Carbon exchange in some invasive species in the Himalayan foothills

NILENDU SINGH^{1*#}, N. R. PATEL², JOYEETA SINGH¹, P. RAJA³, P. SONI¹ & J. S. PARIHAR⁴

¹Forest Research Institute, Dehradun 248 006, India ²Indian Institute of Remote Sensing, Dehradun 248 001, India ³ICAR-Central Arid Zone Research Institute, Jodhpur 342003, India ⁴Space Applications Centre, ISRO, Ahmadabad 380 015, India

Abstract: This study focuses on analyzing the behavior and seasonality in the canopy carbon exchange of a subtropical ecosystem at the Himalayan foothills and comprises three important invasive species: Lantana camara, Ageratum conyzoides and Bidens biternata. Systematic sampling on the daily CO₂ exchange process and biophysical parameters formed the basis of this investigation. The analyses based on year-round in-situ measurements showed that mean daily net canopy carbon exchange (net primary productivity) of the system (all species in totality) was 11.8 g C m⁻² day⁻¹ (41.5 t C ha⁻¹yr⁻¹). All species had almost equal contribution to the system NPP and they were in order of A. conyzoides (14.6 t C ha 'lyr'), B. biternata (13.8 t C ha-1yr-1) and L. camara (13.1 t C ha-1yr-1). Light use efficiency (LUE) exhibited a bimodal trend with peaks in early (Jun - Jul) and post-monsoon (Oct - Nov) season. Mean LUE of L. camara was 20.8 ± 10.9 mmol CO₂ mol⁻¹ PAR, while that of A. conyzoides and B. biternata were $24.7 \pm$ 9.9 and 22.8 ± 10.4 mmol CO₂ mol⁻¹ PAR, respectively. Maximum net canopy assmilation (Cnar) was observed in the post-monsoon period and minimum in the winter (Dec). 15 - 50 % of the Cnar was lost as night-time plant respiration across an annual growth cycle with maximum during winter and minimum in the post-monsoon season. These species together absorbed comparably equal or even more carbon than that of mature forests. However, the carbonretaining capacity of these species is limited due to the short growth cycle.

Key words: Ecophysiology, invasive species, *Lantana camara*, net canopy carbon exchange, photosynthesis, respiration, subtropics.

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Introduction

Many carbon exchange and productivity studies have been carried out over the major forest ecosystems involving eddy covariance system, ground biomass inventory and ecosystem modeling techniques (Baldocchi 2003; Chanda et al. 2013; Kaul et al. 2009; Malhi et al. 1999; Nayak et al. 2010; Piao et al. 2009; Sahu et al. 2015).

However, little attention has been paid to the invasive understory species within these ecosystems.

Large scale and rapid expansion of invasive species as well as their critical importance in the alteration of carbon budget of the native ecosystem accentuates the need of more accurate accounting of net ecosystem CO_2 exchange (NEE) by the individual invaded species and their contribution

^{*}Corresponding Author; e-mail: nilendu_singh@yahoo.com

[#]Present Address: Centre for Glaciology, Wadia Institute of Himalayan Geology, 33-GMS Road, Dehradun 248 001, Uttarakhand.

to the whole system (Chanda et al. 2013; Peltzer et al. 2010). Leaf-level gas exchange measurements employing IRGA chambers (infrared gas analyzers) are perhaps the best alternative to the eddy covariance towers in small, invaded patches due to the lack of minimum footprint area. Leaf-scale measurements of carbon assimilation provide ample scope for deriving canopy photosynthesis by integrating the hourly carbon assimilation measured by an IRGA chamber, and scaling by leaf area.

Lantana camara (Verbenaceae) (L. camara from here on) is one of the most widespread invasive plant species in Southeast Asia. It has colonized the forests in the subtropical Himalayan foothills of India, particularly the Dudhwa, Corbett and Rajaji National Parks (Kimothi et al. 2010). In the last decade, it had extended up even higher in the outer Himalayan ranges (up to 1700 m) (Bhatt et al. 1994; Joshi 2002). It has also invaded the fallow lands (Sharma & Raghubanshi 2006) and forest ecosystems of the peninsular, northeast India and western ghats (Murali & Setty 2001). According to a forest survey (Rawat & Bhainsora 1999), the average density of L. camara bushes found in different parts of Himalayas were 18.0 per 100 m² in Dehradun valley followed by Shiwaliks (9.2 per 100 m²) and the outer Himalayas (7.0 per 100 m²).

