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ORIGINAL ARTICLE

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Impact of rainfall gradient on aboveground biomass and soil organic carbon dynamics of forest covers in Gujarat, India

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Abstract Alterations in precipitation are affecting forest ecosystems' soil carbon cycling. To understand how shifts in rainfall may alter these carbon pools, aboveground biomass (AGB), soil organic carbon (SOC), and microbial biomass carbon (MBC) of tropical forest covers were measured across a rainfall gradient (543–1590 mm) in Gujarat (India), a state falling under semi arid to tropical dry–wet conditions. Species diversity, tree density and soil texture were also measured. Field visits and data collection were carried out for 2 years (2009–2011) in 95 plots of 250 × 250 m in the forest covers across four distinct rainfall zones (RFZs). Data analysis showed that differences seen in the values of the measured parameters across the RFZs are statistically significant ($P < 0.05$). Positive correlations were observed between mean annual precipitation (MAP) and tree density, species diversity, AGB, SOC, and MBC. Across the RFZs, AGB ranged between 0.09 and 168.28 Mg ha^{-1}; SOC values (up to 25 cm soil depth) varied between 2.94 and 147.84 Mg ha^{-1}. Soil texture and MBC showed a significant impact on the dynamics of SOC in all the RFZs. MBC is more influenced by SOC rather than AGB. Both vegetation type and MAP have an important role in the regulation of SOC in tropical soils. Together, these results reveal complex carbon cycle responses are likely to occur in tropical soils under altered rainfall regimes.

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Keywords Rainfall · Forests · Biomass · Soil carbon · Microbial biomass carbon

Introduction

Increase in the frequency, duration, and/or severity of precipitation associated with climate change could fundamentally alter the composition, structure, and biogeography of forests in many regions (Allen et al. 2010). Food and Agricultural Organization (FAO, UN) classified tropical forests into six ecofloristic zones (the tropical rain forests, the moist deciduous forests, the dry zone, the very dry zone, the desert zone and the hill and mountain forests). These regions have a major impact on global biodiversity and carbon cycling. Variability in the amount of rainfall and its intensity are often considerable in tropical areas (Murphy and Lugo 1986) and spatial variability of rainfall strongly influences tropical ecosystem structure and function (Murphy and Lugo 1986; Meng et al. 2011). However, there are limited observations on how variation in mean annual precipitation (MAP) influences carbon stocks in tropical dry forests, particularly in India. Observing soil organic carbon (SOC) and above-ground biomass (AGB) across MAP spatial gradients can provide key insights to this problem.

Gómez-Aparicio et al. (2011) highlighted about the limited understanding of how growth of coexisting tree species varies along environmental gradients in Mediterranean water-limited forest ecosystems, and its implications for species interactions and community assembly under current and future climatic conditions. Water-limited ecosystems are likely to be highly responsive to altered precipitation regimes (Thomey et al. 2011). Drought may be responsible for the decrease in above-ground net primary productivity in forest ecosystems (Whittaker et al. 1974). This is likely to alter the standing biomass of the forests. The role of tropical forests is critical because they are carbon-dense and highly productive (Malhi and Grace 2000; Lewis 2006).

Reichstein et al. (2013) reported that sensitivity of the forest biome to climate extremes (such as drought or heavy precipitation) strongly affects standing biomass and carbon fluxes. Behaviour of these major land covers as one of the important carbon sinks in the near future is uncertain as erratic MAP is considerably affecting most of these mechanistic processes of these regions in an unprecedented manner.

Significant change in carbon stock followed by land-use and land-cover change has been reported earlier at global scale (Haberl et al. 2007; Don et al. 2011) as well as in India (Ravindranath et al. 1997, 2001; Chhabra and Dadhwal 2004; Bijalwan et al. 2010). Estimates indicate that forest covers in India store 3.43 Pg C in AGB while it is 20.99 Pg C in soil (up to 30 cm depth) (Ravindranath et al. 1997; Lal 2004). There is a pressing need to monitor the rate and extent of changes in forest covers in India for understanding its impact on terrestrial carbon storage. Given the implications of Kyoto Protocol and the imminent need to determine sources and sinks of carbon resulting from land-use change (and, perhaps, from natural processes as well), methods that can determine biomass accurately, repeatedly, and inexpensively are desperately needed (Houghton et al. 2001). Fast developing countries like India have to address these issues as a priority as they may be more severely affected by these changes.

AGB and SOC are directly linked as changes in vegetation cover alter inputs of organic matter into the top layers of soil (Jobbágy and Jackson 2000; Chaturvedi et al. 2011; Pan et al. 2011; Schmidt et al. 2011; Mehta et al. 2013). Tropical forests show a distinct pattern of distribution as carbon is partitioned more or less equally between the vegetation and soil (Malhi et al. 1999), unlike temperate or boreal forests, where soil carbon dominates. For example, Piao et al. (2009) found that ∼58 % of the tropical carbon stock lies in biomass with the rest in soil organic matter. Further, AGB is directly impacted by deforestation and degradation (Gibbs et al. 2007). Alterations to vegetation covers because of deforestation, reforestation, and agriculture are prone to alter carbon storage of soils (Bashkin and Binkley 1998; Post and Kwon 2000; Paul et al. 2002, 2003; Degryze et al. 2004; Richards et al. 2007). Globally, soil organic matter contains more than three times as much carbon as either the atmosphere or terrestrial vegetation (Schmidt et al. 2011). Pan et al. (2011) reported that tropical forests have 56 % of carbon stored in biomass and 32 % in soil, whereas boreal forests have only 20 % in biomass and 60 % in soil. Combinations in MAP and forest types lead to differences in the allotment of carbon between AGB and SOC. We hypothesize that variations in MAP are likely to change this distribution.

The carbon stock in terrestrial ecosystems represents the difference between the input from net primary production (in terms of quality and quantity) and the output through decomposition (Couteaux et al. 1995). Soil microbes play a pivotal role in litter decomposition processes. Schmidt et al. (2011) reported that environmental change can influence soil carbon cycling through changes in both metabolic activity and community structure of soil micro-organisms. Climatic factors such as precipitation and temperature have an influence on decomposition and microbial activities in soil (Aerts 1997; Berg 2000). Mehta et al. (2013) showed that vegetation type influences the SOC input through selective decomposition by microbes. Study of soil microbial biomass carbon (MBC) along with SOC, would be indicative of microbial activities at different depths in soil. Dinakaran and Krishnayya (2008) showed that soil texture influences SOC content. Dan-Dan et al. (2010) reported that understanding how spatial scale influences commonly-observed effects of soil texture on SOC storage is important for accurately estimating the SOC pool at different scales.

While several studies on the status of carbon stocks and forest biomass have been done earlier in Indian forests (Ravindranath et al. 1997, 2001, 2008; Chhabra and Dadhwal 2004; Lal 2004; Das et al. 2008; Patil et al. 2012), the impact of rainfall variation on AGB and SOC of tropical forests has not been addressed specifically. In this study, we measured AGB, SOC, MBC, and soil physical properties in established plots to ask,

- How do gradients in annual rainfall influence AGB?
- How are these gradients linked to soil texture, MBC and SOC?
- What are the implications of these variations on changing precipitation across tropical dry forests of India?

Methods

Study area

The study had been carried out across forest covers of Gujarat, a state falling in the western part of India, lying between 20°07′–24°41′N latitude and 68°10′–74°28′E longitude. The total geographical area of the state is 1,96,024 km^2, which is 6 % of total land cover of the country. The state is divided into 26 administrative divisions called Districts (Supplementary Material, Fig. S1). Human population of the state has increased from 26.7 (1971 census) to 60.4 million (2011 Census of India, http://www.censusindia.gov.in; http://www.censusgujarat.gov.in). The monthly minimum and maximum temperatures recorded in the state range between 2–15 °C and 38–45 °C across the state. The state experiences three distinct seasons in a year, Summer (March–June), Monsoon (July–October) and Winter (November–February). Mean annual precipitation (MAP) of the state is 699 mm (ranges between 380 and 1957 mm) across 26 districts (coming from the data of Indian Meteorological Department, http://www.imd.gov.in). 22 out of 26 districts of the

Gujarat state have been covered in this study (Supplementary Material, Fig. S1). Four districts falling in the arid zone (< 450 mm MAP) have been excluded as the vegetation cover there was negligible.

The study area, comprising of 22 districts of Gujarat state has been classified into four major rainfall zones (RFZ-1,2,3,4) (Fig. 1) based on MAP. MAP (coming from 50 year meteorological dataset, 1960–2010; Indian Meteorological Department, http://www.imd.gov.in) received at each zone (1–4) is 543 (474–633), 665 (518–788), 875 (818–951), 1590 (965–1957) mm respectively (Table 1). RFZ-1 includes 4 districts (Jamnagar, Porbandar, Rajkot, Surendranagar), RFZ-2 has 6 districts (Ahmedabad, Amreli, Bhavnagar, Gandhinagar, Junagadh, Sabarkantha), RFZ-3 has 5 districts (Anand, Bharuch, Dahod, Kheda, Panchmahals) and RFZ-4 has 7 districts (Dangs, Narmada, Navsari, Surat, Tapi, Vadodara, Valsad). These 22 districts cover ~66 % of geographical area of Gujarat (Fig. 1, Supplementary Material, Fig. S1). Geographical area occupied by each RFZ (1–4) is 19, 22, 12, and 13 % respectively (Gujarat Forest Statistics 2010–2011).

Geologically, the state consists of flows of basaltic rock surrounded by a fringe of alluvium. Major soil type is alluvial (sandy, sandy loam, sandy clay loam in texture). Soil colour ranges from light brown to dark brown, yellowish red to black. Soils are little acidic, neutral to highly alkaline in nature (data from Gujarat State Agricultural Marketing Board, http://agri.gujarat.gov.in). The state has a forest cover of 9.76 % (year 2011, Forest Survey of India (FSI), http://www.fsi.org.in; Forests and Environment Department, http://www.envforguj.in). More than 90 % area of this recorded forest cover is occupied by trees (Forest Survey of India (FSI), http://www.fsi.org.in; Forests and Environment Department, http://www.envforguj.in). As per the FAO classification, the forest cover is broadly categorised as tropical moist deciduous forest, tropical dry deciduous forest, tropical thorn forest and tropical littoral and swamp forest. Forests in the Gujarat state are unevenly distributed. The spread corresponds to the MAP received by each zone.

The forest cover has experienced many alterations during the past few decades. According to Gujarat Forest Statistics (2010–2011 Report), forest area (proportionate to geographical area) of RFZ-1 and 2 is 7.5 and 7.9 %; RFZ-3 and 4 is 10.6 and 34.3 %, respectively. About 40 % of the studied plots were coming from areas managed by the state forest department. These activities include plantation, measures to prevent

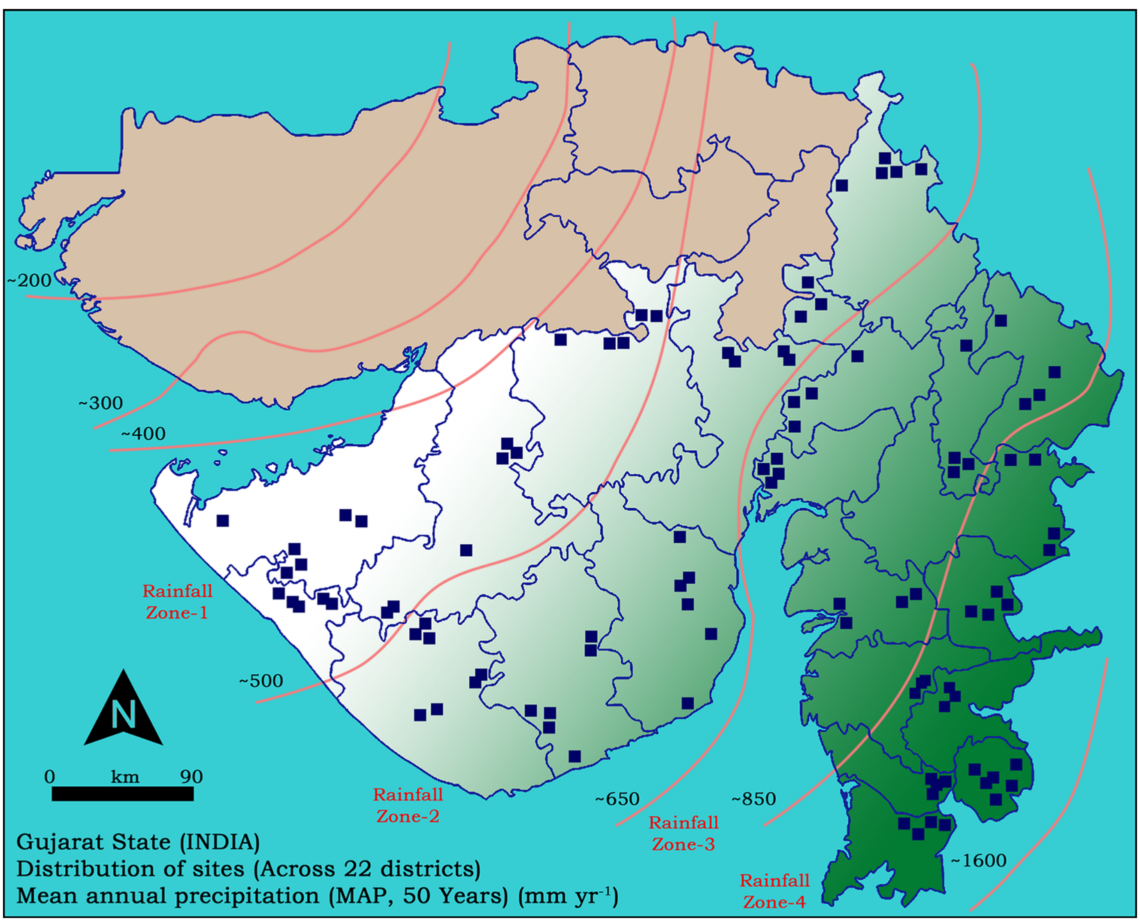

Fig. 1 Map of study area (Gujarat) showing distribution of 95 plots (*blue bullet points*) and mean annual precipitation (MAP, mm year^{-1}) of each rainfall zone (RFZ) (Rainfall data: Indian Meteorological Department data)

forest fire, allowing tribals to harvest forest produce judiciously. Plots are similarly influenced by human activities among all RFZs.

The state forest department has taken up massive reforestation and afforestation programs. At some parts of the state, species like *Tectona grandis*, *Dendrocalamus strictus*, *Butea monosperma*, *Diospyros melanoxylon*, *Eucalyptus globulus*, *Acacia catechu* have been extensively planted. Nearly 130 years ago, *Prosopis juliflora* was planted in arid and semi-arid regions of the state broadly to minimise the spread of desertification (Tewari et al. 2001). Over a period of time, this species spread widely and has become an invasive species. Nearly 700 km^2 area is occupied by this species, having a dubious distinction of ranking first in terms of distribution. Keeping the dominant impact of MAP on AGB of RFZs 1–4 aside, these activities also are likely to have an impact on AGB of these existing forest covers.

Field data collection

The research team of the National Vegetation Carbon Pool Assessment (NVCPA, IIRS, Dehradun) has marked sample plots of 250 × 250 m across these 22 districts of the study area. In each RFZ, sample plots having NDVI values (came from MODIS data of 2006–2008) ranging from 0.05 to 0.65 were marked. By utilizing the latitude and longitude of these 250 × 250 m plots, a total number of 95 sample plots were laid down across the state for this study (Table 1).

Field visits and data collection were carried out for 2 years (2009–2011). Four representative quadrats of 0.1 ha (31.62 × 31.62 m) had been randomly identified within each 250 × 250 m plot (Supplementary Material, Fig. S2). A total of 380 (95 × 4) 0.1 ha quadrats were laid down across the four RFZs. Each quadrat was demarcated by a measuring tape. Density and diversity of vegetation in each quadrat was noted. As per the protocol developed for the assessment of vegetation carbon pool (VCP) of the entire nation, all individual trees having > 10 cm GBH (girth at breast height) were included in the sampling (Field manual 2008, NVCPA project, IIRS-NRSC, ISRO Geosphere Biosphere Programme). Biophysical parameters for trees such as GBH and height and spread of canopy cover were measured. Girth (cm) over the bark of each tree was measured by a measuring tape at a height of 1.37 m from the ground level. Height (m) of the tree was measured by using Vertex Hypsometer. Spread of canopy cover was measured in 4 opposite directions from the bole surface to the peripheral end of canopy in respective directions. Many of the representative trees were marked by metal strips for long-term monitoring. Total number of primary, secondary, tertiary (or more according to the branching pattern) branches of individual trees were noted down and their length and circumference were measured. Ultimate and penultimate twigs (5–7 cm girth) with intact leaves were collected as a part of the semi harvest method for AGB estimation. Girth of these twigs (few centimetres above base) and length were recorded to obtain their volume. Two 5 × 5 m (diagonal corners of 0.1 ha quadrat) and five 1 × 1 m (4 corners and one at the centre of 0.1 ha quadrat) quadrats were demarcated within each 0.1 ha quadrat for the sampling of shrubs and herbs respectively (Supplementary Material, Fig. S2). Procedure followed for biophysical measurements of shrubs was nearly the same as of trees. Out of five 1 × 1 m quadrats laid down for herbs, two quadrats were sampled for biomass calculations. All the collected plant samples were brought to the laboratory in sealed bags. After washing, the samples were oven-dried at 70 °C until they showed a constant weight. Average number of trees (< 10 cm GBH) across all the plots was three.

Soil samples (up to 25 cm depth at 5 cm interval) were collected from each of the 0.1 ha quadrat. They were collected by following the trench method (for details refer Dinakaran and Krishnayya 2008). Samples were collected from 4 different locations randomly placed in the 0.1 ha quadrat. Each location represents the type of vegetation cover seen in the 0.1 ha quadrat. Samples coming from a particular depth of a quadrat were pooled together. This was treated as a composite sample for the soil at that particular depth. Litter debris was excluded from the soil samples of 0–5 cm. For each 250 × 250 m plot, there are 4 composite samples coming from the 4 quadrats of 0.1 ha. Total number of soil samples collected for all the plots were 95 × 4 × 5 (plots × quadrats × number of depths). Collected soil samples were brought to the laboratory in sealed covers. Samples were air dried and subsequently stored in a dry (humid free) environment until further analysis.

Above-ground biomass (AGB) calculations

Estimation of biomass was done by following semi harvest method developed in the National Vegetation Carbon Pool assessment program. In this method, the

Table 1 Number of districts selected, mean annual precipitation (MAP, mm $year^{-1}$) of past 50 years, number of plots (250 × 250 m) and quadrats (0.1 ha i.e., nearly 31.62 × 31.62 m) laid down across all rainfall zones (RFZs)

RFZ	Districts	MAP (1960–2010) (mm $year^{-1}$)	Plots (250 × 250 m)	Quadrats (0.1 ha)
1	4	543	22	88
2	6	665	31	124
3	5	875	20	80
4	7	1590	22	88

collected ultimate and penultimate twigs (5–7 cm in girth) were oven dried till constant weight obtained. Volume and biomass ratio was obtained. This ratio was utilised to convert the measured volume of a tree into AGB of the tree. Similar procedure was followed for estimating AGB of shrubs. Values of tree biomass were compared with values generated by using region and species-specific volumetric equations (developed and published by Forest Survey of India (FSI) 1996; Patil et al. 2012). Error values in these estimations were <10 %. To minimise the uncertainty associated with AGB estimates, we included GBH, height, and specific gravity in the calculations (as suggested in the 'biomass-diameter-height regression model' by Chave et al. 2005). The equation followed was:

$$V = a + b\, D^2 H$$

where V = volume (m^3) under bark; D = diameter at breast height (m) over bark (calculated by using GBH data); H = height of tree (m); a and b are statistical constants.

Region and species-specific gravity (wood density, g cm^{-3}) values (provided by Indian Institute of Remote Sensing, IIRS, Dehradun, India) were used to convert volume into biomass of each tree. Pooled AGB values of trees in a quadrat were considered as AGB of the quadrat. These were extrapolated to express AGB as Mg ha^{-1}.

Soil analysis

Soil characteristics

Soil pH was measured with a soil:water ratio of 1:5 (weight/volume) by using a digital pH meter. Analytical precision of the instrument was ± 0.01. Soil particle size (sand, silt and clay fraction) separation was done by pipette method (Kilmer and Alexander 1949) (for details check Supplementary Material, Mehta et al. 2013). Variations in the proportion of particle size were used to define soil texture. Soil bulk density was calculated by using an online soil calculator (CENTURY, model 4.0, http://www.nrel.colostate.edu/projects/century/) by incorporating soil particle size data.

Soil organic carbon (SOC) estimation

Estimation of SOC content in the collected soil samples was done by wet oxidation method (Walkley and Black 1934). The actual percentage of SOC content was calculated by multiplying the values of easily oxidizable carbon content obtained by Walkley and Black method with a correction factor (1.32). Replicates (n = 3) of each sample were estimated and mean values were calculated. The mean percentage of SOC was then converted to Mg C ha^{-1} of 5, 10, 15, 20, 25 cm depths of sampled soils. For better understanding of the changes in SOC at deeper depth, we extrapolated obtained values of SOC to 100 cm soil depth. The extrapolation has been done by using the following equations (Jobbágy and Jackson 2000, 2001; Yang et al. 2011).

$$Y = 1 - \beta^{d} \tag{1}$$

$$SOC_{100} = \left[\left(1 - \beta^{100}\right)/\left(1 - \beta^{25}\right)\right] * [SOC_{25}] \tag{2}$$

where, Y = cumulative proportion of the soil carbon pool from the soil surface to depth d (in this study 25 cm); β = the relative rate of decrease in the soil carbon pool with soil depth; SOC_{100} = the soil carbon pool in the upper 100 cm (Mg ha^{-1}); SOC_{25} = the soil carbon pool measured in this study up to 25 cm depth (Mg ha^{-1}). β value was calculated by Eq. 1 based on data generated in this study. β value differed for each sample plot (depending on the rate of decrease in SOC from one soil depth to another). Our β values ranged between 0.83 and 0.99.

Soil microbial biomass carbon (MBC) estimation

Soil microbial biomass carbon (MBC) estimation was done for the replicates (n = 3) of collected soil samples by chloroform fumigation extraction method (Witt et al. 2000) (Supplementary Material for further description). The method estimates organic carbon coming from active soil microbes. Obtained values indicate changes in the activity of soil microbial community across the soil profile.

Data analysis

One way ANOVA had been carried out using SPSS software to check whether the differences seen in the measured parameters (tree density, species diversity, AGB, SOC, MBC) across RFZs 1–4 are significant or not. Simple regression analysis was carried out to describe the pattern of relationship (linear or logarithmic) between the measured variables. Coefficient of correlation (Pearson's) was calculated to look at the relationships between variables.

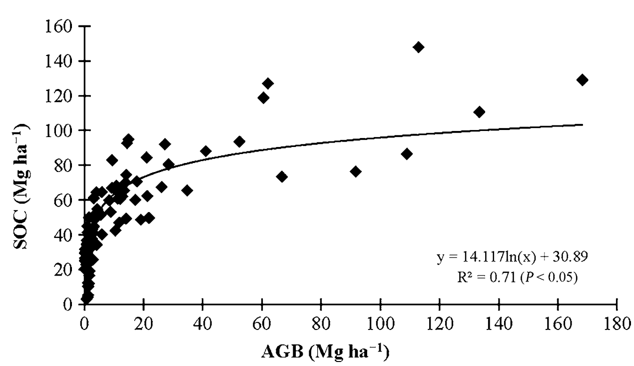

Fig. 2 Relationship between above ground biomass (AGB, Mg ha^{-1}) and soil organic carbon (SOC, Mg ha^{-1}) up to 25 cm soil depth, n = 95 across the rainfall zones (RFZs)

Results

Forest composition

In this study, 5,324 trees (> 10 cm GBH) were sampled and found to belong to one of 75 tree species belonging to 34 families (Supplementary Material, Table S1). 25 % of these (as representatives of plots across RFZs) have been marked with metal tags for future studies. Amongst the 75 tree species, 20 species were common to all plots. Few of these species were planted by the State Forest Department (Supplementary Material). Maximum species richness was found in the wettest zone, RFZ-4 (48 species, 29 families), while minimum diversity was found in RFZ-1 (8 species, 5 families). Recorded density of trees was also maximum in the wettest RFZ-4 (270 trees ha^{-1}) followed by RFZ-3 (218 trees ha^{-1}), RFZ-2 (135 trees ha^{-1}) and minimum in RFZ-1 (122 trees ha^{-1}) (Supplementary Material, Table S3).

