

Carbon dynamics in an *Imperata* grassland in Northeast India

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Abstract

Carbon stocks and soil CO₂ flux were assessed in an *Imperata cylindrica* grassland of Manipur, Northeast India. Carbon stocks in the vegetative components were estimated to be 11.17 t C/ha and soil organic carbon stocks were 55.94 t C/ha to a depth of 30 cm. The rates of carbon accumulation in above-ground and below-ground biomass were estimated to be 11.85 t C/ha/yr and 11.71 t C/ha/yr, respectively. Annual soil CO₂ flux was evaluated as 6.95 t C/ha and was highly influenced by soil moisture, soil temperature and soil organic carbon as well as by C stocks in above-ground biomass. Our study on the carbon budget of the grassland ecosystem revealed that annually 23.56 t C/ha was captured by the vegetation through photosynthesis, and 6.95 t C/ha was returned to the atmosphere through roots and microbial respiration, with a net balance of 16.61 t C/ha/yr being retained in the grassland ecosystem. Thus the present *Imperata* grassland exhibited a high capacity to remove atmospheric CO₂ and to induce high C stocks in the soil provided it is protected from burning and overgrazing.

Resumen

En un pastizal de *Imperata cylindrica* en Manipur, noreste de India, se evaluaron las reservas de carbono (C) y el flujo de CO₂ en el suelo. Las reservas de C en la vegetación fueron estimadas en 11.17 t/ha y las de C orgánico hasta una profundidad de 30 cm en el suelo, en 55.94 t/ha. La tasa de acumulación de C en la biomasa sobre el suelo se estimó en 11.85 t/ha por año y en la biomasa debajo el suelo en 11.71 t/ha por año. El flujo anual de CO₂ del suelo fue de 6.95 t C/ha, siendo fuertemente influenciado por la humedad, la temperatura y el C orgánico del suelo, así como por las reservas de C en la biomasa aérea. El estudio del balance de C en este ecosistema de pastizal mostró que anualmente son capturadas 23.56 t C/ha por la vegetación a través de la fotosíntesis, y de ellas 6.95 t C/ha son retornadas a la atmósfera a través de las raíces y el proceso de la respiración microbiana, con un saldo neto de retención por el ecosistema de 16.61 t C/ha por año. Por tanto, los pastizales de *I. cylindrica* en el noreste de India tienen alta capacidad para capturar CO₂ atmosférico y acumular cantidades considerables de C en el suelo, siempre y cuando se encuentren protegidos de la quema y el sobrepastoreo.

Introduction

The world's grasslands are important terrestrial biomes, occupying an area of about 33 x 10⁶ km², and play an important role in global carbon balance because of their large area and significant sink or source capacities (Nagy et al. 2007). Land use change contributes to increases in atmospheric CO₂ as a consequence of deforestation as well as conversion and cultivation of new arable land (Schimel et al. 2001). Plants play a significant role in

regulating sinks of carbon by withdrawing atmospheric CO₂ and converting it into assimilates and biomass during photosynthesis, translocation and storage (Watson et al. 2000). Research on long-term CO₂ flux has focused on forest ecosystems with the neglect of grassland ecosystems worldwide. However, grasslands cover approximately 32% of the total land area (Adams et al. 1990) and play a significant role in balancing the global C budget (Scurlock and Hall 1998). A number of studies have been conducted on the carbon stocks in different grasslands of the world (Fisher et al. 2007; Fidelis et al. 2013; Toma et al. 2013). Long et al. (1992) studied grassland sites in Kenya, Mexico and Thailand and found they accumulated 144 g C/m²/yr when protected from fires and concluded these grasslands were potentially significant C sinks.

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However, Fisher et al. (1994; 1995) showed that African grasses introduced into savannas in South America increased soil organic matter and accumulated more C in soil than native grasses, highlighting their greater potential in this respect.

In India, grasslands have originated from forest ecosystems as a result of deforestation and abandoned agricultural systems and are maintained at various succession levels by grazing, burning and harvesting. In Northeast India, a few studies have been carried out on the biomass and productivity of grasslands (Yadava and Kakati 1984; Pandey 1988; Ramakrishnan and Ram 1988) but no information is available on carbon storage in the grasslands of the area.

As *Imperata* grasslands (native grasslands) are widely distributed in Northeast India and other Asian countries, occupying an area of about 35×10^3 km² in Asia, we attempted to study the carbon dynamics of *Imperata* grassland ecosystems in Manipur, Northeast India. The main objectives of the present study were to: (i) assess the above-ground and below-ground biomass and their relevant carbon stocks; (ii) estimate the rate of carbon accumulation; and (iii) evaluate the carbon flux in the soils and its relationship with abiotic and biotic variables.

Materials and Methods

Site description

The study site, located at 24°55' N, 94°06' E in Shabungkho Khunou about 20 km from Imphal city in Imphal East District of Manipur, is dominated by *Imperata*

cylindrica and was well protected from grazing or harvesting during the experimental period. The climate of the area is monsoonal with a warm moist summer followed by a monsoon rainy season and a cool dry winter. Climatological data during the study period are given in Figure 1. Mean monthly maximum temperature varied from 22.3 (December) to 30.3 °C (May) and the mean minimum temperature from 4.8 (January) to 22.3 °C (July). Average annual rainfall is 1,408 mm with most received in the rainy season (June–October). A comparison of medium-term (2003–2012) and short-term (study period) data shows that temperatures during the study were similar to the medium-term figures but rainfall (1,167 mm) was lower than the medium-term mean.

Soil sampling and analysis of physico-chemical characteristics

Five soil samples were collected randomly from the study site at monthly intervals from November 2011 to November 2012 for the analysis of physico-chemical characteristics. Soil texture was determined by soil hydrometer (model 152 H, Zeal, UK). Soil pH was measured by a pH meter in 1:5 soil:water suspension. Bulk density was determined by dividing the weight of oven-dry soil by its volume and soil moisture content was determined by the gravimetric method (oven-dry at 105 °C for 24 h).

Soil organic carbon was estimated by the Walkley-Black method (Anderson and Ingram 1993). Total soil nitrogen was measured by the 2100 Kjeltex system and available soil phosphorus following the method of Bray and Kurtz (1945).

