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Primary Productivity of the Pygmy Bamboo *(Arundinaria pusilla)* in the Dry Dipterocarp Forest at Sakaerat, Nakhon Ratchasima

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ABSTRACT

The aboveground and belowground biomass of *Arundinaria pusilla* in two strata of the dry dipterocarp forest were monthly harvested and net primary production, accumulation and disappearance rates by compartment were estimated. These data were further utilized for determination of system transfer functions and the efficiency of energy capture. The results indicated that the aboveground standing crop of standing live, standing dead and litter varied considerably through different sampling intervals within and between each stratum. More belowground biomass was concentrated in the upper soil layer and the amount declined with an increase in depth. The community annual aboveground net primary production was estimated on ash-free basis to be 210 gm^{-2} on stratum 1 and 329 gm^{-2} on stratum 2 and the belowground net production was 2,844 gm^{-2} on stratum 1 and 2,884 gm^{-2} on stratum 2. The accumulation of standing dead (256 gm^{-2}) and litter (214 gm^{-2}) on stratum 1 was greater than the standing dead (198 gm^{-2}) and litter (137 gm^{-2}) on stratum 2. Annual disappearance of litter was also higher on stratum 1 (149 gm^{-2}) than that of stratum 2 (119 gm^{-2}). But the belowground disappearance was much greater on stratum 2 (2,794 gm^{-2}) than that of stratum 1 (2,573 gm^{-2}). Annual efficiency of energy capture was estimated to be 1.77 percent on stratum 2 and 1.86 percent on stratum 1based on 50 percent usable solar insolation. It was shown that the belowground portion of *Arundinaria pusilla* played an important role in the dynamics of the system as a whole. This study confirmed that the belowground biomass in this kind of plant community should be considered as being very important in the study of the ecosystem functions.

Key words : biomass, primary production, system transfer function, energy flow

INTRODUCTION

With the rising demand for food in the world and increasing competition for the use of natural and agricultural land, the efforts of many scientists concerned with food production have been directed towards raising production and improving the efficiency of productivity from existing areas of cultivated land. Hence, primary productivity of natural communities remains a major area for ecological research.

Optimal use of primary producers depends on accurate understanding of the amount and dynamics of herbage biomass. Analyses of ecosystem processes are also dependent on the accuracy of biomass estimates and the seasonal patterns of biomass dynamics. The most important fact, however, is that, without a knowledge of

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primary productivity, the ecosystem functioning is not known as well as the calculation of an energy budget for any ecosystem as a whole is impossible.

The present study was concerned with the estimation of the primary productivity of *Arundinaria pusilla* the predominant perennial grass community (known in Thai as Yaaphet) in the dry dipterocarp forest at Sakaerat Environmental Research Station (SERS), Pak Thong Chai, Nakhon Ratchasima.

The objective of the study was to determine: 1) seasonal variation in the aboveground and belowground plant biomass; 2) aboveground and belowground net primary producton and turnover; 3) net accumulation and disappearance rates; 4) system transfer functions; 5) the calorific content of biomass compartments; 6) efficiency of energy capture; and 7) annual energy flow.

MATERIALS AND METHODS

According to the differences in size, height and density of the stands, the study area was divided into two strata. Stratum 2 is normally located on soil which displays greater prominence of sandstone boulders or rock out crop than that of stratum 1. Three replications of 25 × 30 m were randomly selected on each stratum. The aboveground and belowground biomass were harvested monthly. On each sampling date, ten sample plots of the aboveground biomass were randomly selected and clipped at ground level by using 0.25 × 1.00 m rectangular quadrats on each replication. Three samples of belowground biomass were also collected in each plot by using a soil core method to a depth of 40 cm, and divided into 0-10, 10-20, 20-30 and 30-40 cm sections. All plant materials were oven-dried at 70°C for 48 hours and then weighed to the nearest 0.01 g. The energy content of each compartment was determined by using Parr adiabatic bomb calorimeter.

The aboveground net primary production (ANP) was estimated using three methods, the community peak standing crop (Odum, 1960; Hadley and Kieckhefer, 1963), the sum of positive increase in biomass (Kelly *et al.*, 1974) and the sum of positive change in biomass plus mortality. According to Singh and Yadava (1974) the sum of positive increases in standing dead for only those sampling intervals which correspond to a positive change in biomass is called mortality. The belowground net primary production (BNP) was determined by a summation of the positive changes in the belowground biomass on successive sampling dates (Sims and Singh, 1971; Singh and Yadava, 1974). The turnover rate of belowground biomass was calculated by using the ratio between belowground net production and maximum belowground biomass which poposed by Dahlman and Kucera (1965).