Across India, monsoon is a major climatic factor that alters the moisture and warmth of different climatic regions and consequently influences adaptability of these species (Zobel & Singh 1997). Thus, it would be interesting to study the gas exchange processes in *L. camara* and other invasive species from diurnal to seasonal scale. Additionally, functional traits such as higher foliar nitrogen content, litter decomposition rates, light and water use efficiencies are keys to evolving *L. camara* for enhanced carbon sequestration and drought tolerance (Peltzer *et al.* 2010; Sharma *et al.* 2005).

The lack of research on the ecophysiological traits of invasive species, their seasonal and annual productivity, warrants research that could address the full spectrum of functional traits. Moreover, a complete study on diurnal and seasonal variability in photosynthetic and respiratory processes of *L. camara* and other similar invasive alien species is also essential for drawing meaningful conclusions on the about carbon storage in the ecosystem. Here, we determined how light use efficiency (LUE), plant productivity and leaf area index (LAI) varied on

the seasonal time scale, and what are the critical biophysical and environmental controls of canopy photosynthesis, respiration and net canopy carbon exchange.

Materials and methods

Study site

The observational site (7.0 ha) comprised a stand dominated by Lantana camara located within the campus of Forest Research Institute, Dehradun, India (30° 20' 04" N, 78° 00' 01" E; 640 m). The experimental site also included two more invasive alien species: Ageratum conyzoides and Bidens biternata. The percent area occupied by the species was found to be in the order: L. camara (~75 %) followed by A. conyzoides (~15 %) and B. biternata (~10 %). The land management practice such as clearing of vegetation was carried out during October - November 2010. The vegetation reappeared again in the spring season (March-April 2011). L. camara was present in the system from April to December 2011, until its canopy discolored and dried out in winter. The other two herb species (A. conyzoides and B. biternata) had a short life cycle with emergence in June and dried out in winter due to frosts and lower temperature. During the study period (2011), for the experimental purpose no clearing of vegetation was carried out.

The characteristic climate of the site is subtropical. The mean monthly air temperature varies between 11.5 °C (January) and 27 °C (June). The mean monthly relative humidity ranges from 52 % (April) to 85 % (August). The mean annual rainfall is ~2020 mm and July to September is the monsoon season. Maximum rainfall occurs in August (~570 mm) and minimum in November (~4.0 mm). Sunshine hours vary from 4.4 h day-1 to 9.3 h day-1 with minimum observed during July-August and maximum during May. The mean monthly open pan evaporation varies from 1.2 mm to 7.2 mm with the lowest during December and the highest during May.

The soil is deeply weathered Mollisols (3 - 8 m thick), which is nutrient rich with a porosity range of 40 - 60 % and having pH in the acidic range (4.5 to 6.0). The texture is sandy clay loam with 35 % sand, 40 % clay and 25 % silt. The bulk density is \sim 1.03 g cm⁻³. The moisture content ranges from 10 % in peak summer days to above 24 % during rainy season (mean of 3 depth level: 5, 20 and 45 cm).

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In-situ measurements

Systematic sampling was conducted measuring leaf-level gas measurements such as photosynthesis and respiration together with leaf area index and photosynthetically active radiation. We established thirteen $(5 \times 5 \text{ m})$ randomly selected permanent quadrats for L. camara, four (1 \times 1 m) for A. conyzoides and three (1 \times 1 m) for B. biternata. The leaf area index (LAI) of each species was measured at 10 - day interval (dekadal) from the growth initiation phase of *L. camara* in April. The LAI measurements for A. conyzoides and B. biternata began in June on 10 - day interval basis and lasted up to the senescence phase of each species. The LAI measurements were performed using plant canopy analyzer (LAI - 2000; Li-Cor, Inc., Lincoln, NE). In each of the quadrat, the mean LAI was obtained by taking average of eight readings (two above and six below canopy) in different directions. The mean LAI of quadrats belonging to each species derived to represent temporal dynamics of LAI (Unger et al. 2013).