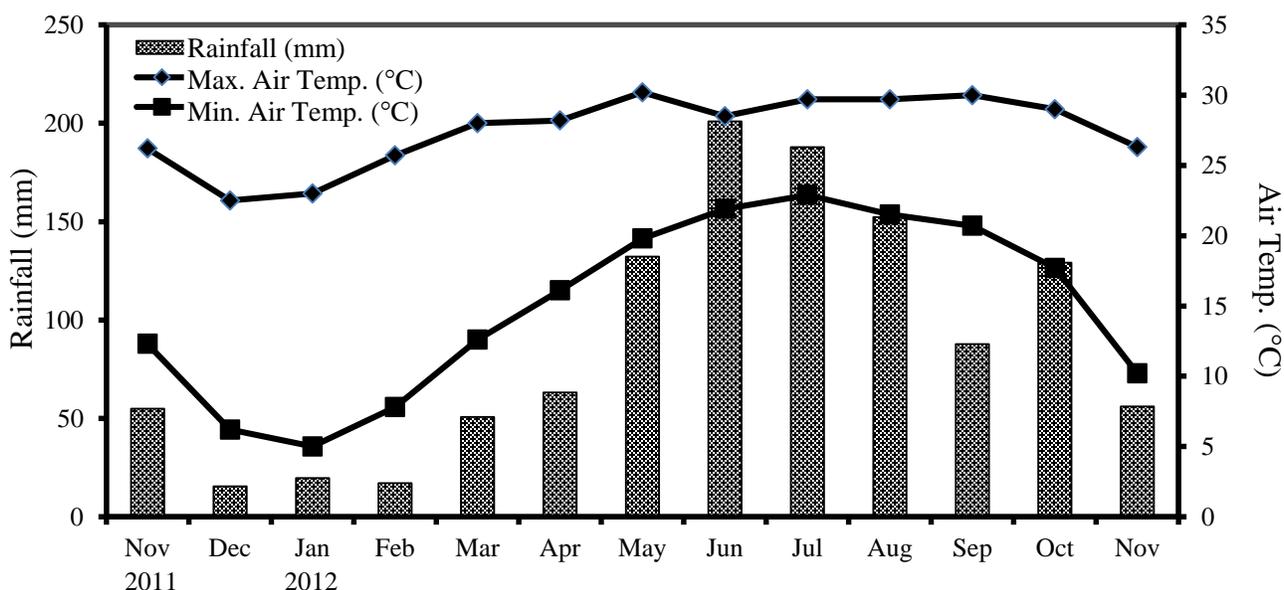


Figure 1. Monthly data for rainfall and air temperature during the study period (November 2011–November 2012).

Estimation of biomass and productivity

Biomass sampling commenced in November 2011 and continued at monthly intervals until November 2012. For the study of above-ground plant biomass, material from 15 random quadrats (40 x 40 cm) was collected according to the method described by Milner and Hughes (1968). The standing vegetation in the quadrats was harvested at ground level using a sharp sickle and the harvested material was placed in polythene bags and transported to the laboratory, where it was divided into live and standing dead. Litter was also collected from within the quadrats. All collected material was placed in perforated paper bags and oven-dried at 80 °C to constant weight.

Below-ground biomass was estimated by taking 15 monoliths of 15 x 15 cm size to a depth of 30 cm, coinciding with samplings for above-ground biomass and at the same locations. The monoliths were brought to the laboratory and divided into 3 sections, representing each 10 cm of depth, and soaked in water for 24 h before washing with a fine jet of water using a 1 mm mesh screen to isolate the roots. The below-ground organic material including live and dead roots was oven-dried at 80 °C until constant weight.

Net above-ground production was estimated by summation of positive increments in total biomass (live biomass plus standing dead material) in the different months and below-ground net production was estimated by the summation of positive increases in root biomass by depth over the course of the study period using the method of Singh and Yadava (1974).

Estimation of carbon stocks in vegetation and soil

The vegetative components, i.e. samples of above-ground and below-ground parts, were oven-dried and powdered and analyzed for carbon using a TOC analyzer (model multi N/C 2100, Analytik Jena, Germany). Carbon stocks were calculated by multiplying the biomass values by 0.45 as per the concentration of carbon obtained from the TOC analyzer for grassland vegetation. The soil organic carbon stocks were estimated from the bulk density (g/cm³), organic carbon concentration (%) and the corresponding soil depth (cm).

Measurement of soil CO₂ flux

Soil CO₂ flux was measured by the alkali absorption method (Singh and Gupta 1977). Open-ended aluminum cylinders, 13 cm diameter and 25 cm tall, were inserted

into the soil up to 15 cm depth. The surface area enclosed in each experimental cylinder was 132.7 cm². Five cylinders were used in the study site, with one serving as a control (blank). Fifty mL of 0.25N NaOH solution was kept in a 100 mL plastic vial in the top of the cylinder, which was made airtight with anchor grip and left for 24 h to absorb CO₂ released. The carbon dioxide absorbed was then determined by titrating NaOH solution with 0.25N standard dilute HCl solution using phenolphthalein as an indicator. Carbon dioxide absorbed from the soil was calculated by using the formula:

$$\text{mg CO}_2 = V \times N \times 22$$

where: V = volume of the acid; and N = normality of the acid.

Statistical analysis

All statistical analyses were carried out using the software IBM SPSS 20. ANOVA was used to determine the differences in biomass and soil CO₂ flux in different months and seasons of the year. Multiple regressions were used to find out the relationship between soil CO₂ flux rate and abiotic and biotic factors.

Results

Physico-chemical characteristics of soil

The grassland soil was generally acidic and clay loam in texture, highly leached and nutrient-poor. Soil pH ranged from 5.3 to 5.8, soil temperature from 27.6 to 28.0 °C, moisture content from 13.2 to 14.5%, bulk density from 1.19 to 1.41 g/cm³ and organic carbon from 1.76 to 1.96%. Total soil nitrogen and available soil phosphorus ranged from 0.019 to 0.029% and 17 to 27 ppm, respectively.