Total net primary production (TNP) was determined simply by adding the aboveground net production (ANP) and belowground net production (BNP). System transfer functions, net accumulation and disappearance rates were determined following the method described by Grodins (1963), Golley (1965), and Sims and Singh (1971). The poduction of standing dead (SD) was calculated by the summation of positive changes in the standing crop of standing dead on successive sampling dates, which represents the transfer of standing live to the standing dead compartment. Litter production (L) was estimated from the sum of positive differences in litter through the successive sampling dates. Litter disappearance (LD) has been derived by adding the negative differences in the litter values between different sampling intervals. Root or belowground disappearance (RD) was represented by the summation of significant negative changes in the belowground biomass on successive sampling dates. Total disappearance (TD) was the sum of litter disappearance (LD) and root disappearance

(RD). In order to estimate the efficiency of energy capture and the flow of energy in the system, all biomass values in gm^{-2} were converted to energy values by multiplying those values with the appropriate calorific content of the harvested samples and expresses in kcal m^{-2}.

RESULTS AND DISCUSSION

Seasonal variation in the aboveground biomass

The aboveground standing crop of live, dead, and litter, both on stratum 1 and stratum 2, varied considerably through different sampling intervals (Tables 1 and 2).

The standing live standing crop on both strata peaked in November at 364 gm^{-2} on stratum 1 and 313 gm^{-2} on stratum 2. The average standing live vegetation was 259 gm^{-2} on stratum 1 and 196 gm^{-2} on stratum 2.

Ruangpanit (1981) estimated that the live herbage of *Arundinaria pusilla* was 275 gm^{-2}, divided into 128 gm^{-2} stem biomass and 147 gm^{-2} leaf biomass. The standing live vegetation decreased on all sampling dates after the peak with minor fluctuations through to the last sampling date in March.

Standing dead material was evaluated in the same manner as standing live on both strata. The standing dead on stratum 1 peaked in March at 202 gm^{-2} and at 194 gm^{-2}in February on stratum 2. The rapid increase of this component in the dry season was probably caused by the transfer of standing live vegetation into this compartment after life cycles were completed. The maximum rate of increase of standing dead material on stratum 1 and stratum 2 was 3.01 and 3.77 gm^{-2} day^{-1}, respectively, both being recorded in January.

The standing crop of ground litter on both strata peaked in May at 237 gm^{-2} on stratum 1 and 199 gm^{-2} on stratum 2. The amount of litter on both strata then declined steadily through the wet season starting from May and increased again during the dry season in February. Fluctuations in the amount of litter were the net result of litter production and disappearance by decomposition. The increase in the amount of litter in the early part of the growing season was probably caused by the addition of material from the standing dead crop and the death of green vegetation. It is also possible that part of the litter could have been carried over from the previous year. The gain in the amount of litter during the dry season was indicative of the transfer from standing dead to litter. The decline during the growing season represents the decomposition of litter. Lewis (1969) pointed out that litter fall was most rapid during the dormant season, but decomposition proceed more rapidly during warm, moist periods.

Seasonal variation in the belowground biomass

The belowground biomass in the upper 40 cm of soil profile on both strata exhibited the same seasonal trend (Tables 3 and 4); only the maximum and minimum amounts of biomass occurred on different dates. The seasonal peak on both strata was recorded in February; with 3,623 gm^{-2} on stratum 1 and 3,481 gm^{-2} on stratum 2. On the average, there were about 2,668 gm^{-2} of belowground biomass in the upper 40 cm of soil profile on stratum 1 and about 2,589 gm^{-2} on stratum 2.

Both strata had a greater belowground biomass during the early wet season followed by a decline and increase immediately following the decline again thereafter. Generally, the mid-season dip in belowground biomass and subsequent recovery was probably the result of stored carbohydrates being utilized for growth and then the carbohydrates were restored later in the same season.

The variation of belowground biomass on both strata occurred primarily in the top 10 cm of

Table 1 Seasonal variation in standing live, standing dead and litter standing crop (gm^{-2} dry mater ± SE[1]) (ash-free dry wt in parenthesis) of *Arundinaria pusilla* in the dry dipterocarp forest stratum 1.