The photosynthetically active radiation (PAR) was measured coincident to the LAI measurements. Photosynthetic photon flux density (Q_p) was measured above and below the canopy (at six locations randomly within each quadrat) using a point (LI-190SB; LI-Cor, Lincoln, NE) and a line quantum sensor (LI-191SB; Li-Cor, Lincoln, NE) respectively. Intercepted photosynthetic photon flux density (PAR_{abs}) for each specific vegetation was evaluated as the difference between above and below canopy Q_p (Unger *et al.* 2013). The difference between intercepted and absorbed PAR is usually small for LAI < 1.0. Therefore, the PAR_{abs} (mol m⁻² s-1) in the study period was estimated as per Lagergren et al. (2005):

$$PAR_{abs} = Q_p(1 - exp^{-\kappa \times LAI}) \tag{1}$$

 $PAR_{abs} = Q_p(1 - exp^{-k \times LAI})$ (1) where, k is the vegetation extinction coefficient, which was averaged as 0.75 in this study. The k was estimated from LAI and PAR measurements above and below the canopy as per Lagergren et al. (2005), (eqn: 2), at 10-day interval as mean of the quadrats.

$$k = \ln \frac{Q_p}{PAR_{abs}} / (-LAI) \tag{2}$$

Light use efficiency, LUE (mmol CO₂ mol⁻¹ PAR)=
$$\frac{c_{nar}}{PAR_{abs}}$$
 (3)

where, Cnar represents the daytime net canopy assimilation rate and its computation has been discussed in the next section (eqn: 4).

Photosynthesis and respiration (gas exchange) rates were recorded continuously for 24 - hours, at

10 - day interval during the growth cycle (10th April 2011 to 20th December 2011). On each day of measurement, daytime (0600 to 1800 hrs LMT) net photosynthesis and night-time (1830 to 0530 hrs LMT) respiration was measured. On hourly time scale, sampling of a species consisted of 360 to 480 readings made from portable photosynthesis system (LI-Cor, Lincoln, NE, model LI-6400 XT) distributed across three plants in three random quadrats. The hourly sampling scheme consisted of three random quadrats with one plant in each quadrat. Each plant has been divided into three vertical layers (top - middle - bottom). About 40 -50 readings were made within 1.5 to 2.0 minutes for each layer (3 - 5 leaves). Thus, each plant in a quadrat was sampled for about six minutes consisted of 120 to 150 readings. Readings from each layer were stored separately in the photosynthesis system for further data processing and upscaling. Thus, three different quadrats were sampled at each hour for each species at fifteenminute interval and averaged for that hour.

Computation of net primary productivity

Photosynthesis data averaged over daytime hours by LI-6400 XT portable photosynthesis system represents daytime canopy net assimilation (Cnar), which is (GPP) minus daytime plant respiration (Rd_{day}).

$$Cnar = GPP - Rd_{day} (4)$$

Net primary productivity (NPP) of the vegetation was thus computed by subtracting night plant (canopy) respiration (NPR) from daytime canopy net assimilation (Cnar) as:

$$NPP = Cnar - NPR \tag{5}$$

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

Cnar =
$$L_{nar}^{sunlit} \times LAI_s + L_{nar}^{shaded} \times LAI_{sh}$$
 (6)
Sunlit leaf area index in the vegetation canopy

(LAIs, in m² leaf m⁻² ground) is,

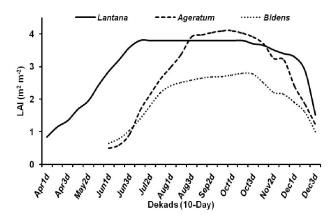


Fig. 1. LAI dynamics of the three invasive species during their life cycle at 10-day interval.

$$LAI_{s} = I'_{A}/K \tag{7}$$
where $K = Cos(\Omega) \Omega = loof$ and a (moon tilt

where, K = Cos (θ) , θ = leaf angle (mean tilt angle), $I_A' = 1 - \exp(-k \times LAI)$, k was computed from LAI and PAR measurements above and below the canopy following Lagergren $et\ al.\ (2005)$.

The shaded LAI (LAI_{sh}) was calculated as: $LAI_{sh} = LAI - LAI_s$ (8)

Results

LAI dynamics

Systematic canopy measurements carried out during the growth cycle of species has enabled the understanding of temporal and seasonal dynamics of the LAI (Fig. 1). Results show that the LAI followed a plateau-shaped seasonal pattern in the L. camara while unimodal in the A. conyzoides and B. biternata. LAI ranged from 0.85 to 3.8 in L. camara and the peak LAI (3.8) reached before the onset of monsoon and remained static for at least five months (July to November). The LAI during growth cycle of A. conyzoides had a wide range (0.5 - 4.1) but peak LAI persisted over short period for both A. conyzoides and B. biternata as compared to that of L. camara. These variations reflected in higher values of seasonal mean LAI: L. camara (3.06), A. conyzoides (2.78) and B. biternata (2.05). Declining trend in LAI and thereby PAR absorbance by the canopy was observed after setting of dormant winter season when leaves gradually (Fig. 1). In brief, foliage development in L. camara almost reached plateau just before the beginning of monsoon and LAI remained high until November. In small patches that A. conyzoides formed, LAI was higher than other two species but was stable for only two months from

August end to October end. The duration when LAI of *B. biternata* was stable at high level was intermediate but its peak LAI was the lowest (Fig. 1).

