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ORIGINAL ARTICLE

Environmental factors associated with seasonal variations of night-time plant canopy and soil respiration fluxes in deciduous conifer forest, Western Himalaya, India

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Abstract

In situ carbon flux studies are typically rare over the Himalaya but are important to understand carbon (C) balance. We investigated night-time canopy respiration (R_{nc}) and soil respiration (R_s) of a deciduous coniferous forest in response to environmental factors. A comprehensive investigation has been carried out on C balance indicators by employing systematic and concurrent measurements over an annual growth cycle of pine (Nov 2010–Dec 2011). The study site consists of uniformly distributed young deciduous *Pinus roxburghii* plantation having understory as *Lantana camara* (an invasive shrub). Results underlined that both R_{nc} and R_s fluxes were highest in the post-monsoon season. Evaporative fraction (EF) and temperature explained maximum variability of fluxes during warm-moist monsoon. Our key finding depicts an inverse significant correlation between day-time canopy photosynthesis (A_c) and R_{nc} across the seasons ($r = 0.83$–0.99). This can be explained by the mechanistic physiological phase of optimal anabolism (A_c) with favorable environmental conditions and minimum level of catabolism (R_{nc}). The respiration-photosynthesis ratio (R_{nc}/A_c) typically ranged from 0.25 ± 0.11 (peak growing season) to 0.71 ± 0.16 (winter season) with mean of 0.26 ± 0.10. The ratio R_s/A_c was highest during the winter season (2.69 ± 0.43), while minimum during peak growing season (0.64 ± 0.29). The R_{nc}/A_c ratio and night-time temperature (AT) also revealed that the ratio could increase when AT crossed 24 °C. These responses indicate that under climate warming, it may have a significant influence on net plant C uptake. Presence of understory shrub minimizes the R_{nc}/A_c ratio, and indicative of a more positive C-balance. Nevertheless, the observations could certainly lend useful insight into C-balance and ecological function in the region. Further, it may be useful in parameterizing and validating C-cycle models.

Keywords Nigh-time plant respiration · Soil respiration · *Pinus roxburghii* · Understory · Subtropical Himalaya · Respiration-photosynthesis ratio

Abbreviations

R_{nc}	Night-time canopy respiration
R_s	Soil respiration
LE	Latent heat
SH	Sensible heat
ET	Evapotranspiration
EF	Evaporative fraction
AT	Air temperature
ST	Soil temperature
SM	Soil moisture
VPD	Vapor pressure deficit
RH	Relative humidity
C	Carbon
CO_2	Carbon dioxide
A_c	Day-time canopy photosynthesis
GPP	Gross primary production
Rd_{day}	Day-time plant respiration
R_e	Ecosystem respiration
LAI	Leaf area index

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10-days interval	Dekads
EC	Eddy-covariance

Introduction

Mechanisms controlling the terrestrial carbon (C) cycle components and their responses to the changing environment across the Himalayan ecosystems are usually unknown. Over the last few decades, ecosystems of the Himalaya have experienced three times more warming than the global average (Bhutiyani et al. 2007; Xu et al. 2009; Shrestha et al. 2012). Increased diurnal temperature and change in precipitation patterns in response to climate warming have altered the regional vegetation in Himalaya (Yadav et al. 2004; Basistha et al. 2009). In view of such environmental change and their impact on C-cycle components, it demands field-based measurements data for understanding the underlying C-cycle processes and controlling environmental factors. In this viewpoint, Indian Space Research Organization (ISRO) undertook an initiative to characterize energy–water–carbon exchange, and their control on mid-altitudinal western Himalayan forests by establishing an INSAT (Indian National Satellite) linked micrometeorological tower of 13 m height at the Forest Research Institute campus, Dehradun, India (Bhattacharya et al. 2013).

The deciduous conifer forest, *Pinus roxburghii* (sarg.) is the dominant vegetation in the lower western Himalayan region (elevation of 500–2000 m) that covers ~ 18,650 km^2 area, and constitutes ~ 6% of the total forested area of India (Forest Survey of India 2011). Given its climatic and ecological importance, understanding on energy-water-carbon exchange fluxes becomes critical to ascertain various environmental controlling factors. In our earlier studies, radiation-energy balance and inter-linkages of C (canopy photosynthesis, A_c), and water fluxes were investigated across the seasons. Results underlined that the degree of coupling between water and C exchange was stronger during post-monsoon and spring seasons (Singh et al. 2014a, b). In this study, we aimed to investigate seasonal dynamics of the canopy (plant) and soil respiration fluxes based on in situ field measurements data and to characterize the dynamics of these fluxes in relation to physical environmental factors, biophysical, and ecophysiological variables.

One of the critical C-balance components is plant respiration, which is a pivotal constituent of forest C-balance. Change in this component would alter atmospheric CO$_2$ concentration, and thereby, it may have a significant effect on global C-cycle strength. Photosynthetically fixed C is allocated to a variety of plant usages, and 50–80% of C is returned immediately to the atmosphere through canopy respiration (Hagihara and Hozumi 1991; Turnbull et al. 2002; Atkin et al. 2007; DeLucia et al. 2007). It is well known that the day-time and night-time canopy respiration (R_{nc}) are not equal in magnitude, and the R_{nc} alone constitutes a major fraction of canopy respiration, as day-time respiration is strongly inhibited by light (Sun et al. 2015; Wehr et al. 2016). Measurement of R_{nc} becomes essential to understand net ecosystem C-balance as the respiration rates obtained during night-time is more stable because the impact of sugar synthesis and transport is minimum (Will and Ceulemans 1997). It is also likely that the temperature-induced changes in R_{nc} and soil respiration (R_s) could have a large impact on C-exchange and storage (Cox et al. 2000; Piao et al. 2010; Anderegg et al. 2015). Further, there is seasonal constancy in respiration-photosynthesis (R_{nc}/A_c) ratio until unless perturbed by some external factors (Gifford 2003; Atkin et al. 2007; DeLucia et al. 2007; Van Oijen et al. 2010). It would be interesting to investigate environmental controls on respiration fluxes in the Himalaya, where seasonal transition phases are prominent and changes in annual phenology are drastic.

R_s is the flux of microbially and plant root-respired CO$_2$ from the soil surface to the atmosphere, and it represents a major flux of C into the atmosphere (Schlesinger and Andrews 2000; Bond-Lamberty and Thomson 2010). The variability of R_s is affected by a multitude of factors; however, soil temperature and moisture are the prime determinants (Baldocchi et al. 2001; Curtin et al. 2000). Changes in precipitation-temperature and consequent changes in vegetation phenology-productivity may also influence the variability of R_s. It is thus crucial to understand how annual dryness-wetness cycle, temperature-moisture conditions influence R_s in the subtropical coniferous forests.

Several studies have analyzed the patterns of leaf respiration to reduce C-exchange uncertainty in different biomes over the globe (Wright et al. 2004; Reich et al. 2006; Atkin et al. 2008, 2015). Nonetheless, Himalayan ecosystems remain elusive with respect to C-balance, and even respiration-photosynthesis ratio for basic model parameterizations. Thus, in situ field data are needed to understand the likely effects of future climate change on pine forests. Further, we have limited knowledge, as of how R_{nc} and R_s respond to environmental factors, such as, moisture/wetness conditions (dewfall, night-time vapor pressure deficit, evaporative fraction) and temperature conditions (night-time air/soil temperature). To characterize these environmental controls on R_{nc} and R_s in a young homogenously distributed *Pinus roxburghii* forest ecosystem having understory, we have used 14 months' of micrometeorological, ecophysiological, and biophysical data comprising an annual growth cycle from November 2010 to December 2011.

