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Matter dynamics with respect to influences of C_3 and C_4 plants in four subtropical grasslands of Nilgiri Biosphere Reserve, the Western Ghats, India

Subramanium Paulsamy[1,*], Bong-Soup Kil[2] and Munusamy Sivashanmugam[1]

[1]Department of Botany, Kongunadu Arts and Science College, Coimbatore 641 029, India
[2]Division of Life Science, Wonkwang University, Iksan 570-749, Korea

Abstract

Biomass changes, net primary production and transfer dynamics of dry matter in four subtropical humid montane grasslands at Ebbenadu, Korakundah, Thiashola and Wenlockdown in Nilgiri Biosphere Reserve (NBR), the Western Ghats, India, were investigated. Despite the early report of a higher density and dominance of C_4 species over C_3 species in these grasslands, no functional study of matter production had previously been carried out. Therefore, in order to determine the roles played by these two groups of species, the present study was attempted. The study revealed that the dry matter and net primary production contributed by C_4 species were much greater than those of its C_3 counterpart in all the grasslands. The turnover rate of aboveground dry matter for both C_3 and C_4 species was generally rapid, whereas it was slow for belowground parts, and litter components of C_3 and C_4 species together. In all grasslands, generally about 60% and 10% of the input were channeled to aboveground and belowground parts, respectively, by the C_4 species, whereas the C_3 species transferred only about 22% and 8% of dry matter to aboveground and belowground parts, respectively. The total disappearance of dry matter was 2.73, 2.10, 3.19, and 1.96 g m^{-2} day^{-1} in Ebbenadu, Korakundah, Thiashola and Wenlockdown grasslands, which was 48.83%, 44.30%, 54.81%, and 41.09% of the total input, respectively, in these grasslands. This resulted in a considerable surplus dry matter production in all the grasslands studied. This balance sheet of dry matter in community function indicates that all the four studied grasslands were supporting the existing wild animals adequately in terms of pasture supply. The study further revealed that the stronger establishment of C_4 species rather than their C_3 counterparts, in terms of higher density and dominance, has driven them to play major roles in matter dynamics and system transfer functions in all the four grasslands studied. This fact evidenced that pasture from C_4 species for wild animals was determined to be higher in comparison to that of C_3 species.

Key words: C_3 and C_4 species, Nilgiri Biosphere Reserve, primary production, subtropical grassland, system transfer function

INTRODUCTION

Quality and quantity of herbage are important for the successful inhabitation of wild animals, by establishing effective food chains and in turn, these attributes are mainly influenced by species composition and distribution of rainy days in tropical and subtropical regions (Sala et al. 1988, Knapp and Smith 2001, Singh et al. 2005). In addition to these factors, the predominant type of photosynthetic metabolism (C_3 or C_4 or CAM types) which takes

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*Corresponding Author
E-mail: paulsami@yahoo.com
Tel: +91-9944687080

place in ecosystems is also reported to play a major role in net primary production (Murphy and Bowman 2007, Niu et al. 2008) Owing to this fact, the analysis of grasslands for primary production contributed by C_3 and C_4 species is essential to assess their production capability. The Nilgiri Biosphere Reserve (NBR) of the Western Ghats is the first established biosphere reserve in India (1986), and covers an area of 5,520 km^2, harboring many types of vegetation, such as scrub jungles, deciduous forests, wet evergreen forests, shoals (subtropical montane evergreen forests), grasslands etc. (Bor 1938). Among them, the grasslands (1% of geographical area of NBR) provide the major sources of fodder to the rich variety of wild herbivores, like sambar, Nilgiri tahr, spotted deer, great Indian gaur, etc., which in turn support many consumers such as the fox, tiger, panther which are local to the region (Singh 1994). In spite of the higher density and dominance of lower species, the role of C_4 species in community metabolism, with particular reference to primary production and system transfer function (STF), and hence, fodder availability, have not been studied in the grasslands of NBR so far. Hence, in the present study, an attempt has been made to study four major grasslands of NBR to determine the level of primary production and other associated processes of matter dynamics which are dependent on C_3 and C_4 species. This is the first ever attempt to quantify the primary production and fodder status in NBR. The information generated by this study will be used as baseline data for forestry and wildlife planners in the preparation of management plan for grasslands and wildlife.

