulosa (6.3%)* *Abies densa (4.1%)* *Taxus baccata (0.3%)*	*Quercus lanata (63.5%)* *Quercus griffithii (29.6%)*
Dominant Understory species	*Ilex dipreyana (0.2%)* *Rhododendron arboreum (0.1%)*	*Symplocus sp. (0.8%)* *Lyonia ovalifolia, (2.2%)* *Rhododendron arboreum (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 carbon (t ha^{-1}) 0-30 cm	127.2 ± 17.4	91.2 ± 6.2
Soil organic nitrogen (t ha^{-1}) 0-30 cm	6.8 ± 0.6	4.2 ± 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.

Biogeosciences Discuss., doi:10.5194/bg-2016-291, 2016
Manuscript under review for journal Biogeosciences
Published: 8 August 2016

Biogeosciences
Discussions
Open Access

Site	Soil moisture levels	**Temperature Range (°C)**	**Q_{10}**	**R_{10} (µmol CO_2 kgC^{-1} S^{-1})**
Coniferous forest	Intermediate (32 Vol. %)	5.0 - 25.0	2.58 ± 0.22[a]	0.09 ± 0.01[a]
	Dry (12 Vol. %)	5.0 - 25.0	1.59 ± 0.07[b]	0.07 ± 0.00[a]
	Wet (56 Vol. %)	5.0 - 25.0	2.12 ± 0.14[a]	0.12 ± 0.01[b]
Broadleaved forest	Intermediate (31 Vol. %)	5.0 - 25.0	2.35 ± 0.09[a]	0.13 ± 0.01[a]
	Dry (12 Vol. %)	5.0 - 25.0	1.60 ± 0.11[b]	0.09 ± 0.01[a]
	Wet (55 Vol. %)	5.0 - 25.0	2.05 ± 0.14[a]	0.16 ± 0.01[b]

Table 2. Q_{10} and R_{10} parameters (Eq. (1)) derived from laboratory incubation. Letters indicate significant differences in R_{10} and Q_{10} between soil moisture levels of the mineral soil samples.

Biogeosciences Discuss., doi:10.5194/bg-2016-291, 2016
Manuscript under review for journal Biogeosciences
Published: 8 August 2016

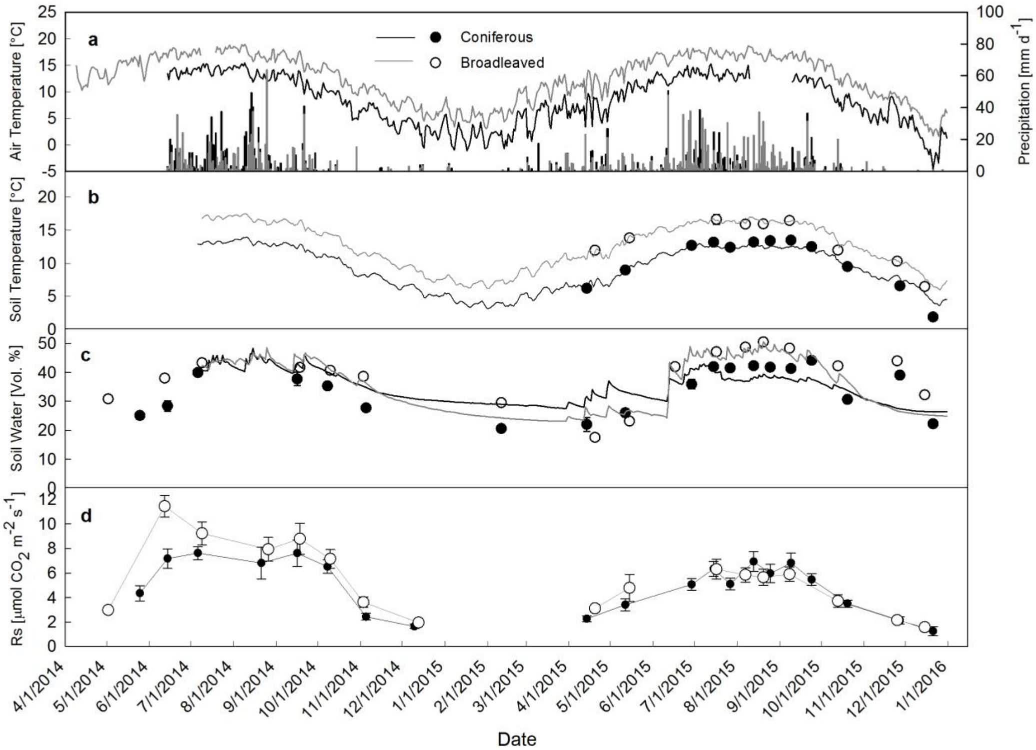


Figure 1. Seasonal course of air temperature and precipitation (a), soil temperature (b), volumetric soil water content (c), and soil respiration (d) measured at a coniferous and a broadleaved forest in Bhutan Himalayas in 2014 and 2015. Circles represent daily mean values of manual measurements. Solid lines (a, b, c) represent daily mean values of continuous measurements. Error bars indicate standard error of the mean.