Changes in above-ground plant biomass

Above-ground live biomass declined from 615 g DM/m² in November 2011 to 221 g/m² in January 2012 and then increased progressively to 813 g/m² in September, before declining to 696 g/m² in November 2012 (P<0.001, Figure 2).

In general the amount of standing dead material followed a similar pattern to that of live material and was mostly greater than the mass of live material, except during July–October 2012. Highest yields of standing dead followed the peak in mortality of aerial parts of plants and death of annuals during November with significant differences between months (P<0.001).

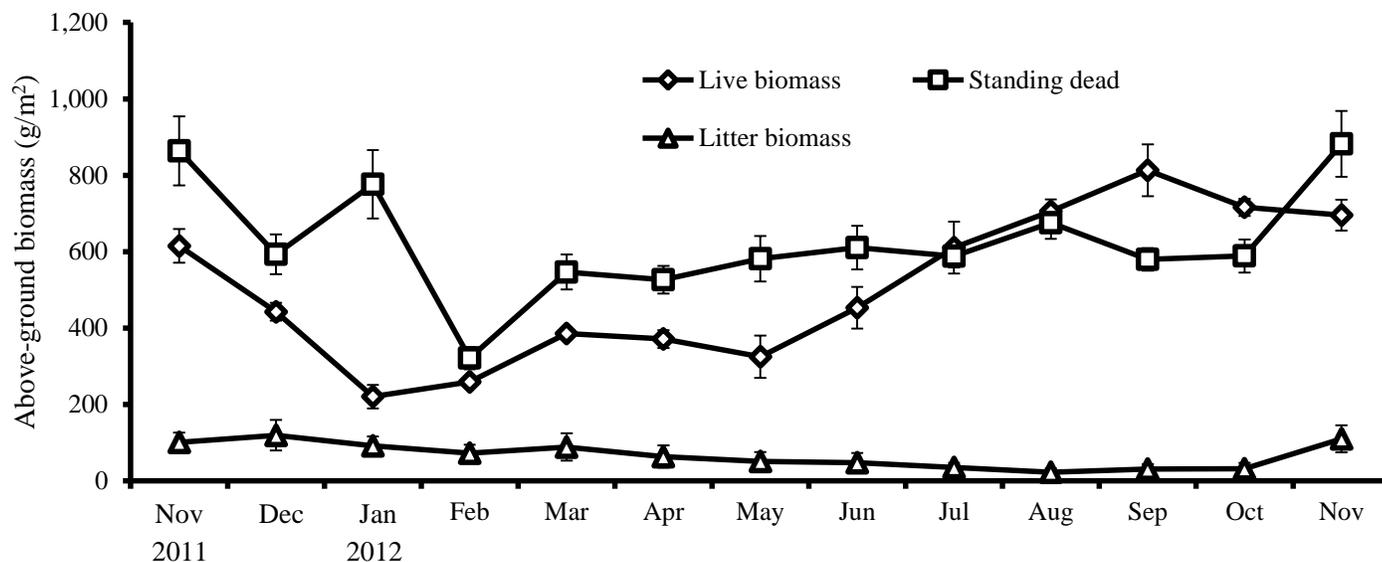


Figure 2. Variation in components of above-ground biomass throughout the year in *Imperata* grassland of Manipur, Northeast India. Standard deviations are indicated by vertical bars.

Surface litter fluctuated between months ($P < 0.001$), with highest values in November–December and lowest values in August (Figure 2).

Total above-ground biomass (live + standing dead + litter) was estimated to be lowest in February (653 g DM/m^2) and highest in November ($1,688 \text{ g/m}^2$).

Changes in below-ground plant biomass

There was very little variation in below-ground biomass in the 10–20 and 20–30 cm soil layers during the year, with the major changes occurring in the 0–10 cm horizon (Figure 3). Total below-ground biomass fluctuated from $1,600 \text{ g/m}^2$ in November 2011 to 800 g/m^2 in January and June 2012, with an interesting spike in April 2012. Of the total below-ground biomass, 78.3% was stored in the 0–10 cm horizon.

Seasonal and annual above-ground and below-ground net primary production

Seasonal above-ground net primary production was highest during the monsoon rainy season (466 g DM/m^2), followed by summer (368 g/m^2) and winter (351 g/m^2), whereas below-ground net primary production exhibited a reverse trend, i.e. highest during the winter season (707 g/m^2), intermediate during the rainy season (300 g/m^2) and lowest during summer (164 g/m^2). Annual values for above-ground and below-ground net primary production

were estimated at $1,185 \text{ g DM/m}^2$ and $1,171 \text{ g/m}^2$, respectively.

Carbon stocks in above-ground biomass, below-ground biomass and soil

Carbon stocks in above-ground and below-ground biomass were recorded to be 5.40 and 5.77 t C/ha , respectively, and soil organic carbon stocks were found to be 55.94 t C/ha to a depth of 30 cm. Of the total carbon in the vegetation-soil system at a given time, 16.7% occurred in vegetative biomass and 83.3% in soil (Table 1).

Table 1. Estimated carbon stocks in *Imperata* grassland of Manipur, Northeast India.

Component	C stock (t/ha)	Proportion (%) of the total
Above-ground biomass	5.40	8.1
Below-ground biomass	5.77	8.6
Soil organic carbon (0–30 cm)	55.94	83.3
Total	67.11	

Rate of carbon accumulation

The annual rates of carbon accumulation in above-ground and below-ground parts of grassland vegetation were estimated to be 11.85 t C/ha and 11.71 t C/ha , respectively, giving an annual total of 23.56 t C/ha .