MATERIALS AND METHODS

Description of the study area

In NBR, the Western Ghats, India (11°13′ N and 76°39′ E), the grasslands are generally restricted in their distribution to between 2,050 and 2,220 m above m.s.l., and have a geographical area of 4,700 ha. These four major grasslands, situated in the high altitudes of NBR, namely Ebbenadu (265 ha), Korakundah (195 ha), Thiashola (280 ha) and Wenlockdown (480 ha), are classified as southern-montane subtropical wet type (Champion and Seth 1968), and were selected as the representatives of the present study. These four grassland have been selected as representative of the biosphere reservation due to their occupying about 200 ha each, as well as the high degree of species variation contained therein. The rest of the grasslands, numbering around 85, each occupy an area of less than 75 ha.

The climatic data for the study areas are given in Table 1. The Thiashola and Korakundah grasslands lie adjacent to each other and at more or less same altitude (2,150 m), and hence, the climatic conditions of these two areas are considered to be the same. However, due to the wide spatial separation (15 km) and variation in altitude, the climatic factors vary for other two grasslands, Ebbenadu and Wenlockdown (2,050 and 2,070 m above m.s.l., respectively). The temperature in the study areas varied between 10.4°C (Korakaundah and Thiashola grasslands during January, 2010) and 24.9°C (Wenlockdown grassland during May, 2010). The average rainfall of the past 20 years in NBR ranged between 900 mm and 3,000 mm/y. Generally, December to February is the dry season, but unusually, in the month of December 2009 during the study period, adequate rainfall occurred in the high ranges of NBR, including the study areas. Copious rainfall occurs during the south-west (June-September) and north-east (October-November) monsoon seasons. The humidity of the studied grasslands was always high, at around 90%. High velocity wind prevails during the south-west monsoon period in the study areas. The soil is black, loamy, shallow, and acidic.

The perennial grass, *Chrysopogon zeylanicus* (Ness) Thw. dominates in Ebbenadu and Korakundah grasslands, and two further perennial grasses, *Cymbopogon nardus* (L.) Rendle and *Ischaemum indicum* (Houtt.) Merr., were determined to be dominant in Thiashola and Wenlockdown grasslands, respectively. The total number of plant species encountered in the grasslands were 108 in Ebbenadu, 88 in Korakundah, 107 in Thiashola, and 77 in Wenlockdown. In all grasslands the C_3 species contribute more to diversity (61 in Ebbenadu, 52 in Korakundah, 62 in Thiashola and 49 in Wenlockdown). Altogether, the family Poaceae accounted for the highest species contribution, of 22, 20, 31, and 17 species, respectively, in Ebbenadu, Korakundah, Thiashola and Wenlockdown grasslands. The other families with generally more than 5 species are Asteraceae, Lamiaceae, Acanthaceae and Rubiaceae. Families such as Caesalpiniaceae, Brassicaceae, Crassulaceae, Piperaceae, Caryophyllaceae, Ranunculaceae and Solanaceae contributed one species each to the respective communities studied. However, including the aforementioned dominant perennial grasses in the respective grassland, the C_4 species exhibited significantly higher density and dominance than C_3 species (Ganesan et al. 2002, Suresh 2008). A rich variety of wild animals, such as Nilgiri tahr, thoda buffalo, panther, sambar, wild boar, block bear, spotted dear, barking dear, Nilgiri lan-

Table 1. Climatic data of Ebbenadu, Korakundah, Thiashola and Wenlockdown grasslands in Nilgiri Biosphere Reserve for the year, 2009-2010