Sampling date	Standing live	Standing dead	Litter	Total
Apr.	155.24 ± 14.26	80.51 ± 7.32	113.61 ± 9.11	349.36
	(143.43)	(73.83)	(100.09)	(317.35)
May	307.56 ± 28.27	135.01 ± 17.40	236.65 ± 19.03	679.22
	(287.57)	(126.06)	(183.14)	(569.77)
Jun.	290.90 ± 38.98	138.44 ± 21.44	215.02 ± 21.44	644.36
	(267.69)	(131.02)	(174.60)	(573.31)
Jul.	290.13 ± 2.31	87.55 ± 13.09	147.07 ± 18.70	524.75
	(265.50)	(83.25)	(118.92)	(467.67)
Aug.	343.40 ± 38.09	79.84 ± 9.44	166.95 ± 16.37	590.19
	(319.08)	(73.39)	(149.52)	(541.99)
Sep.	315.89 ± 29.81	142.65 ± 13.59	160.32 ± 11.43	618.86
	(292.64)	(132.75)	(136.98)	(562.37)
Oct.	282.46 ± 28.58	123.95 ± 12.04	141.75 ± 14.38	548.16
	(256.93)	(113.72)	(118.57)	(498.22)
Nov.	364.27 ± 30.03	69.61 ± 5.76	90.84 ± 6.30	524.72
	(335.82)	(65.48)	(81.62)	(482.92)
Dec.	320.38 ± 28.54	50.93 ± 6.81	71.42 ± 8.72	442.73
	(290.62)	(48.10)	(64.37)	(403.09)
Jan.	268.01 ± 25.21	103.83 ± 13.99	92.40 ± 8.24	464.24
	(244.53)	(97.20)	(82.32)	(424.05)
Feb.	107.61 ± 23.53	197.12 ± 15.63	116.90 ± 6.84	421.63
	(100.53)	(182.22)	(103.69)	(386.44)
Mar.	58.87 ± 8.21	202.02 ± 13.85	184.73 ± 10.02	445.62
	(55.56)	(187.90)	(164.65)	(408.21)
Average	258.73	117.62	144.81	521.15
	(238.33)	(109.58)	(132.21)	(471.12)

[1] Standard error of the mean.

the soil profile and decreased with an increase in depth. It was possible that the size and amount of rhizome of *Arundinaria pusilla* which dominated the belowground biomass caused more variation. Bartos and Sims (1974) believed that the variation in the amount of root mass in the grassland range could come from the fluctuation in the amount of plant crowns. The dynamics of belowground biomass, however, may be interpreted either using concepts of growth and decomposition, or the concept of translocation of photosynthate material down to or up from the root, or the combination of both.

Table 2 Seasonal variation in standing live, standing dead and litter standing crop (gm^{-2} dry mater ± SE[1]) (ash-free dry wt in parenthesis) of *Arundinaria pusilla* in the dry dipterocarp forest stratum 2.

Sampling date	Standing live	Standing dead	Litter	Total
Apr.	209.54 ± 18.39	90.59 ± 7.80	101.41 ± 11.24	401.54
	(191.06)	(82.07)	(91.23)	(364.36)
May	191.23 ± 21.84	120.01 ± 19.66	199.44 ± 23.99	510.68
	(178.15)	(113.17)	(155.74)	(447.06)
Jun.	184.78 ± 26.18	125.11 ± 20.59	188.09 ± 19.94	497.98
	(170.04)	(117.49)	(143.66)	(431.19)
Jul.	227.24 ± 29.40	92.04 ± 14.30	164.36 ± 20.10	438.64
	(212.08)	(86.51)	(133.30)	(431.89)
Aug.	286.30 ± 25.54	112.24 ± 17.35	141.56 ± 18.35	540.10
	(267.52)	(103.03)	(124.88)	(495.43)
Sep.	206.71 ± 20.04	139.03 ± 16.32	113.49 ± 10.23	459.23
	(191.27)	(127.91)	(92.72)	(411.90)
Oct.	228.76 ± 31.23	100.82 ± 15.46	123.17 ± 12.40	452.75
	(210.19)	(94.22)	(106.73)	(411.14)
Nov.	312.74 ± 30.86	91.42 ± 17.94	116.68 ± 11.28	520.84
	(287.60)	(84.94)	(105.40)	(477.94)
Dec.	255.63 ± 24.52	58.27 ± 6.96	71.17 ± 8.59	385.07
	(232.39)	(54.64)	(64.67)	(351.70)
Jan.	147.84 ± 23.03	76.93 ± 11.01	75.16 ± 9.26	299.93
	(133.25)	(70.76)	(66.40))	(270.41))
Feb.	55.79 ± 5.79	193.86 ± 20.63	143.49 ± 8.44	393.14
	(51.94)	(175.99)	(122.97)	(350.90)
Mar.	50.08 ± 9.56	115.50 ± 13.59	123.92 ± 8.19	289.50
	(46.92)	(105.94)	(108.33)	(261.19)
Average	196.38	109.65	130.16	436.19
	(181.03)	(101.39)	(109.67)	(392.09)