Seasonality in photosynthesis and respiration

The distinct variations in leaf-scale gas exchange at different phenophases resulted in seasonal variation in the up-scaled canopy assimilation and plant respiration. During the initial phase of leaf emergence in L. camara, net canopy assimilation (Cnar) and night-time plant respiration (NPR) were low i.e. 3.7 and (-) 1.9 µmol CO₂ m⁻² s⁻¹ respectively. The resultant rate of net carbon accumulation (NPP) amounts to 1.78 µmol CO₂ m⁻²s⁻¹ (Fig. 2a & Fig. 3). As the growing season advanced, the net carbon accumulation increased rapidly following the growth of canopy. Magnitude of Cnar during summer ranged between 6.15 and 7.5 µmol CO₂ m⁻² s⁻¹. Stomatal regulation of carbon/ water vapour exchange in these species might be dominating factor when environmental constraints like low soil moisture and high vapour pressure deficit prevailed in summer. Even though the LAI of species were sufficiently high, the reduced availability of solar radiation due to cloudiness in monsoon season caused a decline in the rate of carbon assimilation and finally productivity of all three species (Fig. 3). Persistence of heavy clouds could bring down the productivity level (Zhang et al. 2009). This behavior strongly suggested that radiation regime is the major environmental control on productivity in subtropics and especially during monsoon. However, these potential invasive species improved their exchange rates quite quickly with the improvement of atmospheric conditions. Adverse effect of low light intensity on the productivity was less pronounced in L. camara than the other two herb species (for example on Jul 3d, Fig. 3). After a dip in the Cnar during early part of monsoon, it increased rapidly in the later part and remained high until October in all the observed species. It is thus summarized that warm-moist environment and the favorable biophysical conditions comprising factor such as soil moisture availability, intensity of radiation and full canopy development have helped the invasive alien species to maintain high net photosynthesis. Productivity was highest during the post-monsoon season. From mid-November onwards, productivity showed a decreasing trend and was reduced to a minimum level by the middle of December (Fig. 2a & Fig. 3). By the last 10 days (third dekad) of December, the canopy had dried out and conseSINGH et al. 267

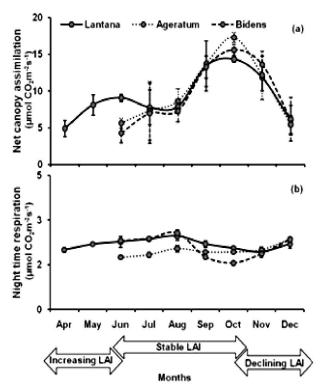


Fig. 2. Mean monthly (a) net canopy assimilation rate, (b) night-time respiration during various phenophases of the species (bar represents SD).

quently the net canopy carbon exchange became almost zero.

The respiratory carbon loss of the plants was relatively stable (1.5 - 2.5 µmol CO₂ m⁻² s⁻¹) across the seasons and phenophase (Fig. 2b). However, some variations were observed in the interseasonal NPR. Respiratory carbon loss of L. camara varied between 1.87 and 2.6 µmol CO2 m⁻² s⁻¹. Initially (i.e. leaf emergence phase) NPR varied between 1.95 and 2.1 µmol CO₂ m⁻² s⁻¹. Respiratory loss increased during summer (2.2 - $2.4 \mu mol CO_2 m^{-2} s^{-1}$) and in rainy season (2.4 - 2.6μmol CO₂ m⁻² s⁻¹). Improved atmospheric conditions in the post-monsoon resulted in increased anabolic rate and reduction in respiratory losses (1.87 - 2.09 μmol CO₂ m⁻² s⁻¹). As canopy senescence advanced during winter, the respiration rate again increased to ~2.3 µmol CO₂ m⁻² s⁻¹. The two herbs exhibited similar behavior as that of L. camara. During the increasing LAI phase, NPR of the species varied within a range of 27 to 53 % of Cnar (B. biternata > L. camara > A. conyzoides) and this ratio decreased in the stable LAI phase, with range of 15 to 20 % (L. camara > B. biternata > A. conyzoides). Night respiration to daytime net assimilation ratio again increased during senescing phase and varied

between 29 and 38 % ($B.\ biternata > A.\ conyzoides > L.\ camara$) (Chu et al. 2011).

