

Soil organic carbon dynamics in two functional types of ground cover (grasses and herbaceous) in the tropics

J. Dinakaran, Nirav Mehta and
N. S. R. Krishnappa*

Ecology Laboratory, Department of Botany, Faculty of Science,
The M.S. University of Baroda, Vadodra 390 002, India

We studied the soil organic carbon (SOC) dynamics in two types of tropical ground cover (grasses predominantly as C₄ functional type and herbaceous predominantly as C₃ functional type), located in a permanent plot of the Department of Botany, the M.S. University of Baroda, Vadodra, India. The aboveground biomass (AGB) and belowground biomass (BGB, as root biomass), soil respiration (R_s), microbial biomass carbon (MBC), dissolved organic carbon (DOC) and SOC were measured for 12 months in the selected types of ground cover. Differences in AGB and BGB allocation indicated the functional difference in both these ground covers. Higher R_s values during monsoon seen in the present study (in both the covers) are attributed to higher biomass production which increases fresh inputs into soil. In both the covers, correlation ($R^2 > 0.6$) was seen between BGB and MBC. DOC in both the covers showed higher values during monsoon coinciding with biomass production. Results of ANOVA showed significant differences ($P < 0.05$) in the measured parameters of both types of ground cover, indicating functional differences. Higher SOC values (15.6–23.2 g kg⁻¹) in herbaceous cover indicated larger inputs of dead organic matter coming from the death of ephemerals. Lesser and relatively stable quantities of SOC (7.8–9.8 g kg⁻¹) in grass cover have been attributed to lower inputs and/or uniformity in their proportion of expenditure of fixed carbon. The findings of the present study indicate that soil carbon dynamics in these ground covers is governed by fluctuations in organic carbon input (fresh and dead), and its pattern of utilization by soil biological/microbial community. The study highlights the importance of herbaceous (C₃ functional type) ground cover in improving soil fertility in the tropics.

Keywords: Biomass, ground cover, soil organic carbon.

SOILS are considered as the largest carbon reservoirs of the terrestrial carbon cycle storing 2344 Pg (1 Pg = 10¹⁵ g) of carbon (C) up to 3 m depth¹. This amount is more than twice that in vegetation (359 Pg) and atmosphere (760 Pg) combined²⁻⁴. The size of the soil organic matter pool is determined by the rate of input of fresh organic matter, the proportion of humified carbon and the rate of efflux of carbon⁵. Changes in the dominant plant life

forms or community type (e.g. ground cover, shrubs and trees) greatly influence soil carbon content, chemistry and distribution. This is because of differences in plant life forms, litter chemistry, patterns of detrital input and rooting depth⁶. There are several studies on the contribution and impact of forest cover (boreal, temperate and tropical) on the carbon cycle⁷⁻¹⁰. Most of these studies focused on temperate and tropical forests, whereas ground cover has been less addressed. Ground cover can be broadly classified into grasslands and forb/herbaceous cover. Savannas/grasslands are a major component of the world's vegetation, covering one-sixth of the land surface and accounting for ~30% of the primary production of all terrestrial vegetation¹¹. Grasslands are considered as a major potential sink for carbon¹²⁻¹⁴. Grassland (temperate and tropical, mostly C₄) soils store more carbon compared to forests soils^{4,14} and have the potential to sequester about 0.5 Pg C yr⁻¹.

Herbaceous vegetation is therophytic in nature, exhibiting maximum number of species during the rainy season¹⁵. Unlike grasslands, herbaceous cover (broadleaved ephemerals, C₃ functional type) is a lesser studied system for its potential in influencing organic carbon levels of the soil. Diversity of herbaceous cover is higher in the tropics. It is an important component of the terrestrial ecosystem and plays a vital role in primary production and turnover¹⁶. Most of these species are ephemerals, completing their life cycle within a year, and adding reasonable quantities of litter into the soil. The cyclical events happening in ground cover are rapid with shorter durations. It is important to look at how different types of ground cover (C₃ and C₄ functional types) influence C allocation and storage in the soils.

Belowground allocation of biomass regulates soil respiration. Soil respiration constitutes the second largest flux of carbon between terrestrial ecosystems and the atmosphere¹⁷. We lack precise knowledge of the sources of and controls upon the release of CO₂ from the soils¹⁸. It has been reported that tropical ecosystems are sustained by photosynthetic fixation of carbon aboveground, most of which is released by respiratory processes occurring belowground^{7,19}. Jha and Mohapatra²⁰ reported that soil moisture is the most important regulating factor of soil respiration in semi-arid ecosystems. Minor changes in soil respiration are likely to alter CO₂ efflux affecting the global carbon cycle. An earlier study¹⁸ mentioned that the flux of 'new' carbon is an important driver of biological processes in the soil, as are the much slower fluxes of carbon arising from the decomposition of shoot and root-derived litter. Organic matter in the soils coming from fresh inputs or from partly decomposed structures can be predominantly utilized by microbes. The soil microbial biomass is surrounded by about 50 times its mass of soil organic matter, but can only metabolize it slowly⁵. These aspects get influenced more in ground cover because of their variations in structure and functional role. There is

*For correspondence. (e-mail: krish14@gmail.com)

necessity for a better understanding of the relationship between carbon input and microbial activity in ground covers showing seasonality in growth. The present study has been carried out to test whether plant functional types (herbaceous cover as C₃ functional type and grasses as C₄ functional type) have any differences in the addition of inputs (fresh and dead organic matter) to the soil, and how these differences will affect soil organic carbon (SOC) dynamics.