[1] Standard error of the mean

Aboveground net primary production

The annual net production based on the community peak standing crop, sum of positive changes in biomass plus mortality and summation of positive biomass increase on dry matter basis were 364, 342 and 287 gm^{-2}, respectively, on stratum 1 and 313, 228 and 208 gm^{-2} on statum 2 (Table 5). In every case the estimate of annual aboveground net production on stratum 1 was more productive than that on stratum 2, probably because the larger number of rock outcrops on stratum 2 retarded the growth and distribution of *Arundinaria pusilla.* It should be pointed out that the community peak standing crop gave maximum estimates of net

Table 3 Belowground biomass (gm^{-2} dry mater ± SE[1]) (ash-free dry wt in parenthesis) of *Arundinaria pusilla* in various soil depth in the dry dipterocarp forest stratum 1.

Sampling date	Soil depth (cm) 1 - 10	10 – 20	20 – 30	30 - 40	Total
Apr.	1306.84 ± 181.08 (1108.72)	354.95 ± 32.03 (275.62)	140.52 ± 10.35 (108.79)	74.24 ± 12.00 (55.72)	1876.55 (1548.85)
May	1376.57 ± 111.08 (1101.53)	1055.36 ± 100.93 (818.33)	155.77 ± 12.62 (119.72)	108.48 ± 10.61 (85.32)	2696.18 (2124.90)
Jun.	1602.60 ± 181.45 (1290.41)	1331.37 ± 181.45 (1041.93)	125.28 ± 11.90 (96.29)	66.50 ± 11.88 (52.30)	3125.75 (2480.93)
Jul.	1511.66 ± 132.04 (1262.39)	674.76 ± 83.33 (554.45)	163.06 ± 10.13 (125.33)	89.04 ± 9.92 (70.03)	2438.52 (2012.20)
Aug.	1877.28 ± 210.27 (1619.53)	824.70 ± 120.17 (710.00)	180.70 ± 6.33 (137.77)	118.87 ± 7.53 (93.55)	3001.58 (2551.85)
Sep.	1393.01 ± 136.13 (1204.26)	760.53 ± 106.53 (623.41)	181.62 ± 4.97 (138.49)	114.45 ± 13.19 (90.07)	2449.61 (2056.23)
Oct.	1793.69 ± 166.93 (1535.94)	649.91 ± 85.35 (543.78)	176.53 ± 17.29 (134.57)	98.10 ± 8.20 (77.20)	2718.23 (2291.49)
Nov.	1846.65 ± 204.39 (1624.68)	569.64 ± 95.75 (493.42)	142.51 ± 16.38 (106.55)	92.58 ± 14.55 (72.80)	2651.38 (2297.45)
Dec.	1446.77 ± 181.60 (1192.76)	594.01 ± 72.17 (491.37)	151.79 ± 20.01 (113.49)	85.95 ± 13.69 (63.29)	2278.52 (1861.01)
Jan.	1986.78 ± 213.36 (1660.95)	718.91 ± 111.49 (582.46)	174.55 ± 17.71 (130.51))	70.48 ± 11.99 (55.43))	2950.72 (2429.35)
Feb.	2516.78 ± 322.57 (2195.39)	842.26 ± 140.86 (634.14)	159.30 ± 8.66 (123.33)	104.95 ± 8.28 (78.78)	3623.29 (3031.64)
Mar.	1338.66 ± 183.66 (1174.67)	616.70 ± 69.88 (491.39)	158.64 ± 7.83 (122.82)	94.34 ± 9.58 (70.81)	2202.34 (1859.69)
Average	1666.44 (1414.28)	749.43 (604.28)	159.19 (121.47)	93.17 (72.11)	2668.22 (2212.13)

[1] Standard error of the mean

production over the other two methods. On stratum 1, net production based on the community peak was 6 percent more than the sum of positive change in biomass plus mortality and 21 percent more than the summation of positive biomass increase. A similar trend occurred on stratum 2, where net production based on the community peak was 17 and 34 percent more than estimated by the sum of positive changes in biomass plus mortality and summation of positive biomass increase

Table 4 Belowground biomass (gm^{-2} dry mater ± SE[1]) (ash-free dry wt in parenthesis) of *Arundinaria pusilla* in various soil depth in the dry dipterocarp forest stratum 2.