Biogeosciences Discuss., doi:10.5194/bg-2016-291, 2016
Manuscript under review for journal Biogeosciences
Published: 8 August 2016

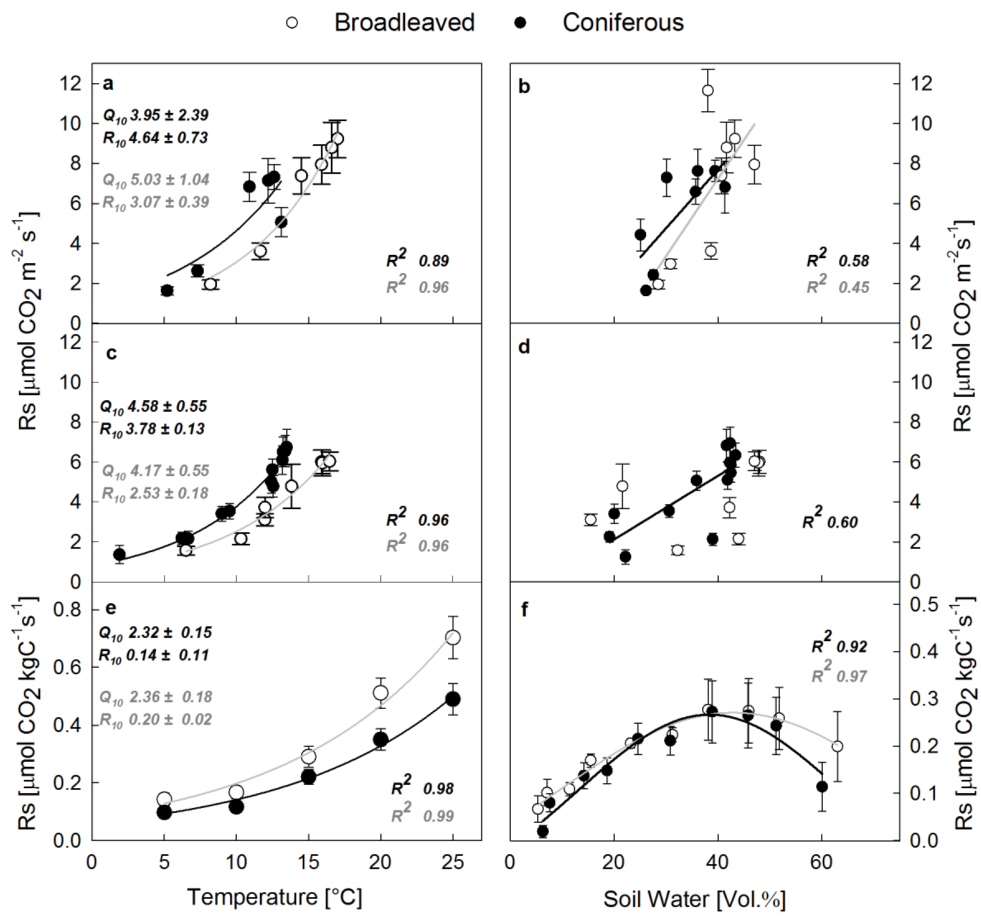


Figure 2. Relationship between soil CO_2 efflux and soil temperature and soil water content for a broadleaved forest and a coniferous forest in Bhutan Himalayas, measured during field campaigns in 2014 (a, b) and 2015 (c, d), and during a laboratory incubation experiment (e, f). Relations between CO_2 efflux and temperature were fitted with an exponential function,Eq.(1) and model parameters (R_{10}, Q_{10}) are shown. Relations between CO_2 efflux and volumetric water content were fitted with linear and Gaussian functions Eq. (2). Error bars represent standard error of the mean.

Biogeosciences Discuss., doi:10.5194/bg-2016-291, 2016
Manuscript under review for journal Biogeosciences
Published: 8 August 2016