GBH values ranged from 10 cm to 357.87 cm across the study area. RFZ-1 showed lowest mean of GBH (19.96 cm) ranging between 11.40 and 51.20 cm. Mean GBH values were the highest (46.60 cm) in RFZ-4 ranging between 10 and 357.87 cm. 8 % of the total recorded trees (across the four RFZs) fell in the GBH range of 10–13 cm (Supplementary Material, Table S2). Percentage of young trees (GBH, 10–13 cm) was in the range of 5–10 % across RFZs 1–4. It was almost the same (~9 %) for RFZ-1 and 4. Trees with higher GBH class (41–60 cm) are relatively higher in RFZ-3 and 4 (Supplementary Material, Table S2). Height of the trees was recorded in a range of 2.1–25.2 m across the study area. Average stand height of RFZ-4 is about two fold higher than RFZ-1.

Prosopis was the most common species followed by *Acacia spp* and *Diospyros* across RFZ-1 and 2. *Prosopis* was found to be very common in RFZ-1 with 60 % plots showing its dominance, while only 30 % of plots in RFZ-2 showed dominance of *Prosopis*. With increase in MAP, RFZ-3 and 4 showed more diverse vegetation with *Tectona* and *Butea* as dominating species followed by *Acacia spp*, *Wrightia, Diospyros, Holarrhaena, Terminalia, and Lagerstroemia*. From a functional type perspective, RFZ-1 and 2 had trees that were generally short and thorny with small leaves (showing xeric features), while RFZ-3 and 4 had trees that were taller and bearing well spread canopy and larger leaves (showing mesophytic features).

Above-ground biomass (AGB)

Herbs, shrubs and trees (saplings) of < 10 cm GBH accounted for < 5 % of the total AGB calculated across the plots, and were hence excluded from further consideration of AGB values. Mean AGB values of quadrats laid increased with an increase in the MAP (Fig. 3). AGB values were ranged between 0.61–2.72, 0.09–14.41, 0.70–66.73, 4.18–168.28 Mg ha^{-1} for RFZs 1–4 respectively (Supplementary Material, Fig. S3a–d). AGB values were influenced by tree characteristics such as GBH, height and wood density. RFZ-1 showed the lowest (1.57 ± 0.8 Mg ha^{-1}) value. Maximum mean value (47.63 ± 39.77 Mg ha^{-1}) for AGB was found in RFZ-4 (Fig. 3). Plots of RFZ-1 were mostly dominated by *Prosopis*. Native species could not establish well in these plots. AGB of these plots largely came from *Prosopis*. AGB values of plots dominated by *Prosopis* were nearly 7 times lower than the plots not dominated by *Prosopis* (< 10 %), for similar density values in RFZ-RFZ-2. In this zone, mean AGB value of *Prosopis* dominated plots was 0.72 Mg ha^{-1} while for plots with lesser density of *Prosopis* it was 5.46 Mg ha^{-1}. We found significant influence of species richness on AGB across these zones, especially at RFZ-3 and 4. Plots with 6–10 species showed mean AGB value of 20.5 ± 4.3 Mg ha^{-1} and plots with 17–37 tree species diversity showed 36.9 ± 4.6 Mg ha^{-1}.

Soil properties and carbon content

pH values for RFZs 1–4 ranged between 5.51 and 7.44. Soil texture was differing with wider dominance of sand fraction (40–60 %). Mean fraction of silt and clay was

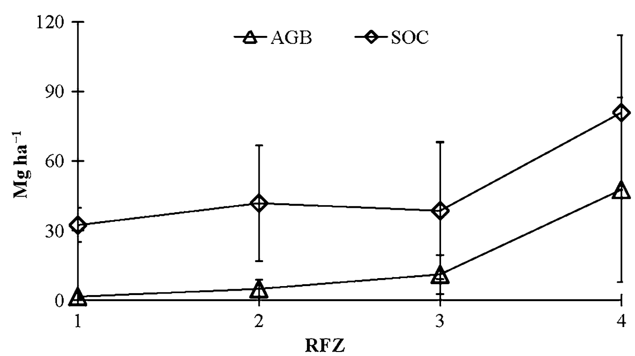

Fig. 3 Mean above ground biomass (AGB, Mg ha^{-1}) and mean soil organic carbon (SOC, Mg ha^{-1}) in each rainfall zone (RFZ)

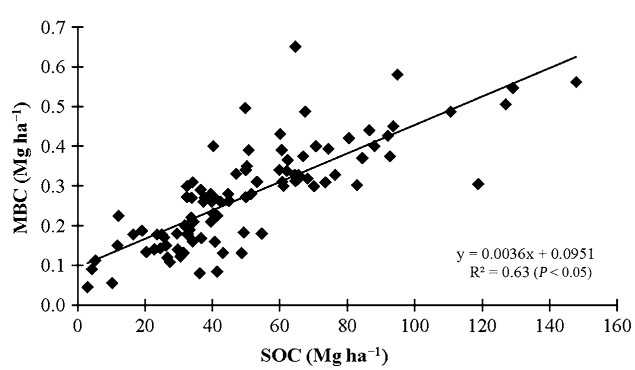

Fig. 4 Relationship between soil organic carbon (SOC, Mg ha^{-1}) and soil microbial biomass carbon (MBC, Mg ha^{-1}) up to 25 cm soil depth, n = 95 across the rainfall zones (RFZs)

the highest at RFZ-4 and was correlated with SOC. Bulk density values ranged between 1.13 and 1.80 (mean 1.42) g cm^{-3}.

SOC values measured at different depths across the study area are given in fig. S4 (Supplementary Material). RFZ-1 showed lowest values for SOC between 16.86 and 43.08 (mean SOC 32.37 ± 7.4) Mg ha^{-1} up to 25 cm depth. RFZ-2 and 3 showed mean SOC values of 41.78 ± 24.9 (5.88–92.64) Mg ha^{-1} and 38.56 ± 29.5 (2.94–92.01) Mg ha^{-1} respectively (Fig. 3). Higher SOC values were seen at RFZ-4 where mean SOC value was 80.81 ± 33.3 Mg ha^{-1} ranged between 34.08 and 147.84 Mg ha^{-1} (Fig. 3). Variations in SOC values across RFZs 1–4 coincided with the differences seen in AGB values (Supplementary Material, Fig. S3a–d). Across the zones, SOC values showed a typical vertical distribution, with higher values in the top layer as compared to the one beneath.

SOC values (up to 25 cm depth) were relatively lesser in plots of RFZ-2 dominated by *Prosopis* as compared to the ones occupied by native species stands. Species richness variation seen in RFZ-3 and 4 influenced SOC content up to 25 cm soil depth. Plots with lower diversity (~8 species, ranged between 6 and 10) showed 49.8 ± 27.8 Mg ha^{-1} SOC. Mean SOC was 82.9 ± 21.7 Mg ha^{-1} for plots with higher diversity (~20 species, ranged between 17 and 37) across RFZ-3 and 4.

We extrapolated the SOC data of this study (measured up to 25 cm depth) to obtain SOC values up to 100 cm depth (Jobbágy and Jackson 2000, 2001; Yang et al. 2011). This helps in knowing the amount of carbon stored across these RFZs up to 100 cm as this is the depth mostly referred in Global carbon cycle models (Jobbágy and Jackson 2000; Guo and Gifford 2002). Values projected indicate that the existing forest cover of Gujarat holds 5.28–421.85 Mg ha^{-1} SOC (up to 100 cm) across RFZs. RFZ-1 and 2 hold 61.50 (19.26–184.22) Mg ha^{-1} SOC up to 100 cm soil depth. Mean SOC value for RFZ-3 and 4 was 92.21 (5.28–421.85) Mg ha^{-1} up to 100 cm soil depth.

Mean soil MBC was maximum (0.11 Mg ha^{-1}) in top 5 cm and minimum (0.03 Mg ha^{-1}) in 20–25 cm depth across the four RFZs (Supplementary Material, Fig. S5a–b). Field observations indicate that this is related with large fresh organic carbon inputs (in the form of fallen litter) to the top soil. Maximum (0.40 Mg ha^{-1}) and minimum (0.16 Mg ha^{-1}) mean values of MBC were found in RFZ-4 and RFZ-1 respectively. MBC values across the zones differed in tune with MAP, AGB and SOC. However, MBC values did not show significant variation corresponding to species richness across RFZ-3 and 4.

Relationship of precipitation and carbon

One way ANOVA showed that differences seen in the values of the parameters (AGB, SOC, MBC) across the RFZs 1–4 are statistically significant ($P < 0.05$). Both linear and logarithmic regressions were performed to find the best fit line describing the relationship between parameters. AGB and SOC pair showed the best fit curve with logarithmic regression within a RFZ and across RFZs 1–4 (Fig. 2, Supplementary Material Fig. S3a–d). SOC and MBC values were more linearly related. SOC and MBC values coming from 0 to 5 cm and 0 to 25 cm showed higher R^2 values (0.78 and 0.71) as compared to the one coming from 20 to 25 cm ($R^2 = 0.59$) (Fig. 4, Supplementary Material Fig. S5a–b). This is attributed to the quantity and quality of litter reaching these depths.

MAP values of RFZs 1–4 regressed with mean values of density, diversity, GBH, SOC and MBC showed linear relationship (Supplementary Material, Table S4), while mean values of AGB showed logarithmic increase with the changes in MAP of RFZs 1–4 (Supplementary Material, Table S4). Coefficient of correlation values of these regression lines ranged between 0.77 and 0.99. MAP and AGB ($r = 0.99$, $R^2 = 0.98$) and, MAP and SOC ($r = 0.93$, $R^2 = 0.86$) showed the highest correlationship compared to MAP and diversity ($r = 0.77$, $R^2 = 0.59$) (Supplementary Material, Table S4). Higher coefficient of correlation for the parameters density, diversity, GBH, AGB, SOC and MBC with MAP indicated their sensitivity towards fluctuations in rainfall (Supplementary Material, Table S4). All of the regressions are statistically significant ($P < 0.05$).

Discussion

Rainfall, vegetation cover and above-ground biomass

The study area falls under semi arid to tropical dry and wet conditions (Koppen's classification system 1931). Differences seen in the MAP of RFZs 1–4 indicate the broad range of precipitation received by these RFZs annually. These differences showed a distinct demarcation on the diversity and distribution of forest tree cover across the four RFZs. Our observations on the dominant trees across RFZ-1 and 2 showed their adaptability to water scarcity by having smaller leaves, open canopy, short stature with relatively slower growth. Greater representation by *Prosopis* in these zones indicate its suitability to grow better in these zones. Dominant trees of RFZ-3 and 4 are distinct in their habit having broad leaves, thick and wide spread canopy and robust growth. These tree forms are comparable with tree species reported earlier for semi arid and tropical dry forests with similar range of rainfall (Jha and Mohapatra 2010; Chaturvedi et al. 2011; Conti and Díaz 2013). Density and diversity of trees were lesser in RFZ-1 and the highest at RFZ-4 showing a linear relationship with MAP. The density values of trees are in coherence with earlier reports (Chave et al. 2005; Patil et al. 2012) for a similar rainfall range. Density of the trees positively correlated with species diversity across RFZs reemphasizing the importance of diversity on the functioning of tropical systems. RFZ-1 was dominated by trees with lower GBH (10–30 cm) accounting for about 85 % of total trees (Supplementary Material, Table S2). Lower GBH values of RFZ-1 can be attributed to slower growth of trees because of lesser MAP. GBH values increased with an increase in MAP. More than 60 % of the trees in RFZ-4 are with high GBH (> 30 cm) (Supplementary Material, Table S2). The positive correlation of GBH with MAP across the RFZs found in this study is comparable with the one reported (Slik et al. 2010). Greater proportion of trees with lower GBH even at RFZ-2 reiterates the importance of MAP on the growth and biomass accumulation of trees in semi arid to tropical dry conditions. GBH values in this study match with other studies on tropical forests with similar MAP (Chave et al. 2005; Chaturvedi et al. 2011; Feldpausch et al. 2012; Patil et al. 2012).

Variations seen in vegetation cover across RFZs showed a direct impact on AGB values. It was reported earlier, that tree species with their differences in canopy spread, height, and GBH influence AGB (Pande 2005; Chaturvedi et al. 2011; Feldpausch et al. 2012). Chave et al. (2005) reported that the most important predictors (in decreasing order of importance) of AGB of a tree are, its trunk diameter, wood specific gravity, total height, and forest type (dry, moist, or wet). AGB values recorded in this study (across RFZs) were affected similarly with the trees' characteristics reaffirming this conclusion. Contribution of trees to total AGB in all the plots was much higher (~95 %) as compared to that of herbs and shrubs together (~5 %). Similar values had been reported earlier for trees (> 93 %) and shrubs & herbs (< 7 %) in tropical deciduous forests (Pande 2005). AGB values recorded in this study coincide with the ones recently reported for tropical dry forests in India (Chhabra and Dadhwal 2004; Bijalwan et al. 2010; Chaturvedi et al. 2011; Patil et al. 2012). The AGB values fall in the range of global data sets reported for tropical forests (Cairns et al. 2003; Haberl et al. 2007; Powel et al. 2010; Saatchi et al. 2011; Becknell et al. 2012; Feldpausch et al. 2012). The AGB at RFZ-4 was about 40 times the AGB recorded for the RFZ-1. Becknell et al. (2012) reported that over 50 % of the variation in AGB could be explained by a single climatic variable, MAP, in seasonally dry tropical forests. Similar conclusion can be drawn from the data set of this study. Logarithmic trend line between MAP and AGB showed an increase in AGB values with an increase in MAP. Increase in MAP has differed impact across RFZs 1–4. The impact is higher at RFZ-1 and 2 as compared to RFZ-3 and 4. We infer that identical increase in MAP has higher positive impact on AGB at RFZ-1 as compared to RFZ-4. Our data set indicates that rainfall has significant influence on AGB, coinciding with the inferences of some of the recent studies (Chave et al. 2003; Slik et al. 2010; Schmidt et al. 2011; Condit et al. 2013; Yang et al. 2014).

In the present study, along with natural regeneration of the trees across the RFZs, we observed several plantations of native and non-native species. Amongst these, *Prosopis* is the major one as it is most widely spread (especially in RFZ-1 and 2) and contributes significantly to the AGB of RFZ-1. *Prosopis* is currently considered as an invasive species for a major part of RFZ-1 and 2. The scanty MAP of RFZ-1 is not conducive for the growth of native species. Easy establishment of *Prosopis* in RFZ-1 would positively augment AGB of these areas. Relatively higher MAP of RFZ-2 is suitable for some of the native species. Vast differences observed in the AGB values of RFZ-2 plots dominated by *Prosopis* or native species indicated the negative impact of this invasive species at RFZ-2. Effective management of *Prosopis* would ensure the distribution and establishment of other species better. Yang et al. (2010) raised concerns about sustainable soil productivity due to forest management practices of larch plantations. A similar inference can be made for the spread of *Prosopis* at RFZ-2. Vegetation covers of RFZ-3 and 4 showed species that are naturally diverse and others altered by plantations. MAP of these zones supported larger diversity and better growth of the trees. This resulted in larger AGB values of these plots.

Above-ground biomass and Soil organic carbon

AGB and SOC have an inherent relationship, specifically in forest covers. Variations in the density and diversity of species, their biophysical features (especially of canopy spread and foliage), soil moisture, soil texture, MBC showed a positive impact on the addition of litter and with fluctuations of SOC across the RFZs. Impact of rainfall was distinct on the AGB and SOC values of RFZ-1 and 2 as compared to that of RFZ-3 and 4. According to Schmidt et al. (2011), spatial heterogeneity of biota, environmental conditions and organic matter have dominant influence on carbon turnover. Previous studies reported that soil carbon gets influenced by AGB, litter quality (Pérez-Harguindeguy et al. 2000; Moorhead and Sinsabaugh 2006; Zhang et al. 2008; Austin and Ballaré 2010; Mahaney 2010; Mehta et al. 2013), soil quality, microbial activity (Moorhead and Sinsabaugh 2006; Schmidt et al. 2011), climatic conditions, and land-use and land-cover changes (Jobbágy and Jackson 2000; Post and Kwon 2000; Schmidt et al. 2011; Yang et al. 2011). Our observations coming from the generated data confirm these findings for tropical forests of India.

SOC values reported here are comparable with earlier studies (Jobbágy and Jackson 2000; Chhabra and Dadhwal 2004; Pande 2005; Fontaine et al. 2007; Chaturvedi et al. 2011). In their analysis, Jobbágy and Jackson (2000) mentioned that the effect of vegetation type was more important than the direct effects of precipitation. Clearly, however, given the higher relative ratio of AGB:SOC, both vegetation type and precipitation have an important role in the regulation of SOC in tropical soils, similar to Chaturvedi et al. (2011) who showed a positive relationship between AGB and SOC.

The logarithmic relationship of SOC–AGB revealed that in all the RFZs, the increase in SOC slows down with higher AGB, implying a tighter link of AGB to SOC in low AGB, dry regions of our study area. The point at which such saturation occurs is different for each zone indicating the impact of MAP on AGB and consequently on SOC. Quantity of SOC per unit amount of AGB recorded was much higher in RFZ-1 and 2 as compared to RFZ-3 and 4. We attribute this to the quality of litter and soil properties (such as soil texture, MBC, moisture).

Plantations (specifically of broad leaved, economically important species) across disturbed areas of these RFZs are assisting in the maintenance of both AGB and SOC levels. From our field observations it seems that plantation activities have an impact on AGB and SOC but this requires further research focused on plots with known history of deforestation and plantation activities. As the age and size of stand trees increases, AGB of the system improves and subsequently ameliorates organic carbon of the soils beneath. It was reported earlier (Guo and Gifford 2002) that when native forest is cleared for plantation forestry, soil carbon stocks are unaffected by broad leaf plantations in low rainfall areas but decline when rainfall exceeds 1500 mm year^{-1}. In a similar manner Paul et al. (2003) concluded that under plantation, as the stand develops, long-term soil carbon accumulates. Higher AGB and SOC seen in the plots with plantation activities in RFZs 1–4 support these views.

Projected SOC values (up to 100 cm depth) are comparable with published reports (Jobbágy and Jackson 2000, 2001; Dinakaran and Krishnayya 2008, 2011; Yang et al. 2011). These estimates come from the differences in the SOC values of top layer and bottom layer (25 cm). Any change in land-use and land-cover will alter SOC values of the top layer and this effect can get reflected in the estimates made up to 100 cm. We infer that any periodic changes (such as selective logging, plantation) in land-use and land-cover of these forest covers can be accounted better in landscape projection models for carbon by using these calculations.

Soil properties and soil organic carbon

The three measured parameters (pH, MBC, particle size) of soil samples showed differences across RFZs, reflecting the role that precipitation plays in soil texturing. Higher AGB values of RFZ-4 can be attributed to this feature because of its better water holding capacity, soil biological activity and nutrient supply. Across the RFZs, MBC was significantly higher at 0–5 cm as compared to 20–25 cm, as fresh litter inputs into the top layer have large quantities of easily decomposable organic matter, priming microbial activity. Proportion of recalcitrant organic matter increases with depth, having a negative impact on microbial growth and existence. Schmidt et al. (2011) reported that microbial activity may be reduced by suboptimal environmental conditions, energy scarcity, lesser availability of organic matter because of its sparse density or association with reactive mineral surfaces. Similarly, our results indicate that lesser availability of easily decomposable organic matter (resulting in energy scarcity) could be negatively affecting MBC. It was reported earlier (Yang et al. 2010) that plantation area supports lesser MBC as compared to natural secondary forests. Results of our study coming from RFZ-1 and 2 are in congruence with these findings. Higher MBC values of RFZ-3 and 4 (as compared to RFZ-1 and 2) are attributed to their litter diversity, higher AGB and SOC. Availability of carbon has been assumed to be the most common limiting factor for microbial growth in soil (Demoling et al. 2007). Lower MBC values seen at RFZ-1 and 2 and the linear correlation of MBC to SOC can be attributed to this factor. AGB and MBC did not show any correlation either at 0–5 cm or up to 25 cm depth ($R^2 < 0.3$) across RFZs. This indicates that soil microbial activity is more affected by SOC rather than AGB in these tropical forest covers.

Implication for changing precipitation

Our results highlight that MAP spatial variability strongly dominates modes of carbon variability across space, further balanced by the role of vegetation cover, plantations, and invasive species. Significant sustained changes in MAP are likely to lead to shifts in tropical forest structure and function. Climate projections of drier conditions (e.g. from RFZ-2 to RFZ-1) would lead to shift in species dominance to those found in RFZ-1, with lower species diversity, biomass, and height, leading to decline in litter input, and eventually decreases in total SOC and MBC. This effect may be hastened by the spread of invasive species, such as *Prosopis*. In cases of previous severe human disturbance (deforestation), plantation of suitable tree species acclimatized to a rainfall zone is likely to have an ameliorating effect on AGB of the region. This again requires further research.

Conclusions

Mean annual precipitation is the driving factor that influences the quantity of biomass and soil carbon across forested regions of Gujarat, India, through the influence precipitation has on diversity, density and diameter of trees. Consequences of these changes are seen in SOC and MBC. Thus, shifts in precipitation are likely to promote significant changes of tropical Indian forest cover and carbon stocks in the future. These effects are more pronounced in the dry regions, as shown by the logarithmic relationship of soil organic carbon to aboveground biomass.

Our study found that plantation of *Prosopis* in the driest sites not only improved the green cover but also showed a positive impact in the increase of vegetation and soil carbon stocks in this arid region, while the same species showed a negative impact on above-ground biomass at the wetter region as its presence hinders the growth and distribution of native species. Further work is needed to disentangle how processes of afforestation, forest plantation management, and spread of invasive species influences the ability of tropical ecosystems to adapt to changing precipitation regimes, especially in dry regions.

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ORIGINAL ARTICLE

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Changes in litter decomposition and soil organic carbon in a reforested tropical deciduous cover (India)

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Abstract Soil organic carbon (SOC) up to 1 m depth originates from contemporary vegetation cover dating from past millennia. Deforestation and reforestation with economically important species is influencing soil carbon sequestration. An attempt has been made in this study to evaluate the impact of vegetation cover change (due to replacement of natural heterogeneous cover by teak and bamboo) on SOC using carbon isotopes ($\delta^{13}C$, ^{14}C) in a tropical system (India). A litter decomposition study was carried out to understand the impact of differences in vegetation characteristics (specifically of leaves) on decomposition. Both experiments were carried out to look at the impact of changes in vegetation characteristics (specifically of leaves) on litter decomposition, and how these influence near term litter decomposition rates (k values) and long-term SOC content of the soil system beneath. Leaves of teak, bamboo and eight other species were selected for this study. The proportion of structural carbohydrates (lignin and cellulose) in leaves significantly (at 5 % level) influenced k values. The SOC and carbon isotope data collected in this study indicate that C_3 vegetation cover in the study area could be contemporary and dominant for the past few centuries. This can be extended up to ~2,200 years from the recorded ^{14}C values of teak cover. The study confirms that k values of leaf litter influence SOC present beneath the vegetation cover at the decadal/century time scale.

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Introduction

Soil organic carbon (SOC) is affected greatly by the vegetation cover present. Human-induced alterations to vegetation cover (deforestation, reforestation, agriculture) are significantly changing carbon storage in soils (Bashkin and Binkley 1998; Post and Kwon 2000; Paul et al. 2002, 2003; Degryze et al. 2004; Richards et al. 2007). Paul et al. (2003) reported that the mean rate of soil carbon change after 40 years of afforestation was 0.09 % per year (0.006 t C ha^{-1} per year). Changes in vegetation cover alter inputs of organic matter into the top layers of soil. This is likely to modify soil biological activity, which, in turn, affects litter decomposition. Bruggemann et al. (2011) reported that aboveground litter layer of an ecosystem is composed of a continuum of fresh litter to completely humified organic matter and serves as a bottleneck for a significant portion of primary productivity sent belowground. An understanding of how changes in vegetation cover alter plant litter decomposition is important as it is one of the important processes of the carbon cycle.

Litter degradability is an important regulator of litter decomposition (Aerts 1997; Berg 2000; Gartner and Cardon 2004; Zhang et al. 2008; Sanaullah et al. 2009). Vegetation type and phenology of the plant signifies the quality of the litter. Schmidt et al. (2011) reported that the persistence of organic matter in soil is due largely to complex interactions between organic matter and its environment, such as the interdependence of compound chemistry, reactive mineral surfaces, climate, water availability, soil acidity, soil redox state and the presence of potential degraders in the immediate micro-environment. The findings of Santiago (2007) indicate that the decomposability of leaf tissues in tropical forest varies from thin, easily decomposable leaves with high nutrient concentrations and high photosynthetic rates to thick, relatively recalcitrant leaves with greater physical toughness and low photosynthetic rates. Degradation of structural carbohydrates such as lignin is thought to be critical for litter decomposition rates and the build-up of soil organic matter (Klotzbucher et al. 2011).

The carbon stock in terrestrial ecosystems represents the difference between the gain from net primary production (in terms of quality and quantity) and the loss through decomposition (Couteaux et al. 1995; Amundson 2001). Moorhead and Sinsabaugh (2006) reported that soils may sequester more carbon if decay rates slow or inputs of organic matter increase. It is important to see how land use-land cover (LULC) changes such as reforestation, stand replacement and social forestry will change or influence litter dynamics.