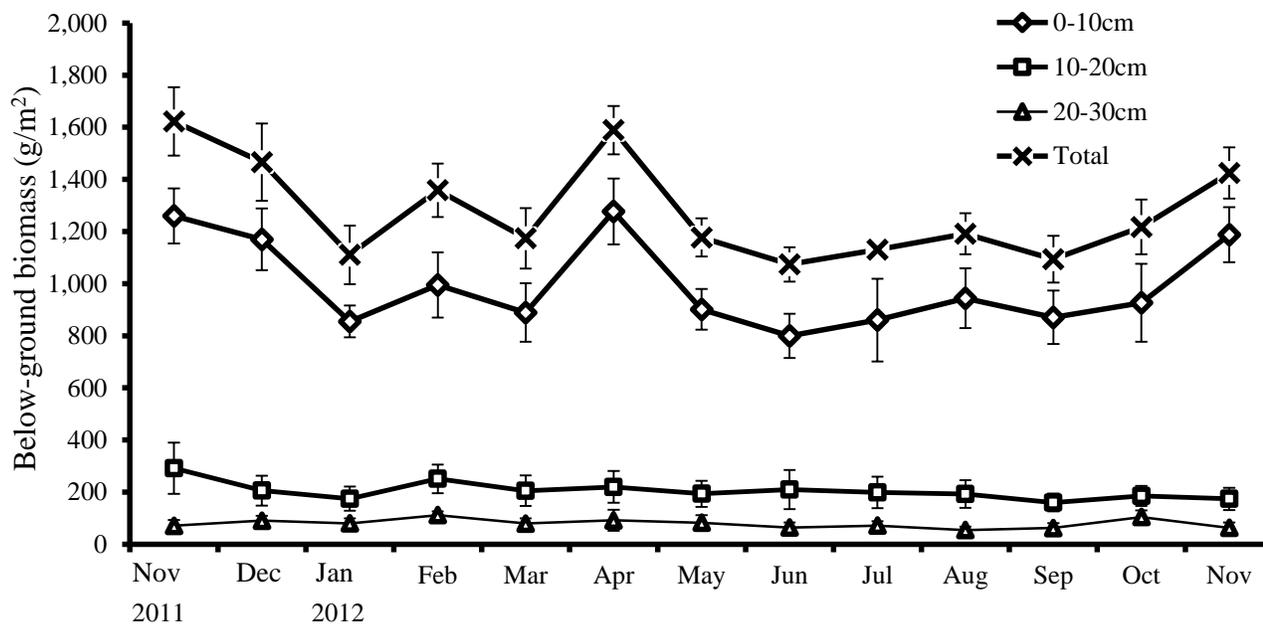


Figure 3. Variation in below-ground biomass in different soil layers throughout the year in *Imperata* grassland of Manipur, Northeast India. Standard deviations are indicated by vertical bars.

Soil CO₂ flux

Soil CO₂ flux for the grassland site varied between 124 ± 11.3 and 586 ± 63.0 mg CO₂/m²/h, attaining peak values in September and lowest values in the dry, cool winter season in January ($P < 0.001$) (Figure 4, Table 2).

Table 2. Seasonal changes in the rate of soil CO₂ flux (mg CO₂/m²/h) in *Imperata* grassland of Manipur, Northeast India.

Season	Soil CO ₂ flux
Summer (March–May)	248 ± 16.8
Rainy (June–October)	427 ± 33.7
Winter (November–February)	153 ± 11.6
Annual	291 ± 12.0

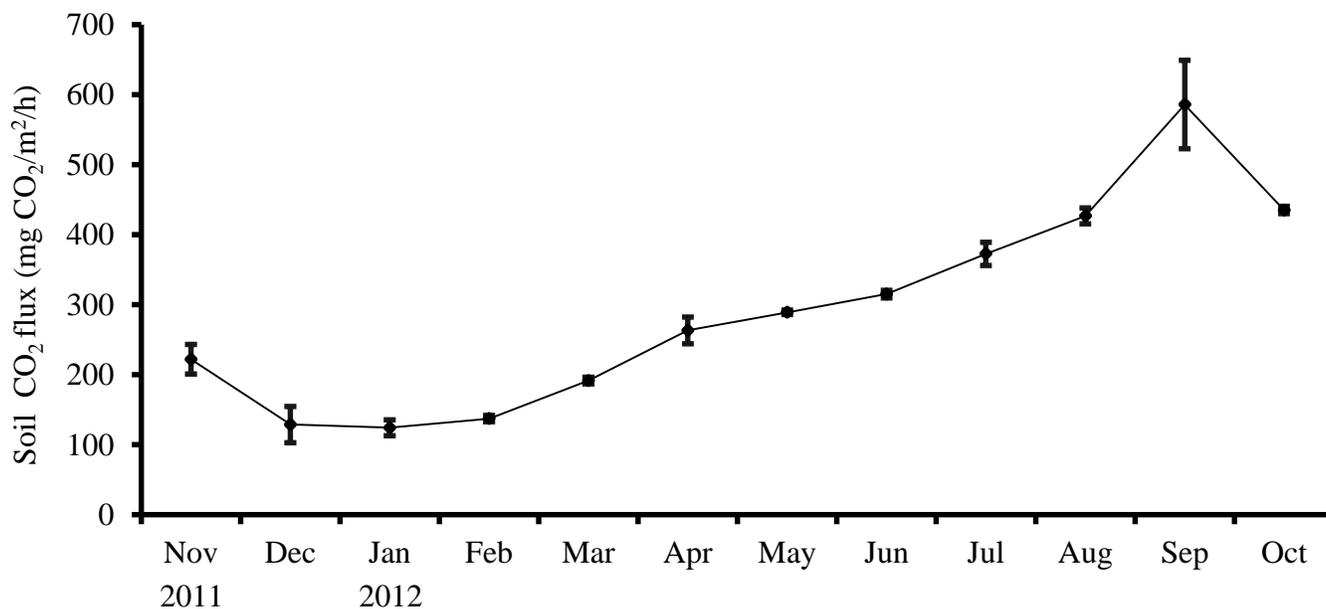


Figure 4. Variation in soil CO₂ flux throughout the year in *Imperata* grassland in Manipur, Northeast India. Standard deviations are indicated by vertical bars.