Given the complex topography, canopy structure of the pines with understory, we utilized manually intensive chamber-based methodology (Speckman et al. 2015), however, at a longer time-interval (continuous 24 h cycles at 10-day interval). Hereafter, dekads should be read as 10 days in a month, for instance, Nov1d can be read as data over 1st to 10th of November. The uncertainty of eddy-covariance (EC) technique during night poses an additional challenge to understand seasonal variation of R_{nc} and R_s (Berkelhammer et al. 2013; Speckman et al. 2015), but the chamber-based measurements are useful when individual ecosystem components and environmental factors or disturbances need to be discerned (Speckman et al. 2015). To best of our knowledge, this is the initial comprehensive study with chamber-based field measurements over the conifers in the western Himalaya to characterize environmental controls on seasonal variations of plant and soil respiration fluxes.

Materials and methods

Site description and climate

The experimental site was located within reserve forest at the Forest Research Institute (FRI), Dehradun, India (30°20′04″N and 78°00′02″E) with a mean elevation of 640 m (Fig. S1). The site has a micrometeorological tower (13 m) with multi-level, slow-response sensors, designed to measure sub-hourly radiative-convective flux, state parameters and sub-surface thermal profiles. The biophysical (LAI: leaf area index, PAR: photosynthetically active radiation, phenology) and ecophysiological properties (photosynthesis, leaf respiration, and soil respiration) of young (~ 8.5 years old), homogenously distributed chir pine (*Pinus roxburghii* Sarg.) plantation patch (~ 5 hectares) were measured at 10-day interval through systematic manual sampling. The patch has an understory cover of *Lantana camara* L. (Verbenaceae), which was cleared during 2010 (October–November). To study the effects of understory cover on ecosystems carbon, water, and energy fluxes, it was not cleared in the year 2011. To have systematic biophysical and ecophysiological measurements, the site was homogenously divided into nine sampling quadrats (10 m × 10 m) in different directions. The micrometeorological tower was placed centrally.

Climate of study site

Study site lies in a heavy rainfall zone in the western Himalayan region (70-year average: 2020 ± 423 mm). Typically, cold winter season comprises December to February, while hot summer season comprises March to May. The summer monsoon season months are from June to September, while the post-monsoon season months are October and November (Basistha et al. 2009). The seasonal pattern of temperature (AT) and precipitation (P) accorded concurrently with peaks of both P and AT (mean 25.5 °C) during July–September (Fig. S2). Such coincident variation (moist–warm condition) is the environmental characteristic of the region.

Vapour pressure deficit (VPD: 1.1 ± 0.85 kPa) remain high (3.7 kPa) only during dry summer (April–May) and minimum (0.37 kPa) during the summer monsoon. Soil water content (w/w; mean of 3 depth: 0.1, 0.2 and 0.45 m, manually collected only once in a month, because of failure of automatic field sensor) during the study period varied between 11% (May) and 24% (August). Sunshine hours vary from 4.4 to 9.3 h day^{-1} with a minimum during July–August and maximum during May. Mean monthly open pan evaporation varies from 1.2 to 7.2 mm with lowest during winter and highest during hot summer. Seasonal VPD and soil moisture dynamics were found inversely but significantly related ($R^2 = 0.69$, $p < 0.001$). Evaporative fraction (EF: the ratio between the evapotranspiration (ET) and the available energy at the land surface), an indicator of annual dryness–wetness cycle (range 0–1), remained above 0.38 throughout the study period with a mean of 0.5 ± 0.16. It varied between 0.38 (winter dekads) and 0.9 (summer monsoon dekads). Further, stronger ET and AT relationship than ET–VPD relation, defined this subtropical pine ecosystem as energy-limited rather than water–limited. The energy and water limitation phase during an annual growth cycle occurs in continuum with a shorter water limited period (confined only to the summer months: April–June) (Fig. S3).

Ecophysiological measurements and data processing

Night-time canopy respiration (R_{nc})

R_{nc} rates of both over and understory were measured from the active tissues (foliage) except the woody tissues (stem) of young pine (understory growth has a little woody tissue). Rates of respiration were manually but intensively measured at 10–day interval from 10th November 2010 to 31st December 2011 for 12 h (18:30 h–05:30 h) using the LI-6400 XT portable photosynthesis system (LI-COR, Lincoln, NE, model LI-6400 XT, Standard leaf chamber area: 2 cm × 6 cm). During measurements, block temperature and VPD was maintained under prevailing ambient conditions. The airflow rate and reference CO_2 was set at 400 and 380 µmol mol^{-1}, respectively.

The hourly sampling of a species (overstory: Pine and understory: *Lantana*) consisted of 360 to 450 readings made from a portable photosynthesis system (LI-Cor, Lincoln, NE, model LI-6400 XT). Hourly readings of the species represent three plants sampled in three different quadrats. Each plant was divided into three-vertical layers (top, middle, and bottom). Three to five needles/leaves per vertical layer of a plant around each canopy position were measured from the photosynthesis system. About 40–50 readings were made within 1.5–2.0 min on each layer. Thus, each plant in a quadrat was sampled for about 6 min consisted of 120–150 readings.

Leaf-level respiration data from photosynthesis system were up-scaled to canopy level on the basis of LAI (Law et al. 2001; Cavaleri et al. 2008) as well as on total canopy leaf area basis ("Biophysical measurements") (Chambers et al. 2004).

Soil respiration (R_s)

R_s rates were measured for 24 h at 10-day interval using a soil chamber (LI-6400-09) combined with a LI-6400 IRGA (Li-COR, Lincoln, NE, USA), randomly in different quadrats for maximum possible spatial coverage. This data were also supplemented intermittently by applying another closed, static chamber based (25 cm × 25 cm) on infrared gas analyzer (IRGA) CO_2 sensor (GasAlertMicroIR5, BW Tech., Honeywell Inc., CA, USA). Within a quadrat, systematic sampling was done to cover both root and non–root zone (based on the distance from trees). Chambers were slipped into collars inserted into the soil 24 h prior to the measurements.

Biophysical measurements

Phenology At weekly intervals, digital field photographs taken from all quadrats were analyzed to determine the transition dates of growth stages of Pine. The green stage of Pine corresponds to May–September and characterized by green, matured and elongated needles. During this period, the crown was mostly covered by green needles so that total photosynthetic area (computed by mechanical counting of all needles in the crown) was equated with green vegetation fraction (GVF) of 1.0 (as 100%). Traces of brown needles began to appear in October, and thus GVF of October was 0.92. As winter approached, browning of leaves increased rapidly because of a physiologically dormant stage and accordingly, the GVF was calculated. By the end of March, the GVF was calculated ~ 0.17. The emergence of new needle buds commenced in March, while the growing season referred the period from April to October.

The understory *Lantana camara* was cleared in the last week of October 2010. New leaves were emerged from the tuberous underground root in the onset of spring. By March end, *Lantana* attained a height of 0.3–0.4 m. *Lantana* canopy was completely developed before the onset of summer monsoon, and attained a height of 1.0 m. It attained maximum height (~ 1.5 m) during the post-monsoon. In Nov–Dec, 2011, when *Lantana* was not cleared, leaf browning was observed after November.

Leaf area index (LAI) The LAI was measured at the 10-day interval in overstory pine and in understory *Lantana*. We used plant canopy analyzer (PCA) (LAI-2000; Li-Cor, Inc., Lincoln, NE, USA) for measuring the LAI. The detailed sampling plan and the correction factor for the clumping of needles in the pine canopy were described in Singh et al. (2014b). Overall, we followed the procedure as per LAI-2000 PCA instruction manual.