Organic carbon present in the top 1 m of soils is produced mostly from the vegetation present in that area for the past centuries to millennia. Alterations in vegetation cover (either naturally or by LULC changes) will influence litter decomposition rates (*k* values), which, in turn, affect organic carbon levels in soil. Decadal to century scale patterns in SOC, incorporated through humification, can be studied using both stable and radioactive isotopes of carbon ($\delta^{13}C$ and ^{14}C) as tracers (Wang and Hsieh 2002). Changes in major types of vegetation cover (C_3/C_4) can also be determined by $\delta^{13}C$. Generally, the $\delta^{13}C$ of SOC increases with depth (1–3 ‰) in soil that has remained under the same plant community for a long period (Boutton et al. 1998; Ehleringer et al. 2000; Powers and Schlesinger 2002; Bruggemann et al. 2011). Terrestrial plants discriminate against $^{13}CO_2$ during photosynthesis and the extent of this discrimination depends on their photosynthetic pathway. RUBISCO (C_3 plant species) and PEP carboxylase (C_4 plant species) play an important role in discriminating $^{12}CO_2/^{13}CO_2$ uptake during photosynthesis (Marshall et al. 2007). $\delta^{13}C$ values of C_3 plants range between −35 and −20 ‰ (Bernoux et al. 1998), while they range from −19 to −9 ‰ for C_4 plants (Boutton 1991). The isotopic composition of soil organic matter is comparable to that of the plant material from which it was derived (Martin et al. 1990). Bowling et al. (2008) hypothesized that $\delta^{13}C$ of leaves can be used as a reference point for plant and ecosystem carbon pools and fluxes. Bruggemann et al. (2011) stated that, during litter decomposition, the isotopic signatures would shift towards an enriched signal due to sorption of older SOC to the remaining leaf litter. Garten et al. (2000) hypothesized that litter quality indirectly controls the extent of isotopic fractionation during soil organic matter decomposition in temperate forest ecosystem. It would be worthwhile to know how litter quality (SLA, contents of structural and non structural carbohydrates) influences isotopic changes during its decomposition in tropical forests.

Radiocarbon dates of SOC represent the mean age of all carbon pools with different levels of stability. Radiocarbon age increases with depth, indicating a high concentration of old and more stabilized organic carbon in deeper layers (Rumpel et al. 2002, 2004; Krull et al. 2003). ^{14}C analysis gives an estimate of age of SOC. Changes in stable isotope ratios indicate vegetation flux from C_3 to C_4. Combination of these methods gives a better understanding of vegetation history/landscape change and its impact on organic carbon present in the top 1 m soil. Generating similar kind of data in tropical systems is very important because of rapid developmental activities across these regions.

Response times of tropical forests are shorter and are sensitive to global perturbations (Malhi and Phillips 2005). In the past century, there have been significant changes in the forest areas of India (Chhabra and Dadhwal 2004). Don et al. (2011) reported that land-use changes are the second largest source of human-induced greenhouse gas emissions, mainly due to deforestation in the tropics and subtropics. They also reported that the effect of land-use changes on SOC is poorly quantified. Deforestation and/or reforestation, social forestry are affecting the functionality of tropical systems in terms of its capacity to sequester carbon (either by acting as a sink or a source of carbon).

Tropical forest covers are diverse (Shi and Singh 2002). Most areas are covered with mixed species. Prior to the current levels of anthropogenic activities, composition of these covers remained largely heterogeneous (for the past millennia). Many of these areas have been cleared and replaced by plantations of commercially viable species such as teak (C_3 plant) and bamboo (C_3 plant). These are two important species used widely in plantations across India and parts of other Asian countries. Depending on human pressure, these covers are harvested after 40–80 years of growth. Often, the same species is replanted. Both species are deciduous in nature and their cover contributes significant amounts of leaf litter (average litter fall for teak and bamboo covers are 6.37 and 4.4 t ha^{-1} respectively) (Singh et al. 1993; Cordero and Kanninen 2003; Zhou et al. 2005; Dinakaran and Krishnayya 2010). In India, 9.77 million ha are occupied by teak and 10.03 million ha by bamboo (Keswani 2001; Chand and Sood 2008).

Disturbance levels of the stands (mixed, teak, bamboo) indicate differences. Teak and bamboo are subjected to relatively higher disturbance owing to their economic value. Mixed vegetation cover is less disturbed under mostly quasi semi-state conditions. Dynamics of SOC levels of soils occupied by mixed species and planted teak and bamboo covers can give an indication about the impact of LULC changes on carbon sequestration. It is important to understand how the vegetation cover shift (from mixed to commercially viable teak and bamboo) will influence SOC. It is equally interesting to look at how changes (if any) in leaf characteristics influence litter decomposition. To address these issues, the present study was carried out at two sites in India affected by LULC changes. One site (Vadodara) was chosen to investigate the influence of leaf characteristics (of different species) on litter decomposition. Another site located in a protected area [Shoolpaneshwar

Wildlife Sanctuary (SWS)] was taken to compare variations in SOC contents across soils (up to 1 m depth) under three vegetation covers. The present study was carried out to look at the impact of changes in vegetation characteristics (specifically of leaves) on near-term *k* values and, how these influence the long-term SOC content of the soil system beneath.

Methods

Study site description

The study was carried out at two sites in Gujarat (India): Vadodara, the site of the litter decomposition study, lies at 22°19′15.26″N, 73°10′47.63″E at an altitude of 37 m above mean sea level, and SWS, the site of the SOC study, (21°29′–21°52′N latitude and 73°29′–73°54′E longitude) situated ~185 km from Vadodara (Supplementary Material, Fig. S1). According to the Holdridge life zone system of classification, the vegetation cover of these study sites falls into the tropical dry forest type (Holdridge 1947). Both study sites are similar in their climatic conditions. The mean annual rainfall is 920 mm (in the months of July–October), and the mean annual minimum and maximum temperatures are 7 and 42 °C, respectively. The Vadodara site has been slowly urbanized over the past century. Existing tree cover has come mostly from human intervention as gardens, etc. This site was considered for the litter decomposition experiment. SWS is covered with wild vegetation. A few areas within the sanctuary have been altered by tribal settlements. In these areas, teak and bamboo plantations were created for the livelihood of local people. The SWS site was selected to look at the dynamics of SOC due to LULC change and carbon isotope analysis (^{13}C, ^{14}C). Three protected plots in Vadodara (Botanical garden, Arboretum, Farm house) with similar vegetation cover were identified for the litter decomposition study. The microbial biomass carbon (MBC) contents of soils at the three sites differ significantly, ranging between 44.88 and 190.08 mg kg^{-1}. MBC levels at the SWS site ranged from 53.2 to 390.4 mg kg^{-1}. Soils are loamy with light-brown to gray/black color and are well drained (Gujarat State Forest Department, unpublished data). The bulk density of the soils at different depths ranges from 1.14 g cm^{-3} at the surface to 1.39 g cm^{-3} at 1.25 m. The soils are slightly acidic with pH ranging from 6.60 to 6.96 (see Supplementary Material for further description).

Selection of plant species and vegetation cover

The selected plant species for litter decomposition study at the Vadodara site were a combination of species used widely in stand replacement (teak and bamboo) and differ in leaf characteristics [such as specific leaf area (SLA) and chemistry]. The selected species are trees (*Tectona grandis* L., teak; *Madhuca indica* J.F.Gmel., madhuca and *Mangifera indica* L., mango), perennial grass (*Dendrocalamus strictus* Nees., bamboo), shrubs (*Hibiscus rosa-sinensis* L., hibiscus; *Datura stramonium* L., datura and *Bougainvillaea glabra* L., bougainvillea) and herbs (*Cyperus rotundus* L., cyperus; *Spinacia oleracea* L., spinach and *Catharanthus roseus* L., vinca). Leaves of the chosen species also have large differences in the proportion of structural carbohydrates.

Three vegetation covers distributed in SWS were identified to investigate SOC level up to 1 m depth. Vegetation covers of teak and bamboo are widespread. Their occupancy increased as they are preferred for stand replacement in these parts. Another cover considered is mixed species. This cover shows natural species distribution with less human intervention compared to the replanted sites. Mixed cover, which did not show significant human influence, was considered as a baseline for comparing changes (if any) in SOC contents because of stand replacement.

Measurement of leaf characteristics

We measured leaf area and carbohydrate concentration. Leaf area was measured by a leaf area meter (CI-203 Area Meter, CID-Bioscience, Camas, WA). Dry weights of leaves were measured and SLA was calculated (leaf area/leaf dry weight). Analytical precisions for leaf area and leaf weights are ±0.001 cm^2 and ± 0.1 mg, respectively. Structural carbohydrate (lignin and holocellulose [cellulose + hemicellulose]) and non structural carbohydrate constituents were estimated by following the method of Booker et al. (1996). Non structural carbohydrate constituents were extracted from dried and powdered leaf samples using 50 % methanol. Subsequently structural carbohydrate constituents were extracted using H_2SO_4 (see Supplementary Material for further description). These measurements were done in newly senesced leaves and leaves on the verge of senescence. Contents of senescent leaves indicate quantities of biochemicals available to the organisms in the soil. Lignocellulose index (LCI, lignin/lignin + cellulose, Moorhead and Sinsabaugh 2006) was calculated for the litter remaining in the litter bags (at 0, 90, 180 and 270 days) to look at the degradability of the material (LCI value towards 0 indicates high decomposition and towards 1 indicates less decomposition of the material).

Leaf litter decomposition experiment

Leaves (newly senesced and on the verge of senescence) of selected plant species were air-dried in the laboratory. We placed 25 g dried leaf material (intact or broken) of each species in a standard perforated litter bag (1 mm mesh size). These bags were placed in the soils at the three points (Arboretum, Botanical Garden and Farm house). Normally, soil biological activity (of micro flora, micro fauna and other microbes) is more in the top layers and decreases as the depth increases mainly because of variations in the availability of easily decomposable material. Litterbags were kept at two depths (0–5 and 15–20 cm) to find out whether the soil biological activity shows any difference (up to 25 cm depth) affecting litter decomposition. Sets (n = 3) of each species were kept at each site, at both depths (3 × 3× 2). Each set had triplicate samples/bags. The total number of litter bags used for the ten selected species was 540 (10 × 3×3 × 3× 2). A uniform distance was maintained between the sets at each depth to avoid disturbance during sampling. The litter bag experiment started in the month of June 2009. Soil moisture content is lowest in this month and we assumed that soil biological activity would be minimal. The experiment was terminated when the data showed that half of the species had < 20 % material left. At 90 days, one set (10 × 3×3 × 2) of litter bags was removed and brought to the laboratory. Bags were cleaned by removing adhered soil carefully (using a brush and magnifying glass). Remaining litter was weighed after drying. This step was repeated at 180 and at 270 days. Remaining litter (at 90, 180 and 270 days) was subjected to chemical analysis (structural and non structural carbohydrate constituents). Soil samples were collected from the three sites before placing the litter bags in the field and after picking up decomposed samples (at 90, 180 and 270 days). These samples were analyzed for MBC by the fumigation method (Witt et al. 2000) (see Supplementary Material for further description).

Soil carbon analysis

Soil samples were collected from the three vegetation covers of SWS (For details of soil sample collection refer to Dinakaran and Krishnayya 2010). SOC was estimated by the wet oxidation method (Walkley and Black 1934). Stable isotope ratio of carbon ($^{13}C/^{12}C$) was measured using a mass spectrometer (GEO-20-20). The isotopic composition was expressed as $\delta^{13}C$ relative to the Vienna Pee Dee Belemnite (VPDB) standard. Mass spectrometer used was Dual-Inlet Stable Isotope Ratio Mass Spectrometer (Europa Scientific Geo 20-20, Crewe, UK). The standards (for stable isotope) used were ANU sucrose ($\delta^{13}C$ = −10.45 per million wrt VPDB) and Oxalic acid II ($\delta^{13}C$ = −17.8 per million wrt VPDB). Mean values of the sample and standard $\delta^{13}C$ are within the acceptable range. The difference between $\delta^{13}C$ of sample and oxalic acid II is 3–13 per million and it is 10–17 per million between sample and ANU Sucrose. ^{14}C was estimated by liquid scintillation counter (Quantulus 1220, Perkin Elmer, Beaconsfield, UK). International standard NBS oxalic acid II was used as a standard for ^{14}C (see Supplementary Material for further description). For details of analysis, refer to Yadava and Ramesh (1999). The Rayleigh equation $\delta = \delta_0 + \varepsilon \ln[C/C_0]$ (where, δ_0 and C_0 represent initial signature and initial carbon content) describes the gradual enrichment resulting from isotopic fractionation associated with soil organic matter decomposition. Enrichment factor indicates any kind of shift in vegetation cover (from C_3 to C_4 or vice versa). We fitted the Rayleigh equation (Accoe et al. 2002; Diochon et al. 2009) to the measured carbon contents and corresponding $\delta^{13}C$ signatures at different depths in the soil profile.

Data analysis

Decomposition constants, k values (g g^{-1} year^{-1}) were calculated using the exponential decay equation (Olson 1963).

$$k_t = (1/t)\ln(X_0/X_t)$$

where, t denotes unit time (90, 180, 270 days), k_t is the decomposition rate when time is t, X_0 is the weight of litter at initial time, X_t is the mass remaining when time is t.

Statistical analysis was done by using SPSS software. Linear regression analysis was performed between measured structural and nonstructural carbohydrates of leaves and their respective k values. Linear regression analysis was also done between log transformed SOC and $\delta^{13}C$ values obtained from SWS. ANOVA was carried out to check the following hypothesis; H_0: expected values of SLA, structural and nonstructural carbohydrates, k values among the ten species are the same; H_1: expected values of SLA, structural and nonstructural carbohydrates, k values among the ten species are not the same. Similar analysis was carried out to check differences in MBC values across three sites (at two depths). H_0 was accepted when calculated F value is less than tabled value at 5 % level of significance.

Results

Measured leaf characteristics

Measured leaf characteristics are expressed as mean values derived from ten leaves for each species (Table 1). Leaf area showed a range of 12.87–1,079.63 cm^2. Leaf dry weights were 0.04–10.62 g (for a single leaf). SLA for the selected species was between 100.52 and 300.54 cm^2 g^{-1}. Dried leaf samples contained 22.98–57.44 % nonstructural carbohydrates and 42.56–77.02 % structural carbohydrates. Amongst the structural components, lignin was 3.41–34.91 %, and holocellulose was 31.42–42.41 %. LCI ranged between 0.08 and 0.46. LCI values increased after 270 days of decomposition. Our ANOVA results showed that differences seen in all these parameters are statistically significant (at 5 % level; H_1 accepted). MBC levels of the soil samples (prior to placing the litter bags) across sites (at two depths) were significantly different (at 5 % level) and ranged from 44.88

Table 1 Measured leaf characteristics for selected species

Species	SLA	Component (%)				LCI	*k* values[a]
		Nonstructural	Structural	Holocellulose	Lignin		
Teak	101.68 ± 15.18	32.33 ± 1.85	67.67 ± 1.85	40.36 ± 1.01	27.31 ± 1.59	0.40 ± 0.02	1.68 ± 0.85
Mango	100.52 ± 0.07	39.56 ± 1.42	60.44 ± 1.42	32.57 ± 4.35	27.88 ± 4.06	0.46 ± 0.13	2.63 ± 0.35
Madhuca	101.95 ± 4.04	36.42 ± 3.94	63.58 ± 3.94	36.27 ± 3.89	27.32 ± 0.55	0.43 ± 0.03	1.45 ± 0.29
Bamboo	220.34 ± 9.27	22.98 ± 1.16	77.02 ± 1.16	42.11 ± 4.60	34.91 ± 5.45	0.45 ± 0.07	1.86 ± 0.93
Hibiscus	279.55 ± 6.20	48.82 ± 4.72	51.18 ± 4.72	42.41 ± 4.72	8.77 ± 0.97	0.17 ± 0.02	–
Datura	151.44 ± 6.19	49.65 ± 1.23	50.35 ± 1.23	39.03 ± 2.74	11.33 ± 3.86	0.22 ± 0.07	3.09 ± 0.55
Bougainvillaea	176.68 ± 23.32	40.16 ± 1.30	59.84 ± 1.30	34.45 ± 1.10	25.39 ± 1.14	0.42 ± 0.01	1.86 ± 0.08
Cyperus	300.54 ± 21.42	42.03 ± 1.12	57.97 ± 1.12	38.38 ± 1.45	19.59 ± 0.12	0.34 ± 0.11	2.42 ± 0.63
Spinach	245.83 ± 23.91	57.44 ± 0.69	42.56 ± 0.69	39.15 ± 2.47	3.41 ± 1.91	0.08 ± 0.05	3.83 ± 0.42
Vinca	250.37 ± 24.54	55.93 ± 3.59	44.07 ± 3.59	31.42 ± 1.16	12.65 ± 2.94	0.29 ± 0.05	2.50 ± 0.61

Values are mean ± standard deviation from the mean
SLA Specific leaf area ($cm^2\ g^{-1}$), *LCI* lignocellulose index
[a] *k* values: decomposition rate ($g\ g^{-1}\ year^{-1}$)

to 190.08 $mg\ kg^{-1}$. Among the three plots at Vadodara, farm house showed the highest MBC followed by arboretum and botanical garden.

All ten species (categorized as trees, shrubs and herbs) showed distinction in the measured parameters. SLA estimates were smaller in value in trees (100.52–101.95 $cm^2\ g^{-1}$) followed by shrubs (151.44–279.55 $cm^2\ g^{-1}$) and herbs (245.83–300.54 $cm^2\ g^{-1}$). The SLA value of bamboo was 220.34 $cm^2\ g^{-1}$. Structural carbohydrates were high in trees (60.44–67.67 %) followed by shrubs (50.35–59.84 %) and herbs (42.56–57.93 %). Nonstructural carbohydrates showed the reverse pattern. Bamboo (perennial grass) had the highest content of structural carbohydrates (77.02 %).

Decomposition rates (*k* values)

Differences seen in the weight loss of leaf litter of a species placed at two soil depths (0–5 and 15–20 cm) at each site did not show any significant difference (at 5 % level; H_0 accepted). In spite of differences in MBC values, decomposition rates for each species coming from the three points (arboretum, botanical garden and farm house) did not show significant variations. Hence, data are presented as the mean of samples from two depths and at three sites ($3 \times 3 \times 2 = 18$ samples) (Fig. 1). Outliers were discarded (2 highest and 2 lowest, 25 % lower or higher than the median value of 18 observations). Mean values are derived from 14 observations for each species at each sampling time (90, 180 and 270 days). After 90 days of being placed in the soil, the minimum *k* value observed was 1.31 (for mango) while maximum was 4.50 (for *Hibiscus*) (Supplementary Material, Fig. S3). The *k* values ranged from 1.45 to 3.83 (Table 1) at 270 days. The *k* values were higher in herbs followed by shrubs and trees (Supplementary Material, Fig. S3). Decomposition was faster in spinach (1.47 g remaining), while much of the original material remained for the same amount of time with *Madhuca* (8.54 g remaining). Sample collection was improper for *Hibiscus* at 270 days and therefore, it was excluded.

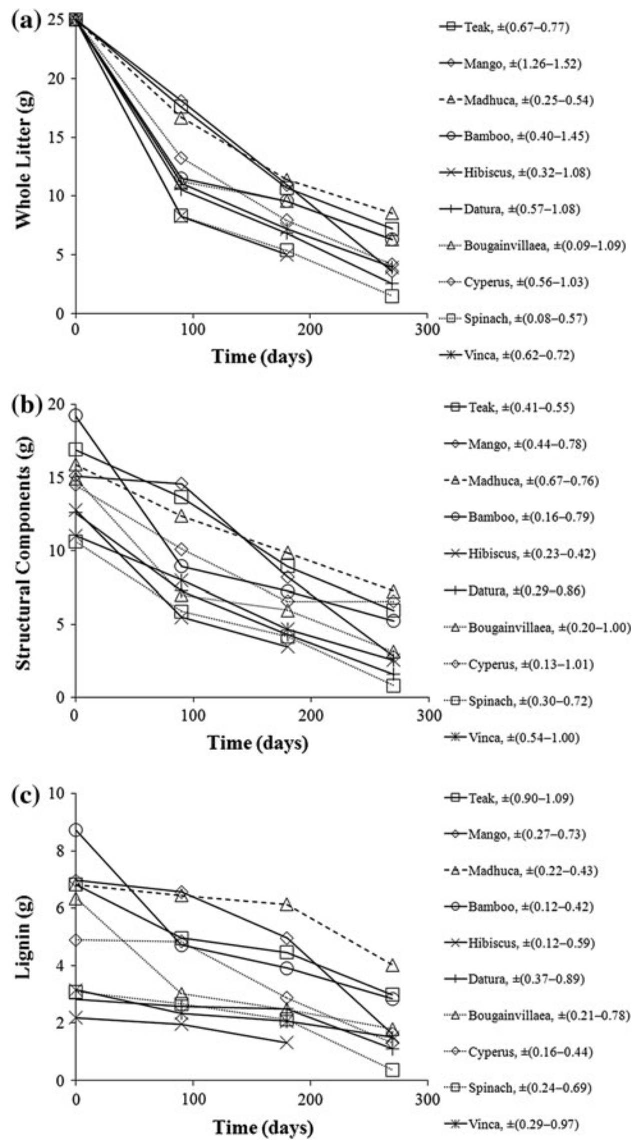

Fig. 1 Weight loss of **a** whole litter mass, **b** structural components and **c** lignin during decomposition (from 0–270 days, Vadodara site) of selected plant species. Values in *parenthesis* indicate range of standard deviation from the mean

Nonstructural carbohydrates decomposed relatively faster than structural carbohydrates ranging in k values from 1.54 to 4.16 (Supplementary Material, Fig. S2). The structural carbohydrates are utilized slowly (k values ranging from 1.07 to 3.49) (Fig. 1). Leaves of different species with similar proportion of structural carbohydrates showed no significant difference in k values. The k values of lignin are 0.71 to 2.88 for all the species at 270 days. MBC values increased 12–150 % (from the initial values) by the end of 90 days of decomposition. During 90–180 days interval, MBC values remained stable. At 270 days MBC values gradually decreased (6–43 % from peak levels at 180 days) and at some points values decreased to initial levels (Supplementary Material, Fig. S4).

Correlation analysis: litter chemistry and decomposition study

SLA showed positive correlation when plotted against k values of all species ($R^2 = 0.74$ at 270 days). k values were correlated positively ($R^2 = 0.67$) with nonstructural and negatively ($R^2 = 0.67$) with structural components. Holocellulose did not show any correlation ($R^2 = 0.02$) with k values. Lignin content had a strong negative correlation ($R^2 = 0.74$) with k values across all species. LCI was inversely proportional to k values ($R^2 = 0.73$) (Supplementary Material, Table S1).

Soil organic carbon

SOC values at different depths coming from the three different vegetation covers of SWS showed significant differences (Table 2). SOC content was high in the top layers and decreased with increasing depth. SOC content was higher in teak sites than in bamboo and mixed vegetation.

Table 2 Soil parameters of teak, bamboo and mixed vegetation covers

Parameters	Teak	Bamboo	Mixed
SOC (g kg^{-1})			
0–2 cm	33.7 ± 0.4	30.8 ± 0.1	30.8 ± 0.7
8–10 cm	25.4 ± 0.1	27.1 ± 0.1	26.7 ± 0.1
20–25 cm	21.6 ± 0.1	23.8 ± 0.1	18.4 ± 0.1
45–60 cm	15.1 ± 0.2	15.4 ± 0.3	9.7 ± 0.3
75–90 cm	10.1 ± 0.1	7.1 ± 7.1	7.9 ± 0.1
90–100 cm	9.3 ± 0.2	6.8 ± 0.2	6.5 ± 0.2
DF [$\delta^{13}C_{soc} - \delta^{13}C_{litter}$ (‰)]			
0–2 cm	3.91	6.84	−0.1
8–10 cm	5.96	2.50	1.64
20–25 cm	7.02	3.66	1.62
45–60 cm	5.64	7.63	2.97
75–90 cm	2.24	6.23	2.21
90–100 cm	6.68	6.90	2.63
Radio carbon age (years BP)			
0–2 cm	Modern		
45–60 cm	1,470 ± 80		
90–100 cm	2,200 ± 80		
Mean residence time (years)			
0–2 cm	230		
45–60 cm	1,311	–	–
90–100 cm	2,015		

Values are mean ± standard deviation from the mean
SOC Soil organic carbon, *DF* discrimination factor

Stable carbon isotopes

The stable carbon isotope composition of plant litter and soils (at six different depths) of teak, bamboo and mixed vegetation cover ranged from −27.9 ‰ to −20.9 ‰, −28.4 ‰ to −20.7 ‰ and −26.7 ‰ to −24.0 ‰, respectively (Fig. 2). Enrichment values of $\delta^{13}C$ were cross-checked with Rayleigh equation fitted between observed SOC and corresponding $\delta^{13}C$ signatures at different depths in the profile (Accoe et al. 2002; Diochon et al. 2009). R^2 value of mixed cover is high (0.68) (Supplementary Material, Fig. S5). Differences in $\delta^{13}C$ values at different depths and between vegetation covers were statistically significant (at 5 % level). The discrimination factor ($\delta^{13}C_{soc} - \delta^{13}C_{litter}$) (Garten et al. 2000) at six different depths of teak, bamboo and mixed vegetation cover is given in Table 2.