Year and month	Temperature (°C)						Rainfall (mm)			Rainy days			Relative humidity (%)		
	Max.			Min.											
	Ebben-adu	TS and KO	Wenlock-down	Ebben-adu	TS and KO	Wenlock-down	Ebben-adu	TS and KO	Wenlock-down	Ebben-adu	TS and KO	Wenlock-down	Ebben-adu	TS and KO	Wenlock-down
2009															
Jun	22.9	22.6	22.8	17.8	17.3	17.6	312.5	360.3	390.7	15	18	12	90	93	92
Jul	21.6	21.4	21.5	16.7	16.2	16.8	310.7	308.6	317.1	14	16	17	95	96	94
Aug	19.4	19.6	19.4	17.8	17.2	17.4	261.3	280.1	247.4	13	12	16	95	96	96
Sep	21.7	21.3	21.8	16.9	16.3	16.6	186.8	212.3	195.8	15	17	14	94	93	93
Oct	16.2	16.7	16.9	15.3	15.2	15.8	398.3	420.5	360.7	19	20	18	97	98	98
Nov	16.8	16.7	16.6	15.9	15.6	15.6	240.3	215.3	206.3	13	12	14	96	94	95
Dec	15.6	15.1	15.3	12.3	11.4	11.9	82.4	91.7	82.4	4	5	4	92	90	91
2010															
Jan	14.2	13.9	14.6	10.6	10.4	10.9	0	0	0	0	0	0	85	87	86
Feb	15.9	15.4	15.6	12.8	11.4	11.7	51.3	45.9	43.6	7	6	8	78	85	82
Mar	16.7	16.4	16.8	13.4	12.8	13.1	148.6	160.6	156.4	11	12	13	75	83	80
Apr	22.2	21.7	21.9	14.9	14.6	14.7	42.1	45.4	43.6	6	8	5	83	86	84
May	24.3	23.8	24.9	16.1	15.2	15.7	89.3	95.4	92.4	9	7	6	90	91	92

TS, Thiashola; KO, Korakundah.
Figures in the table are the mean values of the past 20 y.

gur, Malabar giant squirrel, wild dog, porcupine, and the palm civet cat etc., are reported to inhabit the study areas (Singh 1994).

Methods

In each grassland, 1ha plot was established to sample the vegetation. The plants available in the experimental plots of the grasslands were identified as being either C_3 and C_4 on the basis of photosynthetic type, by employing iodine tests of the leaves (Bolhar-Nordenkampf 1982). The harvest method (Milner and Hughes 1968) was used for the estimation of biomass and the optimum quadrat size, 50 × 50 cm was obtained through the species-area curve method (Greig-Smith 1964). Ten quadrats were sampled randomly in the study plots of each grassland during the last week of every month from June, 2009 to May, 2010. The quadrats were uniformly positioned in each plot in order to cover the entire area. Harvested samples were sorted, into C_3 and C_4 species and were further separated into aboveground and belowground compartments. However, the litter component was treated as single compartment for both C_3 and C_4 types. For the estimation of belowground biomass, 10 monoliths (50 × 50 × 30 cm) were excavated in the harvested quadrats. The monoliths were soaked in water for few hours and were then washed in water carefully. Since the soil was sandy loam, it was not difficult to separate the roots of C_3 and C_4 plants by this method. The respective biomass values were determined after oven drying the samples at 80°C for 48 h.

The aboveground net primary production (ANP) was determined by summing up positive changes in biomass plus mortality (Billore and Mall 1977). Belowground net primary production (BNP) and litter production were obtained by summation of positive increments of the respective biomass. Net accumulation, transfer and disappearance rates of dry matter were estimated by using the methods of Singh and Yadava (1974) and Sims and Singh (1978).

1) Transfer of live shoots to dead shoots was calculated by the summation of the positive changes in the dead shoots on successive sampling dates
2) Transfer of dead shoots to litter (L) was calculated by summation of negative changes in dead shoots
3) The disappearance of litter (LD) = initial litter biomass + litter production – final litter biomass
4) The disappearance of belowground biomass (BD) = initial belowground biomass + belowground net production – final belowground biomass

5) Total disappearance (TD) = litter disappearance + belowground disappearance

The turnover rate of organic matter was calculated by following the method of Dahlman and Kucera (1965), and the 'STFs' were computed by the method of Singh and Yadava (1974). STF is the factor by which the system block multiplies the input to generate the output (Golley 1965) and reflects the orientation of the functioning of an ecosystem in space and time (Sims and Singh 1971).