Net canopy photosynthesis (A_c): measurements, upscaling and errors

Measurements The samplings of photosynthesis and night respiration were carried out at 10-day interval during the growth cycle (i.e., Nov 1d 2010 to Dec 3d 2011) continuously for 24-h. On each day of measurement, daytime (06:00–18:00 h LMT) net photosynthesis and respiration in the next night (18:30–05:30 h LMT) were measured hourly. Hourly sampling of a species (overstory: Pine and understory: *Lantana*) consisted of 360–450 readings made from a portable photosynthesis system (LI-Cor, Lincoln, NE, model LI-6400 XT). Hourly readings of the species represent three plants sampled in three different quadrats. Each plant was divided into three-vertical layers (top, middle and bottom). Three to five needles/leaves per vertical layer of a plant around each canopy position were measured from photosynthesis system. About 40–50 readings were made within 1.5–2.0 min on each layer. Thus, each plant in a quadrat was sampled for about 6 min consisted of 120–150 readings. The readings from each layer were stored separately in the photosynthesis system for data processing and upscaling.

Upscaling Leaf level photosynthesis (L_{nar}) data acquired with LI-6400 XT portable photosynthesis system was upscaled to canopy level according to Campbell and Norman (1998) by assuming single light assimilation response relation for all the leaves in the canopy. Canopy was divided into sunlit and shaded class based on canopy sub-division into three layers (top–mid–bottom). Based on observations on LAI and light penetration, almost always leaves/needles at lowest canopy positions were considered as a shaded class. Photosynthesis contributions from each class (sunlit and shaded) were computed separately. Assimilation rate was summed up according to the fraction of leaf area in each class:

$$A_{\mathrm{c}} = L_{\mathrm{nar}}^{\mathrm{sunlit}} \times \mathrm{LAI}_{\mathrm{s}} + L_{\mathrm{nar}}^{\mathrm{shaded}} \times \mathrm{LAI}_{\mathrm{sh}}.$$

Sunlit leaf area index ($\mathrm{LAI}_{\mathrm{S}}$) in the vegetation canopy (m^2 leaf m^{-2}ground) can be expressed as:

$$\mathrm{LAI}_{\mathrm{s}} = I_{\mathrm{A}}' / K$$

where $K = \cos(\theta)$, $\theta =$ leaf angle (mean tilt angle) and $I_{\mathrm{A}}' = 1 - \exp\,(-k \times \mathrm{LAI})$, k for over and understory vegetation were computed from LAI and PAR measurements above and below the canopy of understory and overstory as per Lagergren et al. (2005).

The shaded LAI was calculated as:

$$\mathrm{LAI_{sh}} = \mathrm{LAI} - \mathrm{LAI_s}.$$

The day-time net canopy assimilation (A_c) calculated as gross primary production $\left(\mathrm{GPP_{day}}\right)$ minus day-time plant respiration ($\mathrm{Rd_{day}}$). Mathematically, it can be written as:

$$A_c = \mathrm{GPP_{day}} - \mathrm{Rd_{day}}.$$

Seasonal variability of A_c has been also provided in Text S1 (supplementary) and may be referred to Singh et al. (2014b).

Using A_c, we have computed two indicators, namely, R_{nc}/A_c (an indicator of canopy carbon balance) and R_s/A_c (an indicator of soil carbon balance). These indicators were described in "Seasonal variation of A_c and respiration-photosynthesis ratios". The total ecosystem respiration (R_e) was computed as sum of R_{nc} and R_s. Further, the ecosystem respiration-photosynthesis ratio (R_e/A_c) was computed that indicative of net canopy C balance.

We have also provided associated errors of canopy photosynthesis in supplementary (text S2) and Table S1.

Micrometeorological observations

Sensors on the micrometeorological tower provide automated measurements of basic variables and radiation components. ET was computed following Bowen ratio energy balance (BREB) method. It consists of various multi-level probes comprising both above-ground (net radiometer, rain gauge, anemometers, AT-RH sensors) and below-ground sensors (soil heat flux plates, thermometers) and details are discussed in Singh et al. (2014a). In our previous study, we analyzed half-hourly averaged micrometeorological data, where we computed ET and EF based on BREB method (Singh et al. 2014b).

Notably, this study has analyzed new environmental variables in the canopy environment, such as, night-time air/soil temperature, night-time VPD, night-time latent heat flux (hereafter, called as "dewfall"). Night-time latent heat ($\mathrm{W\ m^{-2}}$) flux was computed as the sum of daytime ET subtracted from the 24 h sum divided by night-time hours.

Statistical analysis and uncertainty estimate

To examine the relationship between C-cycle components and environmental-biophysical factors, Pearson's correlation analysis was performed. Additionally, one to one interaction between significantly correlated C components and environmental-biophysical predictors were assessed using linear regression analysis. We used multiple regression and ANOVA to identify the best environmental-biophysical factors as predictor variables. Significant statistical differences were set with $p < 0.001$ unless otherwise stated. All statistical analyses were performed using SPSS (ver. 14) and MATLAB R2012 (The MathWorks, Inc., Natick, MA, USA) software. Further, we explored the possibility of temporal coupling between canopy photosynthesis (A_c) and soil respiration (R_s) using wavelet coherence analysis in wavelet analysis software (Torrence and Compo 1998; Grinsted et al. 2004).

Results

Seasonal variations of R_{nc} associated with environmental variables

The annual behaviour of R_{nc} across the seasons, such as winter 2010 (no understory), pre- to post-monsoon (comprising growing period: April–October), and Nov–Dec, 2011 (with understory) has been shown in Fig. 1. The corresponding standard errors (SE) were also shown. The results showed that annual behaviour of R_{nc} was unimodal (maximum in post-monsoon). R_{nc} was maximum (4.44 μmol $\mathrm{CO_2\ m^{-2}\ s^{-1}}$) in the mid–August, while it was minimum (0.76 μmol $\mathrm{CO_2\ m^{-2}\ s^{-1}}$) in March (no understory). Combined mean R_{nc} of both over and understory during growing season was 3.47 ± 0.48 μmol $\mathrm{CO_2\ m^{-2}\ s^{-1}}$, while with understory (Nov–Dec, 2011), it was two times higher (3.41 ± 0.21 μmol $\mathrm{CO_2\ m^{-2}\ s^{-1}}$) than without it during winter 2010 (1.55 ± 0.29 μmol $\mathrm{CO_2\ m^{-2}\ s^{-1}}$).

Monthly variations of R_{nc} and night-time AT were shown in Table 1, wherein, R_{nc} rates were separated as overstory

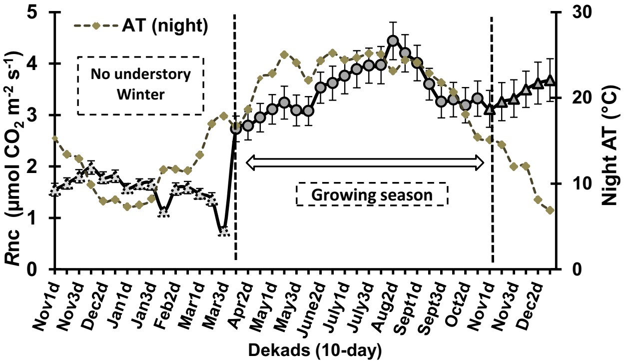

Fig. 1 Variations in night-time canopy respiration ($R_{nc} \pm \mathrm{SE}$) in relation to night-time air temperature (AT) at 10-day (dekads) interval over the study period (November 2010 to December 2011). Solid circles indicate growing period (April–October), dotted triangle denotes winter 2010 (no understory), but solid triangle denotes November–December, 2011 (with understory). It may be noted that only November month data points have been aggregated with winter season as the canopy browning was observed in November

(Pine) and understory (*Lantana*). Results showed that R_{nc} rates were consistently higher from the understory. Mean condition (March–October) indicates that the R_{nc} rates from understory were higher by a factor of 1.70. But, the uncertainty associated with understory R_{nc} was also higher (SD ± 1.8). Month-wise corresponding standard deviation (SD) and coefficient of variation (CV) were also tabulated along with both R_{nc} and night-time AT. Maximum rates of R_{nc} were observed during the month of July and August (summer monsoon season). Therefore, these results indicate that peak values were associated with wetness conditions (soil moisture 20–24%) rather than the night-time AT.