Correlation analysis: carbon isotopes study

The mean $\delta^{13}C$ values of litter and SOC of three types of vegetation covers were plotted against the logarithm of their respective mean carbon content (Fig. 3a–c). The slope of this regression line is called the beta (β) value. The beta value was higher in mixed vegetation cover followed by teak and bamboo covers. Beta values are correlated positively with k values of three types of vegetation cover (Fig. 3d).

Radiocarbon (^{14}C) age of SOC

Calculated radiocarbon age and mean residence time (MRT) at three different depths of teak vegetation cover

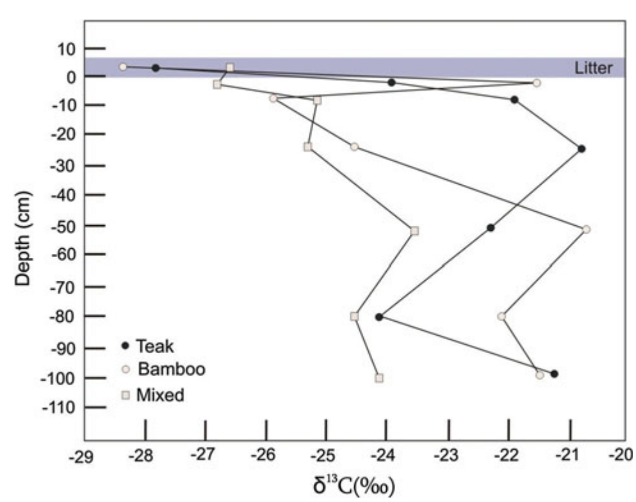

Fig. 2 The $\delta^{13}C$ values of litter and soil at six different depths of teak, bamboo and mixed vegetation covers

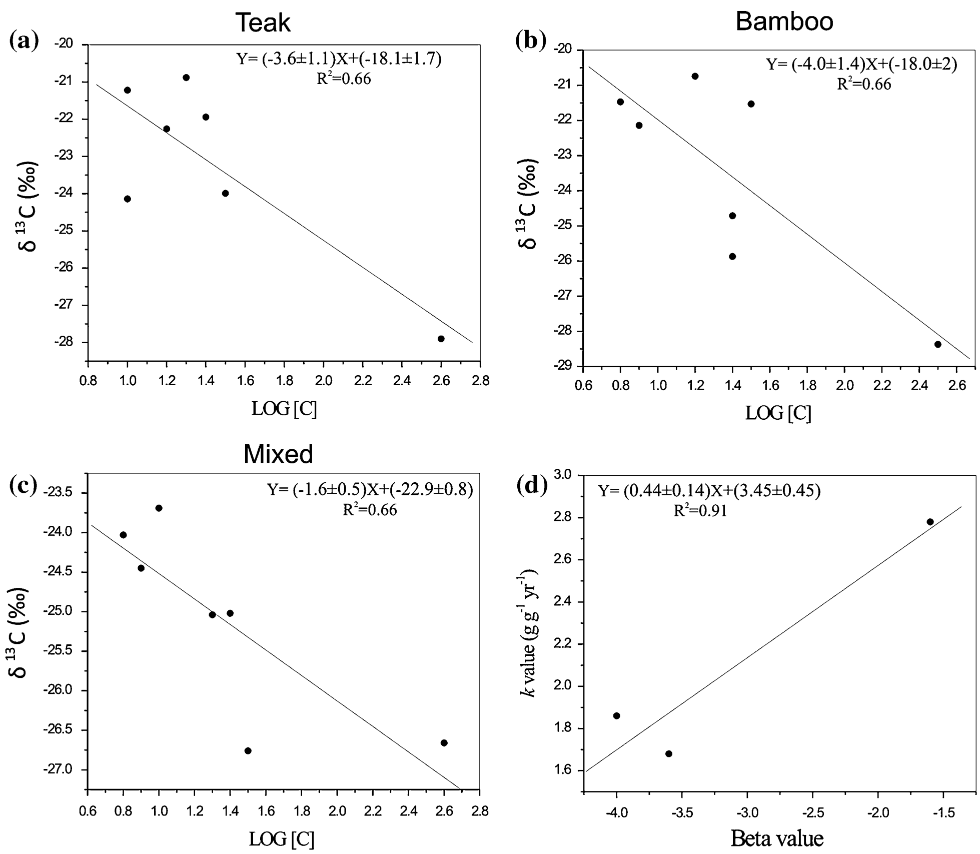

Fig. 3 Relationship between δ^{13}C and log-transformed carbon (g kg^{-1}) of litter and soils at six different depths of **a** teak, **b** bamboo and **c** mixed types of vegetation cover. **d** Relationship between the beta value and litter decomposition rate (k) value of three types of vegetation cover. *Lines* Linear regression fit. Here, beta (β) value is slope of the regression line between mean δ^{13}C values of litter, soil organic carbon (SOC) and the logarithm of their respective mean carbon content of three types of vegetation covers of the Shoolpaneshwar Wildlife Sanctuary (SWS) site

are presented in Table 2. Radiocarbon age increased with increasing soil depth. The top soil (0–2 cm) contains a significant portion of carbon fixed in recent decades as indicated by the presence of bomb carbon (pMC = 100.80 ± 0.95). The radiocarbon age increased almost linearly with depth reaching to a value of ~2,200 (years BP) at a depth of 100 cm.

Discussion

Changes in litter quality and decomposition rate

As observed in this study, alteration in vegetation cover leads to differences in leaf litter quality and decomposition rates. Variations in the characteristics of leaf materials recorded in this study influenced decomposition rates. We found SLA to be an important leaf trait affecting litter decomposition. A plant's economic strategy can be understood from SLA values. Cornwell et al. (2008) reported that leaf 'economic' traits lead influential 'afterlives', affecting the rate of decomposition, which is a key component of the global carbon cycle. In this study, higher SLA values were associated with herbs and lower values with trees. A positive correlation seen between SLA and k values in this study revealed its importance in leaf litter decomposition, confirming the importance of SLA to litter decomposition reported earlier (Cornelissen et al. 1999; Santiago 2007). Recently Salinas et al. (2011) reported that species type influences the decomposition rate, most probably through its influence on leaf quality and morphology. A similar conclusion can be drawn from the results of this study. We found that differences in vegetation characteristics (leaf longevity, proportion of non structural carbohydrates, LCI and SLA) influenced the k values of litter in the short term. Over the study period, most of the leaf material showed decomposition up to 80 %. Our understanding is that LCI determines the quantity of undecomposed/slowly decomposing litter added to the soil. This will have a positive impact on steady state carbon storage in the soil.

Litter chemistry strongly influences litter mass loss (Pe'rez-Harguindeguy et al. 2000; Moorhead and Sinsabaugh 2006; Zhang et al. 2008; Austin and Ballare 2010; Mahaney 2010). This is evident in the results of this study. Of the three chemical constituents measured, nonstructural carbohydrates degraded faster, followed by holocellulose and lignin. Mass loss observed across the different species is exponential at initial stage and linear later. This is correlated with changes occurring in litter chemistry during decomposition. Moorhead and Sinsabaugh (2006) proposed a guild-based decomposition model. This model describes three microbial guilds in the context of decomposition: (1) a guild of opportunist microorganisms grow quickly having high affinity for soluble substrates, (2) a guild of decomposer specialists grow more slowly having affinity for holocellulose substrates, and (3) a guild of miners grow very slowly and is specialized for degrading lignin. Higher k values of non-structural carbohydrates, relatively smaller k values of structural carbohydrates, initial increase and subsequent decrease in MBC values recorded in our litter decomposition study support this model.

Amongst the ten species selected, the species with lower LCI decomposed faster and other species with higher LCI values decomposed at slower rate. LCI can serve as an indicator in evaluating the impact of changes in vegetation cover on current litter decomposition. Stand replacement with teak and bamboo in this study would have slowed down litter decomposition as their LCI are relatively high. These observations can be extended for stand replacements with species having similar LCI values. k values of a species kept at two different depths of a site did not differ significantly, indicating that, in these ecosystems, soil biological activity has nearly the same impact on litter decomposition at least up to 25 cm depth.

Soil organic carbon

Pattern of SOC distribution across the top 1 m of the three covers at SWS remained nearly the same without any large fluctuations. Unpublished records of local federal agencies indicated large-scale stand replacement (by teak and bamboo) activities in the past 150 years. Our observations indicate that replantation after deforestation at a disturbed site under non-steady-state soil carbon dynamics will not alter SOC at decadal/century time scale. From our decomposition study at the nearby site, we can infer that differences in vegetation composition will result in very little impact on the overall soil carbon level. Paul et al. (2002) reported that, in plantations older than 30 years, carbon content was similar to that under the previous systems within the surface 10 cm of soil. Our study suggests that stand replacement (<5 years after logging) has minimal influence on SOC. However, these results are based on sampling at one point of time and, therefore, a better designed study to answer the question if plantation following deforestation alters SOC contents at the decadal/century time scale is needed.

Stable carbon isotopes ($\delta^{13}C$)

The range of $\delta^{13}C$ values in soils of teak, bamboo and mixed land cover is comparable with the $\delta^{13}C$ values of C_3 plant communities, i.e., -35 to -20 ‰ (Boutton 1991). The enrichment of $\delta^{13}C$ values associated with the observed data in the upper 100 cm soil profile of teak, bamboo and mixed land cover indicate that these areas were occupied predominantly by C_3 vegetation. The enrichment factors in this study are higher than those reported for C_3 red spruce forest (Diochon et al. 2009). The β value predicts the expected change in the $\delta^{13}C$ value, or isotopic discrimination, for every ten-fold increase in carbon concentration (Garten et al. 2000). β-values of mixed cover showed correlation when plotted against composite k values of all other species selected in this study. A similar trend was seen in teak and bamboo covers. The positive correlation seen between β values and k values of three types of vegetation cover indicated the influence of decomposition rate on soil carbon turnover and storage. $\delta^{13}C$ values of teak cover (up to 1 m depth) indicate that the area is occupied predominantly by C_3 vegetation. ^{14}C values of the same samples place them as ~2,200 years old. From these observations, we conclude that the study area has been covered predominantly by C_3 vegetation for the past ~2,200 years.

Conclusions

Only limited data exist on multiple species litter decomposition at tropical sites in India or the SOC contents of forests under teak and bamboo plantations. Through our experiments we have shown that SLA, leaf chemistry, and LCI are important leaf characteristics with significant impact on litter decomposition. Our understanding is that short-term differences in k values have minimal impact on long-term changes in SOC. We did not detect a difference in the patterns of SOC distribution across the top 1 m after stand replacement. Radio carbon ages and $\delta^{13}C$ values indicate that the study area has been populated predominantly by C_3 vegetation during the past ~2,200 years. Future research can be carried out to understand the influence of leaf traits of diverse tropical vegetation on k values, and their impact on long-term SOC dynamics.

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Seasonal variations in phenology and productivity of a tropical dry deciduous forest from MODIS and Hyperion

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ABSTRACT

Tropical dry deciduous forests exhibit diverse phenological behaviour that has significant impact on Gross Primary Productivity (GPP). However, satellite remote sensing of GPP may be impacted by spectral and spatial resolution of sensor. The Vegetation Photosynthesis Model (VPM) was applied to time-series of Hyperion and MODIS (MOD09A1_500 m) reflectance values to evaluate spatial and spectral resolution impacts on inference of seasonal variation in phenology and GPP for Teak, Bamboo and Mixed tropical deciduous vegetation ecosystems of Shoolpaneshwar Wildlife Sanctuary (SWS), Gujarat, India. Seasonal dynamics coinciding with the phenological cycle were seen in Enhanced Vegetation Index (EVI) and Land Surface Water Index (LSWI), though with greater dynamic range in Hyperion than MODIS MOD09A1_500 m, as a result primarily of spectral properties. In contrast, GPP values from MOD17A2_1000 m did not similarly track observed phenological changes. Hyperion EVI resampled at multiple resolutions (30 m; 60 m; 120 m; 250 m; 500 m) maintained synchrony with variations in the phenological events of canopy. All three covers showed lower GPP estimates in dry season despite higher Photosynthetically Active Radiation (PAR) values suggesting that water availability rather than PAR is the critical factor governing GPP of tropical dry deciduous forests. Given the patchy landscape and moisture-driven seasonal cycle of phenology and GPP, spatial resolutions of better than 250 m and narrowband spectral features like Hyperion are necessary for monitoring phenology and GPP of tropical dry deciduous forests, providing a basis for improving methodologies of photosynthesis products from upcoming EnMAP and HyspIRI programs.

1. Introduction

Tropical forests are one of the most diverse habitats on Earth (Bradshaw et al., 2009; Whitmore, 1998). They are responsible for about one-third of global terrestrial primary productivity (GPP) and exhibit a wide variation in patterns of vegetative and reproductive phenology on both large and small geographic scales (Beer et al., 2010; Morellato et al., 2000). Small changes within the tropical forest biome can potentially lead to major global impacts on both the rate and magnitude of climate change and the conservation of biodiversity (Lewis, 2006). These changes will also have a compelling impact on the Gross Primary Productivity (GPP) of tropical forest covers, whose magnitude and variability are still poorly understood, especially outside the Amazon basin.

Among these forests, dry deciduous forests are the most disturbed and least protected ecosystems on earth (Murphy and Lugo, 1986), and a system that has been understudied in terms of GPP. The knowledge gap is due in part to the complexity of tropical forest ecosystems, the underdevelopment of scientific and engineering infrastructure in the geographical areas that coincide with these forests, and the tendency of many countries to treat tools for conservation and resource management as a low priority relative to immediate economic needs (Sánchez-Azofeifa et al., 2003).

A particular challenge to GPP estimation in tropical dry deciduous forest is that individual species within these exhibit diverse phenological behaviour, owing to wide-ranging response of plants to limitation in water availability and duration and intensity of

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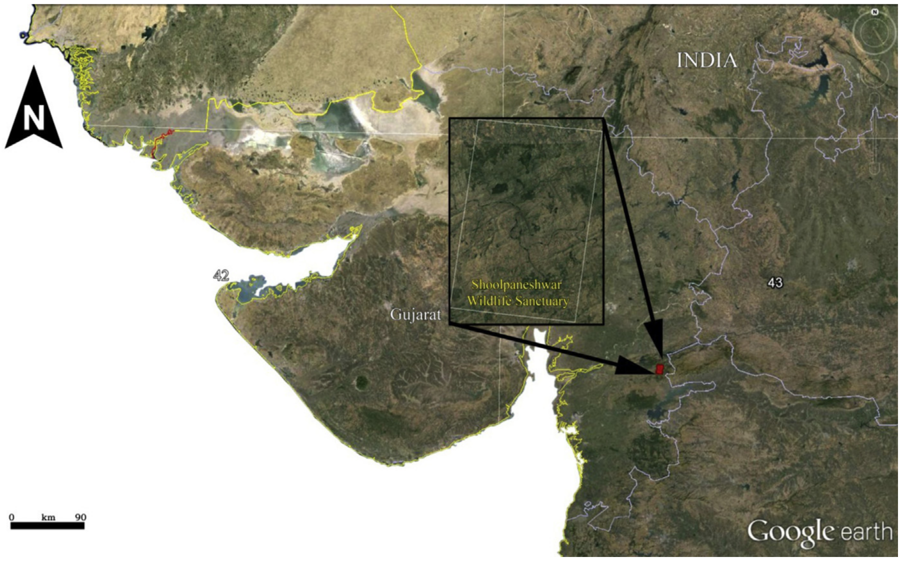

Fig. 1. Location of the study area (21.7017N, 73.735E, India, displayed in Google map image with UTM projection).

seasonal drought (Mooney et al., 1995). Water is commonly considered to be the most important environmental factor affecting growth and distribution of trees (Hinckley et al., 1991) largely by affecting the timing of phenological events in dry forests (Murphy and Lugo, 1986). In tropical forests, leaves are shed during the early dry season and new shoots are produced with the onset of wet season (Reich and Borchert, 1984). Observed phenological events of many tropical dry forests confirm to these expectations (Frankie et al., 1974). Temporal dynamics of cyclical events such as leaf emergence and leaf fall have also been suggested as a possible mechanism to explain the dry-season maxima of carbon and water fluxes (Xiao et al., 2005a; Hutyra et al., 2007).

While eddy covariance flux towers can provide direct estimates of ecosystem carbon exchange (Baldocchi et al., 2005), there are limited flux towers in tropical dry deciduous forest. In complex and difficult to access ecosystems, satellite remote sensing can provide consistent and systematic observations of phenology (Jeong et al., 2011) and ecosystem productivity. However, the accuracy of remote sensing-based models in tropical dry deciduous forests is not known. There are many models based on satellite remote sensing developed for GPP estimation using different parameters, including the Moderate Resolution Imaging Spectroradiometer (MODIS) product termed MOD17A2 (Zhao and Running, 2006), the Vegetation Photosynthesis Model (VPM, Xiao et al., 2004a), Temperature and greenness (TG) model (Sims et al., 2008) and the Vegetation Index (VI) model (Wu et al., 2010). TG and VI models are vegetation index-based models. MOD17A2 and VPM are Light Use Efficiency (LUE) based models (Running et al., 2004).

Here, we examine the fidelity of existing broad band, multispectral, coarse spatial resolution vegetation indices, such as those from MODIS, by comparing them to the EO-1 Hyperion sensor, a narrow band, hyperspectral, higher spatial resolution product, and evaluate their ability to detect phenological and moisture variations of tropical dry deciduous forests. We selected six different days of year (DOY) that span across the phenological cycle of trees of our study area, and also where the two sensors overlap in imaging time with limited variation in sun-sensor geometry, and finally, when direct phenological observations were made. Further, we applied the VPM model to MODIS and Hyperion to evaluate how these differences in vegetation index seasonality and magnitude influence a commonly used GPP model. Finally, we assessed how this GPP model compares to the standard MOD17A2_1000 m LUE based GPP model.

Our primary objective is to compare vegetation index, phenology, and GPP estimates coming from these three different datasets in a tropical dry deciduous forest. We asked:

1. What differences are observed in seasonal variation in Enhanced Vegetation Index (EVI), Land Surface Water Index (LSWI), and modelled GPP estimates of a tropical dry deciduous forest coming from optical sensors of different spatial and spectral resolutions?
2. How are these seasonal variations in remotely sensed reflectance related to variations in observed plant phenology, biomass, and water stress?
3. To what extent do these estimates of GPP differ among model structure, spatial resolution, and parameter and interpolation assumptions?

2. Methods

2.1. Study area and vegetation characteristics

The study area, Shoolpaneshwar Wildlife Sanctuary (SWS, 21°29′N–21°52′N and 73°29′E–73°54′E) is located in Gujarat, India (Fig. 1). The SWS is one of the important protected areas supporting sizeable biota. It is spread over an area of 675 sq. km. Topography of the study area is undulated with continuous and discontinuous hilly tracts up to an elevation of ~800 m (a.s.l.) intermingled with valleys, streams and sporadic clearings for agriculture. Mean annual precipitation of the area is 1107 mm (coming from 1991 to 2006, 15 years meteorological dataset). For the study year 2006, mean annual precipitation was slightly higher, at 1493 mm (Fig. 2). Minimum and maximum mean temperatures in winter and summer season were 15° C and 35° C, respectively. The study area follows strong seasonal dynamics. The four month wet season is usually from July to October. The rest of the year (November–June) acts as dry season (winter, summer).

The forest cover of the sanctuary can be classified as the tropical dry deciduous forest, dominated by *Tectona grandis* L.f. Linn. (Teak), *Dendrocalamus strictus* (Roxb.) Nees (Bamboo) and other Mixed tree species cover (semi-evergreen and deciduous). Like in any tropical area, heterogeneity in species distribution is unique to the study area. Mixed species cover consists of species like *Adina cordifolia* (Roxb.) Hook. f., *Morinda tomentosa* B. Heyne ex Roth., *Dalbergia sissoo* DC., *Terminalia bellirica* (Gaertn.) Roxb., *Anogeissus*

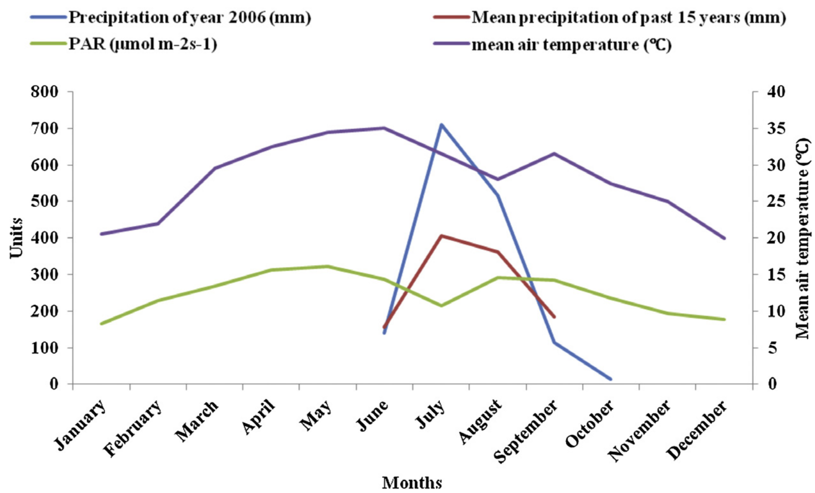

Fig. 2. Monthly rainfall (of year 2006), mean monthly rainfall (of 15 years, 1991–2006), PAR values and mean monthly air temperature (°C, of year 2006) of the study area, indicating a strong wet and dry cycle, with otherwise relatively constant temperature. 2006 had nearly twice the precipitation in the wet season than 15 Y average. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

latifolia (Roxb. ex DC.) Wall. exBedd., *Butea monosperma* (Lam.) Taub., *Mitragyna parvifolia* (Roxb.) Korth., *Garuga pinnata* Roxb., *Lagerstromia parviflora* Roxb., *Wrightia tinctoria* R.Br., *Terminalia arjuna* Roth. and *Ficus glomerata* Roxb. Few individuals of Teak and Bamboo are also present in this Mixed species cover. Bamboo was originally used as a plantation species and now has become a naturalized cover of the area as it combines good growth and drought tolerant properties towards longer dry periods. Sizeable stretches of the marked study area have large expanses of Teak and Bamboo covers as homogenous patches. These are interspersed with Mixed species covers.

2.2. Field data collection

An extensive field survey was done to collect information on homogenous vegetation patches, heterogeneous covers and any signs of human disturbance. Field surveys were carried out on all the six dates coinciding with the EO-1 Hyperion data acquisition time and across seasonal differences in the phenology. A total of 140 quadrats were laid down across the study site (91.50 km^2). 68 quadrats were laid down for Teak, 31 for Bamboo and 41 for Mixed species cover. The number of quadrats laid down for each cover was proportional to its distribution in the study site. Quadrats laid down were randomly spread across the selected area. Each quadrat was of 30 m × 30 m size, matching the spatial resolution of Hyperion sensor. Each quadrat of a vegetation cover was aligned to a 2 × 2 or 3 × 3 pixel window of the same cover. In all the quadrats, we estimated tree diameter at breast height (DBH). Quadrats of a cover having closer DBH were pooled together and mean values of DBH were obtained. These ground based DBH values were correlated with satellite based GPP of a particular day for a specific cover.

2.3. Satellite data

2.3.1. Hyperion data acquisition and pre-processing

Six narrow band EO-1 Hyperion images were acquired on 88/2006, 93/2006, 294/2006, 304/2006 and 309/2006 DOY. To fill in the gap in phenological cycle of these deciduous covers, a Hyperion image for January (22/2011) was inserted into the time series, leading to covering a phenological cycle with DOY 22, 88, 93, 294, 304, and 309, spanning the seasonal cycle of leaf emergence, leaf flushing (both in number and growth), leaf expansion and maturation, senescence and defoliation. The spatial resolution of the sensor was 30 m and the spectral resolution was 10 nm with a wavelength range of 356–2578 nm (242 bands). At the time of image acquisitions, the study area had less than 25% cloud cover. Of the six DOY, three fall in Dry season (22, 88, and 93 (later half of winter, summer)) and the other three in Wet season (294, 304, and 309 (end of monsoon, first half of winter)). The Hyperion radiance values from the 179 Hyperspectral narrow bands (after excluding uncalibrated, overlapped and water absorptive bands) were converted to surface reflectance using FLAASH (Fast Line-of-sight Atmospheric Analysis of Spectral Hypercube, USA), a Modtran-4 based program to remove atmospheric scattering and absorption effects (Saini et al., 2014).