Grazing by wild herbivores like gaur, sambar, Nilgiri tahr, spotted deer etc. were observed in the study plots. The information collected from the public in near by settlements also confirmed the frequent grazing of these animals in the study areas. However, no data was collected on the quantum of herbage removal by these herbivores through grazing. A population census of these herbivores which graze upon the study areas was also not available. Hence, the results presented in this paper exclude the grazing loss made by wild animals.

RESULTS AND DISCUSSION

Monthly changes in the mass of aboveground dry matter (live and dead shoots) and belowground dry matter of C_3 and C_4 species, and total litter (C_3 + C_4 species) in the four studied grasslands are exhibited in Figs. 1-3. Gener-

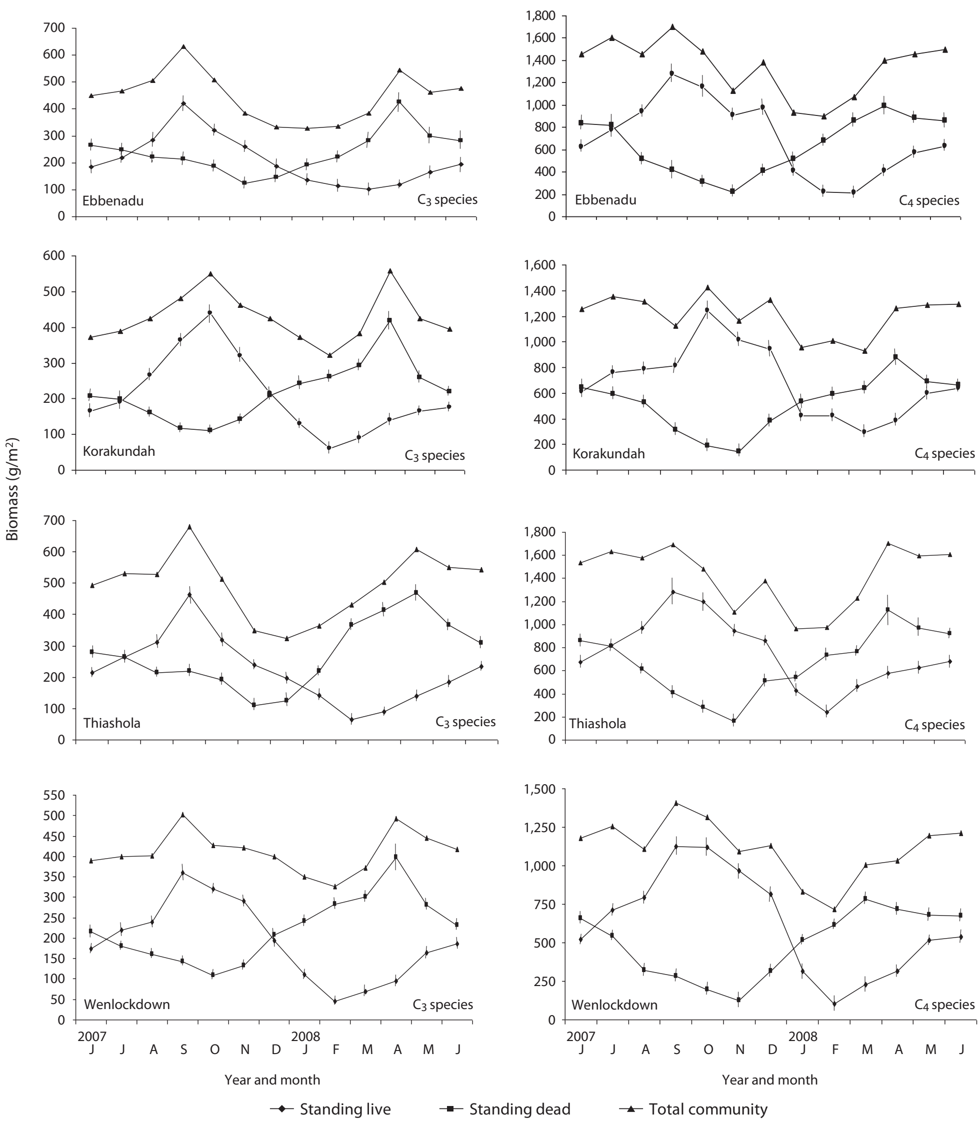

Fig. 1. Aboveground biomass (standing live and standing dead) of C_3 and C_4 species and total community in four grasslands of Nilgiri Biosphere Reserve, the Western Ghats.

ally, the aboveground biomass of the C_4 plants are nearly three-fold greater than that of the C_3 counterparts in all four studied grasslands (103-1,238 g/m^2 for C_4 species against 45-463 g/m^2 of the C_3 species (Fig. 1). It is well known that in homogenous communities the species of higher density exert a greater effect on community organization and metabolism (Stout and Brooke 1985). Sivashanmugam (2008) has previously encountered greater number of C_4 species than C_3 species per unit area in all four studied grasslands. La Pierre et al. (2011) reported that the predominance of C_4 grasses may be attributed to the effects of precipitation and temperature during periods relevant to the phenology and growth cycle of these species.