During the winter season, R_{nc} and AT (night-time) were negatively correlated, which might be due to senescence induced higher respiratory fluxes that increased with the decline in temperature (Fig. 2a). By contrast, during hot summer season (March–May) and peak growing season (June–October), R_{nc} and AT (night-time) were positively correlated ($r = 0.89$ and 0.64) that suggestive of an increase in R_{nc} under increasing night-time AT. Albeit, the relationships were statistically significant with moderate r value (0.64) especially during peak growing season, it suggests that night-time AT alone may not control the rates of R_{nc} (explained only ~ 40% of the variability). So, in this energy-limited environment, other wetness factors, such as dewfall and EF had a major role to play.

Night-time latent heat flux [expressed as latent heat (W m^{-2}) or dewfall] is an important component of the daily water cycle, but the least studied phenomenon in the Himalayan ecosystem. Typically, dewfall and rainfall (or soil moisture) were inversely correlated. It was observed that dewfall and night-time VPD were positively correlated ($r = 0.83$, $p < 0.001$) during the growing period (April–October). We observed that the night-time VPD (kPa) and R_{nc} were negatively correlated across all seasons except the hot summer season (Fig. 2b). Their relationships were quite identical along with R_{nc} and dewfall (Fig. 2c). Moreover, R_{nc} and dewfall were negatively correlated irrespective of winter or growing seasons (Fig. 2c). Their relationships were stronger during peak growing season ($r = 0.92$, $p < 0.001$), while moderate during winter 2010 ($r = 0.69$, $p < 0.01$). With understory during Nov–Dec, 2011, their relationship was weaker. By contrast, in hot summer season (March–May), we observed a positive correlation ($r = 0.73$, $p < 0.001$), and it suggests that with increasing dewfall, the R_{nc} rate increases. R_{nc} and EF were strongly and positively correlated (Fig. 2d) during growing and hot summer seasons ($r = 0.85$–0.90, $p < 0.001$). However, during the winter season 2010 (no understory), there was no correlation as most of the data points were clustered, when EF ranged from 0.4 to 0.5. In the case of Nov–Dec, 2011, it becomes negatively correlated ($r = 0.94$). Inverse R_{nc}–EF relation during winter might be due to the senescence-induced higher respiratory fluxes with an overall decrease in temperature and EF. Notably, under increased wetness conditions, subtropical pine forests exhibited an increase in R_{nc} rates.

Multiple linear regression (ANOVA) analysis between R_{nc} and combinations of night-time AT, dewfall, VPD (night-time), and EF environmental variables could explain 83% of the R_{nc} variability ($p < 0.001$) across the peak growing season. Nevertheless, we infer that about 17% of this unexplained variation of R_{nc} may be related to other environmental variables including species-specific physiological traits. Hence, these relationships have significance in predicting R_{nc} in relation to any alteration in the environmental parameters.

Seasonal variations of R_s associated with environmental variables

The annual behaviour of R_s across the seasons over the study period has been shown in Fig. 3. Results showed that the annual cycle of R_s was bimodal (maximum in post-monsoon and pre-monsoon). The mean R_s across the 14 months period

Table 1 Month-wise variations of R_{nc} of the foliage (μmol CO_2 m^{-2} s^{-1}) and night-time air temperature (°C) during March to October 2011

Months	R_{nc} (mean ± SD), CV (%)		Night-time AT (mean ± SD), CV (%)
	Overstory: Pine	Understory: *Lantana*	
March	1.20 ± 0.38, 32.0	–	16.0 ± 2.4, 15.0
April	0.82 ± 0.04, 5.0	2.0 ± 0.07, 3.6	19.2 ± 2.8, 14.7
May	0.95 ± 0.02, 2.8	2.19 ± 0.05, 2.6	23.9 ± 1.1, 4.6
June	1.13 ± 0.13, 11.6	2.27 ± 0.18, 8.0	23.8 ± 1.6, 6.8
July	**1.50 ± 0.14, 9.8**	**2.36 ± 0.06, 2.8**	24.7 ± 0.36, 1.4
August	**1.73 ± 0.09, 5.2**	**2.47 ± 0.17, 7.0**	24.1 ± 0.9, 4.0
September	1.42 ± 0.27, 19.0	2.2 ± 0.10, 7.0	22.9 ± 1.1, 5.0
October	1.20 ± 0.02, 2.0	2.0 ± 0.04, 2.4	18.0 ± 2.6, 14.5
Mean (March–Oct)	1.25 ± 0.32, 26.0	2.2 ± 1.8, 8.0	22.4 ± 2.9, 13.0

The SD and CV refer to standard deviation and coefficient of variation. The bold indicates maximum R_{nc} rates

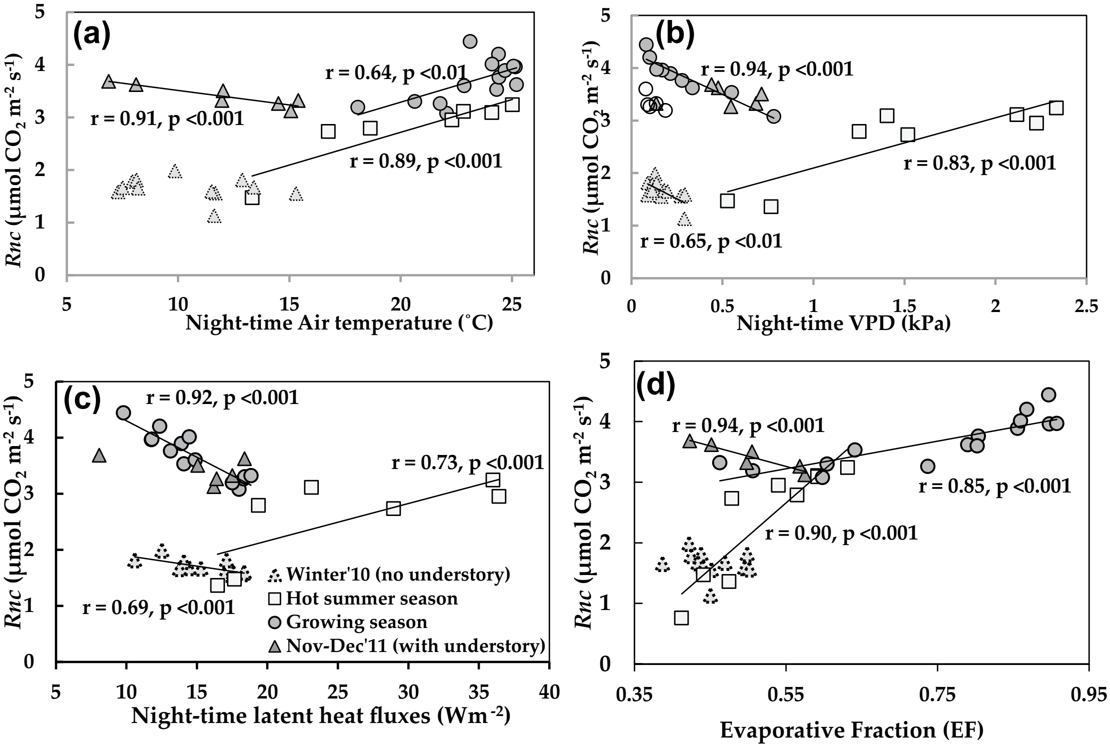

Fig. 2 Relationship between R_{nc} with night-time AT (**a**) and night-time VPD (**b**). Solid circles indicate across peak growing season with understory (June–October), dotted triangle denotes winter 2010 (no understory), solid triangle denotes November–December, 2011 (with understory), and square denotes hot summer season (March–May). In case of night-time VPD (**b**), September–October data were shown separately with open circles. Relationship between R_{nc} with night-time latent heat fluxes (dewfall) and evaporative fraction (EF) were shown in subplot (**c**) and (**d**), respectively