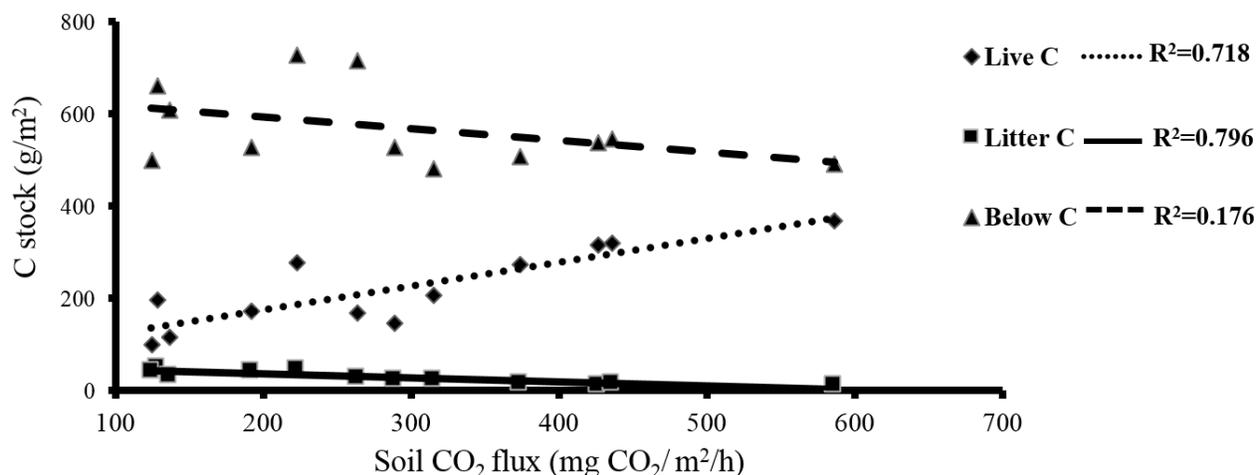


Figure 5. Relationship between soil CO₂ flux and C stock in live above-ground biomass, litter and below-ground biomass.

Relationship of soil CO₂ flux with abiotic and biotic variables

The relationships between the rates of soil CO₂ flux (mg CO₂/m²/h) and soil properties, i.e. soil temperature (X₁), soil moisture (X₂) and soil organic carbon (X₃) were analyzed by multiple regression as follows:

$$Y = -683.446 + 1.229X_1 + 3.557X_2 + 498.496X_3$$

($r_1 = 0.81$; $r_2 = 0.68$; $r_3 = 0.97$ at $P < 0.01$).

Soil CO₂ flux was positively related to C stocks in live above-ground biomass ($R^2 = 0.72$; $P < 0.001$) and negatively related to C stocks in litter ($R^2 = 0.80$; $P < 0.001$) and below-ground biomass ($R^2 = 0.18$; $P < 0.001$) (Figure 5).

Discussion

This study has provided valuable information on the carbon dynamics of an *Imperata* grassland in India. It has shown the ability of these grasslands to extract CO₂ from the atmosphere and incorporate it in vegetative material, which then has the potential to be stored as soil carbon, depending on management factors.

The present data for live above-ground biomass in humid grassland (221–813 g DM/m²) fell within the range recorded for most Indian grasslands, being lower than the 72–1,596 g/m² reported from the Bundelkhand region by Gupta and Ratan (2005) but considerably higher than the 16–373 g/m² for Western Garhwal Himalaya (Dhaulakhandi et al. 2000).

Our data for carbon stocks in above-ground biomass (5.65 t C/ha) were higher than the 4.0–4.4 t/ha reported by Ramsay and Oxley (2001) in Ecuadorian paramo grasslands but lower than the 6.5 t/ha reported by Gibbon

et al. (2010) for a grassland-cloud forest transition zone in the high Andes of Peru. We found that *Imperata* grassland contained up to 3.40 t C/ha in dead biomass (litter + standing dead biomass), contributing 29% of the total carbon stock in the vegetation, while Fidelis et al. (2013) recorded a figure of 28.9% in a Brazilian Cerrado wet grassland. This highlights the importance of quantification of litter and standing dead biomass in improving the understanding of carbon dynamics. In the event of fire, a common management practice in tropical native grasslands, much of the carbon in this dead plant material can be released as CO₂ into the atmosphere. Long et al. (1992) found that C accumulation in pastures was 144 g C/m²/yr in the absence of fire and 40 g C/m²/yr, when burnt every second year.

As was expected, the maximum above-ground live biomass occurred in September, coinciding with peak growth of the grassland species during the rainy season, with the minimum in January, when conditions were cool and dry. The gradual decline in live biomass from October to January followed the pattern of maturing of perennial species and completion of the life cycle by annual plants after the cessation of the monsoonal rains. As a result, in all regions, the maximum biomass value occurred either in September or October, as growth was triggered by the advent of monsoonal rains in May-June throughout the country.

The highly significant differences between months in terms of above-ground live biomass, standing dead and litter result from the interactions and balances between growth of new material, maturation and death of pasture species, transfer of standing dead to litter and breakdown of litter by microorganisms. The variation in standing dead material throughout the study resulted from a

combination of addition of new biomass as plants matured and senesced and transfer of standing dead to litter. This then influenced litter levels, which fluctuated throughout the year as a net result of transfer of standing dead material to the litter component and the rate of disappearance of litter. The peak values for surface litter in December probably reflect the transfer of standing dead material to litter from the high standing dead levels recorded in November, combined with slow decomposition rates in litter as temperatures declined, as shown by low values for CO₂ flux in November to February. As contributions from standing dead declined and litter breakdown increased as temperatures rose into summer, litter levels declined to a minimum in August.

Carbon stocks in below-ground biomass (5.75 t C/ha) in the present study were similar to the data reported for *Leymus chinensis* grassland of Northern China (5.57 t C/ha) by He et al. (2008), lower than the 6.75 t C/ha reported for Neotropical savannas of Brazil by Delitti et al. (2001) and higher than the 2.58–2.77 t C/ha reported by Fidelis et al. (2013) in a Brazilian Cerrado wet grassland.

The minimum value for below-ground biomass (BGB) in June may be due to the translocation of reserve food materials for the growth and development of new grass tillers in the pre-monsoon period and decomposition of dead below-ground materials, while the maximum value in November would result from the translocation of material from aerial parts of plants into the below-ground parts with the onset of the post-monsoon period. The increase in the amount of BGB during April may be due to early development of absorptive rootlets, which rapidly compensate for the translocation (Menaut and Cesar 1979), combined with slow rate of decomposition of roots. This adaptation in tropical grasslands allows accumulation of reserve material in the roots during unfavorable climatic conditions experienced in cool and dry winter seasons (Redmann 1975).