It was further observed that the higher aboveground biomass of both the C_3 and C_4 species was recorded during the monsoon period (June-November) in all the grasslands studied. Ganesan et al. (2002) previously reported the vigorous sprouting of rhizomes of perennials, and the germination of seeds of both annuals and perennials after the advent of monsoon in these grasslands and this response of constituent species could perhaps be the reason for this fact. The aboveground standing dead biomass of C_3 and C_4 species varied between 108 g/m^2 (Wenlockdown) and 468 g/m^2 (Thiashola), and 125 g/m^2 (Wenlockdown) and 1,124 g/m^2 (Thiashola), respectively, with the peak amount occurring during post-monsoon and dry periods (December, 2009-May, 2010). Furthermore, the biomass of this compartment was noted to be inversely proportional to the standing live compartment. This may be attributed to the conversion of the standing live compartment into the standing dead compartment during the dry season, when the vegetative growth of the green shoots is low or almost nil (Singh and Krishnamurthy 1981, Karunaichamy and Paliwal 1994, Paulsamy et al. 2001). In all the grasslands, the standing crop biomass of belowground parts of C_3 and C_4 species varied greatly during the study period (Fig. 2). The C_4 species contributed significantly to belowground dry matter (513-960 g/m^2) at all times of sampling, and was greater than that of its C_3 counterpart in all the grasslands studied (167-398 g/m^2). The higher density of C_4 species in all grasslands may be accounted for by this fact. In addition, it has been noted that the peak biomass of both C_3 and C_4 species occurred in the month of October, 2009, after the attainment of peak live shoot biomass in September, 2009. Trlica and Singh (1979) and Gupta (1987) explained that this may be due to the transfer of higher amounts of assimilate to roots, wither concomitant with or succeeding the maturity of shoots. The variation in litter biomass of