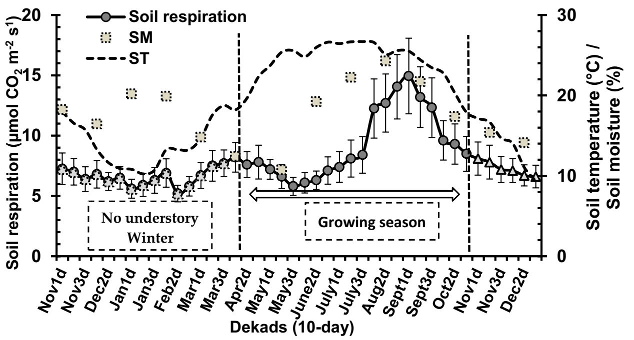

Fig. 3 Variations in night-time soil respiration ($R_s \pm$ SE) in relation to night-time soil temperature (ST) and soil moisture (SM) at 10-day interval over the study period (November 2010–December 2011). Solid circles indicate growing period (April–October), dotted open triangle denotes winter 2010 (no understory), but solid triangle denotes November–December, 2011 (with understory)

was 7.97 ± 2.4 µmol CO_2 m^{-2} s^{-1} (CV: 30%). A smaller peak (7–8 µmol CO_2 m^{-2} s^{-1}) was observed in March–April as the ecosystem entered growing season. The highest peak (12–15 µmol CO_2 m^{-2} s^{-1}) was noted in post-monsoon season, concurrent with the peak in plant respiration (R_{nc}) (Fig. 1). R_s declined with the advancement of summer season (April–May), may be due to decreasing soil moisture. It again gradually increased with the arrival of summer monsoon before declining to a lowest in winter (November–February) (Fig. 3). During winter 2010 and Nov–Dec, 2011, R_s was 6.5 ± 0.70 and 7.25 ± 0.59 µmol CO_2 m^{-2} s^{-1}, respectively. The CVs in these periods were 10.7% and 8.2%, respectively, reflecting the feeble role of photosynthates from understory and overstory on R_s during winter physiological dormancy.

The relationships between R_s and environmental variables were shown in Fig. 4. The results showed that irrespective of the seasons, both soil and air temperatures have a substantial control on R_s rates, wherein r values exceeded 0.81 ($p < 0.001$) (Fig. 4a). In winter season 2010 and in Nov–Dec, 2011, we observed a positive correlation between R_s and temperatures with r-value of 0.71 in 2010 (no understory), while 0.95 in Nov–Dec, 2011 (with understory). In case, if we plot all seasons together (excluding hot summer water-limited period), the relationship between R_s and temperatures (soil and air) becomes stronger, wherein night-time ST (or AT) predominantly explained 85% of the R_s flux variation (Fig. 4b). During hot summer season water-limitation

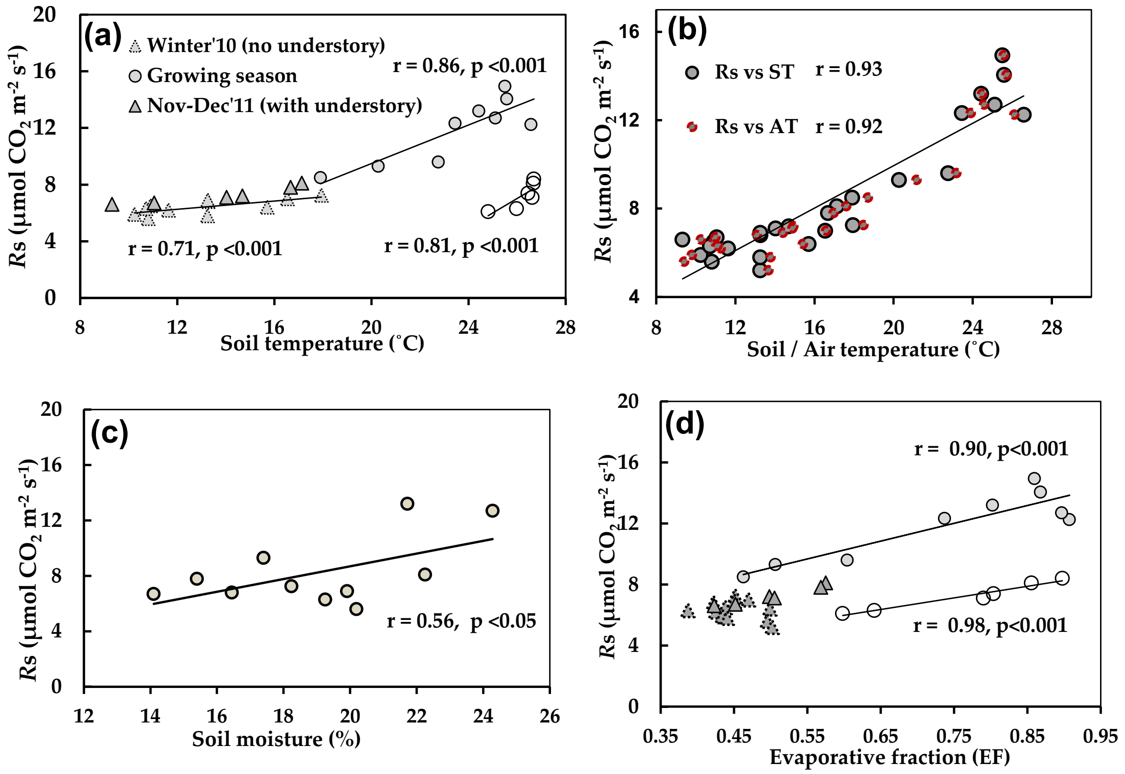

Fig. 4 Variations of R_s in relation to night-time soil temperature (ST) and day-time air temperature (AT) at 10-day interval over the period from November 2010 to December 2011 (**a, b**). Variations of R_s in relation to soil moisture (SM) and EF were plotted in subplots (**c**), (**d**). Open circles indicate growing season (June–July), while solid circles indicate growing season (August–October). In all plots, hot summer season covering the period March–May was excluded

period (April–May), R_s rates declined with increasing temperature. Thereby, we infer that temperature has no control over R_s rates. As mentioned earlier, during this period, soil moisture mostly controlled R_s variability.

In this moisture abundant environment, R_s was moderately correlated with soil moisture ($r = 0.56$, $p < 0.05$) across all seasons except the hot summer (Fig. 4c). It is worth to repeat here that because of the failure of the automatic field moisture sensor, we collected monthly soil moisture samples. Excluding hot summer time water-limitation period, EF alone explained 85% of the flux variability (Fig. 4d). During growing season, over the period of June–July and August–October, r–values were observed as 0.98, and 0.90, respectively, between R_s and EF. In winter season 2010 (no understory), there was no correlation, while in Nov–Dec, 2011, it showed a strong correlation under the presence of understory ($r = 0.98$). We also performed multiple regression analysis between R_s and environmental controlling factors (night-time soil temperature and EF), and the results underlined that these two factors could explain about 89% ($p < 0.001$) of the R_s variability. These results reasonably indicate that the seasonal transitions phases are critically important for the R_s flux.