Sampling date	Soil depth (cm) 1 - 10	10 – 20	20 – 30	30 - 40	Total
Apr.	1692.41 ± 191.10	655.75 ± 105.00	149.80 ± 16.94	74.46 ± 16.01	2582.42
	(1402.67)	(513.49)	(115.98)	(55.89)	(2088.03)
May	1624.87 ± 146.98	1299.42 ± 163.92	156.87 ± 13.18	82.85 ± 21.04	3164.01
	(1263.01)	(960.53)	(120.57)	(65.16)	(2409.27)
Jun.	1353.51 ± 158.80	684.31 ± 84.05	104.06 ± 23.71	26.07 ± 9.74	2167.95
	(1127.20)	(560.04)	(79.98)	(20.50)	(1787.72)
Jul.	1498.93 ± 157.73	705.59 ± 93.30	142.07± 8.10	83.30 ± 6.57	2429.89
	(1285.78)	(586.91)	(109.20)	(65.52)	(2047.41)
Aug.	1589.14 ± 136.67	997.70 ± 219.67	175.43 ± 16.24	97.22 ± 11.28	2859.49
	(1325.50)	(845.35)	(133.73)	(76.51)	(2381.09)
Sep.	1516.36 ± 162.50	608.88 ± 95.58	170.35 ± 15.75	85.51 ± 16.46	2381.10
	(1325.50)	(503.94)	(129.86)	(67.30)	(2004.90)
Oct.	1291.40 ± 129.04	574.61 ± 146.30	188.24 ± 19.08	95.23± 10.72	2149.48
	(1104.15)	(480.03)	(143.49)	(74.95)	(1802.62)
Nov.	1946.21 ± 176.01	530.47 ± 101.24	116.00 ± 14.78	75.72 ± 11.01	2668.40
	(1761.51)	(462.04)	(86.73)	(59.55)	(2369.83)
Dec.	1287.35 ± 119.09	478.67 ± 63.66	86.83 ± 19.95	37.12 ± 15.64	1889.97
	(1042.11)	(395.76)	(64.92)	(29.19)	(1531.98)
Jan.	1760.75 ± 275.88	637.65 ± 134.14	144.72 ± 17.61	90.59 ± 8.90	2633.71
	(1458.43)	(527.97)	(108.21))	(71.24)	(2165.85)
Feb.	2579.15 ± 254.65	605.50 ± 69.39	186.04 ± 8.04	109.81 ± 7.24	3480.50
	(2221.42)	(446.62)	(144.03)	(82.42)	(2894.49)
Mar.	1994.53 ± 242.17	433.63 ± 47.48	157.31 ± 8.13	80.20 ± 7.12	2665.67
	(1618.16)	(337.84)	(121.79)	(60.20)	(2137.99)
Average	1677.88	685.18	148.14	78.17	2589.38
	(1409.48)	(551.71)	(113.20)	(60.70)	(2135.10)

[1] Standard error of the mean

respectively. However, each method of calculation has its own application and the difference in net production varied depending on the method of estimation and the sampling interval utilized.

For further discussion in aboveground net production, however, the estimates obtained by sum of positive changes in biomass plus mortality has been used primarily because this method is well adapted for determining the primary productivity. Singh and Yadava (1974) also found this method

Table 5 Comparison of estimates of aboveground net primary production of *Arundinaria pusilla* based on three methods of estimation in the dry dipterocarp forest strata 1 and 2.

Method of estimating production	Stratum 1		Stratum 2	
	ANP [1/] (g m^{-2})	Rate of production (g m^{-2} day^{-1})	ANP [1/] (g m^{-2})	Rate of production (g m^{-2} day^{-1})
1. Based on the community peak standing crop	364.27 ± 30.03[2/] (335.82)[3/]	0.99 (0.92)	312.74 ± 30.86 (287.60)	0.86 (0.79)
2. Based on the sum of positive change in biomass plus mortality	341.90 (328.84)	0.93 (0.90)	227.75 (210.33)	0.62 (0.58)
3. Based on the sum of positive increase in biomass	287.40 (276.61)	0.79 (0.76)	207.55 (193.81)	0.57 (0.53)

[1/] ANP = annual aboveground net production
[2/] Standard error of the mean
[3/] Ash-free dry weight in parenthesis.

appears to be the best estimate compared to the others. Since this method was the only method in the study that took mortality into account and gave the estimates in between the other two methods, it is reasonable to utilize this method for further discussion.