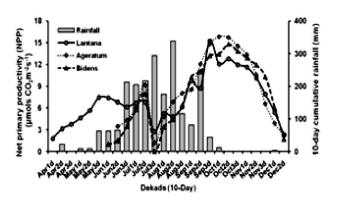


Fig. 3. Net primary productivity of the three species at 10-day interval.

The net primary productivity

Considering individual species responses to environmental conditions, NPP of L. camara in April was 45 (± 5.2) g C m⁻² that later increased to 106 (± 3.2) g C m⁻² in June with full canopy development (Fig. 4). The NPP declined in the monsoon and attained a stable value (85 \pm 11 g C m⁻²). Productivity was maintained above 150 g C m⁻² in the flowering and fruiting phase for next three months (Sep, Oct, Nov) with maximum in October (197 ± 2.8 g C m⁻²). The NPP declined drastically during winter as plant entered physiological dormancy. Mean annual productivity of L. camara was 110 (± 55) g C m⁻² (13.1 t C ha⁻¹ yr⁻¹) and was several fold higher than A. conyzoides and B. biternata (14.6 and 13.8 t C ha-1 yr⁻¹ respectively) on area basis.

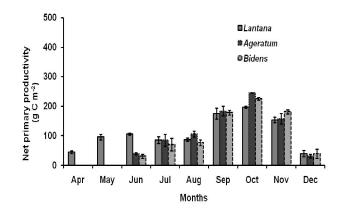


Fig. 4. Monthly primary productivity of the species (bar represents SD).

Light use efficiency (LUE)

The mean LUE obtained were 20.8, 24.7 and 22.8 mmol CO₂ mol⁻¹ PAR for L. camara, A. conyzoides and B. biternata respectively (Fig. 5). Irrespective of growth stages, the LUE was highest in A. conyzoides followed by B. biternata and L. camara. The L. camara attained its highest LUE during early monsoon, while it was during later part for the other two herb species (Fig. 5). It declined as winter approached. Overall, LUE was highly variable ranging from 4.5 to 40.0 mmol CO₂ mol-1 PAR. It remained lowest when the canopy was developing. During growing period, mean LUE of the whole system was 25.0 mmol CO₂ mol⁻¹ PAR with occasional peaks up to 35 - 40 mmol CO₂ mol⁻¹ PAR during cloudy days. These peaks were attributed to the efficient utilization of diffuse fraction of radiation by the canopy. LUE of these species were even comparable to those of natural forests (Lagergren et al. 2005).

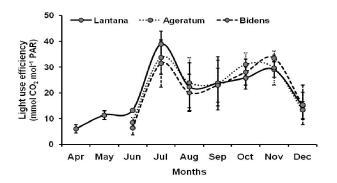


Fig. 5. LUE of the species in different seasons of their life cycle (bar represents SD).

Discussion

LAI cycle of annual herb species (unimodal) differed from that of the perennial shrubs (plateau shaped), which suggests different growth and resource capture-allocation strategies. The species also differed in their responses to the monsoon. The canopy of *L. camara* developed before the onset of monsoon, while in the other two species foliage development and LAI continued to increase over several weeks after the beginning of monsoon. Higher magnitude of LAI in herbs persisted in post-monsoon period only for 30 - 40 days. *L. camara* maintained its peak LAI at least for ~5 months. Ecophysiological attributes among these invasive species appeared to vary over time and thus make an ecosystem efficient in resource

capture. LUE's of these light-loving invaders are comparable and even higher among crops and natural vegetations (Lagergren et al. 2005; Sinclair et al. 1992; Unger et al. 2013). In the present study, A. conyzoides had the highest mean LUE, followed by B. biternata and L. camara (Fig. 5), even though more than 75 % of the area was covered by L. camara. This reflects L. camara is more efficient in PAR utilization, and probable allelopathic effects (Bais et al. 2003). All the three species attained peak LUE in the range of 35 - 40 mmol CO₂ mol⁻¹ PAR during cloudy period, which indicates the role of diffuse radiation in canopy PAR utilization (Sinclair et al. 1992). Bimodal distribution was also noticed in the diurnal behavior of LUE with the lowest and stable value in the noon hours (1130 and 1430 hrs LMT) and higher values towards early morning and late afternoon hours except on heavy cloudy days.