The decrease in BGB with increase in depth of soil with 73.2–83.4% in the upper layer of soil (0–10 cm) is similar to the trend reported by Singh and Yadava (1974) in a tropical grassland of Kurukshetra (54.5–85% in top 10 cm). Our results of 1,074 g/m² (June) to 1,623 g/m² (November) were similar to the 1,001–1,614 g/m² reported by Yadava and Kakati (1984) in *Imperata-Bothriochloa* grassland of Manipur, India but lower than the 1,503–2,005 g/m² for grassland of Western Garhwal Himalaya (Dhaulakhandi et al. 2000) and higher than the 454–1049 g/m² for grassland of Bundelkhand region (Gupta and Ratan 2005). Obviously species composition, location, elevation, soil factors and seasonal climatic conditions impact on the amounts of plant biomass produced

and its rate of breakdown.

The peak in above-ground net primary production (ANP) during the rainy season was to be expected as climatic conditions were favorable for growth of vegetation with optimum temperature and sufficient moisture in the soil. In contrast, the low values in winter result from the drying of the grass and annual plant species with the onset of dry and cold winter conditions and low soil moisture levels. Similar trends in ANP in Indian grasslands have been reported by other workers (Yadava and Kakati 1984; Pandey 1988; Sinha et al. 1991; Bawa 1995). This highlights the key role played by the monsoon rainfall pattern in determining seasonal net primary production patterns of the grassland communities.

On the other hand, peak below-ground net primary production (BNP) occurred during winter, showing that this period is conducive to and favorable for translocation of photosynthates from aerial parts of the vegetation to below-ground parts. Low values in summer result from the translocation of reserve material from roots to support the growth of new sprouts with the advent of monsoon rains during the summer season. At the onset of winter, most perennial grasses and annual plants mature and there is a tendency for accumulation of food reserves in the below-ground parts. Maximum BNP during winter was also reported by many workers in different Indian grasslands (Singh and Yadava 1974; Sah and Ram 1989; Sinha et al. 1991).

Our study shows that the proportions of carbon stocks in AGB and BGB were more or less similar but were small in comparison with the amounts of carbon stored in the soil. More than 80% of the organic carbon in the pasture-soil combination was organic carbon in the soil, a similar result to that reported by Ni (2002) for the grasslands of China. This demonstrates that an *Imperata cylindrica* pasture can induce high C stocks in the soil. Like carbon in the pasture components, this carbon can be lost to the atmosphere if soils are disturbed. The present data on soil organic carbon stocks (55.94 t C/ha) can be compared with the 50–164 t C/ha reported by Chan and McCoy (2010) in pasture in Australia and the 28.1–417 t C/ha in semi-natural grassland in Southern China (Toma et al. 2013).

The positive significant relationship between soil C stocks and live AGB highlights the importance of live biomass in the supply of carbon to the soil, while litter and BGB have a small negative effect (Figure 6).

Soil CO₂ flux showed remarkable seasonal variation, being highest during the rainy season and lowest in winter. Maximum soil CO₂ flux during the rainy season was expected because of the high microbial activity and rapid decomposition of litter under the warm moist conditions.

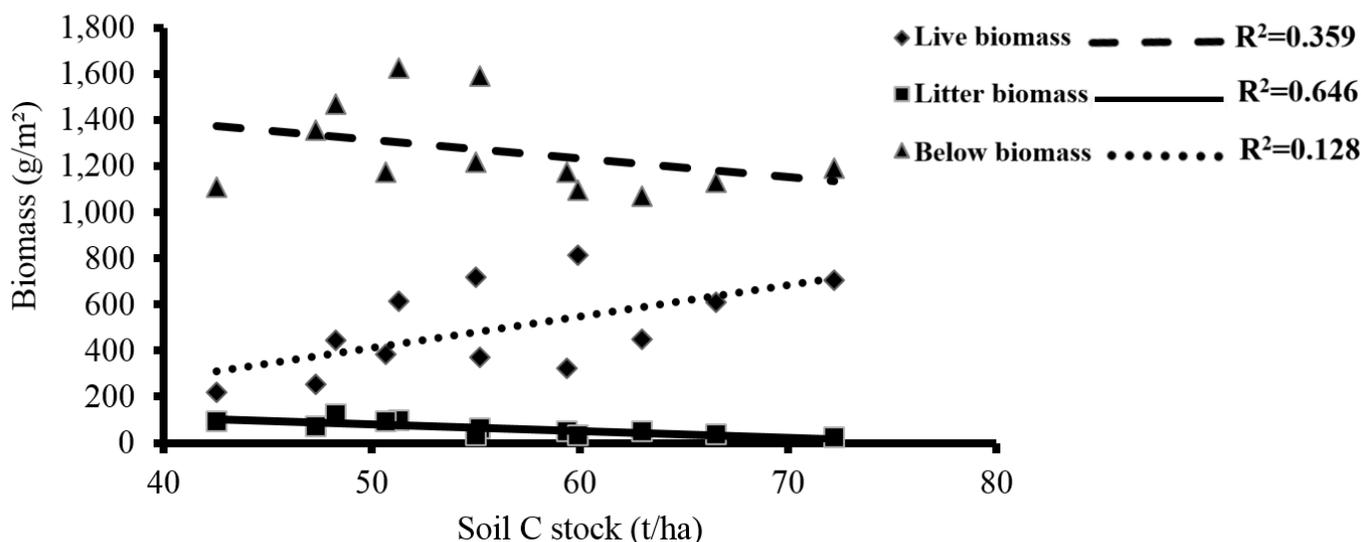


Figure 6. Relationships between soil C stock and live above-ground biomass (AGB), litter and below-ground biomass (BGB).