Belowground net primary production and turnover

Estimates of annual belowground net production on strata 1 and 2 were 3,426 g m^{-2} (9.39 g m^{-2} day^{-1}) and 3,383 g m^{-2} (9.27 m^{-2} day^{-1}), respectively (Table 6). The turnover rate of belowground biomass was calculated by the method proposed by Dahlman and Kucera (1965). The ratio between belowground net production and maximum belowground biomass gave a turnover value. It was estimated that approximately 95 percent of the belowground biomass in stratum 1 and 97 percent in stratum 2 of *Arundinaria pusilla* would be replaced each year (Table 6). The figures were rather high compared to the grassland range in temperate zones. Nilsson (1970) found that about 50 percent of the root would be replaced each year or turnover every two years. Dahlman and Kucera (1965) indicated that 25 percent of the root system in grassland range would be replaced each year, producing turnover rate of roots every four years. In the ungrazed shortgrass prairie, Sims and Singh (1971) reported the turnover rate was 36 percent per year.

Net primary production, accumulation and disappearance rates

Net primary production, accumulation and disappearance rates by compartments for stratum 1 and 2 are presented in Table 7.

These data showed that total net production (3,212 g m^{-2}), aboveground net production (329 g m^{-2}), and belowground net production (2,883 g m^{-2}) as well as their rates of production on stratum 1 were greater than those on stratum 2. The

Table 6 Annual belowground net production and turnover rate of belowground biomass in the dry dipterocarp forest stratum 1 and 2. (ash-free dry weight in (g m^{-2}) parenthesis)

Stratum	Belowground net production[1/] (g m^{-2})	Rate of production (g m^{-2} day $^{-1}$)	Maximum biomass (g m^{-2})	Turnover %
1	3425.65	9.39	3623.29	94.5
	(2883.58)	(7.90)	(3031.64)	(95.1)
2	3382.58	9.27	3480.50	97.2
	(2844.33)	(7.79)	(2894.49)	(98.2)

[1/] Based on the sum of positive changes in biomass on successive sampling dates.

Table 7 Annual net primary production accumulation and disappearance rates (ash-free basis) by compartments of *Arundinaria pusilla* in the dry dipterocarp forest strata 1 and 2.

Compartment	Stratum 1		Stratum 2	
	gm^{-2}	$gm^{-2}day^{-1}$	gm^{-2}	$gm^{-2}day^{1}$
Total net primary production (TNP)	3212.42	8.80	3054.66	8.37
Aboveground net primary production (ANP)	328.84	0.90	210.33	0.58
Standing dead (SD)	256.35	0.70	198.17	0.54
Litter (L)	213.93	0.59	136.82	0.37
Litter disappearance (LD)	149.37	0.41	119.72	0.33
Belowground net primary production (BNP)	2883.58	7.90	2844.33	7.79
Belowground biomass disappearance (RD)	2572.74	7.05	2794.37	7.66
Total disappearance (TD)	2722.11	7.46	2914.09	7.98

rate of accumulation of organic matter in the standing dead compartment was also greater on stratum 1 than on stratum 2. Moreover, accumulation of organic material in the litter compartment was higher on stratum 1 (214 g m^{-2}) than on stratum 2 (137 g m^{-2}). Annual diappearance of litter was also higher on stratum 1 than on stratum 2. But the belowground disappearance as well as the total disappearance, was much greater on stratum 2 than on stratum 1, although the belowground net production on both strata were only slightly different.

There was an annual surplus of 490 g m^{-2} of dry matter on stratum 1, much higher than that on stratum 2 (140 g m^{-2}). This is because the rate of belowground biomass disappearance on stratum 2 (7.66 g m^{-2} day^{-1}) was greater than that on stratum 1 (7.05 g m^{-2} day^{-1}) although there was a higher rate of litter disappearance, 0.41 g m^{-2} day^{-1} on stratum 1 compared to 0.33 g m^{-2} day^{-1} on stratum 2. It was clear that the belowground portion of this kind of grass plays an important role in the dynamic of the system as a whole. This study confirmed that the belowground biomass in this kind of plant

Table 8 System transfer functions of *Arundinaria pusilla* in the dry dipterocarp forest.