The atmospherically corrected images were geometrically registered using the nearest neighbourhood sampling method and second order polynomial model where resultant RMSE was ≤0.5 pixel for all six datasets. For the analysis of the three vegetation covers, a spatial subset of 345 × 256 pixel (91.50 km^2) was generated within each scene. Locations of the 140 quadrats (30 m × 30 m) for three vegetation covers were transferred on to the generated subset (91.50 sq. km). Hyperion reflectance dataset from the registered pixels of the three covers (140 in number) were then used to calculate GPP ($g\,C\,m^{-2}\,d^{-1}$) for each of the six DOY.

To compare effects of spatial and spectral resolution of Hyperion_30 m, coarse resolution reflectance data were developed for the six DOY using the spectral resampling tool available in the ENVI package. For testing the impact of spatial resolution, resampled and native spectral resolution datasets of Hyperion (for six DOY) were upscaled to 60 m, 120 m, 250 m, and 500 m. EVI, LSWI and GPP were calculated for six DOY using these datasets.

2.3.2. MODIS data

MODIS is the primary multispectral (broadband) instrument in the NASA Earth Observing System for monitoring the seasonality of global terrestrial vegetation, acquiring data in 36 spectral bands from 450 nm to 2100 nm. The central point of the Hyperion subset was submitted to https://daac.ornl.gov/cgi-bin/MODIS/GR_col5_1/mod_viz.html. The MODIS land science team provides a suite of eight day composite products (available online), (http://modis-land.gsfc.nasa.gov/) including the eight day GPP product (MOD17A2_1000 m) and the eight day surface reflectance product (MOD09A1_500 m). These Collection 5 data products, MOD09A1_500 m and eight day GPP MOD17A2_1000 m were selected to match with the DOY of Hyperion datasets. These outputs included a subset of 8.5 km × 12.5 km for MOD09A1_500 m and a subset of 9 km × 13 km for MOD17A2_1000 m, matching well with the selected Hyperion subsets.

The MODIS Terra Surface Reflectance atmospheric correction algorithm product (MOD09A1_500 m) is computed from the MODIS Level 1B bands 1 (620–670 nm), 2 (841–875 nm), 3 (459–479 nm), 4 (545–565 nm), 5 (1230–1250 nm), 6 (1628–1652 nm), and 7 (2105–2155 nm) with varying spectral resolution. The MOD09A1_500 m datasets are provided to users in a tile fashion; each tile covers 10° latitude by 10° longitude. The subset of this product includes 425 pixel of 500 m × 500 m size. The 140 quadrats of three vegetation covers fall in 46 quadrats of the MOD09A1_500 m product. These 46 quadrats were used to extract reflectance data. These values subsequently were used to calculate GPP ($g C m^{-2} d^{-1}$) for the three selected vegetation covers using VPM model across the six DOY.

2.4. Sun-sensor geometry comparisons

We compared sun-sensor geometry of the two sensors to rule out solar zenith angle (SZA) variations as driving differences in the studied sensor vegetation indices (EVI and LSWI) (Galvão et al., 2011). Sun-sensor geometry of both the sensors was checked to see whether the variations seen in the reflectance values across spectrum are actually due to cyclical changes in phenology or because of artefacts caused by view illumination geometry. Calculated EVI values of Hyperion_30 m, 60 m, 120 m, 250 m, 500 m and MOD09A1_500 m were correlated with the reflectance values of the bands (blue, red and NIR) used to generate it. We found difference between sun-sensor geometry of the two sensors was 5.1°, and never exceeded 6.6°. Relationship of changes in SZA to EVI are discussed further in Section 3.2.3 and implications discussed in Section 4.4 and the supplementary materials.

2.5. MODIS GPP

The MODIS GPP product (MOD17A2_1000 m, collection 5 is designed to provide an accurate regular measure of the growth of the terrestrial vegetation. To estimate GPP in MOD17A2, the main data inputs to the MOD17A2_1000 m algorithm include: (1) fraction of Photosynthetically Active Radiation (FPAR) and Leaf Area Index (LAI) from the MOD15 LAI/FPAR data product, (2) temperature, incoming solar radiation, and vapor pressure deficit (VPD) derived from a meteorology dataset, (3) land cover classification from the MODIS MCD12Q1 data product, and (4) a Biome Parameter Lookup Table (BPLUT) containing values of ε_max for different vegetation types and other biome-specific physiological parameters.

In this study, the marked study area (a subset of 9 km × 13 km) included 117 pixel of 1 km × 1 km size. The 140 field quadrats mapped onto 25 quadrats of MOD17A2_1000 m product. These 25 quadrats were used to extract daily GPP ($g C m^{-2} d^{-1}$) values for six DOY. GPP values coming from MOD17A2_1000 m product comes from the following equation:

$$GPP = \varepsilon \times APAR \tag{1}$$

where $\varepsilon = \varepsilon_{max} \times T_{MIN}$_scalar × VPD_scalar.

The two parameters for T_{MIN_scalar} (Temperature Minimum and Temperature Maximum) and the two parameters for VPD_scalar are used to calculate the scalars that attenuate ε_{max} to produce the final ε ($kg C MJ^{-1}$) used to predict GPP. APAR (Absorbed Photosynthetically Active Radiation) in MODIS algorithm is expressed as in the following equation:

$$APAR = IPAR \times FPAR \tag{2}$$

where IPAR (Incident Photosynthetically Active Radiation on the vegetative surface) is estimated from incident shortwave radiation (SWRad, provided in the GMAO dataset) as IPAR = (SWRad × 0.45).

An eight day estimate of FPAR (Fraction of Photosynthetically Active Radiation) from MOD15 and daily estimated PAR from GMAO are multiplied to produce daily APAR for the pixel (Heinsch et al., 2003).

2.6. The vegetation photosynthesis model (VPM)

VPM is a model developed for estimating GPP of forest covers by using optical remote sensing data. It has been successfully validated for different ecosystems, including tropical evergreen forest, temperate deciduous forest, and evergreen needle leaf forest using multispectral observations (Xiao et al., 2004a,b, 2005a,b; Wu et al., 2010). The model is built upon the conceptual partitioning of photosynthetically active vegetation (PAV) and non-photosynthetic vegetation (NPV) within the leaf and canopy (Xiao et al., 2004a). It takes advantages of additional spectral bands (e.g., blue and shortwave infrared (SWIR)) that are available from advanced optical sensors (Xiao et al., 2004a,b). VPM has only one parameter (ε_0) that is biome specific (Xiao et al., 2005b)

VPM uses two improved vegetation indices, Enhanced Vegetation Index (EVI) and Land Surface Water Index (LSWI), which have the potential to provide major improvement over other satellite based models that only use the more traditional Normalized Difference Vegetation Index (NDVI) (Xiao et al., 2004a). EVI directly adjusts the reflectance in the red band as a function of the reflectance in the blue band, accounting for residual atmospheric contamination (e.g., aerosols) and variable soil and canopy background reflectance (Huete et al., 1997). Xiao et al. (2005a) assumed that LSWI is capable of tracking changes in leaf water content over the plant growing season.

The VPM model was followed to estimate GPP from the reflectance datasets of MOD09A1_500 m and EO-1 Hyperion datasets across six DOY. It is a LUE based model and estimates GPP as described in the following equation:

$$GPP = \varepsilon_g \times FPAR_{PAV} \times PAR \tag{3}$$

where $FPAR_{PAV}$ is the fraction of photosynthetically active radiation (PAR) absorbed by leaf chlorophyll in the Photosynthetically active vegetation (PAV), PAR is the photosynthetically active radiation ($\mu mol\ m^{-2} s^{-1}$, photosynthetic photon flux density, PPFD), and ε_g is the light use efficiency ($g C mol^{-1}$ PPFD). In this study, monthly PAR values were obtained from MERRA dataset (GMAO, NASA) (Fig. 2). In the VPM, ε_g is determined by the following equation:

$$\varepsilon_g = \varepsilon_0 \times Tscalar \times Wscalar \times Pscalar \tag{4}$$

where ε_0 is the apparent quantum yield or maximum light use efficiency ($\mu mol\ CO_2\ \mu mol^{-1}$ PPFD), and *Tscalar, Wscalar and Pscalar* are the down-regulation scalars for the effects of temperature, water and leaf phenology (leaf age) on the light use efficiency of vegetation, respectively. In this study, input ε_0 (0.65) parameter was selected for all three vegetation covers based on a look up table published for different biomes (Ito et al., 2004).

Tscalar is estimated for each DOY, using the equation developed for the Terrestrial Ecosystem Model (TEM) (Raich et al., 1991). For *Tscalar* calculations, T_{min}, T_{max} and T_{opt} (minimum, maximum and optimum photosynthetic temperature) published for *D. oleifera* (Vargas and Cordero, 2013) were used. For air temperature (T), local meteorological data matching with the dates of optical sensor data acquisition were considered (Fig. 2).

Wscalar and *Pscalar* were calculated using equation given in Xiao et al. (2005a). In this study LSWI was calculated across six DOY for the three vegetation covers (Table 1). Calculated LSWI_Hyperion

Table 1
Details of the spectral bands of optical sensors used for EVI and LSWI.

Vegetation indices	EO-1 Hyperion hyperspectral narrow bands	MOD09A1_500 m broad bands
EVI	854 nm (NIR) 641 nm (red) 468 nm (blue)	Band−2 (NIR: 841–876 nm) band−1 (red: 620–670 nm) Band−3 (blue: 459–479 nm)
LSWI	875 nm (NIR) 1638 nm (SWIR)	Band−2 (NIR: 841–876 nm) Band−6 (SWIR: 1628–1652 nm)

and LSWI_MOD09A1_500 m values for the three selected vegetation covers were used to calculate *Wscalar* and *Pscalar*. In the VPM model, *Pscalar* is included to account for the effect of leaf age/phenological state on photosynthesis at canopy scale. In the study area, foliage expansion is rapid, stays in green state for sometime followed by degreening. To include these distinct changes in model, *Pscalar* was calculated for all the DOY using equation given by Xiao et al. (2005a) where $Pscalar = (1 + LSWI)/2$.

In the current version of the VPM model, $FAPAR_{PAV}$ (Eq. (5)) is assumed to be a linear function of EVI and coefficient α is simply set to be 1.0 (Xiao et al., 2004a,b).

$$FAPAR_{PAV} = \alpha \times EVI \quad (5)$$

where $EVI = 2.5\ \{(R_{nir} - R_{red})/(1 + R_{nir} + 6 \times R_{red} - 7.5 \times R_{blue})\}$

EVI was calculated for EO-1 Hyperion (30 m; 60 m; 120 m; 250 m; 500 m) datasets and MOD09A1_500 m product using Hyperspectral narrow bands and Multispectral broad bands, respectively.

GPP estimates obtained from the reflectance datasets were compared with GPP estimates of MOD17A2_1000 m. ANOVA was carried out to check whether the differences seen in the GPP values of VPM_Hyperion, VPM_MOD09A1_500 m and MOD17A2_1000 m were significantly different.

3. Results

3.1. Phenological variations

Phenological variations are seen in foliage development (leaf emergence–leaf expansion) and abscission (Fig. 3). Phenological cycles of these three vegetation covers (Teak, Bamboo, and Mixed species) are distinct. Most of the deciduous vegetation starts leaf development prior to the onset of monsoon. The vegetation covers reach maximum density of green foliage during monsoon season and thereafter. From the 1st week of November, foliage of some of the trees (Teak, Bamboo, and few species of Mixed cover) start degreening. Progressively the foliage becomes senescent. Leaf fall starts in January in all the three covers. Highest leaf fall was observed in March. Trees show new leaf emergence and flushing in April.

Though Teak and Bamboo have similar phenological pattern, the pace of phenological shift is relatively faster in Teak and than in Bamboo. Both species show maximum leaf fall in the months of March to April. In contrast, mixed species cover showed a mosaic pattern in phenology. In Mixed species cover, *G. pinnata, W. tinctoria, T. bellirica, A. cordifolia, D. sissoo* and *L. parviflora* show leaf fall from the month of February followed by leaf flushing in the month of May. In the month of April, few of the trees in Mixed species cover like *A. latifolia, M. parviflora, T. arjuna* and *B. monosperma* are leafless and many others (*W. tinctoria, A. cordifolia, D. sissoo* and *T. grandis*) are with new leaves of different hues. In subsequent months, crowns of all the species show lush green foliage.

Unlike coarse resolution remote sensing, Hyperion images of six days faithfully reproduced the same pattern as observed in the phenological changes of the field survey (Fig. 4). The differences observed in reflectance of the six DOY of Hyperion coincide with the phenological cycle of trees (Fig. 4). Canopy of the vegetation covers on 294 DOY were covered with green foliage. As the days progressed, degreening strarts. By 88 DOY, the canopy had sparse, mostly dried foliage. Images from 294 DOY to 93 DOY show synchrony with the phenological cycle of the forest cover. 294 DOY image depicts the wet season characteristics of vegetation while 88 DOY image reflects that of dry season.

Remotely sensed phenological stages also correlated well with the recorded rainfall. During the year 2006, rainfall was spread across five months (June–October) and maximum rainfall was observed in the month of July (~800 mm) (Fig. 2). Hyperion NDVI values were higher in monsoon resembling the lush green condition of the forest cover. These NDVI values were lowest in summer depicting leafless conditions.

3.2. Vegetation indices and VPM parameters

3.2.1. Hyperion datasets

EVI_Hyperion_30 m values ranged from 0.13 to 0.46 for three vegetation covers across six DOY. Variations in EVI_Hyperion_30 m values coincided with the shift in the phenology of the study area, with a peak value in wet season (294 DOY) and a lower one in summer (88 DOY, 93 DOY) across the three vegetation covers (Fig. 5). Though the canopy foliage appeared green in the months of October and November, EVI_Hyperion_30 m values showed differences indicating subtle changes in the pigmentation of foliage. A significant difference in values were observed from 309 DOY to 22 DOY and 93 DOY to 294 DOY, whereas the difference was insignificant for 294 DOY to 309 DOY and 88 DOY to 93 DOY. Slightly higher EVI_Hyperion_30 m was seen for the 93 DOY when compared to the 88 DOY. A decrease is observed from the 309 DOY to 88 DOY. Highest EVI_Hyperion_30 m values were observed for Bamboo across six DOY, followed by Mixed species cover, and then Teak. Hyperion_EVI values for native and resampled upscaled (60 m, 120 m; 250 m; 500 m) dataset (Figs. 6 and 7) all reproduced distinct phenological variations across six DOY for three vegetation covers.

Differences in LSWI of the three covers show variations in the canopy water content. LSWI_ Hyperion_30 m of Teak values were positive at three DOY (294; 304; 309) and negative at three DOY (22; 88; 93). Bamboo and Mixed species showed positive values at four DOY (22; 294; 304; 309) and negative values at two DOY (88; 93) (Fig. 8). Maximum LSWI_ Hyperion_30 m values were seen at 294 DOY and minimum at 88 DOY. Like EVI and NDVI, LSWI values coincided with the phenological cycle of the tree covers. Lower LSWI_ Hyperion_30 m values indicated early onset of senescence in Teak cover (22 DOY) and also showed greater dryness in its foliage. Mixed species cover showed relatively higher LSWI_ Hyperion_30 m values. LSWI_Hyperion_(60 m, 120 m; 250 m; 500 m) values for native and resampled upscaled datasets are shown in Figs. 9 and 10.

3.2.2. MOD09A1_500 m datasets

EVI_MOD09A1_500 m values ranged between 0.14 and 0.45 (Fig. 5). Similar to Hyperion dataset, values are illustrative of phenological cycle of tree covers. Maximum EVI_ MOD09A1_500 m values were seen at 289–296 DOY and minimum at 81–88 DOY and 89–96 DOY. Correlation between EVI_ MOD09A1_500 m and NIR reflectance is not as high as the one seen with Hyperion dataset (Suppl. Info. Fig. 2), and differences in EVI_ MOD09A1_500 m values across the three covers were not distinct ($p > 0.05$). The range in LSWI_MOD09A1_500 m values was between −0.15 and 0.19 (Fig. 8). Higher values were seen at 289–296 DOY and lower ones at 81–88 DOY. Variations in the values correlated with phenological changes of canopy cover foliage. The dynamic range observed was not as large as in Hyperion.

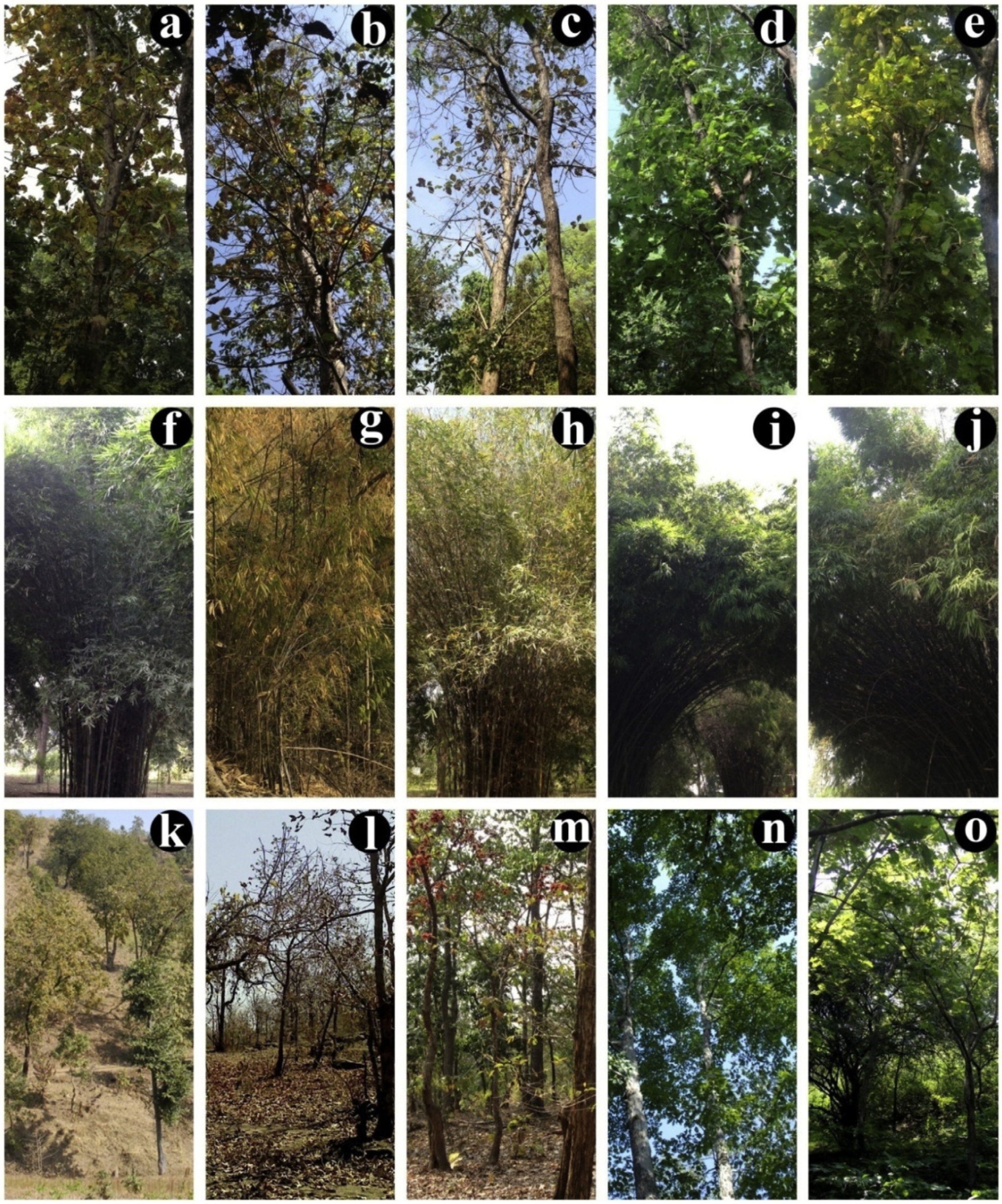

Fig. 3. Field photographs of the study area representing different phenological stages of the three vegetation covers from dry to wet season (22 DOY—a; f; k, 88 DOY—b; g; l, 93 DOY—c; h; m, 294 DOY—d; i; n, 309 DOY—e; j; o). Teak (a–e), Bamboo (f–j) and Mixed species covers (k–o).

3.2.3. Sun-sensor geometry

Increase in EVI values coincide with phenological events across six DOY for selected vegetation covers rather than changes in SZA (Table 2). EVI values of Hyperion_30 m and MODIS_500 m for the three vegetation covers coincided with the shift in the phenology of the study area with a peak value in wet season (294 DOY) and a lower one in summer (88 and 93 DOY). Both sensors showed strong positive relationship between NIR reflectance and EVI values of tropical dry vegetation covers across six DOY (Hyperion_30 m, $r = 0.98$, MOD09A1_500 m, $r = 0.92$, Suppl. Info. Figs. 1 and 2). EVI showed negative relationship with blue and red reflectance values across six DOY (Suppl. Info. Figs. 1 and 2). In dry season (DOY 22, 88, 93), as SZA decreased (51.11°–30.04°), EVI values also decreased for both the sensors. For wet season, no clear pattern was observed. Closer synchrony of DOY of Hyperion and MODIS data acquisition coupled with a comprehensive atmospheric correction ensured the removal of influence coming from other factors (SZA & Solar view angle) (see Suppl. Info.).

Table 2
Solar zenith angles of MODIS and Hyperion across six DOY.

DOY	Solar zenith angle (SZA)	
	Hyperion	MOD09A1_500 m
22	51.11	46.25
88	32.08	26.72
93	30.04	23.38
294	39.87	34.69
304	42.22	37.73
309	43.41	39.45

3.3. Seasonal dynamics in GPP estimates

Dynamics of GPP estimates of six DOY derived from GPP_VPM_Hyperion_30 m matched with the changes in phenological events of vegetation covers observed on the ground. Higher GPP

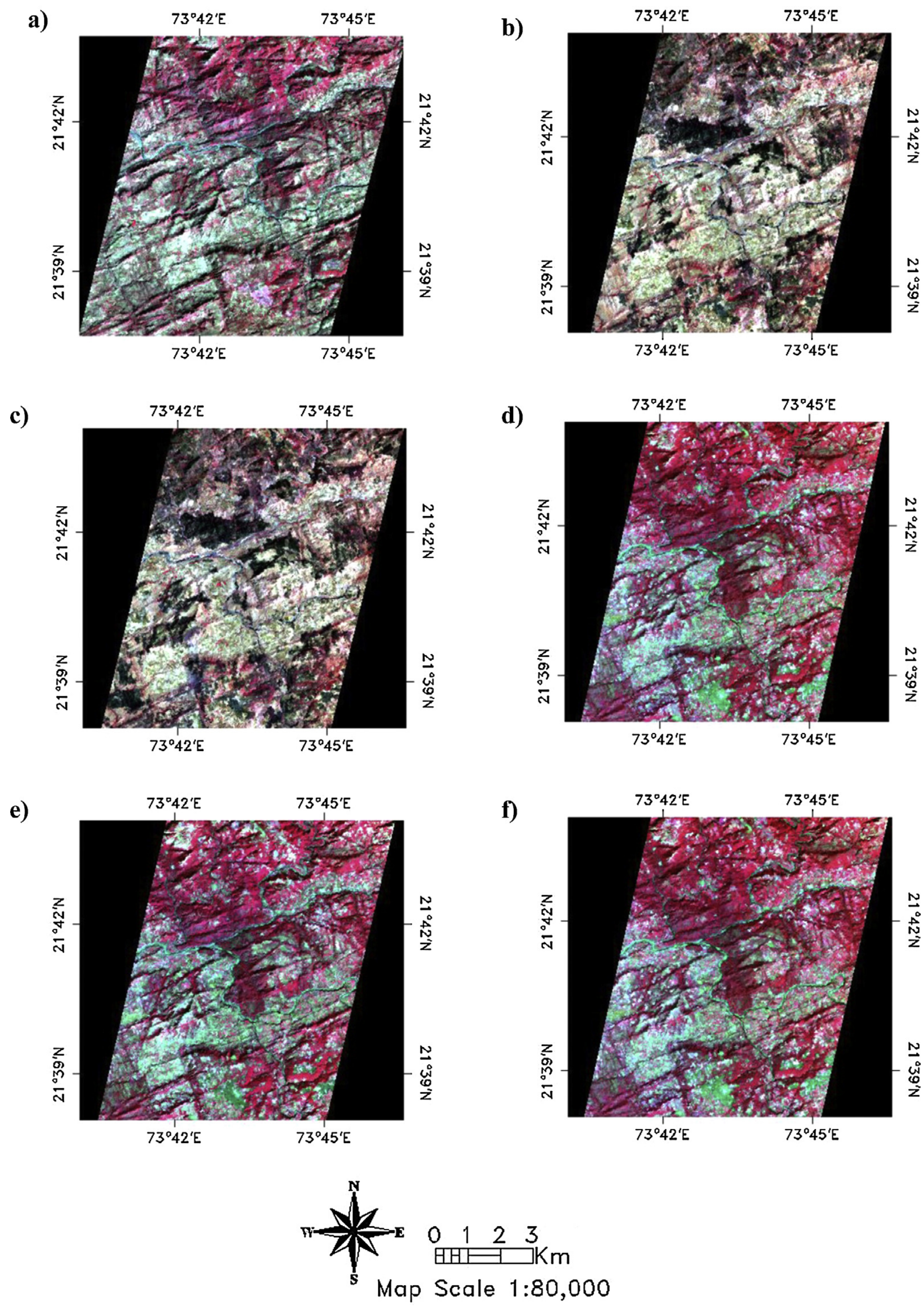

Fig. 4. RGB images (R—813 nm; G—651 nm; B—559 nm) of subset of Hyperion scenes for dry season ((a) 22 DOY, (b) 88 DOY, (c) 93 DOY) and wet season ((d) 294 DOY, (e) 304 DOY, (f) 309 DOY). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

value was observed for 294 DOY and the lowest for 88 DOY for the three covers (Fig. 11). GPP values for 93 DOY (when compared to 88 DOY) were slightly higher across the three vegetation covers coinciding with budburst and for higher PAR values observed in the month of April. Initiation of degreening of canopy foliage in the month of November was also reflected in the GPP values (Fig. 3).