The study was conducted at a permanent plot of the Department of Botany, The M.S. University of Baroda, Vadodara, India lying between lat. 22°19'15.26"N and long. 73°10'47.63"E, at an elevation of 37 m asl. The size of the plot is 4.56 acres. Three distinct seasons are seen in the study area: monsoon (July–October), winter (November–February) and summer (March–June). Rainfall is restricted to the monsoon months (mean annual precipitation is 920 mm). Mean (10 yr) annual minimum and maximum temperatures are 6.3°C (winter) and 41.6°C (summer). The plot is interspersed with trees accounting for an occupancy of nearly 25% area. Grass cover (C₄ functional type) is present in the northeast direction of the plot, occupying an area of nearly 35%. The rest of the area is covered by forbs/broadleaved herbs (C₃ functional type). Grasses present in the study area are *Dichanthium annulatum* (Forssk.) Stapf, *Sporobolus coromandelianus* (Retz.) Kunth, *Oplismenus burmannii* (Retz.) Beauv., *Eragrostis tenella* (L.) Beauv., *Setaria glauca* (L.) Beauv. Forb/herbaceous species present are *Boerhavia diffusa* L., *Antigonon leptopus* Hook. & Arn., *Euphorbia hirta* L., *Aerva javanica* (Burm.f.) Schult., *Tridax procumbens* L., *Achyranthes aspera* Cooke, *Sida acuta* Burm., *Corchorus aestuans* L., *Corchorus fascicularis* Lam., *Ruellia tuberosa* L., *Abutilon indicum* (L.) Sw., *Vernonia cinerea* (L.) Lees, *Alternanthera sessilis* (L.) DC, *Solanum nigrum* L., *Acalypha indica* L., *Oldenlandia corymbosa* L., *Clitoria ternatea* L., *Tephrosia purpurea* (L.) Pers., *Scrophularia* sp., *Amaranthus spinosus* L., *Amaranthus viridis* L., *Peristrophe bicalyculata* (Retz.) Nees, *Blumea membranacea* DC and *Cassia occidentalis* L. Species composition is the same across the grass cover. Herbaceous cover showed a difference in species diversity (15–20%) across the study area. Percentage occupancy is the same. The plot has been allowed for natural regeneration with occasional land management activities for the past 25 years. Area occupied by grasses is treated as grass cover (C₄ functional type), and that occupied by forbs/broadleaved herbs is treated as herbaceous cover (C₃ functional type). Dominant grasses are perennial in nature throughout the area. Area occupied by broad-leaved herbs showed seasonality in occupancy. Most of these herbs stay for less than a year. Temporal variation is seen in the arrival and subsequent demise of the species. Most of the species start their life cycle immediately after the first showers of monsoon. Their existence is seen up to January/February. Some species are late entrants. Few of these

continued their existence in summer months. Overall, herbaceous cover showed maximum occupancy in monsoon through winter and sparse distribution in summer.

Monitoring of both the vegetal covers started with the onset of sprouting of herbs in maximum numbers and continued for 12 months. This study cycle ensured accounting of all ephemeral herbs coming at different seasons of a year (from June 2008 to May 2009). The total area occupied by each cover (grasses and herbs) was divided into 1 m² blocks. Randomized block design was employed while picking up a quadrat for measuring different parameters. Parameters measured are above-ground and belowground biomass (AGB and BGB respectively), total SOC content, dissolved organic carbon (DOC), soil respiration (R_s) and microbial biomass carbon (MBC). For each parameter, 5–10 replicates were taken at each time of observation. For the estimation of BGB, MBC and SOC, only the top 5 cm layer was considered. All the parameters were estimated once in the first week of every month for 12 months (from June 2008 to May 2009).

AGB was estimated by dry weight basis. Whole plant parts were clipped (2 cm above the ground level) from 20 × 20 cm area. The collected samples (five replicates) were oven-dried and dry weights were measured.

For the estimation of BGB, soil cores of 6 cm diameter (up to 5 cm depth) were taken from grass and herbaceous cover. The collected cores (five for each cover) were placed in a 500 ml beaker filled up with water. Large-size roots were hand-picked and other roots were segregated by passing the suspension through sieves of different mesh size (500, 250 and 53 μm). The collected roots were packed in a filter paper, oven-dried and dry weights were measured.

Soil pH was measured at a soil:water ratio of 1:5 (weight/volume). Particle size separation of the soil samples was done using the pipette method²¹.

Soil respiration was measured *in situ* following the alkali absorption method²². Ten cylindrical plastic chambers (18 cm diameter and 20 cm height) were randomly placed in grass and herbaceous cover (ten in each cover). Aboveground vegetation was removed before the measurements. Each cylinder was inserted into a depth of 3 cm of the soil surface. CO₂ efflux was collected in small plastic chambers with 20 ml 1 M NaOH over a 24 h period. The amount of CO₂ absorbed was estimated by titrating with 1 M HCl using phenolphthalein as an indicator.

Prior to SOC estimation, the air-dried soil samples were passed through 2 mm sieve to remove roots and other organic materials. SOC and DOC were estimated by wet oxidation method²³. DOC was extracted following the protocol of Jones and Willett²⁴. Briefly, 20 g soil sample was mixed with 40 ml of distilled water. The mixture was kept on a shaker for 2 h. Subsequently the samples were left static overnight. Supernatant was passed

through Whatman (No. 41) paper. These samples were analysed by wet oxidation method²³. Values obtained were considered as DOC.

MBC was estimated by chloroform fumigation extraction method²⁵. Briefly, 20 g of dried soil samples were taken in 250 ml Schott bottles. Nearly 10 ml of distilled water was added for moistening and triggering microbial activity. In control samples, 0.5 M K₂SO₄ was added immediately and placed on a shaker for 60 min. Subsequently they were filtered and organic carbon in the filtrate was estimated by wet oxidation. To another set of bottles, 3 ml of ethanol-free chloroform was added and sealed. These were incubated for 24 h in darkness. Later the bottles were kept open for the evaporation of chloroform. Then 0.5 M K₂SO₄ was added and the carbon content was estimated. MBC was calculated as the difference in organic carbon content between fumigated (C_f) and unfumigated soils (C_{uf}).

$$\text{MBC (g kg}^{-1}\text{)} = C_f - C_{uf}$$

Statistical analysis was done using SPSS (version 15.0 for windows). Mean values for AGB, BGB, SOC, DOC and MBC come from five replicates and for R_s the number of replicates is ten. ANOVA was done for all the parameters to find out whether the differences observed between the two ground covers are significant or not. Linear regression analysis was performed between two relevant parameters.