Compartments	Stratum 1	Stratum 2
TNP to ANP	0.102	0.069
TNP to BNP	0.898	0.931
ANP to SD	0.780	0.942
SD to L	0.835	0.690
ANP to L	0.650	0.651
L to LD	0.698	0.875
BNP to RD	0.892	0.892
TNP to TD	0.847	0.954

Note : For notation see table 7.

community should be considered as being very important in the study of the ecosystem functions.

System transfer function

The system transfer function is the quantity by which the system block multiplied the input to generate the output (Grodin, 1963) or it is the ratio of output to input (Golley, 1965). The system transfer function for the whole year on strata 1 and 2 is presented in Table 8. The functions were calculated using the compartment values in Table 7.

On the annual basis, the transfer functions on stratum 1 had 10 percent aboveground and 90 percent belowground production campared to 7 percent aboveground and 93 percent belowground production on stratum 2. There was 78 percent of aboveground net production which found its way into the standing dead compartment on stratum 1 and about 94 percent on stratum 2. The annual transfer of standing dead to litter was 84 percent on stratum 1 and 42 percent on stratum 2. This amounted to 65 percent of the aboveground net production on stratum 1 and 39 percent on stratum 2. It is evident that some direct transfer may also occur from the live vegetation to the litter compartment. Galley (1965) stated that a relative amount of litter might be contributed by current live vegetation. Uresk *et al.* (1975) noted that litter may increase from live herbage because of rain, hail, wind and insects. Of the total litter produced, 70 percent on stratum 1 and 88 percent on stratum 2 were decomposed within the same year.

The annual transfer from belowground net production to belowground disappearance was 89 percent on stratum 1 and 98 percent on stratum 2. Within the year, about 85 percent of total net production disappeared from the system on stratum 1 and 95 percent on stratum 2. This gave on annual net gain of total net production of about 15 percent on stratum 1 and 5 percent on stratum 2.

Calorific content of biomass compartments

Calorific content of *Arundinaria pusilla* was determined by a composite sample from both strata. The average calorific values of standing live, standing dead, litter and belowground biomass were 4.312, 4.375, 4.237 and 4.462 kcal g^{-1} ash-free dry weight, respectively. Biomass in g m^{-2} may be converted to energy by multiplying these values by the appropriate calorific equivalents to estimate the standing crop of energy in the community. On an ash-free basis, the energy stored aboveground was 2,029 kcal m^{-2} on stratum 1 and about 1,689 kcal m^{-2} on stratum 2. The

Table 9 Usable solar insolation, annual net primary production and efficiency of annual energy capture (ash-free dry weight) of *Arundinaria pusilla* in the dry dipterocarp forest stratum 1 and 2.

Energy used by compartments	Annual net primary production (kcal m^{-2})		2/ Efficiency (%)	
	Stratum 1	Stratum 2	Stratum 1	Stratum 2
Usable solar insolation 1/	767,845	767,845	-	-
Abeveground net production	1,418	907	0.18	0.12
Belowground net production	12,867	12,691	1.68	1.65
Total net production	14,285	13,598	1.86	1.77

1/ 50% of total solar insolation.
2/ Net production/usable solar insolation.

average energy stored belowground fluctuated around 9,900 to 9,588 kcal m^{-2} on stratum 1 and 2, respectively.

Efficiency of energy capture

In order to determine the energy capture in aboveground and belowground production in kcal m^{-2}, the appropriate mean calorific value mentioned above has been used to convert the aboveground and belowground net production on both strata from g m^{-2} to kcal m^{-2} (Table 9). The efficiency of energy capture was expressed as percentages of energy within the visible portion of the spectrum which was assumed to be 50 percent of the total solar insolation (Golley, 1960; Odum, 1971). The efficiency values have been calculated and presented in Table 9, which includes the aboveground, belowground and total net production on both strata.

The efficiency of annual energy capture for aboveground net production on stratum 1 (0.18%) was more efficient than that on stratum 2 (0.12%). The efficiency of energy capture of aboveground net production was less than that of belowground net production. The efficiency of energy capture in belowground (1.68%) and total net production (1.86%) on stratum 1 was more than that in belowground (1.65%) and total net production (1.77%) on stratum 2.