Quadrats with highest DBH had higher GPP estimates. DBH and satellite based GPP (Hyperion_30 m) values showed positive correlation ranging from 0.60 to 0.75 (Tables 3–5). Seasonal variations of average GPP_VPM_Hyperion_30 m values were ranging from $3.71 \pm 1.15\,g\,C\,m^{-2}\,d^{-1}$ (88 DOY) to $29.84 \pm 3.85\,g\,C\,m^{-2}\,d^{-1}$ (294 DOY) for Teak, $4.13 \pm 1.23\,g\,C\,m^{-2}\,d^{-1}$ (88 DOY) to $33.37 \pm 3.33\,g\,C\,m^{-2}\,d^{-1}$ (294 DOY) for Mixed species and $5.23 \pm 1.46\,g\,C\,m^{2}\,d^{-1}$ (88 DOY) to $34.62 \pm 3.75\,g\,C\,m^{-2}\,d^{-1}$ (294 DOY) for Bamboo (Fig. 11).

Dynamics of GPP estimates of six DOY coming from native and resampled upscaled VPM_Hyperion_60 m, 120 m, 250 m, and 500 m datasets also matched with the phenological variations across

Table 3
Mean DBH and Hyperion_GPP estimates of sample quadrats of Teak cover in the study area.

Sr. no.	DBH (cm)	GPP ($g\,C\,m^{-2}\,d^{-1}$)					
		22/2011	88/2006	93/2006	294/2006	304/2006	309/2006
1	446.07	3.38	2.55	3.41	23.29	19.52	18.57
2	512.64	3.28	3.58	3.75	25.83	19.34	19.23
3	572.27	5.05	2.56	3.98	25.36	20.27	19.33
4	631.10	3.50	2.60	4.12	25.60	20.65	21.00
5	647.60	4.54	2.71	4.06	26.27	22.89	20.91
6	668.77	4.95	2.80	3.67	28.28	20.22	19.66
7	693.70	4.61	3.30	3.95	28.47	21.78	21.56
8	762.14	5.55	3.31	4.23	29.36	21.74	23.49
9	856.09	5.87	3.09	3.91	28.70	20.21	20.04
10	1023.58	4.60	3.62	4.53	27.54	22.73	21.75
11	1524.07	5.19	3.80	4.04	32.28	20.70	20.47
12	1877.39	6.62	3.38	4.22	34.47	25.95	24.64
13	2062.65	6.85	3.85	4.61	31.77	24.26	21.72
14	2157.19	6.88	3.65	4.49	35.37	22.87	24.53
15	2384.94	5.67	4.17	5.25	35.13	24.29	26.85
16	2928.45	6.88	4.38	4.92	29.41	24.72	26.74

Table 4
Mean DBH and Hyperion_GPP estimates of sample quadrats of Bamboo cover in the study area.

Sr. no.	DBH (cm)	GPP ($g\,C\,m^{-2}\,d^{-1}$)					
		22/2011	88/2006	93/2006	294/2006	304/2006	309/2006
1	4,201.69	12.89	4.85	4.74	32.62	26.40	25.64
2	5,013.38	13.89	5.02	4.54	32.00	31.45	29.36
3	5,792.60	15.46	5.15	5.16	33.00	32.49	27.89
4	6,102.00	16.12	4.73	5.30	33.00	31.82	30.86
5	6,226.14	17.99	5.40	5.29	32.63	30.22	30.83
6	6,359.83	15.43	4.56	4.98	33.83	29.73	31.59
7	6,531.72	16.51	5.14	4.89	36.56	31.75	30.60
8	6,803.87	16.70	5.76	5.65	39.07	31.69	32.63
9	7,591.69	17.39	6.03	6.75	36.20	34.13	31.95
10	8,307.89	18.07	6.04	5.56	37.48	34.14	29.89
11	10,023.58	17.64	6.32	6.78	38.70	35.84	34.85

three vegetation covers (Figs. 12 and 13). Both upscaled datasets showed larger variation in mean and standard deviation values. GPP_VPM_Hyperion_60 m, 120 m, 250 m, 500 m of Teak cover at 22 DOY, were higher as compared to GPP_VPM_Hyperion_30 m. For Bamboo GPP_VPM_Hyperion estimates were decreasing with increase in spatial resolution across six DOY. GPP_VPM_Hyperion values for Mixed species cover did not show a well-defined pattern. Differences in GPP estimates with upscaling are more pronounced in dry season.

Compared to Hyperion, when using MOD09A1 reflectance, GPP_VPM_MOD09A1_500 m estimates showed wider range, though resulting GPP largely matched with the phenological cycle of tree covers. Higher values were seen at 289–296 DOY and lower ones at 81–88 DOY. As compared to Hyperion estimates, GPP_VPM_MOD09A1_500 m values were lower in dry season (Fig. 11).

Estimated daily GPP_MOD17A2_1000 m values ($g\,C\,m^{-2}\,d^{-1}$) coming from the selected eight day interval of selected month coinciding with the Hyperion acquisition dates are given in supplementary information (Suppl. Info. Table 1). GPP_MOD17A2_1000 m estimates were narrower in range across the three vegetation covers (0.00–2.16 $g\,C\,m^{-2}\,d^{-1}$). For Bamboo and Mixed species covers, 17–24 DOY showed maximum GPP value while for Teak it was higher at 297–304. Further, GPP_MOD17A2_1000 m values were higher at 305–312 DOY as compared to that of 289–296 DOY. Changes in the GPP_MOD17A2_1000 m values did not coincide with

Table 5
Mean DBH and Hyperion_GPP estimates of sample quadrats of mixed species cover in the study area.

Sr. no.	DBH (cm)	GPP ($g\,C\,m^{-2}\,d^{-1}$)					
		22/2011	88/2006	93/2006	294/2006	304/2006	309/2006
1	409.56	4.64	2.92	3.91	30.85	24.49	24.77
2	435.77	4.78	3.94	4.55	29.55	25.51	23.56
3	499.75	8.51	2.93	3.93	29.22	28.00	24.87
4	536.77	9.29	3.31	5.85	31.10	27.40	27.30
5	568.19	5.38	3.16	3.20	28.85	31.17	25.77
6	806.52	6.88	4.72	6.97	35.57	29.98	30.74
7	889.29	10.79	4.52	6.32	34.33	29.52	33.45
8	942.04	9.77	3.60	5.11	33.41	29.59	28.95
9	1043.74	8.18	5.26	5.72	36.79	30.91	30.93
10	1065.70	8.39	4.42	6.06	32.14	29.74	30.22
11	1091.48	12.44	4.74	6.30	34.85	31.10	31.77
12	1165.47	13.32	4.53	7.27	34.98	29.33	29.20
13	1366.83	12.50	5.65	9.86	38.29	34.59	34.92

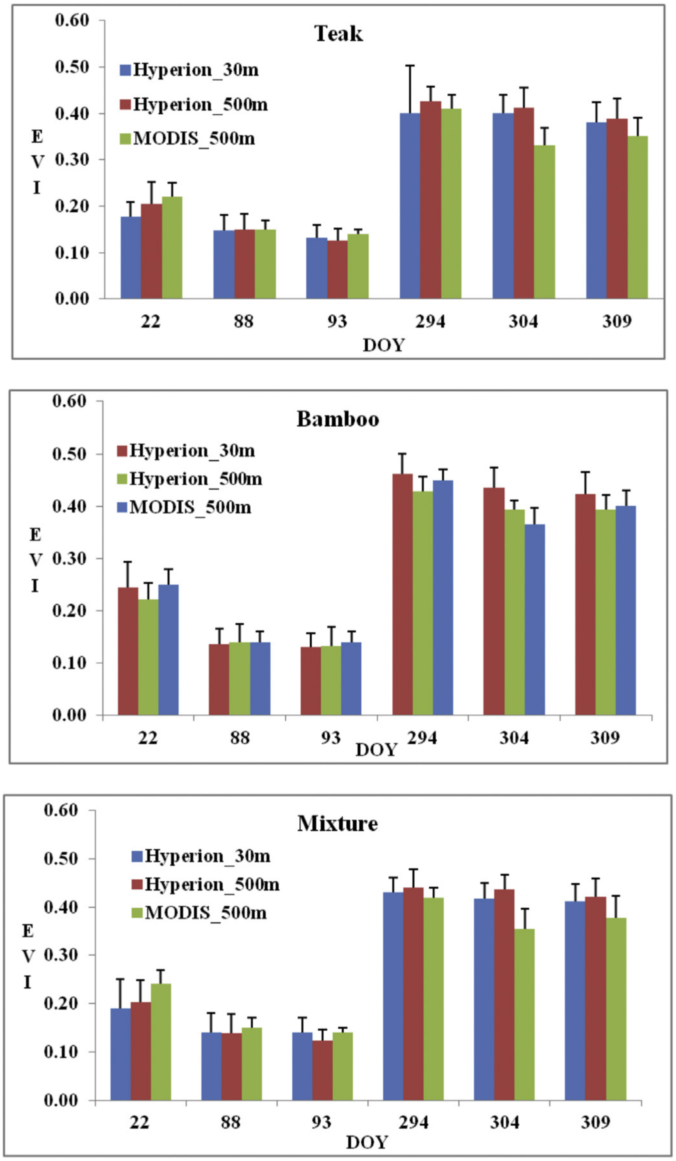

Fig. 5. Comparison of EVI values of Hyperion_30 m, Hyperion_500 m and MODIS_500 m. Shifts from early to late DOY reflect dry to wet season transition. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

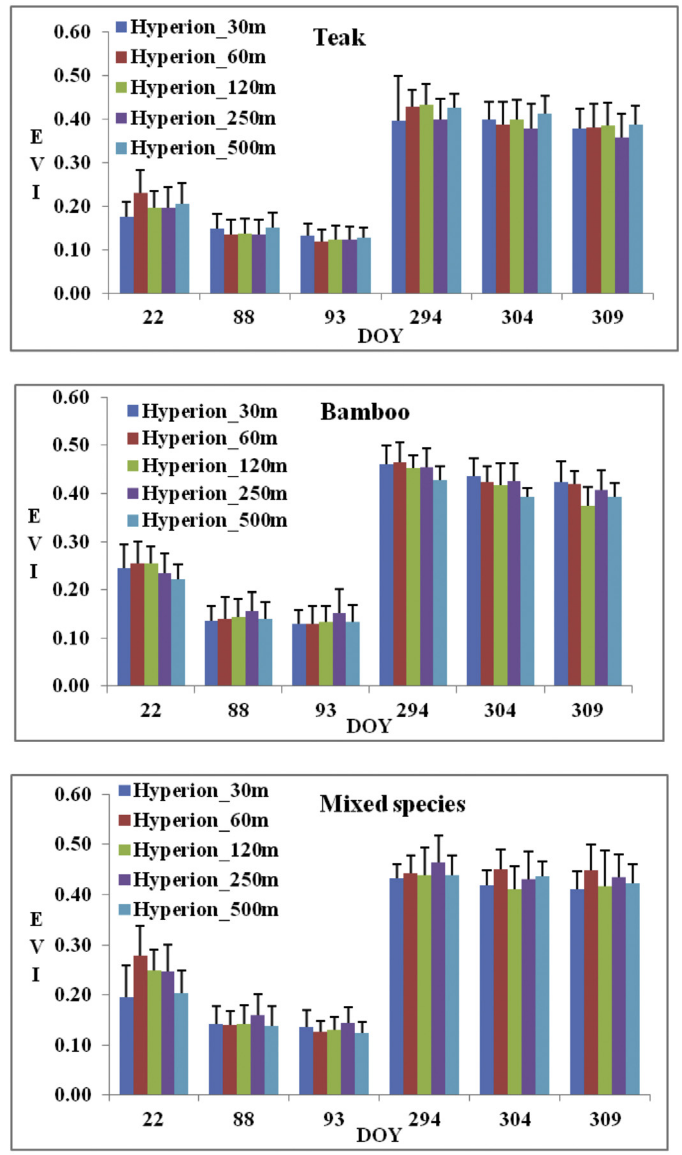

Fig. 6. Hyperion_EVI values for upscaled datasets (30 m, 60 m, 120 m, 250 m, 500 m) for six DOY show limited change in EVI magnitude and tendencies at least up to 250 m.

phenological variations. Extracted ones at 81–88 DOY and 89–96 DOY for Mixed species and Bamboo covers showed nil values.

3.4. Comparison of upscaled time-series Hyperion with MODIS datasets

A positive correlation was observed in EVI values of Hyperion_30 m and MOD09A1_500 m datasets for Teak ($r = 0.96$), Mixed species cover ($r = 0.97$) and Bamboo ($r = 0.98$) across six DOY (Suppl. Info. Fig. 3a–c). The correlation did not change with upscaling of Hyperion to MODIS resolution (Suppl. Info. Fig. 3g–i). Correlation between GPP_VPM_Hyperion_30 m and GPP_VPM_MOD09A1_500 m for Bamboo was $r = 0.98$, for Teak $r = 0.95$ and for Mixed species cover $r = 0.99$ (Suppl. Info. Fig. 3d–f). GPP estimates from VPM_Hyperion_500 m and VPM_MOD09A1_500 m were positively correlated (Suppl. Info. Fig. 3j–l) with high values ($r = 0.95–0.99$) across Teak, Bamboo and Mixed species covers.

4. Discussion

4.1. Dynamics of vegetation indices

EVI and LSWI tracks phenology in both optical sensor values, similar to earlier studies in temperate forests (Xiao et al., 2004b). Observed EVI and LSWI values for tropical dry deciduous forest of SWS are different (higher in wet season and lower in dry season) than that previously observed in evergreen tropical Amazonian forests in Brazil (Xiao et al., 2005a; Galvão et al., 2011), and demonstrate that tropical dry deciduous forest covers can be well differentiated by standard vegetation indices.

Higher EVI_Hyperion_30 m values were observed for wet season and lower for dry season. Unlike the MODIS observations, native upscaled EVI_Hyperion_ (60 m; 120 m; 250 m; 500 m) values also showed similar pattern, indicating that spectral sensitivity is more important than spatial resolution for detection of phenology. Other Hyperion studies also supported the value of spectral sensitivity. Samanta et al. (2012) and Galvão et al. (2011) reported that Hyperion EVI and LAI products are very sensitive to changes in

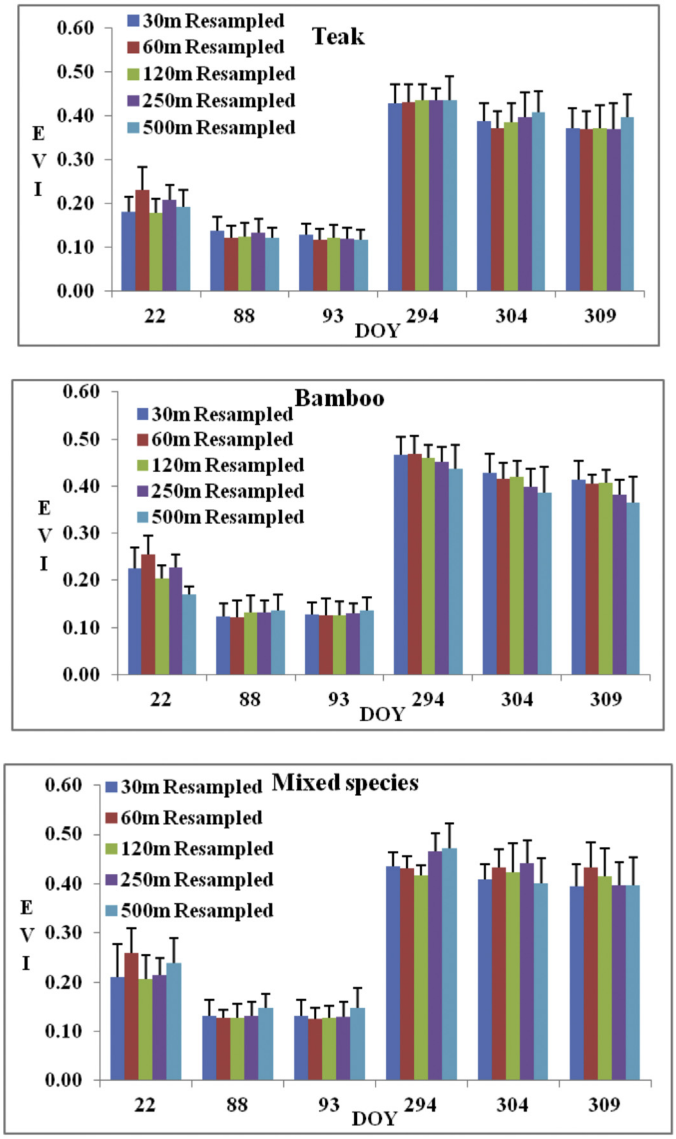

Fig. 7. Similar to Fig. 6, but Hyperion EVI values for upscaled by resampling (30 m, 60 m, 120 m, 250 m, 500 m) for six DOY, showing a similar response as native upscaling.

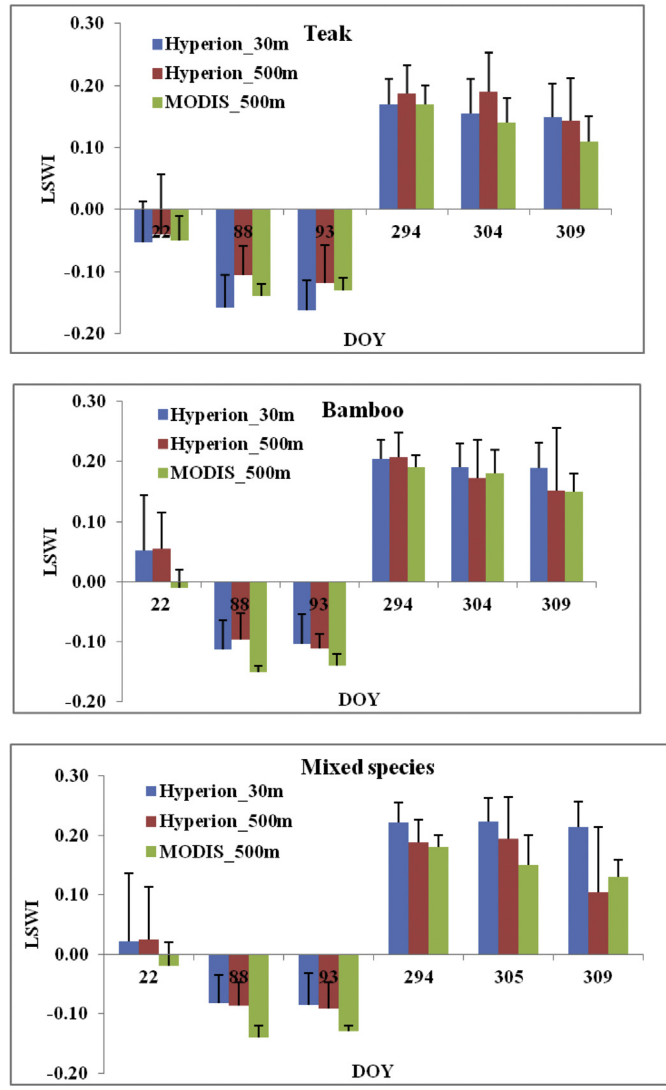

Fig. 8. Comparison of Hyperion_30 m, Hyperion_500 m and MODIS_500 m LSWI values, which has larger variation than EVI.

NIR reflectance. We find that EVI was more responsive to canopy structural changes than NDVI for Hyperion.

LSWI values from Hyperion showed finer changes in leaf optical properties owing to variations in biochemical and biophysical properties of canopy, with higher values in wet season than dry season. An independent study was carried out in our laboratory to monitor monthly changes in the foliage of trees akin to the composition of species seen in adjacent forest covers. Leaf water content, leaf area, leaf weight, chlorophyll were measured for a year at monthly intervals. Changes in the leaf water content of Teak, Bamboo canopies indicated 15–25% fall in leaf water content from October to December (unpublished data). Jin et al. (2013) similarly reported the effective applicability of LSWI data to extract the phenological dynamics of savannah woodlands in Southern Africa across precipitation gradient and woodland species types. Thus Hyperion LSWI can help in monitoring water status/drought stress of forest canopies (Chandrasekar et al., 2010).

Unlike Hyperion, EVI and LSWI estimates from MOD09A1_500 m did not match with similarly sensitivity. Though a general trend of higher values in wet season and lower ones in dry season was observed across the three covers, LSWI_MOD09A1_500 m was relatively insensitive at lower end of values observed during dry season. This is attributed specifically to spectral resolution in narrowband features that best reflect water stress. EVI_MOD09A1_500 m values of dry season did not reflect the phenological events of the three tree covers.

While spectral sensitivity was most important for detection of variation, higher spatial heterogeneity of the covers in SWS requires consideration of optimum spatial resolution. Semi-variogram analysis (Fig. 14) reveals little change in spatial variation of optical properties up until 30 m. The semi-variogram of Hyperion data has high sill variance and short range compared to that of MODIS data. It indicates that the spatial correlation in Hyperion data is limited to a smaller area and the overall variance is higher. This finding captures the expected heterogeneity of data in a tropical dry deciduous environment. Such heterogeneity is not captured well in the MODIS data due to lower spatial resolution.

4.2. Seasonal dynamics in GPP

GPP estimates were synchronous with ground-based phenological events and biomass of tropical dry deciduous forest of SWS, at least for Hyperion, with higher GPP in wet season and lower values

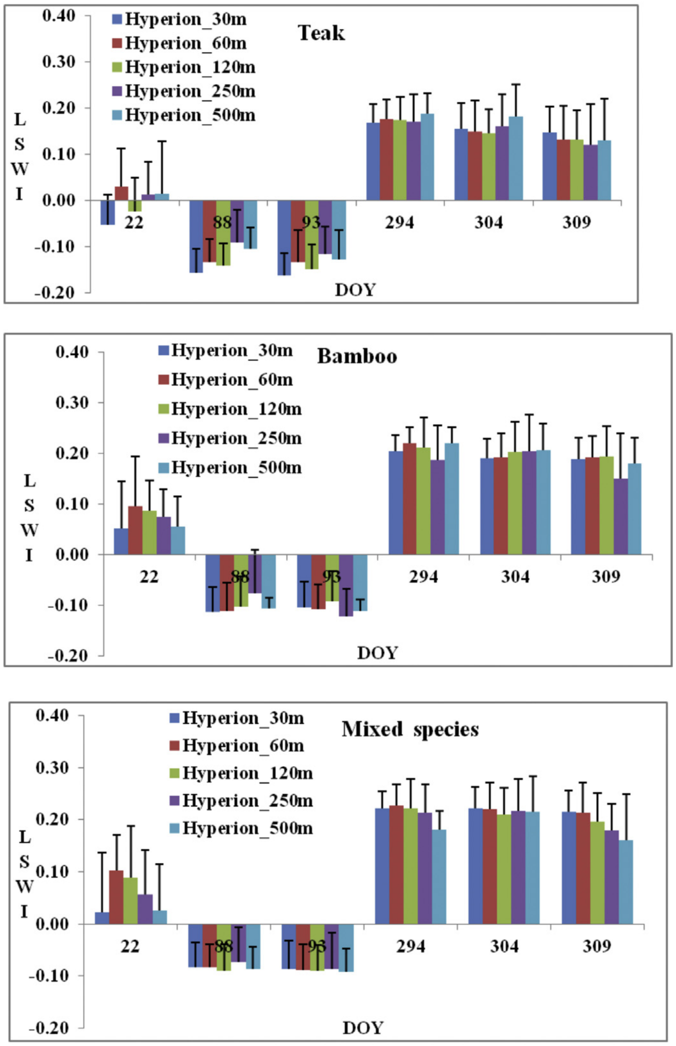

Fig. 9. Hyperion_LSWI values for upscaled datasets (30 m, 60 m, 120 m, 250 m, 500 m) for six DOY.