Grass (C₄ functional type) and herbaceous (C₃ functional type) covers showed distinct pattern in the measured parameters, reflecting the functional nature of the cover. Seasonal influence was observed in all the measured parameters of both the covers. Results of ANOVA showed significant difference ($P < 0.05$) in the measured parameters of both the covers.

Similarity was seen in particle size, pH and bulk density of soil samples coming from both the covers (Table 1). Proportion of sand was higher in grass cover. Proportion of clay was slightly higher in herbaceous cover.

AGB was maximum in grass cover (C₄ functional type) as compared to herbaceous cover (C₃ functional type) (Table 2). In both the covers higher biomass was observed during monsoon and minimal during summer months. In grass cover AGB production peaked during

monsoon and decreased in summer through winter. In herbaceous cover peak production was also observed during monsoon. Unlike grass cover in herbaceous cover the AGB showed a double peak/dip pattern (Table 2). BGB was higher in herbaceous cover compared to grass cover (Table 2). Pattern of variation in BGB was similar to that of AGB.

Soil respiration values were relatively higher in herbaceous cover. Seasonal fluctuations in soil respiration values were similar in both the covers. Higher values were recorded in monsoon and relatively lesser values in winter (Table 3).

SOC content was higher in herbaceous cover (C₃ functional type) than in grass cover (C₄ functional type). Values of SOC in 12 months oscillated in a narrow range in grass cover (7.8–9.8 g kg⁻¹), whereas in herbaceous they moved in a wider range (15.6–23.2 g kg⁻¹, Table 4). Both the covers showed higher SOC values during monsoon season and relatively lesser in the summer season.

MBC in grass cover ranged from 60 to 234.6 mg kg⁻¹ and in herbaceous cover it was 106–343.3 mg kg⁻¹ in different months throughout the year (Table 3). Overall, the MBC values were higher in herbaceous cover than in grass cover. MBC in both the cover types showed similar seasonal pattern, increasing from June to September and decreasing from October to May. Highest MBC values were observed during monsoon and lowest in the summer season for both the cover types. DOC values were higher in grass cover compared to herbaceous cover (Table 4). They were maximum in the monsoon months and decreased gradually in summer through winter in both the covers. Highest DOC value was recorded in September for grass cover and in August for herbaceous cover. Lowest DOC value was noticed in April in both the covers.

Variability in BGB was well explained by AGB in grass cover ($r^2 = 0.71$; Figure 1a), whereas it was not seen in herbaceous cover ($r^2 < 0.1$). Variability in SOC was not explained by any of the measured parameters ($r^2 < 0.5$). Variability in MBC was explained by DOC and BGB in both the covers ($r^2 > 0.6$, Figures 1b, c and 2). Box plots drawn for measured parameters showed variations between the covers (Figure 3). The spread of variation was different in both the covers.

Both the vegetal covers differed in their productivity and tenure of existence. These features showed an impact on organic carbon inputs to the soil. Values of different parameters measured showed the influence of functional nature of ground vegetal cover (C₃ or C₄).

AGB was consistently higher in grass cover, which had a positive impact on fresh inputs of carbon into the soil. AGB values of grass cover recorded in the present study were higher^{12,13} or similar^{26,27} to the published data. Higher AGB values in grass cover were attributed to its standing biomass. AGB values of herbaceous cover were similar to the findings of Sharma and Upadhyaya¹⁵ and Das *et al.*¹⁶. AGB in herbaceous cover moved according

Table 1. Soil properties of grass and herbaceous covers of the permanent plot

Soil property	Grass cover	Herbaceous cover
Soil texture		
Sand (%)	74	63
Silt (%)	24	30
Clay (%)	02	07
Soil pH	6.91	6.92

Table 2. Mean values ($n = 5$) of AGB and BGB of herbaceous and grass covers

Month	AGB		BGB	
	Herbaceous cover	Grass cover	Herbaceous cover	Grass cover
January	677.5 ± 2.5	1792.5 ± 37.8	59.1 ± 2.3	62.4 ± 20.2
February	930.0 ± 102.7	1733.3 ± 68.8	52.7 ± 7.0	42.8 ± 23.1
March	920.8 ± 38.2	1566.7 ± 68.8	82.3 ± 19.1	32.8 ± 1.2
April	387.5 ± 7.2	1558.3 ± 59.1	74.4 ± 2.0	31.6 ± 2.0
May	354.2 ± 15.7	1553.3 ± 5.8	54.2 ± 1.0	26.5 ± 20.0
June	369.5 ± 0.7	1549.2 ± 1.4	103.4 ± 4.2	37.3 ± 2.3
July	775.0 ± 66.1	1558.3 ± 62.9	104.6 ± 14.7	60.3 ± 30.0
August	825.0 ± 66.1	2066.7 ± 50.2	112.4 ± 4.2	113.3 ± 10.6
September	883.3 ± 38.2	2041.7 ± 118.2	94.0 ± 0.6	74.4 ± 8.3
October	803.0 ± 25.5	1954.0 ± 6.9	95.5 ± 16.0	71.7 ± 15.0
November	805.0 ± 8.7	1978.3 ± 30.1	71.7 ± 4.6	62.4 ± 28.0
December	711.7 ± 1.4	1851.7 ± 2.9	66.6 ± 2.0	62.4 ± 10.3

AGB, Aboveground biomass (g m^{-2}). BGB, Belowground biomass (g m^{-2} ; up to 5 cm depth). \pm , Values indicate standard deviation.