The present rates of soil CO₂ flux (124–586 mg CO₂/m²/h) in the grassland ecosystem are comparable with those reported for grasslands of Kurukshetra, India by Gupta and Singh (1981), northern semi-arid grasslands of USA by Frank et al. (2002) and subtropical forests in China by Wang et al. (2011).

The significant positive relationship between soil CO₂ flux rates and soil moisture, soil temperature and soil organic carbon levels reveals that these parameters have a strong influence on CO₂ emissions into the atmosphere, as reported for different ecosystems by other workers, e.g. Oishi et al. (2013) and Zhou et al. (2013). Similarly, soil CO₂ flux is closely related to C stocks in live AGB, litter and BGB indicating the strong influence of these parameters on CO₂ emissions.

Our estimates of annual organic carbon input as litter (347 g C/m²/yr) and annual carbon output (695 g C/m²/yr) as estimated by annual soil CO₂ flux rate suggest that annual output of CO₂ was almost double that produced by annual litter fall. This would mean there should be a net loss of C from the soil as most C entering the soil comes from litter break down. However, Fisher et al. (2007) suggest that the rate at which litter decays is often underestimated so that this figure may not represent the true C input from litter. Litter decomposition is very fast as a result of high microbial activity coupled with congenial climatic conditions prevailing in the region (Devi and Yadava 2007).

The annual carbon budget of the present *Imperata* grassland shows that 23.56 t C/ha was captured by the

vegetation through photosynthesis, while 6.95 t C/ha was released into the atmosphere as CO₂ emissions from soil due to root and microbial respiration with a net balance of 16.61 t C/ha/yr being retained in the grassland ecosystem. Thus subtropical *Imperata* grasslands have a huge potential to help reduce carbon dioxide levels in the atmosphere and could be used as C sinks in Asian countries, provided they are protected from fire, grazing and harvesting and could be one option for mitigating climate change at a global level.

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References

- Adams JM; Faure H; Faure-Denard L; McGlade JM; Woodward FI. 1990. Increases in terrestrial carbon storage from the last glacial maximum to the present. *Nature* 348:711–714. DOI: [10.1038/348711a0](https://doi.org/10.1038/348711a0)
- Anderson JM; Ingram JSI, eds. 1993. *Tropical soil biology and fertility: A handbook of methods*. 2nd Edn. CAB International, Wallingford, UK.
- Bawa R. 1995. Biomass dynamics of Himalayan grassland. *International Journal of Ecology and Environmental Sciences* 21:25–36.
- Bray RH; Kurtz LT. 1945. Determination of total, organic, and available forms of phosphorus in soils. *Soil Science* 59:39–46. DOI: [10.1097/00010694-194501000-00006](https://doi.org/10.1097/00010694-194501000-00006)