Seasonal variation of A_c and respiration-photosynthesis ratios

Overstory pine A_c varied between 1.99 and 10.5 µmol CO_2 m^{-2} s^{-1}, while for understory (*Lantana camara*), it was always higher that varied from 3.7 to 17.3 µmol CO_2 m^{-2} s^{-1}. A_c was lowest during the winter season because of physiological dormancy and combined effects of low temperature, LAI, net radiation and PAR. During growing season (April–October) and with an account of understory growth, mean A_c observed as 15.2 ± 5.7 µmol CO_2 m^{-2} s^{-1} with a peak of 25–26 µmol CO_2 m^{-2} s^{-1}. Peak was observed in the post-monsoon (September–October) on account of optimal conditions of environmental variables, such as clear sky, moderate VPD (0.6–0.8 kPa), and high soil moisture availability (20–24%) including understory growth (peak in LAI cycle). In winter 2010 (no understory), mean A_c was 2.39 ± 0.10 µmol CO_2 m^{-2} s^{-1}. Compared to winter season (2010), A_c was observed as 11.33 ± 4.5 µmol CO_2 m^{-2} s^{-1} in Nov–Dec, 2011, which was five-times higher owing to the presence of understory.

The R_{nc}/A_c (an indicator of canopy carbon balance) and R_s/A_c (an indicator of soil carbon balance) were shown for month-wise and season-wise in the Table 2. These results showed that R_{nc}/A_c varied from 0.14 (±0.01) to 0.87 (±0.02) across seasonal phenophases (minimum during post-monsoon and maximum in winter' 10). During the growing season, it varied from 0.14 (±0.01) to 0.35 (±0.05). These results suggest that the higher fraction of R_{nc}/A_c observed during winter' 10 season (no understory), while the lower fraction of R_{nc}/A_c observed during growing season. The higher fraction of R_{nc}/A_c during winter season was because of lower rates of A_c. During Nov–Dec, 2011, the respiration-photosynthesis ratio was largely lower (0.29 ± 0.19) than the winter' 10 season (0.71 ± 0.16), and this may be explained by the presence of understory. In addition, the respiration-photosynthesis ratio was found much higher for overstory than for understory (*Lantana camara*). Thus, it will be interesting to note the substantial effect of understory vegetation on respiration-photosynthesis ratio (Table 2).

During winter and hot summer seasons, the pattern of R_s/A_c (an indicator of soil carbon balance) was similar as compared to the R_{nc}/A_c, wherein we observed higher soil respiration losses (Table 2). The R_s/A_c ratio was observed as 2.69 (±0.43), 1.45 (±1.14), and 0.74 (±0.30) during winter' 10, hot summer' 11, and Nov–Dec, 2011, respectively. As discussed earlier, the higher fraction of R_s/A_c during winter season was attributed to lower rates of A_c owing to physiological dormancy. During winter' 10 and hot summer periods, it can be noted that the R_s rates exceed the A_c that leads to negative C-balance. Nevertheless, the R_s/A_c ratio stabled at 0.64 (±0.29) during peak growing season, which is suggestive of gain in C-balance.

Seasonal relationship between A_c and R_{nc} rates

The relation between R_{nc} and A_c is shown in Fig. 5 and these results depict an inverse and significant relationship across the seasons. The R_{nc} rates were subtle during winter season 2010 (no understory), while significantly higher during Nov–Dec, 2011 (with understory). In Nov–Dec, 2011, R_{nc} and A_c showed a negative significant correlation ($r = 0.83$), which indicates senescence induced higher respiratory CO_2 release. In particular, the understory has a higher influence on R_{nc} than overstory. During the growing season, we observed that R_{nc} and A_c were inversely related ($r = 0.83$). It suggests that during a phase of optimal anabolism (e.g., A_c), catabolism process (e.g. R_{nc}) reduces to a minimum. As a result, the process could help for constructive

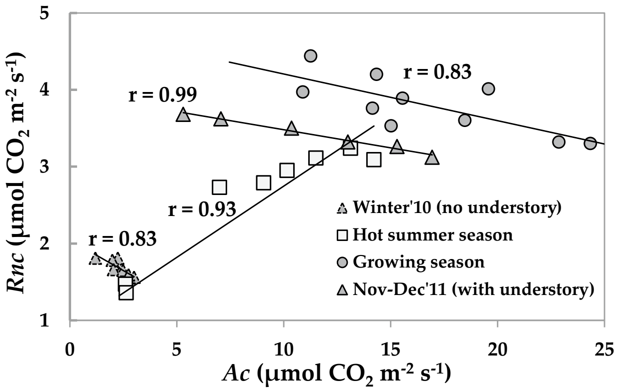

Fig. 5 The relationship between A_c and R_{nc} across the seasons. The coefficients are statistically significant at $p < 0.001$

Table 2 Monthly and seasonal variations of respiration-photosynthesis ratios such as R_{nc}/A_c and R_s/A_c (μmol CO_2 m^{-2} s^{-1}) during November, 2010 to December, 2011

Months	R_{nc}/A_c (mean ± SD), CV (%)		R_s/A_c (mean ± SD), CV (%)	
	Month-wise	Seasonal mean	Month-wise	Seasonal mean
November, 2010	0.68 ± 0.12, 18	**Winter'10 Season** **0.71 ± 0.16, 23**	2.78 ± 0.16, 6	**Winter'10 Season** **2.69 ± 0.43, 16**
December	**0.87 ± 0.02, 3**		**3.12 ± 0.16, 5**	
January, 2011	**0.76 ± 0.08, 11**		2.75 ± 0.19, 7	
February	0.50 ± 0.08, 16		2.13 ± 0.41, 19	
March	0.47 ± 0.12, 26	**Hot Summer Season** 0.35 ± 0.12, 34	**2.92 ± 0.39, 13**	**Hot Summer Season** 1.45 ± 1.14, 78
April	0.33 ± 0.05, 16		0.93 ± 0.22, 23	
May	0.24 ± 0.02, 11		0.51 ± 0.11, 21	
June	0.23 ± 0.02, 10	**Peak Growing Season** 0.25 ± 0.11, 45	0.45 ± 0.05, 11	**Peak Growing Season** 0.64 ± 0.29, 46
July	0.35 ± 0.16, 45		0.72 ± 0.35, 48	
August	0.35 ± 0.05, 15		1.08 ± 0.08, 8	
September	0.17 ± 0.04, 27		0.65 ± 0.16, 25	
October	0.14 ± 0.01, 7		0.38 ± 0.01, 4	
November	0.22 ± 0.03, 16	**Nov–Dec, 2011** 0.29 ± 0.19, 67	0.51 ± 0.04, 7	**Nov–Dec, 2011** 0.74 ± 0.30, 41
December	0.51 ± 0.17, 35		0.96 ± 0.28, 29	
Mean (April–Oct)	0.26 ± 0.10, 39		0.67 ± 0.28, 42	

Bold indicates maximum values

canopy C-balance. However, during the hot summer season (March–May), when the canopy of both overstory and understory started developing, an increase in A_c as well as in R_{nc} was observed ($r = 0.93$).

Discussion

The contribution of night-time plant and soil respiration is potentially immense and worth considering at fine scale to understand the carbon balance dynamics and to improve the global climate-carbon models (Gifford 2003; Atkin et al. 2015; Wehr et al. 2016). There exist a multi-temporal correlations and occasional phase reversal between photosynthesis and soil respiration (Vargas et al. 2011) as the day-time plant respiration is much less than the night-time due to light-inhibition (Sun et al. 2015; Wehr et al. 2016). During night-time, R_{nc} rate is also stable because of the minimum impact of sugar synthesis and transport (Will and Ceulemans 1997). Hence, we examined respiratory fluxes in understudied but dominant vegetation in the mid–altitudinal Himalayan range (500–2000 m) (Forest Survey of India 2011) i.e. the chir pine ecosystem (*Pinus roxburghii*). Measurements were made on night-time canopy respiration (R_{nc}) and soil respiration (R_s) in a homogenously distributed young chir pine plantation (with and without understory).