Table 3. Mean values of MBC ($n = 5$) and R_s ($n = 10$) of herbaceous and grass covers

Month	MBC		R_s	
	Herbaceous cover	Grass cover	Herbaceous cover	Grass cover
January	158.3 ± 2.5	98.0 ± 3.5	11.7 ± 1.1	10.5 ± 0.4
February	106.0 ± 8.0	96.2 ± 5.8	12.6 ± 5.8	12.4 ± 0.5
March	117.5 ± 1.3	65.3 ± 3.1	14.1 ± 1.1	14.1 ± 0.3
April	124.7 ± 5.5	60.0 ± 2.0	13.5 ± 1.1	12.3 ± 0.2
May	151.3 ± 3.1	72.0 ± 5.3	14.1 ± 1.3	11.8 ± 0.2
June	209.3 ± 2.3	170.0 ± 2.0	13.8 ± 1.3	12.8 ± 0.1
July	268.0 ± 8.0	230.6 ± 18.0	13.3 ± 0.8	13.0 ± 0.2
August	343.3 ± 20.8	234.6 ± 12.2	15.4 ± 1.5	15.2 ± 0.3
September	305.3 ± 3.8	220.5 ± 11.0	12.8 ± 1.5	12.0 ± 0.1
October	215.3 ± 2.9	210.0 ± 9.2	15.3 ± 0.9	15.3 ± 0.2
November	160.0 ± 2.0	167.3 ± 1.2	12.1 ± 0.8	12.0 ± 0.3
December	148.0 ± 12.0	155.3 ± 6.9	11.8 ± 1.4	11.9 ± 0.1

MBC, Microbial biomass carbon (mg kg^{-1}). R_s , Soil respiration ($\text{g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$). \pm , Values indicate standard deviation.

to the cyclical pattern of ephemeral vegetation. Species occurrence in this cover was affected by the life-cycle pattern of each species. Peak production of biomass by a species was coupled to its life cycle. These differences showed an impact on AGB values of herbaceous cover. AGB in both the covers was higher during monsoon and lower in summer. This was a typical seasonality impact mostly influenced by the water availability. BGB was relatively higher in herbaceous cover compared to grass cover. BGB values in the present study were less compared to published reports^{13,28}. Ratio of BGB/AGB in both these covers was an indication that the soils are nutrient-rich²⁹. Differences in AGB and BGB allocation indicated the functional difference in both these ground covers. Similar to earlier findings³⁰⁻³³, BGB was higher during monsoon in both the covers. The quantity and periodicity of addition of dead biomass to the soils are influenced by the biomass produced in both the covers. Ephemeral nature of herbaceous cover increased inputs of

organic carbon into these soils. Addition of similar quantities of dead biomass (within a year) was unlikely in the grass cover owing to its longer duration of stay. Variations in the addition of organic carbon to the soil have affected the values of the measured parameters.

R_s values of both the covers were higher than those reported³⁴, indicating the dynamics of tropical ground cover. R_s values measured in the present study include both autotrophic and heterotrophic respiration. It is controlled by organic carbon inputs (fresh and/or dead) and their decomposability. Earlier reports mentioned that R_s is influenced by photosynthetic assimilate supply^{17,35}. A higher R_s value during monsoon seen in the present study (in both the covers) was attributed to higher biomass production, which increases fresh inputs into the soil. Earlier studies^{36,37} also reported that high rate of CO_2 released during the rainy season could be due to a congenial environment for the microorganisms dwelling in the soil decomposing organic matter. Low rate of CO_2 release from

Table 4. Mean values ($n = 5$) of SOC and DOC of herbaceous and grass covers

Month	SOC		DOC	
	Herbaceous cover	Grass cover	Herbaceous cover	Grass cover
January	22.0 ± 2.8	7.8 ± 0.2	114.7 ± 0.8	112.0 ± 2.3
February	18.9 ± 3.5	8.8 ± 0.1	119.3 ± 0.1	106.0 ± 1.8
March	18.9 ± 2.2	9.2 ± 0.1	116.0 ± 2.5	118.4 ± 2.3
April	20.2 ± 3.2	9.6 ± 0.2	98.0 ± 3.2	92.0 ± 1.2
May	20.4 ± 3.2	9.8 ± 0.1	108.3 ± 1.5	140.0 ± 10.5
June	21.0 ± 2.5	9.1 ± 0.1	140.7 ± 0.6	145.3 ± 8.5
July	20.5 ± 4.5	9.6 ± 0.1	151.3 ± 1.6	170.6 ± 11.5
August	23.2 ± 4.8	9.8 ± 0.1	168.7 ± 2.2	152.0 ± 5.8
September	15.6 ± 3.9	9.0 ± 0.1	168.3 ± 19.1	185.0 ± 30.0
October	17.8 ± 3.0	9.6 ± 0.1	152.7 ± 7.4	159.3 ± 6.4
November	16.2 ± 3.4	8.7 ± 0.1	162.76 ± 5.6	151.0 ± 2.3
December	17.0 ± 3.4	8.6 ± 0.3	138.0 ± 3.2	124.0 ± 1.5

SOC, Soil organic carbon (g kg^{-1}). DOC, Dissolved organic carbon (mg kg^{-1}). \pm , Values indicate standard deviation.