- Chan KY; McCoy D. 2010. Soil carbon storage potential under perennial pastures in the mid-north coast of New South Wales, Australia. *Tropical Grasslands* 44:184–191. <http://goo.gl/DBTUF1>
- Delitti WBC; Pausas JG; Burger DM. 2001. Belowground biomass seasonal variation in two Neotropical savannas (Brazilian Cerrados) with different fire histories. *Annals of Forest Science* 58:713–721. DOI: [10.1051/forest:2001158](https://doi.org/10.1051/forest:2001158)
- Devi AS; Yadava PS. 2007. Wood and leaf litter decomposition of *Dipterocarpus tuberculatus* Roxb. in a tropical deciduous forest of Manipur in North-East India. *Current Science* 9:243–246.
- Dhaulakhandi M; Rajwar GS; Kumar P. 2000. Primary productivity and system transfer functions in alpine grassland of Western Garhwal Himalaya. *Tropical Ecology* 41:99–101.
- Fidelis A; Lyra MFS; Pivello VR. 2013. Above- and below-ground biomass and carbon dynamics in Brazilian Cerrado wet grasslands. *Journal of Vegetation Science* 24:356–364. DOI: [10.1111/j.1654-1103.2012.01465.x](https://doi.org/10.1111/j.1654-1103.2012.01465.x)
- Fisher MJ; Rao IM; Ayarza MA; Lascano CE; Sanz JI; Thomas RJ; Vera RR. 1994. Carbon storage by introduced deep-rooted grasses in the South American savannas. *Nature* 371:236–238. DOI: [10.1038/371236a0](https://doi.org/10.1038/371236a0)
- Fisher MJ; Lascano CE; Rao IM; Sanz JI; Thomas RJ; Vera RR; Ayarza MA. 1995. Pasture soils as carbon sink. *Nature* 376:473. DOI: [10.1038/376473a0](https://doi.org/10.1038/376473a0)
- Fisher MJ; Braz SP; Santos RSM dos; Urquiaga S; Alves BJR; Boddey RM. 2007. Another dimension to grazing systems: Soil carbon. *Tropical Grasslands* 41:65–83. <http://goo.gl/2qoVB6>
- Frank AB; Liebig MA; Hanson JD. 2002. Soil carbon dioxide fluxes in northern semiarid grasslands. *Soil Biology and Biochemistry* 34:1235–1241. DOI: [10.1016/S0038-0717\(02\)00062-7](https://doi.org/10.1016/S0038-0717(02)00062-7)
- Gibbon A; Silman MR; Malhi Y; Fisher JB; Meir P; Zimmermann M; Dargie GC; Farfan WR; Garcia KC. 2010. Ecosystem carbon storage across the grassland-forest transition in the high Andes of Manu National Park, Peru. *Ecosystems* 13:1097–1111. DOI: [10.1007/s10021-010-9376-8](https://doi.org/10.1007/s10021-010-9376-8)
- Gupta RK; Ratan N. 2005. Biomass dynamics, net primary production and turnover rate of grassland community in Bundelkhand region (U.P.). *Bulletin of National Institute of Ecology* 16:87–94.
- Gupta SR; Singh JS. 1981. Soil respiration in a tropical grassland. *Soil Biology and Biochemistry* 13:261–268. DOI: [10.1016/0038-0717\(81\)90060-2](https://doi.org/10.1016/0038-0717(81)90060-2)
- He N; Yu Q; Wu L; Wang Y; Han X. 2008. Carbon and nitrogen store and storage potential as affected by land use in a *Leymus chinensis* grassland of Northern China. *Soil Biology and Biochemistry* 40:2952–2959. DOI: [10.1016/j.soilbio.2008.08.018](https://doi.org/10.1016/j.soilbio.2008.08.018)
- Long SP; Jones MB; Roberts MJ. 1992. Primary productivity of grass ecosystems of the tropics and subtropics. Chapman and Hall, New York, USA.
- Menaut JC; Cesar J. 1979. Structure and primary productivity of Lamto savannas, Ivory Coast. *Ecology* 60:1197–1210. DOI: [10.2307/1936967](https://doi.org/10.2307/1936967)
- Milner C; Hughes RE. 1968. Methods for the measurement of primary production of grassland. Blackwell Scientific Publications, Oxford and Edinburgh, UK.
- Nagy Z; Pintér K; Czóbel Sz; Balogh J; Horváth L; Fóti Sz; Barcza Z; Weidinger T; Csistalan Z; Dinh NQ; Grosz B; Tuba Z. 2007. The carbon budget of semi-arid grassland in a wet and a dry year in Hungary. *Agriculture, Ecosystem and Environment* 121:21–29. DOI: [10.1016/j.agee.2006.12.003](https://doi.org/10.1016/j.agee.2006.12.003)
- Ni J. 2002. Carbon storage in grasslands of China. *Journal of Arid Environments* 50:205–218. DOI: [10.1006/jare.2001.0902](https://doi.org/10.1006/jare.2001.0902)
- Oishi AC; Palmroth S; Butnor JR; Johnsen KH; Oren R. 2013. Spatial and temporal variability of soil CO₂ efflux in three proximate temperate forests ecosystems. *Agricultural Forest Meteorology* 171:256–269. DOI: [10.1016/j.agrformet.2012.12.007](https://doi.org/10.1016/j.agrformet.2012.12.007)
- Pandey AN. 1988. Short-term study of recovery of a tropical grassland following seasonal burning. *Tropical Ecology* 29:159–170.
- Ramakrishnan PS; Ram SC. 1988. Vegetation, biomass and productivity of seral grasslands of Cherrapunji in North-East India. *Vegetatio* 74:47–53. DOI: [10.1007/bf00045613](https://doi.org/10.1007/bf00045613)
- Ramsay PM; Oxley ERB. 2001. An assessment of aboveground net primary productivity in Andean grasslands of Central Ecuador. *Mountain Research and Development* 21:161–167. DOI: [10.1659/0276-4741\(2001\)021%5B0161:aaonp%5D2.0.co;2](https://doi.org/10.1659/0276-4741(2001)021%5B0161:aaonp%5D2.0.co;2)
- Redmann RE. 1975. Production ecology of grassland plant communities in western North Dakota. *Ecological Monographs* 45:83–106. DOI: [10.2307/1942332](https://doi.org/10.2307/1942332)
- Sah VK; Ram J. 1989. Biomass dynamics, species diversity and net primary production in a temperate grassland of Central Himalaya, India. *Tropical Ecology* 30:294–302.
- Schimel DS; House JI; Hibbard KA; Bousquet P; Ciais P; Peylin P; Braswell BH; Apps MJ; Baker D; Bondeau A; Canadell J; Churkina G; Cramer W; Denning AS; Field CB; Friedlingstein P; Godale C; Heimann M; Houghton RA; Melillo JM; Moore B; Murdiyarso D; Noble I; Pacala SW; Prentice IC; Raupach MR; Rayner PJ; Scholes RJ; Steffen WL; Wirth C. 2001. Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature* 414:169–172. DOI: [10.1038/35102500](https://doi.org/10.1038/35102500)
- Scurlock JMO; Hall DO. 1998. The global carbon sink: A grassland perspective. *Global Change Biology* 4:229–233. DOI: [10.1046/j.1365-2486.1998.00151.x](https://doi.org/10.1046/j.1365-2486.1998.00151.x)
- Singh JS; Yadava PS. 1974. Seasonal variation in composition, plant biomass and net primary productivity of a tropical grassland at Kurukshetra, India. *Ecological Monographs* 44:351–378. DOI: [10.2307/2937034](https://doi.org/10.2307/2937034)
- Singh JS; Gupta SR. 1977. Plant decomposition and soil respiration in terrestrial ecosystems. *Botanical Review* 43:449–528. DOI: [10.1007/bf02860844](https://doi.org/10.1007/bf02860844)
- Sinha A; Rana RS; Gupta SR. 1991. Growth patterns, net primary production and energy transfer in two grassland communities of sodic soils. *Tropical Ecology* 32:105–116.

- Toma Y; Clifton-Brown J; Sugiyama S; Nakaboh M; Hatano R; Fernández FG; Stewart JR; Nishiwaki A; Yamada T. 2013. Soil carbon stocks and carbon sequestration rates in seminatural grassland in Aso region, Kumamoto, Southern Japan. *Global Change Biology* 19:1676–1687. DOI: [10.1111/gcb.12189](https://doi.org/10.1111/gcb.12189)
- Wang B; Jiang Y; Wei X; Zhao G; Guo H; Bai X. 2011. Effects of forest type, stand age, and altitude on soil respiration in subtropical forests of China. *Scandinavian Journal of Forest Research* 26:40–47. DOI: [10.1080/02827581.2010.538082](https://doi.org/10.1080/02827581.2010.538082)
- Watson RT; Noble IR; Bolin B; Ravindranath NH; Verardo DJ; Dokken DJ, eds. 2000. Land use, land-use change and forestry. A Special Report of the Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press, Cambridge, UK.
- Yadava PS; Kakati LN. 1984. Biomass dynamic and net primary productivity in a grassland ecosystem at Imphal. *International Journal of Biometeorology* 28:123–145.
- Zhou Z; Zhang Z; Zha T; Luo Z; Zheng J; Sun OJ. 2013. Predicting soil respiration using carbon stock in roots, litter and soil organic matter in forests of Loess Plateau in China. *Soil Biology and Biochemistry* 57:135–143. DOI: [10.1016/j.soilbio.2012.08.010](https://doi.org/10.1016/j.soilbio.2012.08.010)

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