Temporal behaviour of the net canopy assimilation (Cnar) showed strong dependence on the phenology and environmental variables namely temperature, vapour pressure deficit (VPD), intensity, and quality of light. It may be interesting to note that species responded quickly to the environmental conditions because of their physiological plasticity (Carrion-Tacuri et al. 2011). In general, light and temperature are the rate-determining factors for the subtropical ecosystems and seasonal variations influences the fluxes of carbon, energy and water vapour (Singh et al. 2012).

Results on the net carbon exchange or net primary productivity (NPP) also emphasize the possibility of differentiating phenotypic plasticity of herbs and shrubs. We found that during heavy clouds and rainy day, NPP of herbs came down to near zero (temporary decline in productivity). However, L. camara maintained critical level of metabolism during same time-period (Fig. 3). Herbs managed to increase their productivity even in low radiation phase of monsoon months, but the productivity of L. camara remained constant at the same time (Fig. 4). Invasive species under investigation had NPP comparable to the natural forest during their growth cycle (Bhatt et al. 1994; Kumar et al. 2012; Singh & Singh 1992). However, their carbon retaining capacity is less, as the turnover rate of carbon in these systems is much higher than that of forests (Ehrenfeld 2003). These species invest more in above ground biomass and it have higher decomposition rates and consequently higher ecosystem respiration (Ehrenfeld 2003). Bhatt et al. (1994) reported that L. camara grows

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well even in the nutrient poor soils and its net primary productivity is comparable to that of forests. Here, we found the mean NPP of *L. camara* at 13.1 t C ha⁻¹ yr⁻¹, which is comparable to that noted by Singh & Singh (1992). Mean NPP of *A. conyzoides* was at 14.6 t C ha⁻¹ yr⁻¹ and that of *B. biternata* at 13.8 t C ha⁻¹ yr⁻¹. Net canopy carbon exchange or NPP of the system stands on mass basis at 11.73 g C m⁻² day⁻¹. Out of this, contribution of *L. camara* is 31 % (3.67 g C m⁻² day⁻¹) and that of *A. conyzoides* and *B. biternata* is 36 % (4.17 g C m⁻² day⁻¹) and 33 % (3.88 g C m⁻² day⁻¹) respectively. However, on area basis contribution of herbs were rather insignificant.

Assuming ecosystem respiration in this subtropical environment at maximum 75 % of NPP (Yu et al. 2005), the, net ecosystem exchange or net ecosystem productivity (NEE/NEP) stands at 2.93 g C m⁻² day⁻¹. Contribution of *L. camara* will be 0.91 g C m⁻² day⁻¹. 1.04 g C m⁻² day⁻¹ for *A. conyzoides* and 0.97 g C m⁻² day⁻¹ for *B. biternata*. This figure is comparable and even more than other ecosystems and biomes of the world that were measured by eddy-covariance system on annual-time scales (Canadell 2000; Yu et al. 2014).

Conclusions

A study was conducted to measure and analyze the seasonality in the canopy carbon exchange in a subtropical ecosystem at the Himalayan foothills comprising three important invasive species: Lantana camara, Ageratum conyzoides and Bidens biternata. Systematic sampling on the daily CO₂ exchange process and biophysical parameters formed the basis of the investigation. The study could be summarized as following. Among environmental controls, the seasonal variation in PAR was the most important rate-determining factor and transition periods between seasons were the critical period for the carbon balances and fluxes. Maximum net canopy assimilation of different species occurred in a phase shift manner. L. camara and other two invasive species attained peak net carbon assimilation during post monsoon period rather than monsoon season. Net canopy carbon exchange of the system stands at 11.73 g C m⁻² day⁻¹ on mass basis. Out of this, contribution of L. camara was 3.7 g C m⁻² day⁻¹(13.1 t C ha⁻¹ yr⁻¹) and that of A. conyzoides and B. biternata was 4.17 (14.6 t C ha-1 yr-1) and 3.88 (13.8 t C ha-1 yr-1)g C m⁻² day⁻¹ respectively.

Though, the carbon retaining capacity of *L.* camara and acclimated alien invasive herbs is

much less than that of forest ecosystem, nevertheless it cannot be ignored as they have fixed more carbon annually than that of subtropical forests in the Himalayan region. Therefore, we reiterate the need of long-term monitoring of ecosystem carbon fluxes in relation to inter-annual climatic variability while accounting for carbon balance in the subtropical Himalayas.

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