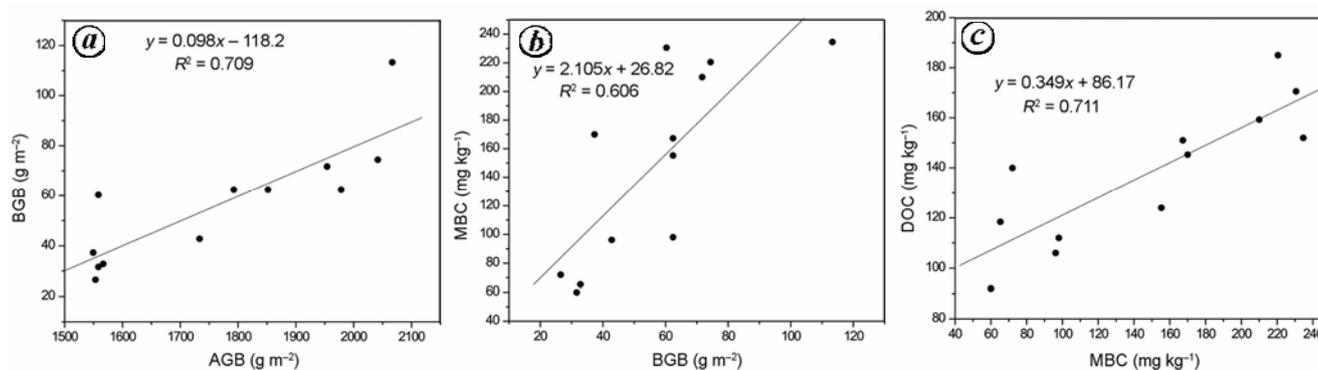


Figure 1. Correlation between AGB and BGB (a), BGB and MBC (b), and MBC and DOC (c) of C_4 cover. AGB, Aboveground biomass; BGB, Belowground biomass; MBC, Microbial biomass carbon and DOC, Dissolved organic carbon.

the soil in the summer months in grass and herbaceous covers seen in the present study is attributed to low moisture content of the soil, temperature and relative humidity, thereby inhibiting the microbial activity and decomposition^{36,38}.

Like R_s , DOC in both the covers showed higher values during monsoon, coinciding with biomass production. Higher values of DOC had a positive impact on MBC (Figures 1 and 2). Higher BGB and MBC also seen during this season correlate with these values (Figures 1 and 2). The microbial contribution to R_s has been shown to respond more rapidly and sensitively to assimilate supply^{39–41}. MBC values in the present study were maximum during monsoon moving together with fresh inputs, and this coincided with R_s values during monsoon. R_s values were relatively higher in herbaceous cover. This was correlated with more organic matter inputs (both fresh and dead; Figure 2 and Table 2). In grass cover longevity of standing biomass lessened dead matter input. Input fall in this cover can also be attributed to larger maintenance costs of higher AGB⁴². Lesser R_s values in winter and

summer seen in both the covers were attributed to a fall in fresh inputs and slower utilization of dead organic matter. An earlier study¹⁸ reported that half of the biological activity in the soil is fuelled by carbon that is fixed through photosynthesis in few hours (grasslands), and the other half by dead organic matter supplied as litter that is fixed months or years earlier. From the R_s values of the present study it can be concluded that in the tropics with similar ground cover, 50:50 division of soil biological activity for the supplied C cannot be seen. It differs as organic matter inputs are controlled by the life-cycle dynamics and functional type (C_3/C_4) variations.

MBC was more in herbaceous cover compared to grass cover. This was attributed to higher chemical diversity (coming from a large number of species) and higher dead organic matter inputs. Stimulation of soil microbial biomass/activity by organic carbon inputs has been well documented^{43–47}. In the present study, a positive relationship was observed between BGB and MBC. This is expected as roots are immediate sources for fresh inputs. Fine root turnover also adds easily decomposable organic

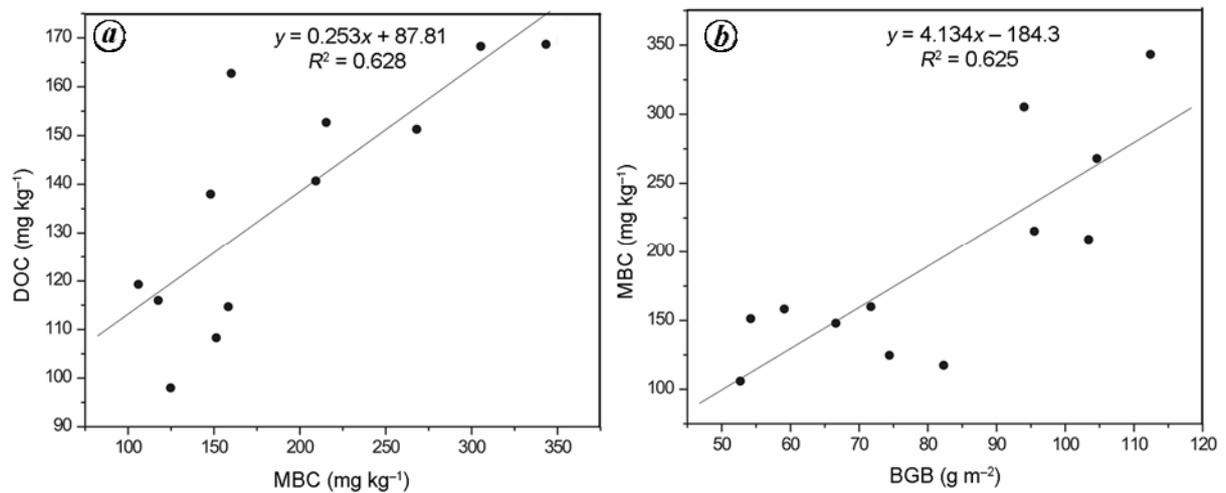


Figure 2. Correlation between MBC and DOC (a) and BGB and MBC (b) of C₃ cover.