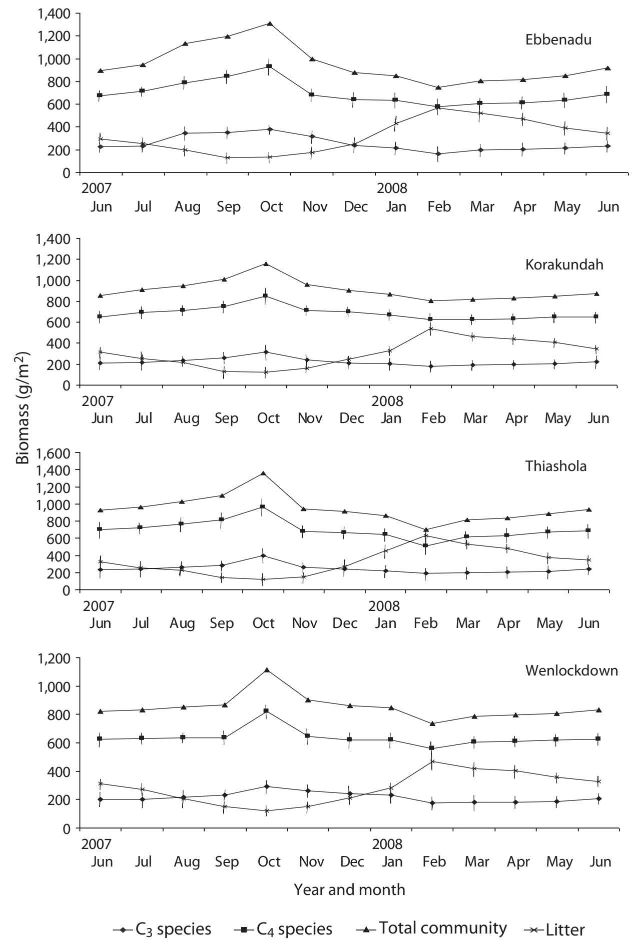

Fig. 2. Belowground biomass of C_3 and C_4 species, and total community and litter biomass (C_3 + C_4 species) in four studied grasslands of Nilgiri Biosphere Reserve, the Western Ghats.

C_3 and C_4 species together ranged between 119 and 628 g/m^2 in Thiashola grassland (Fig. 2). In all grasslands, the higher litter mass was estimated during winter, followed by summer months (December through May) because of the transfer from the live shoot compartment due to senescence and mortality of herbage. Therefore, the time of higher belowground dry matter synchronized with the time of higher aboveground standing dead dry matter in the four grasslands studied. Unfavorable climatic conditions, like low and high temperatures in winter and summer months, and relatively low soil moisture during may explain the higher litter mass during this period (Paulsamy et al. 2001).

The ANP estimated were 2,537, 2,400, 2,791, and 2,310 g m^{-2} y^{-1} in Ebbenadu, Korakundah, Thiashola and Wenlockdown grasslands, respectively (Table 2), and more than 70% of that in every grassland was composed of C_4 species alone. The belowground production ranged between 375 (Korakundah) and 658 g/m^2 (Thiashola) in the studied grasslands (Table 2). The higher performance of C_4 species in terms of net primary production in all the grasslands may be explained due to their significant higher density and dominance over the C_3 counterpart (Sivashanmugam 2008). Ganesan et al. (2002) already reported the dominance of C_4 species in the high level grasslands of NBR. The higher net primary production by C_4 species in the high level grasslands of NBR may also be due to the availability of high intensity light in that region, which is a factor which generally enhances C_4 photosynthetic activity (Chuluun et al. 1999). It is further expected that the energy content in the primary produce of C_4 species may be higher than that of the C_3 species, as the former group assimilated more CO_2 than the later (Osborne and Beerling 2006). This may be due to a reduced loss of energy in the absence of photorespiration in C_4 plants (Holaday and Bowes 1980). The total annual litter production by C_3 and C_4 species together ranged between 350 and 522 g/m^2 (Table 2). This falls well within the reported range of litter production in tropical moist grasslands (Paulsamy et al. 2007, Dhaulakhandi et al. 2010, Melvin et al. 2011).

The turnover rate of dry matter of aboveground parts of both C_3 and C_4 species in the four grasslands was generally rapid (0.99-1.25 g/y) (Table 2). It is well known that humid communities are characterized by a rapid turnover rate of dry matter due to the higher decomposition coefficient (Coupland 1979, Karunaichamy and Paliwal 1994, Paulsamy et al. 2001, Pucheta et al. 2004). On the other hand, the turnover rates of belowground parts of C_3 and C_4 species and litter parts (C_3 + C_4 species) were determined to be slow. It may be explained by the fact that most of the constituent species are perennials, and so, they have rhizomes, which are replaced slowly, as the major belowground parts (Senthilkumar et al. 1998).