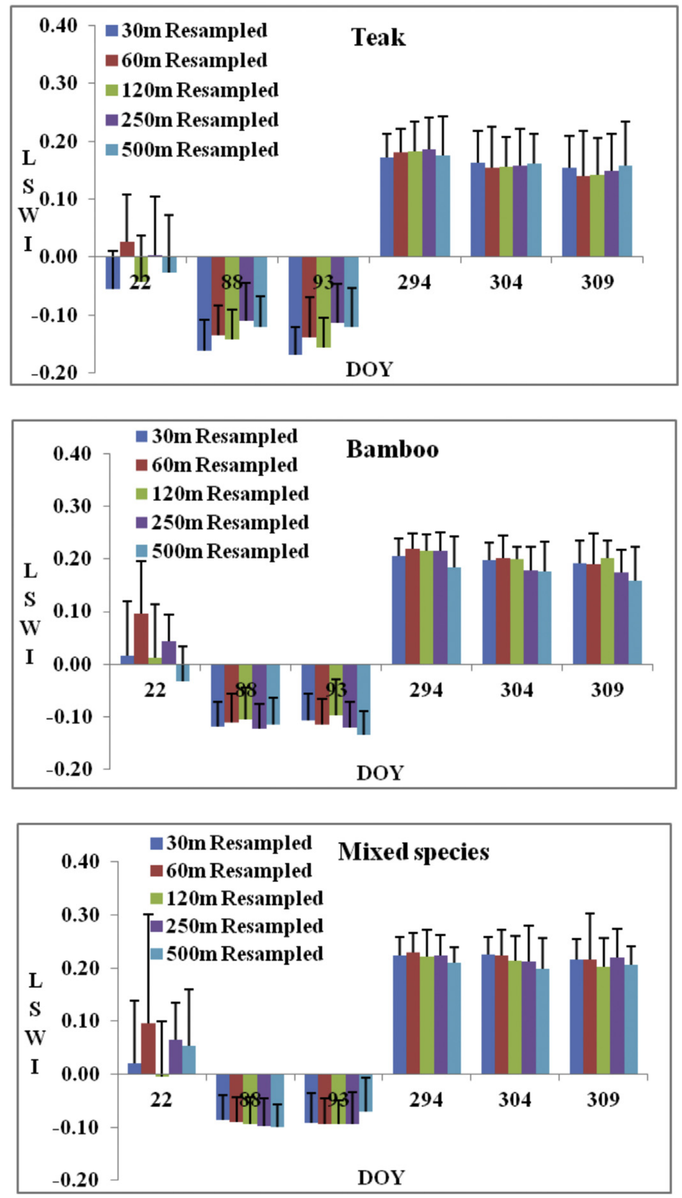

Fig. 10. Similar to Fig. 9, Hyperion resampled LSWI values for upscaled datasets (30 m, 60 m, 120 m, 250 m, 500 m) for six DOY.

in dry season. GPP_VPM_MOD09A1_500 m estimates did not match with the ones coming from GPP_VPM_Hyperion_30 m or its upscaled variants. However, these estimates were more synchronous as compared to MOD17A2_1000 m in terms of following phenological events observed on the ground. While there is a no *a priori* reason why GPP should correlate with biomass or DBH, it is a reasonable first guess, and our analysis uses these to show that a correlation exists in Hyperion that is not seen in MODIS, suggesting a major discrepancy. Regression lines of GPP_VPM_Hyperion_30 m with EVI, LSWI, *Pscalar* and *Wscalar* showed high coefficient of correlation (Pearson's, $r = 0.97–0.99$) reiterating the sensitivity of high spectral and spatial resolution dataset in GPP estimates of tropical deciduous covers. The upscaled GPP (native and resampled) estimates limited deviation in all DOY as compared to GPP_30 m. We thus infer that it is the spectral response that provides greater dynamic range in GPP seasonal estimates from Hyperion over MODIS in tropical dry deciduous forest.

GPP estimates of MOD17A2_1000 m did not match with the phenological events nor with the GPP estimates from Hyperion or MOD09A1_500 m, similar to other results showing lack of reliability of MOD17A2 algorithm in the tropics (Ganguly et al., 2010). Similarly, in the VPM model, we found *Wscalar* and *Pscalar* values derived from Hyperion were more responsive towards phenological changes as compared to the ones of MOD09A1_500 m.

Our VPM model showed that the tropical dry deciduous forest of SWS had higher photosynthesis in the wet season and lesser in the dry season. We also find in VPM that *Wscalar* is the strongest factor influencing GPP estimates of tropical dry deciduous forests. These results contrast those from tropical evergreen forests in the Amazon (Saleska et al., 2003; Huete et al., 2006; Brando et al., 2010), which argue that dry-season leaf-level responses are primarily PAR limited. Instead, in our dry deciduous, monsoon-driven system, higher PAR values did not result in higher GPP in the dry season as water limitation persisted. Rather, plants here are adapted to respond to the intermittent response on monsoonal precipitation. Other papers have noted soil–moisture sensitivity in tropical evergreen forests (Morton et al., 2014). Xiao et al. (2005a) reported that large proportion of young foliage can utilize PAR better because of higher photosynthetic efficiency. Similar conclusion can be drawn for the increase in the GPP estimates of 93 DOY as compared to 88 DOY. The newly flushed leaves increased GPP of these covers.

Our results of higher photosynthesis (as evidenced in GPP estimates) in the wet season appears to be less ambiguous than the

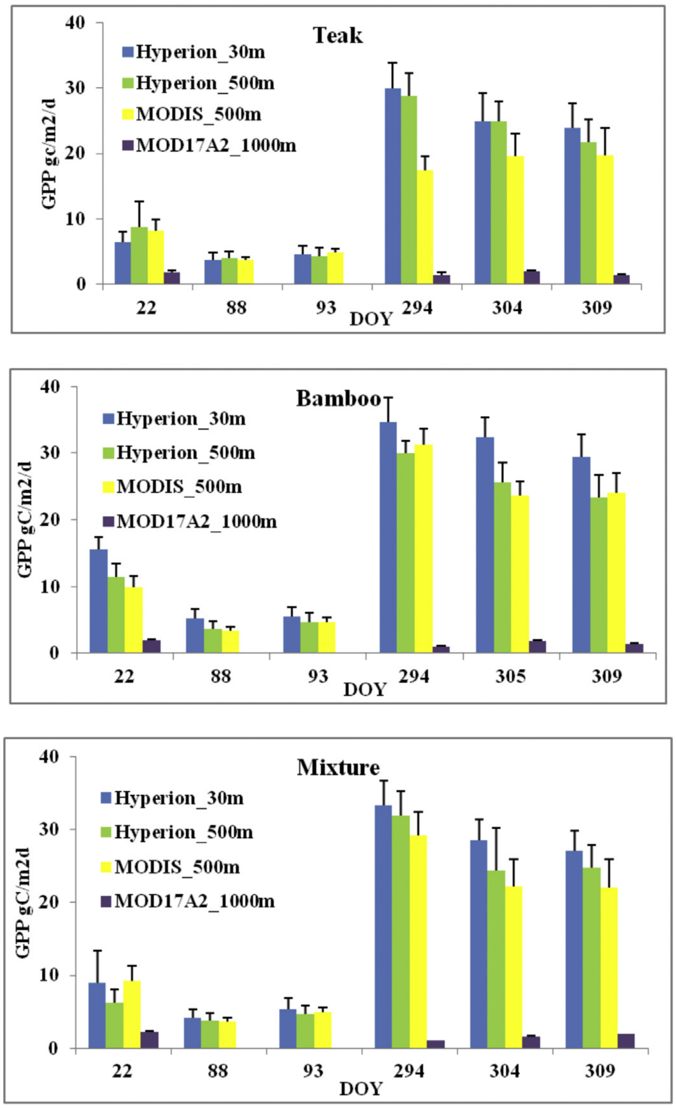

Fig. 11. Comparison of GPP values of Hyperion_30 m; Hyperion_500 m; MODIS_500 m MOD17A2_1000 m GPP values. Clearly the standard MOD17A2_1000 m GPP values are starkly different from the VPM based estimates.

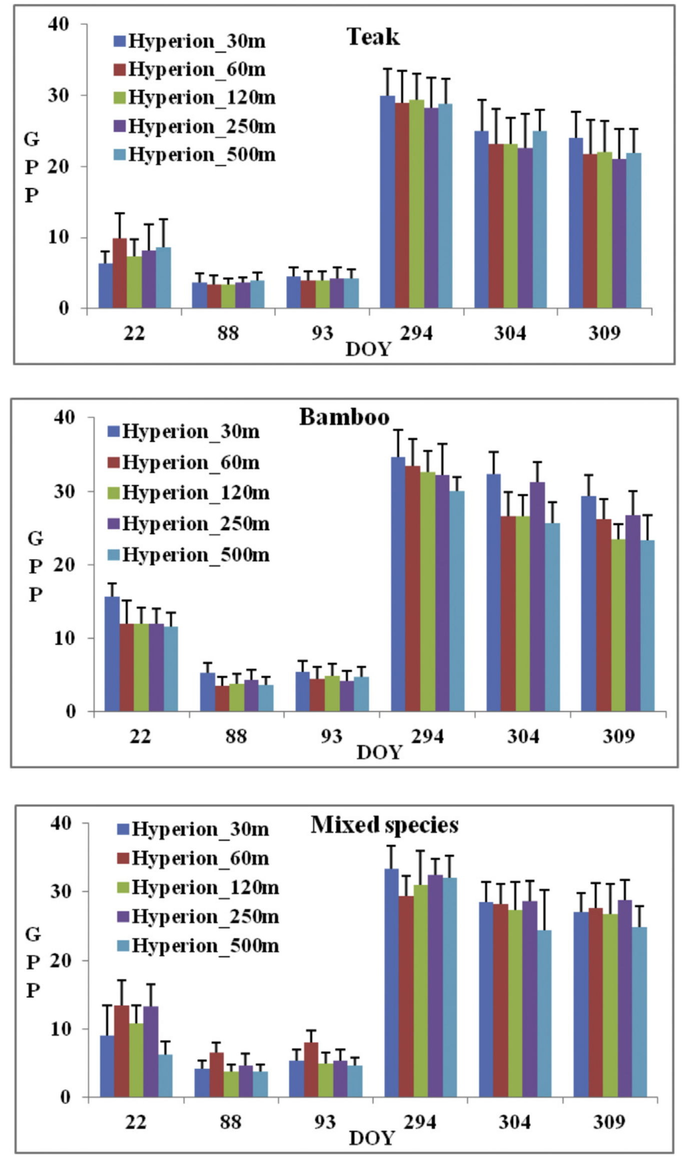

Fig. 12. Hyperion_GPP values for upscaled datasets (30 m, 60 m, 120 m, 250 m, 500 m) for six DOY.

contradictory results of moist tropical evergreen forests, though most studies there also show higher photosynthesis in the dry season than in the wet season (Myneni et al., 2007; Huete et al., 2006; Xiao et al., 2005a; Nemani et al., 2003). These results are consistent with known physiology of tropical dry forests (Frankie et al., 1974; Reich and Borchert, 1984; Murphy and Lugo, 1986; Borchert, 1994). According to Murphy and Lugo (1986) water stress is most frequently cited as the primary factor for the type or timing of phenological events in tropical species.

4.3. Reliability of global MODIS GPP in tropical dry deciduous forests

Previous studies have reported many uncertainties with MODIS GPP (MOD17A2_1000 m) products. These are attributed to lower spatial resolution of the dataset and uncertainty in interpolated or inferred input parameters (LUE, interpolated meteorological data) (Chasmer et al., 2009; Heinsch et al., 2006; Kanniah et al., 2009; Mu et al., 2007; Turner et al., 2006; Zhao et al., 2006). Input data are usually unavailable at the same spatial scale as the remote sensing imagery (Sims et al., 2008; Yang et al., 2007). Also, VPD does not explicitly incorporate soil water deficit in canopy gas exchange, which may lead to an overestimation of GPP (Fensholt et al., 2006; Leuning et al., 2005; Yuan et al., 2007; Coops et al., 2007). MOD17A2_1000 m underestimates water stress, thus overestimating GPP (Mu et al., 2007). Turner et al. (2006) reported that MODIS over estimated GPP in low productivity sites while it underestimated GPP in high productivity sites, consistent with our study.

Part of the low GPP observed in our study region by MOD17A2_1000 m can be attributed to inappropriate biome classification, identified in much of our region as identified woody savannah. This misclassification resulted in low values for the maximum light use efficiency obtained from the look up table. Running et al. (2004) and Sims et al. (2006) reported that the most significant limitation of MODIS GPP algorithm is the improper characterizing of LUE as it uses lookup tables of maximum LUE determination for a given vegetation type and then adjusts those values downwards on the basis of environmental stress factors using interpolated meteorological data.

Morton et al. (2014) reported that correcting optical remote sensing data for artefacts of sun-sensor geometry is essential to

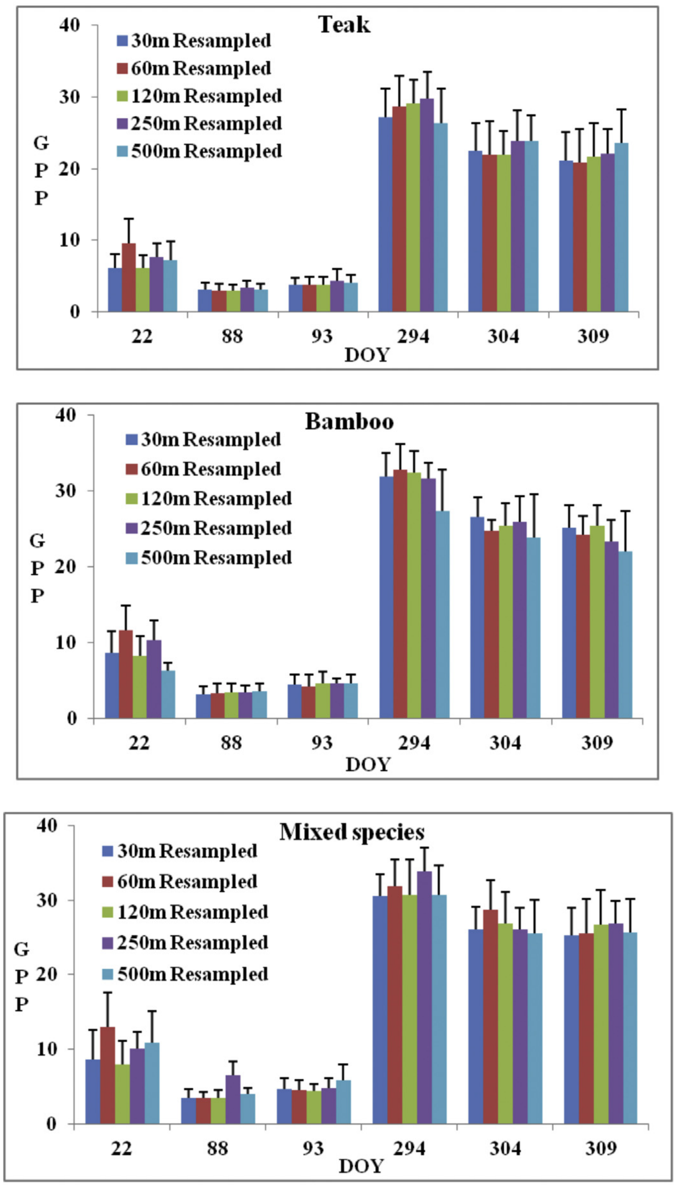

Fig. 13. Hyperion resampled GPP values for upscaled datasets (30 m, 60 m, 120 m, 250 m, 500 m) for six DOY.

isolate the response of global vegetation to seasonal and inter-annual climate variability. They also concluded that GLAS and MODIS dry season observations do not support the hypothesis that changes in canopy reflectance properties from leaf phenology are consistent at larger spatial scales (≥1 km) across the southern Amazon. Similarly, our obtained GPP _MOD17A2_1000 m values at 81–88 DOY and 89–96 DOY were zero for Mixed species cover and Bamboo which can be attributed to the averaging of pixels at large spatial resolution (1 km) with interference of soil and non-photosynthetic vegetation signal.

4.4. Uncertainty analysis

A number of factors complicate multi-sensor analysis. For example, sun-sensor geometry needs to be accounted. However, only limited differences were seen in the sun-sensor geometry between the two sensors and data acquisition synchrony in time reduced the uncertainties induced by Bidirectional Reflectance Distribution Function and atmospheric conditions despite the difference in spectral and spatial resolution of MODIS and Hyperion sensors. Difference between sun-sensor geometry of the two sensors was 5.1°, and never exceeded 6.6°. Differences of this magnitude of angle (<10%) will have minimal impact on the reflectance values of the sensors.

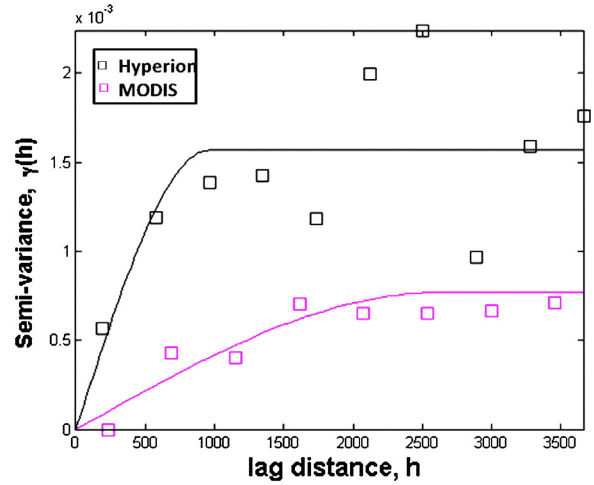

Fig. 14. Semi-variogram generated for EVI of Hyperion_30 m and MODIS_500 m resolution datasets reveals a clear 500–2000 m mode of spatial variability and greater sensitivity to spatial variability in Hyperion, consistent with our findings on the effect of spatial resolution on Hyperion and MODIS EVI, LWSI, and GPP.

Amazon forest studies (Galvão et al., 2011) did not report changes in canopy structure while in our study area structural variations are clearly seen. They also reported that EVI and NIR reflectance values are inversely related to SZA. This has not been observed in our study. Correlation between EVI and reflectance of red, blue and NIR for both the sensors were contrary to the observations made by Galvão et al. (2011). Thus, we conclude that SZA has minimal or no impact on measured parameters (EVI and NIR reflectance values) of tropical dry deciduous forests.

Uncertainty in GPP estimates can also come from spectral and spatial resolution of the optical sensor data, homogeneity or heterogeneity of the tree cover, or scalar values used in finding out ε_g. Based on GPP from two optical sensors (inclusive of upscaled native and resampled) GPP estimates of Hyperion), we find that differences in spectral resolution add greater variance than spatial resolution. While direct ground truth for GPP is not available in this region, the ground-based DBH, biomass, and phenology observations were more consistent with variation in Hyperion than MODIS. Dry season GPP_Hyperion_30 m estimates are the lowest across the covers and appear to be realistic compared to ground based observations of plant phenology and optical foliage photographs. GPP_Hyperion_30 m dataset brought in fine scale variations in scalar values (specifically LSWI), which have a direct impact on GPP estimates. Heterogeneity in tree cover is common in the Tropics. While smaller than 500 m spatial resolution dataset can address many of the shortcomings for GPP estimation in heterogeneous covers, narrowband spectral observations also provide greater dynamic range of phenological and water stress variation.

5. Conclusion

Seasonal water stress determines the timing of phenological events in tropical dry deciduous forests and has a significant impact on the GPP of tropical dry deciduous forest cover, but the mechanism of its action remains poorly understood. Mapping GPP in these systems requires attention to spectral and spatial resolution. Multispectral broadband sensors have significant limitations (Thenkabail et al., 2004; Thenkabail et al., 2000). The need is obvious for targeting specific narrow bands to study the spectral properties of vegetation for these mixed species, moisture sensitive systems (Mariotto et al., 2013).

In theory, observations with a finer spatial resolution should improve regional estimations of GPP since they better capture the variation in a heterogeneous landscape (Schubert et al., 2012) and scaling equations from reflectivity to GPP are non-linear. Instead, our study found that spectral sensitivity is more important than spatial resolution in identifying critical changes in phenological events and vegetation indices. Estimates of GPP coming from Hyperion showed synchrony with phenological events of a tropical dry deciduous forest cover, unlike standard MODIS estimates, or even broadband-based estimates from the VPM model. Water stress drives these phenological variations, which were clearly observed both on the ground and in the estimated Hyperion-based VPM model GPP values for three vegetation covers across the selected dates. Vegetation indices derived from broadband sensors and global look-up table parameters were less sensitive to the unique leaf-, canopy-level changes occurring in our target species. Findings of this study can help on fine tune the methodologies for advanced information products from upcoming EnMAP and HyspIRI programs.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet.2015.08.246

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

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We studied the soil organic carbon (SOC) dynamics in two types of tropical ground cover (grasses predominantly as C_4 functional type and herbaceous predominantly as C_3 functional type), located in a permanent plot of the Department of Botany, the M.S. University of Baroda, Vadodara, 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 (C_3 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 = 10^{15} g) of carbon (C) up to 3 m depth[1]. This amount is more than twice that in vegetation (359 Pg) and atmosphere (760 Pg) combined[2–4]. 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 carbon[5]. 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 depth[6]. There are several studies on the contribution and impact of forest cover (boreal, temperate and tropical) on the carbon cycle[7–10]. 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 vegetation[11]. Grasslands are considered as a major potential sink for carbon[12–14]. Grassland (temperate and tropical, mostly C_4) 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 season[15]. Unlike grasslands, herbaceous cover (broadleaved ephemerals, C_3 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 turnover[16]. 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 (C_3 and C_4 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 atmosphere[17]. We lack precise knowledge of the sources of and controls upon the release of CO_2 from the soils[18]. 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 Mohapatra[20] 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 CO_2 efflux affecting the global carbon cycle. An earlier study[18] 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 slowly[5]. These aspects get influenced more in ground cover because of their variations in structure and functional role. There is

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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 C_3 functional type and grasses as C_4 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 (C_4 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 (C_3 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 (C_4 functional type), and that occupied by forbs/broadleaved herbs is treated as herbaceous cover (C_3 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 m^2 blocks. Randomized block design was employed while picking up a quadrat for measuring different parameters. Parameters measured are aboveground 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 method[21].

Soil respiration was measured *in situ* following the alkali absorption method[22]. 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. CO_2 efflux was collected in small plastic chambers with 20 ml 1 M NaOH over a 24 h period. The amount of CO_2 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 method[23]. DOC was extracted following the protocol of Jones and Willett[24]. 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 method[23]. Values obtained were considered as DOC.

MBC was estimated by chloroform fumigation extraction method[25]. 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 K_2SO_4 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 K_2SO_4 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}).

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

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 (C_4 functional type) and herbaceous (C_3 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 (C_4 functional type) as compared to herbaceous cover (C_3 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.

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

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 (C_3 functional type) than in grass cover (C_4 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 1 *a*), 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 1 *b*, *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 (C_3 or C_4).

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 Upadhyaya[15] and Das *et al.*[16]. AGB in herbaceous cover moved according

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

	AGB		BGB	
Month	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). ±, Values indicate standard deviation.

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

	MBC		R_s	
Month	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 ± 69	11.8 ± 1.4	11.9 ± 0.1

MBC, Microbial biomass carbon (mg kg^{-1}). R_s, Soil respiration (g CO_2 m^{-2} day^{-1}). ±, 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-rich[29]. Differences in AGB and BGB allocation indicated the functional difference in both these ground covers. Similar to earlier findings[30–33], 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 reported[34], 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

	SOC		DOC	
Month	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}). ±, Values indicate standard deviation.

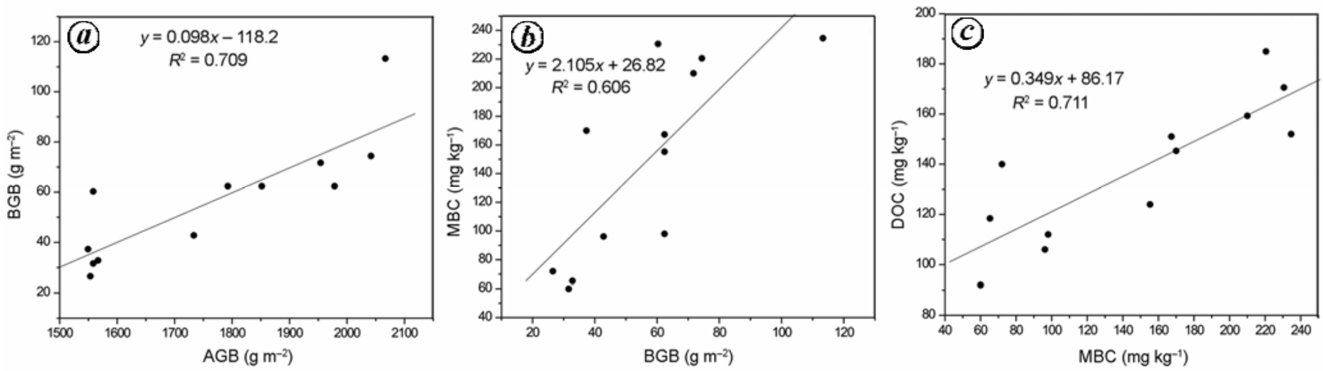

Figure 1. Correlation between AGB and BGB (***a***), BGB and MBC (***b***), and MBC and DOC (***c***) of C_4 cover. AGB, Aboveground biomass; BGB, Belowground biomass; MBC, Microbial biomass carbon and DOC, Dissolved organic carbon.