Our key findings underlined that at daily time-scale over the active growing season, night-time canopy respiration (R_{nc}) and day-time canopy photosynthesis (A_c) are inversely correlated. It suggests that during the phase of optimal anabolism, catabolism reduces to a minimum and environmental conditions which induce a decline in A_c, may concurrently increase R_{nc} and vice-versa. Soil respiration and A_c relations were only sufficiently prominent at seasonal time-scale as evidenced by their de-coupling during hot summer-time water stress. Evaporative fraction-temperature explained maximum variability in fluxes over this energy-limited ecosystem.

The environmental control on the R_{nc} is interesting in this subtropical energy-limited environment with a short distinct phase of hot summer time water-limitation. We found that in growing season, environmental wetness (dew, evaporative fraction) was the strongest statistical driver of R_{nc}. To understand the underlying physiological mechanism, we presented abridgedly the biochemistry of plants (Buchanan et al. 2002). Nocturnal decoupling of leaf water potential with the root water is a common phenomenon in non-water limiting environment (Simonin et al. 2009). This is because of the lowered VPD and absorption of moisture by leaf surface including stomata (Stone 1957; Breshears et al. 2008). Thus, stomata are hypothesized to remain open during the night, however, at a minimal constant level to get the moisture absorbed. Accordingly, if environmental moisture is sufficient, then leaf water potential may reach near saturation. In this water, saturated extracellular condition R_{nc} may increase due to the release of additional CO_2 (in addition to normal TCA/krebs cycle) in the course of formation of pyruvate from malate. Excess extracellular moisture condition and increased HCO_3^- lead to an alternative route of phosphoenolpyruvate oxidation (instead of the normal route of pyruvate formation from phosphoenolpyruvate) (Buchanan et al. 2002). This causes an additional amount of night-time CO_2 efflux in the period of excess moisture availability, and formed the biochemical basis of the observed relation between moisture content and R_{nc} (Fig. 2). This alternative route of phosphoenolpyruvate oxidation becomes the normal way of respiration to replenish the reducing equivalents in the plant mitochondria (Buchanan et al. 2002). It could be concluded that under increased temperature and wetness conditions, subtropical pine forests exhibited an increase in R_{nc} rates. It may be suggestive of an increase in R_{nc} under rising night-time temperature over the Himalaya. This finding is in line with previous observation over evergreen broadleaf tropical forest (Anderegg et al. 2015). So, night-time warming may differentially affect R_{nc} more than photosynthesis (A_c), thereby, reducing C uptake (Peng et al. 2013; Xia et al. 2014).

In the annual cycle, R_{nc} and R_s peaked during post-monsoon concurrent with the peak in productivity. However, on a daily time-scale, our findings indicated a significant inverse relationship between day-time net canopy assimilation and night-time canopy respiration (Fig. 5) except during spring-summer time over and understory canopy development and during winter season (2010) in absence of understory. This inverse relationship could be explained based on mechanistic physiological behavior of optimal anabolism (A_c) and the minimum level of catabolism (R_{nc}) during favorable environmental conditions. Biochemically, Buchanan et al. (2002) had explained that during the phase of optimal anabolism, catabolism (R_{nc}) usually reduces to a minimum. Our findings are also consistent with the temperature manipulation experiment by Turnbull et al. (2002). Sun et al. (2015) found an inverse relation in a conifer species (*Pinus koraiensis*) in north-eastern China. Nevertheless, the relation between the processes of photosynthesis and respiration is a subject of debate, usually linked mechanistically through the impacts that each process has on leaf carbohydrate status (Azcon-Bieto 1992; Goldschmidt and Huber 1992).

Remarkably, hot summer time water stress had an effect on photosynthesis and respiration relationship as it was significantly inverse when both over and understory canopy was still developing. During spring and hot summer seasons, when the canopy of both overstory and understory was developing, we observed an increase in A_c as well as in R_{nc}. This positive relation may be explained by heterotrophy and anaplerotic uptake of CO_2 (dark CO_2 fixation). Heterotrophy is a period in the life cycle of plants when autotrophic inputs are suspended and carbon substrate requirement is met through the remobilization of stored carbohydrate reserves. This state even occurs on a diurnal time-scale and on seasonal time-scale during the spring time bud/leaf burst in plants (Bathellier et al. 2007). During periods of active growth (canopy development), an additional inorganic carbon supply is essential in the tricarboxylic acid cycle (TCA or Krebs cycle) to generate carbon intermediates required for amino acid synthesis. Additional carbon can be sourced either through the scavenging of intracellular respired CO_2 or through the uptake of CO_2 from surrounding atmosphere (or soil air-pores in the case of plant roots). Further, it may be noted that the developing leaves have a higher rate of catabolism (R_{nc}) than mature leaves (Buchanan et al. 2002), therefore, a positive correlation was obtained when photosynthesis and respiration both were increasing with canopy growth initialization. Besides, higher LAI and A_c in understory than overstory may have contributed towards significant positive correlation during the recovery phase in these months. During winter 2010, R_{nc} and A_c showed no clear relation because overstory pine was undergoing physiological dormancy and understory was absent.

Our study found that the presence of understory vegetation tended to reduce respiration-photosynthesis ratio. The understory *Lantana camara* (an invasive shrub species) contributed significantly to the system C balance, as evident by its higher rate of A_c as well as R_{nc} (Table 1; Fig. 2). During growing season, R_{nc} consumed ~ 23% of the net canopy assimilation that increased to 30% during Nov–Dec, 2011 when understory was present but senescing, while, in the same time-period in winter 2010, in the absence of understory, R_{nc} represented ~ 70% of the A_c. Thus, given that pine (overstory) phenology behaved similarly in both the years, the contribution of understory component in C balance in a forest ecosystem is evident.

The ratio R_{nc}/A_c can be used to evaluate canopy C balance in response to variations of environmental factor. Photosynthesis–respiration relation is largely driven by environmental factors than inter–specific genetic variation (Lewis et al. 2011). Canopy respiration usually consumes about half of the fixed carbon, and the remainder supports plant growth (Amthor and Baldocchi 2001). The mean value of 0.28 during the growing season is suggestive of lower respiratory carbon losses from this coniferous ecosystem. The mean varied from 0.12 to 0.52 across the growing season. These results were consistent with the previous studies that reported in the range of 0.1 to 0.3 for different species including herbs, shrubs and trees in the subtropical ecosystems in southeast China (Chu et al. 2011). Ryan et al. (1994) reported that the R_{nc}/A_c ratio varies from 0.32 to 0.64 in pine trees, but from a Himalayan region (pine) we observed it at about 0.44. In line to this, prior studies have evaluated R_{nc}/A_c ratio along with temperature increase and underlined that the ratio increased in response to temperature as well as drought (Zaragoza-Castells et al. 2008; Catoni and Gratani 2014; Reich et al. 2016). Accordingly, our findings were also consistent with those previous studies. Further, based on night-time temperature manipulation experiment, Turnbull et al. (2002) discussed that R_{nc} rate could increase substantially with higher temperature and thereby, the increment in respiration-photosynthesis ratio. These responses indicate that an increase in night-time temperatures under climate warming may have a significant influence on net plant C uptake.

Additionally, we have analyzed R_{nc}/A_c ratio with respect to night-time AT (Fig. 6) and these results indicated that with increasing night-time AT, the respiration-photosynthesis (R_{nc}/A_c) ratio increased especially during growing season and with understory even during Nov–Dec, 2011. Their relationships were significantly positive, which is indicative of the gain of canopy C balance with increasing temperatures. Our results were consistent with previous studies that have reported about the temperature sensitivity on respiration-photosynthesis ratio (R_{nc}/A_c), which discussed the possible adverse impacts on canopy C balance, owing to temperature change (Atkin et al. 2006; Chi et al. 2013).