Table 3 and Fig. 3 showed the data of STFs in the four grasslands studied. Generally, around 60 and 10% of dry matter was channeled to the aboveground and belowground parts of C_4 species, respectively, whereas the C_3 species channeled only around 22% and 8% of dry matter to aboveground and belowground parts in the studied grasslands. The transfer of aboveground production to litter ranged between 15.15% and 18.70%, and the TD from the total net production was determined to exist between 26.6% and 33.72% across the studied grasslands. The transfer of live shoots into the dead compartment, and that of dead shoots into the litter compartment varied between 77.50% (Wenlcockdown) and 83.89% (Thiashola). Thus, there was a net accumulation of 16% to 23% of dry matter in the live shoot compartment alone during the study period of one year. The rates of litter disappearance were 1.19, 1.12, 1.39, and 0.93 g m^{-2} day^{-1} and that of the belowground parts were 1.54, 0.94, 1.80, and 1.03 in Ebbenadu, Korakundah, Thiashola, and Wenlockdown grasslands, respectively. The sum of these values gives a TD of 2.73, 2.10, 3.19, and 1.96 g m^{-2} day^{-1}, respectively, for these grasslands. These TDs of dry matter were 48.8%, 44.3%, 54.8%, and 41.1% of the total input in Ebbenadu, Korakundah, Thiashola and Wenlockdown grasslands, respectively.

Table 2. Annual net production and turnover of dry matter of C_3 and C_4 species of aboveground and belowground parts, and litter parts of C_3 and C_4 of the four studied grasslands of Nilgiri Biosphere Reserve, the Western Ghats

Compartments	Attribute	Ebbenadu species			Korakundah species			Thiashola species			Wenlockdown species		
		C_3	C_4	Total	C_3	C_4	Total	C_3	C_4	Total	C_3	C_4	Total
Aboveground	Annual net production (g m^{-2} y^{-1})	629	1,908	2,537	698	1,702	2,400	781	2,010	2,791	615	1,695	2,310
	Turnover rate	0.99	1.12	1.09	1.25	1.19	1.21	1.15	1.18	1.18	1.23	1.20	1.21
	Turnover time	1.01	0.89	0.91	0.80	0.84	0.82	0.93	0.85	0.85	0.84	0.82	0.82
Belowground	Annual net production (g m^{-2} y^{-1})	224	361	585	147	228	375	219	439	658	122	263	385
	Turnover rate	0.59	0.39	0.45	0.47	0.27	0.32	0.55	0.46	0.48	0.42	0.32	0.35
	Turnover time	1.71	3.09	2.56	2.39	3.66	3.20	2.02	2.25	2.18	2.70	3.19	3.05
Litter	Annual net production (g m^{-2} y^{-1})		448			393			522			350	
	Turnover rate		0.79			0.73			0.83			0.75	
	Turnover time		1.27			1.36			1.20			1.33	

Therefore, the net surplus dry matter in all compartments of the studied grasslands was generally above 50% owing to the slower rate of disappearance than that of the accumulation of dry matter. Similar findings have been reported for other humid grasslands in Western Ghats, India (Karunaichamy and Paliwal 1994, Senthilkumar et al. 1998, Paulsamy et al. 2001). It is known that this accumulation of surplus dry matter in these grasslands proves the concept of disclimax stage in the succession of Nilgiri grasslands, as postulated by Bor (1938) and Champion (1939). Furthermore, from a nourishment point of view, it is understood that these grasslands support many wild animals directly or indirectly, by supplying adequate pasture throughout the year, by having a huge amount of excess fodder in terms of aboveground matter. In this function, the C_4 species in all grasslands played a pivotal role in comparison with C_3 species. The contribution of over 60% of matter by C_4 species with high energy content is more favorable and supportive for wild animals. By considering these four major grasslands has representatives of pasturelands, it is understood that high altitude grasslands in NBR are more productive and energetic due to the presence of greater numbers of C_4 species. In addition to this factor, the ever availability of water in the streams of the grasslands and safety and shelter of the near by shola forests makes these grasslands an ideal habitats for wild