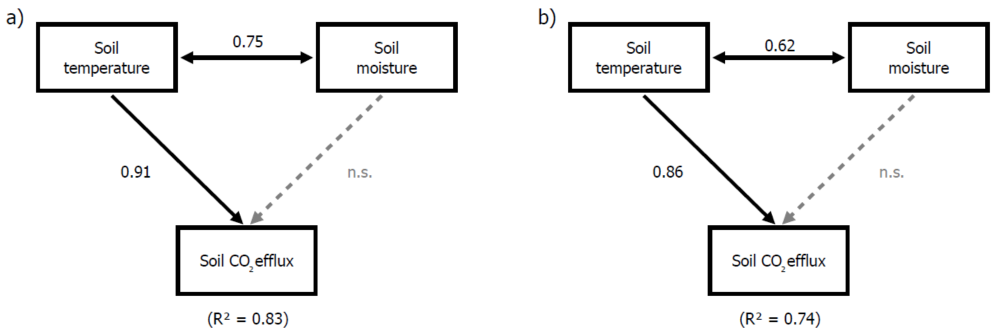
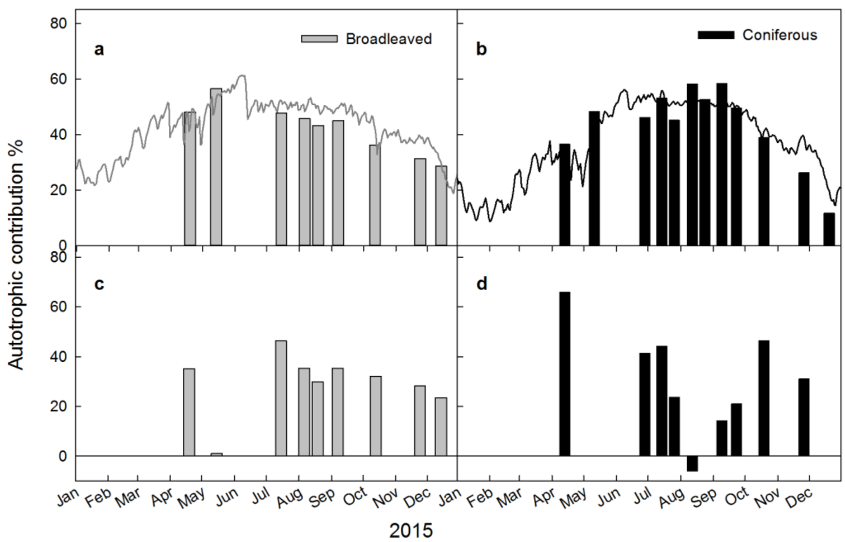


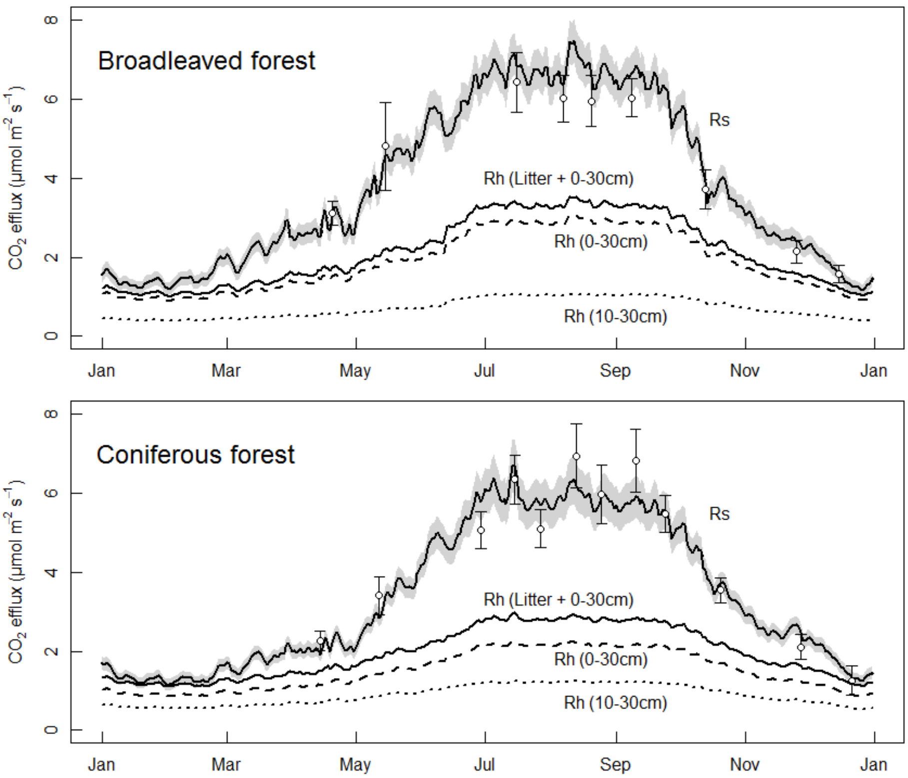
Figure 3. Structural equation models for a broadleaved (a) and a coniferous (b) forest in Bhutan Himalayas, describing the soil climatic drivers of soil CO_2 efflux during measurement campaigns in 2014 and 2015.



606

607 **Figure 4: Monthly contribution of autotrophic soil respiration to total soil CO_2 efflux at a broadleaved and coniferous**
608 **forest in Bhutan Himalayas. Data on autotrophic respiration are derived from the difference of modelled daily soil CO_2**
609 **efflux and modelled heterotrophic soil respiration rates (a, b, solid lines), measured soil CO_2 efflux and modelled**
610 **heterotrophic soil respiration rates (a, b, bars), and measured soil CO_2 efflux from control and trenched plots (c, d) of the**
611 **respective site.**

Biogeosciences Discuss., doi:10.5194/bg-2016-291, 2016
Manuscript under review for journal Biogeosciences
Published: 8 August 2016



612
613 **Figure 5: Seasonal course of modelled soil CO_2 efflux (Rs) and heterotrophic soil respiration rates (Rh) from different soil**
614 **layers at a broadleaved and coniferous forest in Bhutan Himalayas in 2015. Open circles are measured soil CO_2 efflux**
615 **rates. Error bars and shaded area represent standard error of the daily mean.**