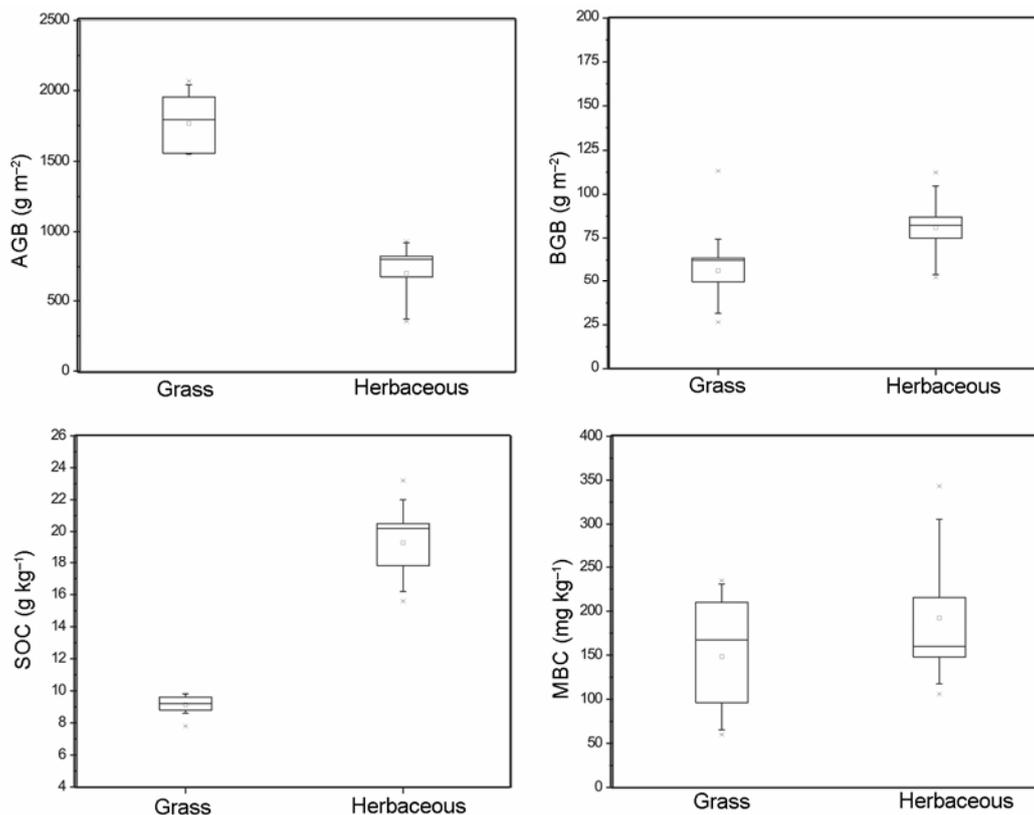


Figure 3. Box plots of AGB, BGB, SOC (soil organic carbon) and MBC.

matter affecting MBC. Organic matter in the soils can be easily utilized by microbes as coming from fresh inputs or from partly decomposed structures. Increased soil C inputs enhance soil microbial activity/MBC¹².

SOC values were remarkably different between the two covers. An earlier study⁴⁸ reported that plant functional traits regulate net soil carbon storage by controlling car-

bon assimilation, its transfer and storage in BGB, and its release from the soil through respiration and leaching. Higher SOC values in herbaceous cover reflect its ability to hold larger quantities of organic carbon improving soil fertility. Relatively stable SOC values seen in grass cover indicate that either the input of organic matter or their proportion of expenditure remains uniform. Higher

standing biomass throughout will also increase photosynthate spending for maintenance⁴². Unlike grass cover, input of fresh and dead organic matter into soils was significantly different in herbaceous cover. Temporal differences in the completion of life cycle of ephemerals have an impact on modulation/timing of inputs. All these are reflected in the SOC values. The observed changes could get accentuated in tropical soils covered with herbaceous (C₃ functional type) ground cover because of climate change (especially to rising CO₂ levels). Both the covers showed significant differences in all the measured parameters across different seasons, indicating seasonal impact. From the values of MBC, biomass inputs (into soil), R_s and SOC in the two functional types of the present study, we can establish that there is a significant difference in the activities of important biological processes in these two covers influencing SOC dynamics.

The study highlights significant differences in the measured parameters in two different functional types of ground cover. Measured parameters showed seasonal variation. These differences were manifested in soil carbon dynamics beneath the respective covers. Observed changes could get accentuated in tropical soils, especially covered with herbaceous (C₃ functional type) ground cover because of climate change (rising CO₂ levels).