Soil respiration (R_s) was bimodal in the annual cycle. First, a smaller peak was observed when the ecosystem left winter, entered summer and a secondary (highest) peak was observed in the post-monsoon at the peak of the growing season. The peak in R_s matched with the concurrent optimal mix of the summer monsoon environmental conditions (warm-moist) and soil metabolic activities. We observed a tight link between plant productivity and soil respiration, which was most in the post-monsoon (Yuan et al. 2011). Interestingly, we noted a complete reversal in R_s and A_c relation (Fig. 1b, Fig. S4), when winter-time temperature-limited

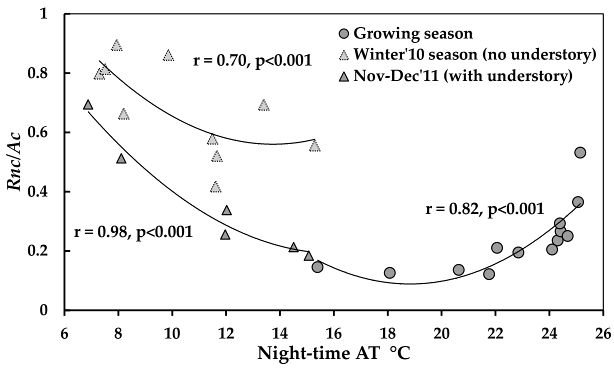

Fig. 6 The relationship between R_{nc}/A_c and Night-time AT across the seasons were plotted using the 2nd order polynomial. Solid circles indicate growing season data. Dotted triangle denotes winter 2010 (no understory), whereas solid triangle denotes November–December, 2011 (with understory)

conditions changed to water-limitation period during hot summer seasons. This behaviour was probably due to the reduction in photosynthate availability (as over and understory canopy was still developing) as well as moisture stress-induced reduction in soil metabolism. Anaplerotic uptake of CO_2 could be another reason (Dark CO_2 fixation: when additional inorganic carbon is essential for amino acid synthesis during plant development, it is either sourced through the scavenging of respired CO_2 or through the uptake of CO_2 from surrounding atmosphere or through the soil air-pores in the case of plant roots). It is reasonable to conclude that during hot summer season, R_s decouples from photosynthetic carbon input and it reduces due to the combined effect of photosynthate availability and water deficit, while over rest of the growing season, R^2 was greater than 0.65 (0.8 in post-monsoon, $p < 0.001$). Understory also played a role in determining the strength of R_s–A_c relation, even during winters. As it was weakest ($R^2 = 0.12$, $p = 0.22$) when no understory was present (winter 2010) and stronger ($R^2 = 0.94$, $p < 0.001$) during Nov–Dec, 2011 with understory (Fig. 1b, Fig. S4). R_s fluxes especially during the summer monsoon season were higher because of the presence of large populations of earthworms, termites, and associated fungi at the site (Bradford et al. 2014) in comparison to other studies from the region (Rout and Gupta 1989). Based on EC technique, Verlinden et al. (2013) suggested that R_s could consume about 46% of A_c of poplar (Populus) trees. Over European forests, Janssens et al. (2001) reported that the mean annual R_s could consume about 55% of A_c. In comparisons to the above estimates, our findings indicate that R_s could consume ~ 67% (range 38–108%) of the A_c in pine trees during the growing season with understory. Multiple regression analysis of R_s and abiotic factors (soil/air temperature, soil moisture, and EF) indicated that the temperatures and EF have a larger control on R_s flux during peak growing season (Wangdi et al. 2017), while soil moisture has a limited control. But, soil moisture has a larger role during hot summer water-limited period. Thus, seasonal transition phases of R_s fluxes in this region were critically associated with soil/air temperature, soil moisture, and EF.

It is also pertinent to mention here the possible source of uncertainty in the measurements and methods. Diffusion-leak may become a significant source of error in the chamber-based methodology. We carefully considered it every time while operating the photosynthesis system and ensured it by ‘valve matching’, as it was routinely performed every 30 min to maintain prevailing ambient conditions and to correct any analyzer offsets. Hourly R_{nc} measurements of over and understory comprised of 360–450 measurements made from a portable photosynthesis system (LI–6400 XT). These probably tended to reduce random measurement error (coefficient of variation). Lack of spatial representativeness is the most important source of systematic error in soil respiration (R_s) measurements. To have sufficient spatial representativeness of both root- and non-root-zone with a single measurement system, these zones were hourly and alternatively sampled in different random quadrats. We were also carried out, another static chamber (25 cm × 25 cm) IRGA-based parallel and periodic soil respiration measurement. Despite all these precautions in systematic chamber-based measurements, the systematic error of ~ 15 to 20% associated with chamber-based methodology (Luo and Zhou 2010) has not been excluded in this study. A systematic source of uncertainty in this study was that we were not able to measure the respiration from woody tissue such as branches and stems. The shrub understory has little woody tissues; however, the woody tissue respiration from chir pines (overstory) must be significant. Several authors (Law et al. 2001; Wang et al. 2004; Acosta et al. 2007), indicated that it can vary between 1 and 15% depending on the age. We, therefore, assumed it as 5% of total ecosystem respiration ($R_{nc} + R_s$) (because of young age: 8.5 year).

Conclusion

We addressed two major carbon balance indicators, namely, night-time canopy respiration (R_{nc}) and soil respiration (R_s) of the deciduous coniferous (chir pine) forest in response to environmental factors. This unique and comprehensive study has employed a combination of systematic ecophysiological measurements and gradients of micrometeorological data within and above the canopy system. It was possible to characterize respiratory carbon fluxes at temporal scales of hours, days and one complete annual phenological cycle from a relatively understudied region of the world. Observations could certainly lend useful insight into carbon balance and ecological functions in the region. Our key findings suggest that at daily time-scale over the active growing seasons, night-time canopy respiration and day-time canopy photosynthesis are inversely correlated. Soil respiration and productivity (A_c) relations are dynamic and maximum coupling was observed during post-monsoon, whereas complete reversal (de-coupling) during hot summer-time water stress. Evaporative fraction-temperature explained maximum variability in fluxes over this energy-limited ecosystem. Furthermore, we found that the R_{nc}/A_c ratio has increased with an increase in night-time temperature that indicative of temperature sensitivity on respiration-photosynthesis ratio. These responses indicated that increase in temperature under climate warming may have a significant influence on net plant C uptake. Alterations in environmental variables at seasonal time-scale to inter-season transition periods may have a significant effect on the C-balance in the region.

Presence of understory (*Lantana*) vegetation largely influenced both R_{nc} and A_c, whereas, it can minimize the respiration-photosynthesis ratio. Thus, the reduced ratio helps in accumulation of C in pine forest across subtropical Himalaya region. Removal of understory is a prevalent forest management practice in the Himalaya, and we propose that this may not be a viable tool for a forest carbon balance point of view. On the contrary, *Lantana* also commonly identified as the worst weed worldwide, which could pose serious problems in the plantation forestry. It can obstruct the growth of prime vegetation and may become dominant species causing a threat to the native flora.

Time-series of data are needed to assess the degree of inter-annual variability in response to environmental conditions. Improved understanding of short and long-term behaviour of C-exchange and regulations in relation to environmental conditions will provide a basis for improving models and exploring the effects of climate change on C-cycling. Nonetheless, these findings may be useful in understanding components of C balance indicators and further parameterizing and validating C-cycle models.

Author contribution statement NS conceived and designed the experiments; NS and BRP analyzed the results and wrote the article.

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Compliance with ethical standards

Conflict of interest Authors declare no conflict of interest.

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