In the shortgrass ecosystem Sims and Singh (1971) reported that the efficiency of total net production based on 50 percent of solar insolation was 0.57 at the Pawnee and 0.19 percent at the Pantex site. Klipple and Costello (1960) found the efficiency based on 45 percent of solar insolation was 1.3 percent. However, for most ecosystems the annual efficiency of solar energy conversion in the visible spectrum into net production potentially was near 1 percent or less (Woodwell and Whittaker, 1968).

These data indicated that the variation of the efficiency values depended on the time intervals and the estimation of solar insolation used in the determination, as well as the community types of vegetation under study.

Annual energy flow

Based on the system transfer functions in table 8, the estimate of the annual energy flow through the primary producer compartments on stratum 1 and 2 of *Arundinaria pusilla* in the dry dipterocarp ecosystem is depicted in Figures 1 and 2, respectively. The usable solar insolation was 767, 845 kcal m^{-2}, based on 50 percent of the

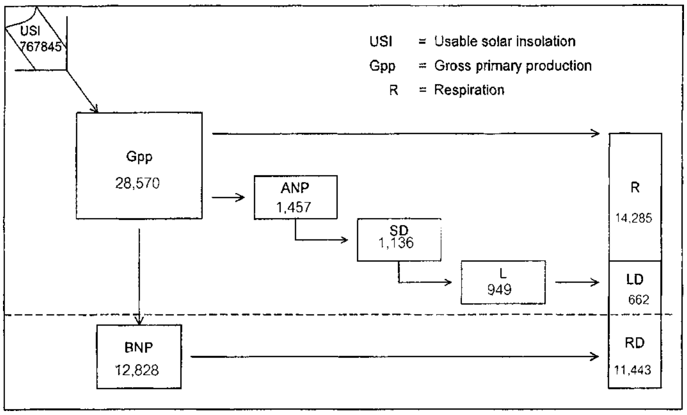

Figure 1 Annual energy flow (kcal m-2) through primary producer compartment of *Arundinaria pusilla* in the dry dipterocarp forest stratum 1.

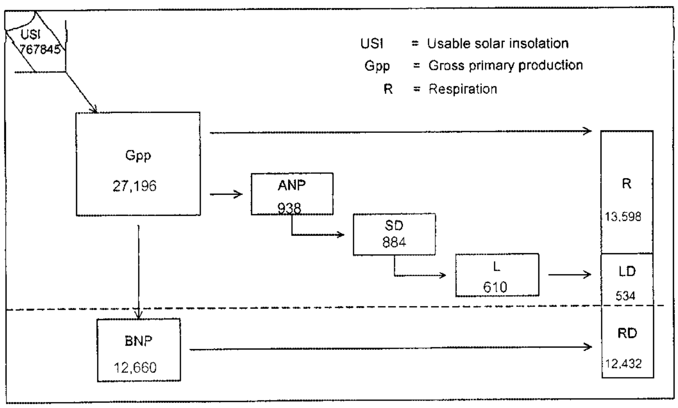

Figure 2 Annual energy flow (kcal m-2) through primary producer compartment of *Arundinaria pusilla* in the dry dipterocarp forest stratum 2.

incident solar energy. Golley (1965) estimated the respiration by analyzing the CO_2 content of the air in a chamber around the plant and found that about 47 percent of gross primary production was lost through respiration. Values of gross primary production and respiation in the present study were based on the assumption that, in general, 50 percent of the gross primary production was dissipated by respiration and the remaining 50 percent was total net primary production (Odum, 1971).

There was a surplus of energy on both sites, 15 percent on stratum 1 and 5 percent on stratum 2. More surplus energy was stored in belowground than aboveground on stratum 1 but on the contrary for stratum 2. *Arundinaria pusilla* on stratum 1 stored 36.5 percent surplus energy in aboveground production and 63.5 percent in belowground production. But *Arundinaria pusilla* on stratum 2 stored 63.9 percent surplus energy in aboveground production and 36.1 percent in belowground production.

Therefore, if these two strata remain

unburned or ungrazed for a long period of time, the surplus of energy in the form of organic matter would probably accumulate and increase soil organic matter and eventually improve soil moisture storage. The excess production, therefore, may change the environmental conditions of the ecosystem in the longrun. But in reality, plants and litter in this dry dipterocarp forest were burned out every year during the dry season. In order to reduce the ground fuel and utilize the surplus energy of the system efficiently, the introducing of cattle raising in this forest at the early of the growing season should be carried out every year. However, a study of the nutrient cycling of the undergrowth in this ecosystem is recommended.

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