1. Jobbagy, E. G. and Jackson, R. B., The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol. Appl.*, 2000, **10**, 423–436.
2. Dixon, R. K., Brown, S., Houghton, R. A., Solomon, A. M., Trexler, M. C. and Wisniewski, J., Carbon pools and flux of global forest ecosystems. *Science*, 1994, **263**, 185–190.
3. Lal, R., Carbon sequestration, terrestrial. *Encycl. Energy*, 2004, **1**, 289–298.
4. Lal, R., Soil carbon sequestration to mitigate climate change. *Geoderma*, 2004, **123**, 1–22.
5. Kemmitt, S. J. *et al.*, Mineralization of native soil organic matter is not regulated by the size, activity or composition of the soil microbial biomass – a new perspective. *Soil Biol. Biochem.*, 2008, **40**, 61–73.
6. Gill, R. A. and Burke, I. C., Ecosystem consequences of plant life form change at three sites in the semiarid United States. *Oecologia*, 1999, **121**, 551–563.
7. Malhi, Y., Baldocchi, D. D. and Jarvis, P. G., The carbon balance of tropical, temperate and boreal forests. *Plant Cell Environ.*, 1999, **22**, 715–740.
8. Lewis, S. L. *et al.*, Increasing carbon storage in intact African tropical forests. *Nature*, 2009, **457**, 1003–1006.
9. Piao, S., Fang, J., Ciais, P., Pcylin, P., Huang, Y., Sitch, S. and Wang, T., The carbon balance of terrestrial ecosystems in China. *Nature*, 2009, **458**, 1009–1013.
10. Han, F., Hu, W., Zheng, J., Du, F. and Zhang, X., Estimating soil organic carbon storage and distribution in a catchment of Loess Plateau, China. *Geoderma*, 2010, **154**, 261–266.
11. Grace, J., Jose, J. S., Meir, P., Miranda, H. S. and Montes, R. A., Productivity and carbon fluxes of tropical savannas. *J. Biogeogr.*, 2006, **33**, 387–400.
12. Xiao, C., Janssens, I. A., Liu, P., Zhou, Z. and Sun, O. J., Irrigation and enhanced soil carbon input effects on below-ground carbon cycling in semi arid temperate grasslands. *New Phytol.*, 2007, **174**, 835–846.
13. Cahill, K. M., Kucharik, C. J. and Foley, J. A., Prairie restoration and carbon sequestration: difficulties quantifying carbon sources and sinks using a biometric approach. *Ecol. Appl.*, 2009, **19**, 2185–2201.
14. Nakagami, K. *et al.*, Soil carbon stock in typical grasslands in Japan. *Grassl. Sci.*, 2009, **55**, 96–103.
15. Sharma, K. P. and Upadhyaya, B. P., Phytosociology, primary production and nutrient retention in herbaceous vegetation of the forestry arboretum on the Aravalli hills at Jaipur. *Trop. Ecol.*, 2002, **43**, 325–335.
16. Das, D. K., Chaturvedi, O. P., Mandal, M. P. and Kumar, R., Effect of tree plantations on biomass and primary productivity of herbaceous vegetation in eastern India. *Trop. Ecol.*, 2008, **49**, 95–101.
17. Bahn, M. *et al.*, Soil respiration in European grasslands in relation to climate and assimilated supply. *Ecosystems*, 2008, **11**, 1352–1367.
18. Hogberg, P. and Read, D. J., Towards a more plant physiological perspective on soil ecology. *Trends Ecol. Evol.*, 2006, **21**, 548–554.
19. Kuzyakov, Y., Sources of CO₂ efflux from soil and review of partitioning methods. *Soil Biol. Biochem.*, 2006, **38**, 425–448.
20. Jha, P. and Mohapatra, K. P., Soil respiration under different forest species in the riparian buffer of the semi-arid region of northwest India. *Curr. Sci.*, 2011, **100**(9), 1412–1420.
21. Kilmer, V. J. and Alexander, L. T., Methods of making mechanical analysis of soils. *Soil Sci.*, 1949, **58**, 15–24.
22. Anderson, J. P. E., Measurement of CO₂ evolution rates (long term assay). In *Methods in Applied Soil Microbiology and Biochemistry* (eds Alef, K. and Nannipieri, P.), Academic Press, London, 1982, pp. 464–465.
23. Walkley, A. and Black, I. A., An examination of the Degtjareff method for determining soil organic matter and proposed modifications of the chromic acid titration method. *Soil Sci.*, 1934, **37**, 29–38.
24. Jones, D. L. and Willett, V. B., Experimental evaluation of methods to quantify dissolved organic nitrogen (DON) and dissolved organic carbon (DOC) in soil. *Soil Biol. Biochem.*, 2006, **38**, 991–999.
25. Witt, C., Gaunt, J. L., Glaiacia, C. C., Ottow, J. C. G. and Neue, H. U., A rapid chloroform-fumigation extraction method for measuring soil microbial biomass carbon and nitrogen in flooded rice soils. *Biol. Fert. Soil*, 2000, **30**, 510–519.
26. Hector, A. *et al.*, Plant diversity and productivity experiments in European grasslands. *Science*, 1999, **286**, 1123–1126.
27. Weigelt, A., Weisser, W. W., Buchmann, N. and Scherer-Lorenzen, M., Biodiversity for multifunctional grasslands: equal productivity in high-diversity low-input and low-diversity high-input systems. *Biogeosciences*, 2009, **6**, 1695–1706.
28. Fiala, K., Tuma, I. and Holub, P., Effect of manipulated rainfall on root production and plant belowground dry mass of different grassland ecosystems. *Ecosystems*, 2009, **12**, 906–914.
29. Schmid, I., The influence of soil type and interspecific competition on the fine root system of Norway spruce and European beech. *Basic Appl. Ecol.*, 2002, **3**, 339–346.
30. John, B., Pandey, H. N. and Tripathi, R. S., Vertical distribution and seasonal changes of fine and coarse root mass in *Pinus kesiya* Royle Ex. Gordon forest of three different ages. *Acta Oecol.*, 2001, **22**, 293–300.
31. Gill, R. A. and Jackson, R. B., Global patterns of root turnover for terrestrial ecosystems. *New Phytol.*, 2000, **147**, 13–31.
32. Luo, Y., Meyerhoff, P. A. and Loomis, R. S., Seasonal patterns and vertical distributions of fine roots of alfalfa (*Medicago sativa* L.). *Field Crops Res.*, 1995, **40**, 119–127.
33. Rytter, R. M. and Hansson, A. C., Seasonal amount, growth and depth distribution of fine roots in an irrigated and fertilized *Salix viminalis* L. plantation. *Biomass Bioenergy*, 1996, **11**, 129–137.