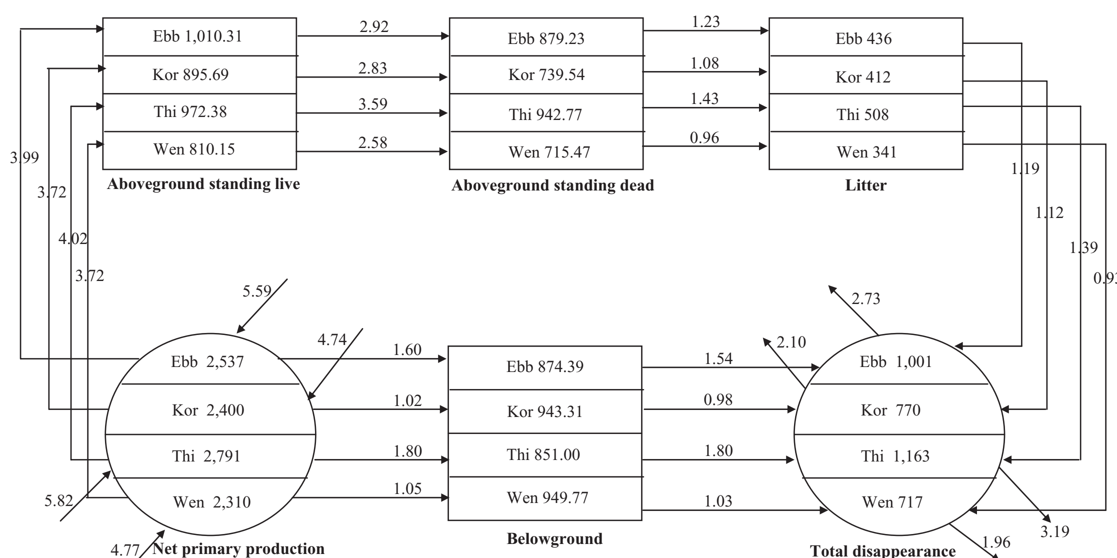

Fig. 3. Diagram depicting net dry matter flow through the various compartments in four humid grasslands of Nilgiri Biosphere Reserve, the Western Ghats. Numbers in boxes are the annual standing crop (g/m^2); numbers in circles are total net primary production and disappearance; numbers on the arrow are net flux rates in g m^{-2} day^{-1}. Ebb, Ebbenadu; Kor, Korakundah; Thi, Thiashola; Wen, Wenlockdown.

Table 3. Matter dynamics of the four studied grasslands of the Nilgiri Biosphere Reserve, the Western Ghats

Components	Ebbenadu species		Korakundah species		Thiashola species		Wenlockdown species	
	C_3	C_4	C_3	C_4	C_3	C_4	C_3	C_4
TNP to ANP	20.14	61.11	25.15	61.33	22.64	58.27	22.82	62.89
TNP to BNP	7.17	11.56	5.29	8.21	6.34	12.72	4.52	9.75
ANP to SD	11.13	30.21	12.61	30.20	10.09	34.25	12.11	28.35
ANP to L	17.65		17.66		18.70		15.15	
SD to L	41.56		37.86		39.55		37.04	
L to LD	97.32		97.17		97.32		97.43	
BNP to BD	96.58		95.47		99.54		97.66	
TNP to TD	32.06		27.74		33.72		26.60	

TNP, total net production; ANP, aboveground net production; BNP, belowground net production; SD, standing dead production; L, litter production; LD, litter disappearance; BD, belowground disappearance; TD, total disappearance.

animals in this biosphere reserve. The build-up of dry matter in the grassland community poses a risk of surface fire during the summer months of February-April. Hence, adequate measures have to be taken by the wildlife wardens to prevent the fire and loss of fodder during the lean period. Periodical monitoring of grasslands is an essential part of this process, estimating fodder supply and achieving a higher standard of wildlife management. As it is the first report of primary production status of certain major grasslands in NBR, the data can be used as a baseline to make evaluations and comparisons in future.

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