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 AGB[42]. 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 study[18] 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

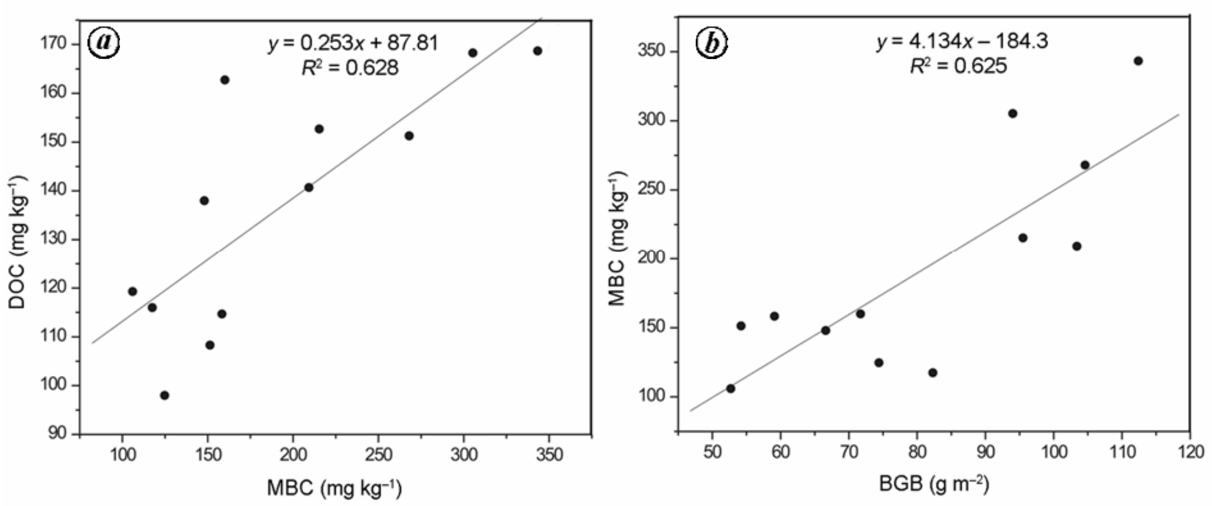

Figure 2. Correlation between MBC and DOC (***a***) and BGB and MBC (***b***) of C_3 cover.

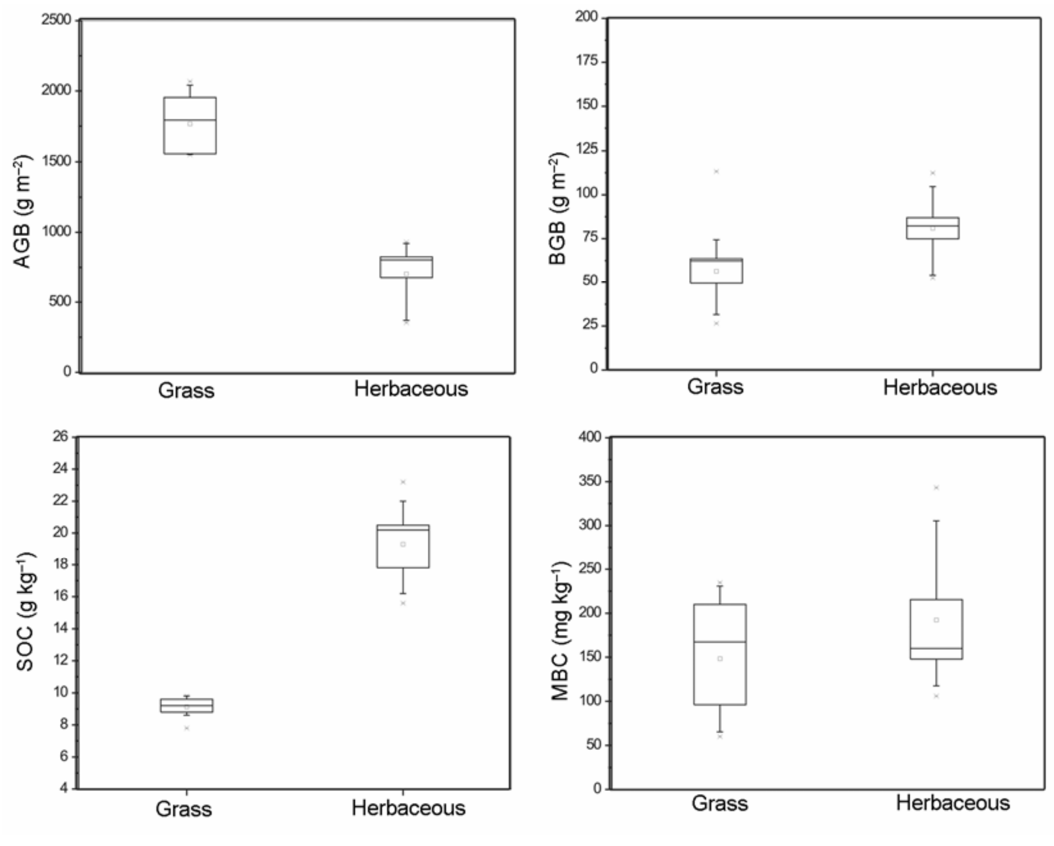

Figure 3. Box plots of AGB, BGB, SOC (soil organic carbon) and MBC.

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/MBC[12].

SOC values were remarkably different between the two covers. An earlier study[48] reported that plant functional traits regulate net soil carbon storage by controlling carbon 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 maintenance[42]. 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 (C_3 functional type) ground cover because of climate change (especially to rising CO_2 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 (C_3 functional type) ground cover because of climate change (rising CO_2 levels).

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

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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 constraints[2]. 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 capacity[3]. 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 maize[4], peas[5] 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.

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RESEARCH PAPER

Allometric equations for estimating leaf area index (LAI) of two important tropical species (*Tectona grandis* and *Dendrocalamus strictus*)

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Abstract: Leaf area index (LAI) of Teak (*Tectona grandis*) and Bamboo (*Dendrocalamus strictus*) grown in Shoolpaneshwar Wildlife Sanctuary of Narmada District, Gujarat, India was obtained by destructive sampling, photo-grid method and by litter trap method. An allometric equation (between leaf area by litter trap method and canopy spread area) was developed for the determination of LAI. Results show that LAI value calculated by the developed allometric equation was similar to that estimated by destructive sampling and photo-grid method, with Root Mean Square Error (RMSE) of 0.90 and 1.15 for Teak, and 0.38 and 0.46 for Bamboo, respectively. There was a perfect match in both the LAI values (estimated and calculated), indicating the accuracy of the developed equations for both the species. In conclusion, canopy spread is a better and sensitive parameter to estimate leaf area of trees. The developed equations can be used for estimating LAI of Teak and Bamboo in tropics.

Keywords: bamboo; canopy spread area; leaf area index; specific leaf area; teak; tropical forest

Introduction

Leaf area index (LAI) is an important parameter in the functioning of forests controlling plant productivity and exchange of energy between vegetation and atmosphere (Moser et al. 2007). It provides apt information for the evaluation of primary production of forest ecosystem. LAI is defined as the cumulative one sided surface area of the leaves in the canopy per unit ground area. Finding out a suitable allometric relationship between leaf area and other biophysical parameters of trees (diameter at breast height (DBH), tree height, and litter mass) is also an important aspect of tree research. However, LAI is one of the most difficult parameters to quantify properly, owing to large spatial and temporal variability (Breda 2003). Many studies were carried out for LAI of temperate forests (Sellin 2000; Temesgen and Weiskittel 2006; Weiskittel and Maguire 2006; Urban et al. 2008). A few studies on the LAI have also been conducted for tropical ecosystems (Maass et al. 1995; Nascimento et al. 2007). LAI can be determined by harvesting, litter trap or by optical methods. The common indirect optical methods are radiation measurement based on Beer-Lambert law, using canopy analysers (Li-Cor, Delta T devices), hemispherical photography, and remote sensing (Blackburn and Steele 1999; Dovey and Toit 2006; Nascimento et al. 2007; Urban et al. 2008). However, all the indirect methods have their own limitations. For instance, optical sensors fail to function perfectly in dense, multi-layered canopy system commonly in tropics (Moser et al. 2007).

Direct methods for leaf area (LA) estimation are expensive and time consuming, and easily lead to the destruction of the sample. It is equally impossible to execute for large tracts of vegetal cover. Therefore, indirect methods have been used to determine LAI with low accuracy for some important tropical forest trees (Maass et al. 1995; Dovey and Toit 2006). The cross-validations between direct and indirect methods have pointed to a significant underestimation of LAI with indirect methods (Breda 2003). Mass-based (direct) approaches are comparatively more accurate than optical (indirect) approaches for LAI measurements across environmental gradients (Khan et al. 2005). Plant ecologists are interested to determine LAI preferably by indirect method (even with lesser accuracy) in order to prevent destruction of the sample. An easy and accurate method is needed to estimate the LAI of vegetation, especially tropical forests. Tropical deciduous trees are unique in having complete leaf shedding in short span of time. In deciduous stands, a non-destructive method consists of collecting leaves in traps distributed below the canopy during leaf fall (Breda 2003). Khan et al. (2005) found a relationship between leaf area, above ground biomass and DBH of mangrove trees. Allometric equations relating to litter mass and DBH can be used to estimate LAI by having specific leaf area (SLA) (Gower et al. 1999). Many studies have shown a relationship between foliage mass and other biophysical parameters such as litter dry matter content, tree diameter and crown surface

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area (Makela and Albrektson 1992; Li et al. 2005; Pretzsch and Mette 2008). For the determination of LAI, exact and accurate estimation of total LA of a tree is essential. The current study was carried out to estimate LAI by developing an allometric relationship between LA and spread of canopy for two important tropical deciduous species, *Tectona grandis* (L.) and *Dendrocalamus strictus* (Nees.).

Materials and methods

Study area

The study was conducted at Shoolpaneshwar Wildlife Sanctuary (SWS) of Narmada District, Gujarat, India (21°29'N–21°52'N and 73°29'E–73°54'). SWS occupies an area of 675 km^2. Annual rainfall of the area is in the range of 900–1200 mm. Rainfall starts from the last week of June and is restricted to the months of June–October. Minimum (8°C) and maximum (42°C) temperatures are recorded in winter and summer, respectively. Vegetation cover of the SWS is mostly deciduous in nature. Teak (*Tectona grandis* L.) and Bamboo (*Dendrocalamus strictus* Nees.) are the most dominant species of the study area. Other species also growing in the sanctuary are *Butea monosperma* (Lamk.), *Holarrhena antidysenterica* (R.) Br, *Mitragyna parviflora* (Korth.), *Dalbergia latifolia* (Roxb.), *Anogeissus latifolia* (Wall.), *Bridelia retusa* (L.), *Albizia lebbeck* (L.), *Madhuca indica* (Gmel.), *Garuga pinnata* (Roxb.), *Pongamia pinnata* (L.) and *Ficus racemosa* (L.). Density of vegetation in the sanctuary is approximately 650 individuals·ha^{-1} Teak trees, 350 individuals· ha^{-1} Bamboo clumps, and 650 individuals·ha^{-1} of mixed trees. Soils are reddish-brown in colour and loamy. Alluvium deposits of clay-loam type are also seen with light brown to grey black colour (Gujarat state Forest Department, unpublished data). Two important species (*Tectona grandis* L. and *Dendrocalamus strictus* Nees.) were chosen to develop an allometric equation between leaf area and canopy spread. A few patches of Teak and Bamboo growing in neighbouring district, Vadodara were also identified to test the validity of the developed allometric equation.

Measurement of Biophysical parameters

Biophysical parameters such as height of the tree, diameter at breast height (DBH) and canopy spread were measured for both the species. About 15 individuals of each species were picked up from a 30 × 30 m plot for measurements. Measurements were carried out at ten plots. Height of the tree was measured by using Ravi's multimeter (indigenous equipment). The instrument works on trigonometric principle. DBH and canopy spread were measured using a metre tape. For each tree, canopy spread was measured in four opposite directions. Subsequently mean canopy spread of each tree was calculated. These values were considered as radius for each tree's canopy area. By using πr^2 canopy spread area of each tree was calculated.

LAI from litter trap method

Litter was collected from the forest floor of Teak and Bamboo at quarterly intervals for one year. More than 95% of litter collected comprised of leaves. Litter fall was the maximum in summer. Litter was collected from randomly laid quadrats of 1 m^2 size on the marked forest floor. We assumed that most of the leaves (>90%) of a tree will fall within its canopy spread area during litter fall. Any exchange would be uniformly compensated. At each point 5–8 quadrats were laid. From the collected litter, pieces of branches (if any) were removed (<5% by weight). The rest (>95%) was of leaves. This was transferred into plastic bags, oven dried for 48 h at 70°C, and dry weights were measured. Extreme values were discarded while pooling the data. Readings of peak litter fall period (summer) were used. Average litter fall values (m^{-2}) were obtained from five readings of each plot. Values coming from 10 plots for each species were pooled again to obtain mean litter weights of unit canopy spread area (m^{-2}). From these pooled average values (of Teak and Bamboo), total weight of the leaves fallen under canopy spread area of each individual tree was calculated. This was considered as foliage biomass of the tree. Independently 15–20 mature leaves of both the species were plucked from five trees with different canopy spread areas. Leaf area and dry weight of these leaves were measured. Subsequently mean specific leaf area (leaf area/ dry weight) for both the species was calculated. Leaf area of each tree was calculated by multiplying obtained foliage biomass of the tree with specific leaf area. LAI was estimating by dividing leaf area of a tree with canopy spread area.

Allometric equation

A simple linear regression equation was developed by taking canopy spread area and estimated leaf area of a tree as variables. Trees with different canopy spread areas were identified. Corresponding leaf area was calculated. Both these values were regressed.

Validation of regression model by destructive sampling and photo-grid method

LAI of the Teak and Bamboo trees growing in Vadodara district was measured by destructive sampling and also by photo-grid method. Twenty trees (12 for Teak, 8 for Bamboo) having similar DBH were considered. Canopy spread and subsequently canopy spread area were measured. Canopy of the Teak was vertically stratified into segments (3-6 depending on canopy height) from the base of canopy up to its tip. From each segment, 20%–25% of leaves were plucked and their leaf area was measured by using graph paper. Leaf area values of each segment were obtained by extrapolating actual readings of 20%–25% of foliage. The leaf area values of all the segments of a tree were summed up to obtain leaf area of the Teak tree. These values were used to calculate LAI of 12 Teak trees. In Bamboo, the number of stumps in each clump (Bunch of individual stem/stump of bamboo) was counted, and 5–6 representative stumps were identified. Leaf samples of these stumps were collected and leaf area was estimated by using graph paper. Average leaf area of a stump was calculated. Subsequently leaf area of each clump was obtained (leaf area of stump × number of stumps in a clump). These values were used to calculate LAI of 8 individuals of Bamboo.

Another 20 trees of similar description were taken for photo-grid method. Each tree was photographed in 4–6 directions. A ruler was included in the canopy while clicking. Number of snaps was proportional to height of the tree. Pictures taken were observed in Adobe Photoshop. Each picture was superimposed on a

1×1 grid. Each grid was considered as a pixel. Actual number of leaves in 5−10 pixels was counted. Mean leaf number of a pixel was obtained. Total number of pixels in photographs of each tree was obtained. Care was taken to avoid repetition of the same area in calculating pixels. Total number of leaves of a tree was obtained (number of pixels× mean number of leaves in a pixel). This number was multiplied with mean leaf area (coming from 20 mature leaves) to obtain leaf area of the tree. Total leaf area of 20 trees was used to calculate LAI of each tree. Canopy spread area of these 40 trees (24 for Teak and 16 for Bamboo) was taken to estimate leaf area of each the tree species by using the allometric equations developed. LAI of these 40 trees was obtained on the basis of the leaf area values. LAI values of 40 trees (coming from destructive sampling, photo-grid method and from allometric equation) were evaluated against each other with the help of Root Mean Square Error (RMSE). RMSE was used to measure the average difference between predicted and observed parameters. RMSE between predicted and observed parameters was calculated by the equation 1.

$$\text{RMSE}=\sqrt{\frac{\sum(P_i-O_i)^2}{n}} \quad (1)$$

where P_i the predicted value, O_i is the observed value. Here, predicted values are obtained from the developed equation while the observed values are from the destructive sampling and photo-grid method.

Results

Litter production increased from September to the peak at the next June. In June the canopy was completely leafless. Dry weight of fallen litter was higher in Teak compared to Bamboo. Dispersion of the values of fallen litter at most of the points is relatively less. Amount of fallen litter was proportional to canopy spread area in both the species. SLA values were more in Bamboo compared to Teak. Biophysical parameters of Teak and Bamboo trees were mentioned in Table 1. Leaf area values of individuals calculated by weights of foliage biomass and SLA values were high and increased with the increase in the size of individual/canopy spread area. Allometric equations were developed between these leaf area values and respective canopy spread area (Fig. 1). Leaf area values of another set of individuals, estimated by destructive sampling and photo-grid method were given in Fig. 2. Here also leaf area increased with an increase in the size of individual. The values of leaf area obtained by both the methods are almost similar for individuals with the same size. Correlation coefficient between leaf area values coming from both the methods was very high (Fig. 2). For all these individuals leaf area was calculated using the allometric equation developed. The calculated values were very close to the values estimated by the direct method (Fig. 3). Similar estimates developed between leaf area and DBH did not give better correlation (Fig. 4). Leaf area values obtained from different trees were used to calculate LAI. LAI values of Teak and Bamboo were 6.56 and 5.08, respectively. LAI values coming from the developed allometric equation and destructive sampling are matching with each other (RMSE 0.90 for Teak; 0.46 for Bamboo). Similar, results were also found among LAI values coming from the developed allometric equation and photo-grid method (RMSE 1.15 for Teak and 0.38 for Bamboo).

Table 1. Biophysical parameters of Teak and Bamboo trees of ten different study plots (n= 150 for both the species)

No	Teak			Bamboo		
	DBH (m)	Canopy Spread (m)	Canopy Spread Area (m^2)	DBH (m)	Canopy Spread (m)	Canopy Spread Area (m^2)
1	0.25±0.01	3.53±0.21	39.02±4.71	1.72±0.26	4.80±0.40	72.35±12.15
2	0.18±0.03	2.40±0.42	18.09±6.24	1.11±0.08	2.93±0.39	26.86±7.12
3	0.21±0.03	2.00±0.20	12.56±2.52	0.80±0.12	3.10±0.64	30.18±12.19
4	0.13±0.02	1.70±0.17	9.07±1.80	1.75±0.14	3.45±0.39	37.37±8.48
5	0.22±0.02	2.93±0.15	26.86±2.84	1.66±0.19	3.35±0.77	35.24±15.77
6	0.17±0.03	2.15±0.29	14.51±3.86	1.11±0.09	3.53±0.40	39.02±8.79
7	0.21±0.04	3.10±0.27	30.18±5.15	1.11±0.09	3.35±0.61	35.24±12.56
8	0.16±0.03	2.30±0.41	16.61±5.85	1.91±0.08	4.95±0.37	76.94±11.45
9	0.19±0.03	2.80±0.44	24.62±7.57	1.78±0.08	4.60±0.50	66.44±14.21
10	0.26±0.03	4.23±0.11	56.05±2.95	2.07±0.06	3.43±0.51	36.83±10.94

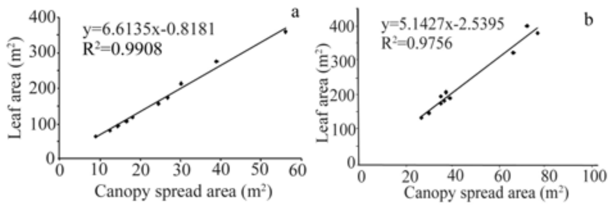

Fig. 1 Allometric relationship of LA to Canopy spread area of Teak (a) and Bamboo (b)

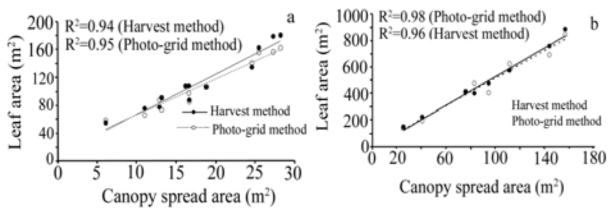

Fig. 2 Correlation of leaf area derived from photo-grid and harvest methods of Teak (a) and Bamboo (b) with canopy spread area.

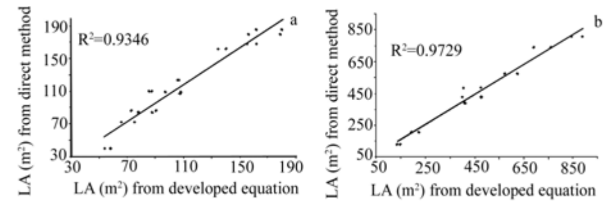

Fig. 3 Correlation between the leaf area of Teak (a) and Bamboo (b) derived from the developed equation and the destructive sampling and photo-grid method.

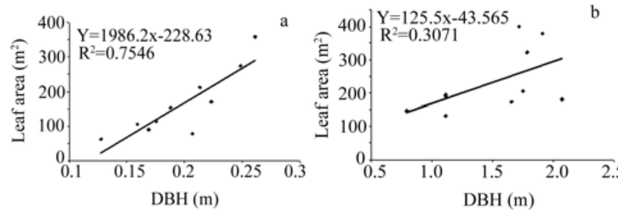

Fig. 4 Allometric relationship of leaf area to diameter at breast height of Teak (a) and Bamboo (b).

Discussion

Results of our study indicate a perfect correlation between leaf area and canopy spread area. Estimation of leaf area index from the developed allometric equation gave values similar to the ones coming from direct methods of estimation. This confirms the better functioning of the developed equations for estimation of LAI of Teak and Bamboo. LAI has a close correlation with many bio-physical changes of a tree; therefore, estimation of LAI is an important aspect for understanding the functioning of tropical trees. Most of the published results come from temperate regions (Sellin 2000; Temesgen and Weiskittel 2006; Weiskittel and Maguire 2006; Urban et al. 2009) and there are only a few reports for tropics (Maass et al. 1995; Moser et al. 2007). It is very important to have standardized equations for the estimation of LAI for tropical trees. Results of this study make an attempt to fill this void. At least for two important species selected the allometric equation worked with high accuracy. Earlier reports (Mussche et al. 2001; Breda, 2003; Asner et al. 2003) concluded that indirect methods underestimated LAI as compared to direct methods. Results of this study indicate that the developed indirect method is equally better with two of the most commonly used direct methods (destructive and photo-grid). There is no under- or over- estimation. Results of SLA showed difference in the leaf morphology of both the species. They differed with variations in the thickness of leaves as reported earlier (Witkowski and Lamont 1991; Wilson et al. 1999). Litter production was the maximum in both the sites at the end of summer, indicating the severity of the season as well as the deciduous nature of trees. Pande (2005) reported that annual litter production of Teak ranged from 3.27–4.53 $Mg{\cdot}ha^{-1}{\cdot}a^{-1}$. In the present study, the litter fall values of Teak were relatively higher (3.28−5.99 $Mg{\cdot}ha^{-1}{\cdot}a^{-1}$). This unique leaf fallen pattern helped us in calculating leaf area with better precision by litter trap method. Breda (2003) envisaged the importance of fallen litter values in estimating LA for deciduous trees. Results of our study support the view. Our estimates of mean LAI for the two tropical species are similar to the values reported earlier (Maass et al. 1995; Yang et al. 2006; Moser et al. 2007; Ganguly et al. 2008). Moreover, the values are in a narrow range irrespective of coming from direct methods or from the allometric equations.

Estimates developed between LA and DBH of trees did not give better correlation (Khan et al. 2005; Gower et al. 1999). We tried to test the correlation between LA and DBH. The correlation coefficient values are much lower (Fig. 4) compared to the ones coming from LA and canopy spread area (Fig. 1). It implies that canopy spread area is relatively more sensitive to LA as compared to DBH. Any small variations are noticeable as canopy spread area is much larger for a tree than its DBH. The relationship between LA and canopy spread area worked well for Teak and Bamboo in this study. Usage of canopy analyser has a major limitation when the tree cover is dense, and has lianas or thick ground cover. The allometric relation developed here will not be affected by any of these factors thereby giving a better estimate for LA of a tree. The study can be extended to other tropical trees for LAI estimation.

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