34. Zhu, J., Yan, Q., Fan, A., Yang, K. and Hu, Z., The role of environmental, root, and microbial biomass characteristics in soil respiration in temperate secondary forests of northeast China. *Trees*, 2009, **23**, 189–196.
35. Bahn, M., Schmitt, M., Siegwolf, R., Richter, A. and Brtiggermann, S., Does photosynthesis affect grassland soil-respired CO₂ and its carbon isotope composition on a diurnal timescale? *New Phytol.*, 2009, **182**, 451–460.
36. Devi, N. B. and Yadava, P. S., Seasonal dynamics in soil microbial biomass C, N and P in a mixed oak forest ecosystem of Manipur, North-east India. *Appl. Soil Ecol.*, 2006, **31**, 220–227.
37. Devi, N.B. and Yadava, P. S., Emission of CO₂ from the soil and immobilization of carbon in microbes in a subtropical mixed oak forest ecosystem, Manipur, North-east India. *Curr. Sci.*, 2009, **96**(12), 1627–1630.
38. Kosugi, Y. *et al.*, Spatial and temporal variation in soil respiration in a Southeast Asian tropical rainforest. *Agric. For. Meteorol.*, 2007, **147**, 35–47.
39. Bahn, M., Knapp, M., Garajova, Z., Pfahringer, N. and Cernusca, A., Root respiration in temperate mountain grasslands differing in land use. *Glob. Change Biol.*, 2006, **12**, 995–1006.
40. Heinemeyer, A., Ineson, P., Ostle, N. and Fitter, A. H., Respiration of the external mycelium in the arbuscular mycorrhizal symbiosis shows strong dependence on recent photosynthates and acclimation to temperature. *New Phytol.*, 2006, **171**, 159–170.
41. Moyano, F. E., Kutsch, W. L. and Schulze, E. D., Response of mycorrhizal, rhizosphere and soil basal respiration to temperature and photosynthesis in a barley field. *Soil Biol. Biochem.*, 2007, **39**, 843–853.
42. Carbone, M. S. and Trumbore, S. E., Contribution of new photosynthetic assimilates to respiration by perennial grasses and shrubs: residence times and allocation patterns. *New Phytol.*, 2007, **176**, 124–135.
43. Goyal, S., Chander, K., Mundra, M. C. and Kapoor, K. K., Influence of inorganic fertilizers and organic amendments on soil organic matter and soil microbial properties under tropical conditions. *Biol. Fert. Soils*, 1999, **29**, 196–200.
44. Chowdhury, M. A. H., Kouno, K., Ando, T. and Nagaoka, T., Microbial biomass, S mineralization and S uptake by African millet from soil amended with various composts. *Soil Biol. Biochem.*, 2000, **32**, 845–852.
45. Garcia-Gill, J. C., Plaza, C., Soler-Rovira, P. and Polo, A., Long-term effects of municipal solid waste compost application on soil enzyme activities and microbial biomass. *Soil Biol. Biochem.*, 2000, **32**, 1907–1913.
46. Peacock, A. D., Mullen, M. D., Ringelberg, D. B., Tyler, D. D., Hedrick, D. B., Gale, P. M. and White, D. C., Soil microbial community responses to dairy manure or ammonium nitrate applications. *Soil Biol. Biochem.*, 2001, **33**, 1011–1019.
47. Tu, C., Ristaino, J. B. and Hu, S., Soil microbial biomass and activity in organic tomato farming systems: effects of organic inputs and straw mulching. *Soil Biol. Biochem.*, 2006, **38**, 247–255.
48. De-Deyn, G. B., Cornelissen, J. H. C. and Bardgett, R. D., Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecol. Lett.*, 2008, **11**, 516–531.

ACKNOWLEDGEMENTS. We thank the Department of Science and Technology, New Delhi, for funding through the SSS Programme and Indian Institute of Remote Sensing, Dehradun, for financial assistance through ISRO–GBP Programme (NVCPA project).

Received 18 November 2010; revised accepted 25 August 2011

Cry1Ac expression in transgenic *Bt* cotton hybrids is influenced by soil moisture and depth

D. Blaise^{1,2,*} and K. R. Kranthi¹

¹Central Institute for Cotton Research, Nagpur 440 010, India

²Present address: Indian Institute of Soil Science, Berasia Road, Bhopal 462 038, India

Cry1Ac toxin concentration was assessed in leaves of *Bt* transgenic cotton hybrid grown on shallow (<60 cm) and deep (>90 cm) black soils of Nagpur, Maharashtra, India. Cry toxin concentration increased up to 80 days after sowing followed by a steep decline. In general, toxin concentration was greater on the deep black soils than the shallow soil. This was because of greater water-holding capacity of the deep soils. Cry toxin concentration was closely related to the soil water content. Beyond (excess moisture) and below (moisture deficit) field capacity, toxin concentration declined. A cubic polynomial best described the relationship between Cry toxin concentration and soil moisture content ($R^2 = 0.95$).

Keywords: *Bt* cotton hybrid, black and shallow soil, Cry toxin, soil moisture.

COTTON cultivation, in India, was transformed after the introduction of *Bt* cotton hybrids. At present, almost the entire cotton acreage is planted under *Bt* transgenic hybrids. Consequently, productivity in the post-*Bt* era increased from 303 kg/ha in 2001–02 to 526 kg lint/ha in 2008–09 (ref. 1). Compared to the world average, however, productivity levels are still low mainly because of the abiotic constraints². Most of the cotton grown in the country is rain-dependent and the crop experiences moisture stress. Furthermore, cotton is grown on soils of varying depths, and it has been observed that productivity is better on deep Vertisols compared to the shallow soils because the former has a better water-holding capacity³. Apart from productivity being affected, Cry toxin expression may also be affected. Water stress has been reported to affect expression of transgenes in transgenic crops such as maize⁴, peas⁵ and cotton^{6–8}. This has serious implications: (i) ineffective pest control; (ii) pest becoming resistant to the *Bt* toxin, and (iii) high pesticide use. Kranthi *et al.*⁹ demonstrated that the toxin expression declined with crop age in all the *Bt* hybrids tested. Under rainfed conditions of central India, rains cease early in September. Thus, the crops grown in deep Vertisols are less likely to experience moisture stress than those grown on shallow soils. However, the impact on the Cry toxin production is less known. To address this issue field studies were conducted to assess the effect of soil depth on Cry toxin expression.

*For correspondence. (e-mail: blaise_123@rediffmail.com)