Carbon Cycling in a Loblolly Pine Plantation

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Summary. The carbon cycle of a loblolly pine plantation in North Carolina was examined during its 12th through 16th years from planting. Net primary production during the study period averaged $2056 \, \mathrm{g C m^{-2}}$ year^{-1}. With autotrophic respiration equal to 2068 g C, the calculated gross production was $4124 \, \mathrm{g C m^{-2}}$ year^{-1}. Heterotrophic respiration of $694 \, \mathrm{g C m^{-2}}$ year^{-1} resulted in net ecosystem production of $1362 \, \mathrm{g C m^{-2}}$ year^{-1}. In carbon cycle comparisons between forest ecosystems, autotrophic respiration rates were found to be closely coupled to regional temperature.

Introduction

Carbon is the basic constituent of organic compounds and the major element involved in the fixation of energy by photosynthesis. The carbon cycle provides a valid means of examining similarities in ecosystem function. Few ecosystems have been studied in sufficient detail to allow development of accurate descriptions of their carbon cycles. Two such studies include the work by Woodwell and Whittaker (1968) in a xeric oak-pine forest at Brookhaven, New York and the work reported by Harris et al. (1975) in a mesic deciduous forest on karst topography at Oak Ridge, Tennessee. This paper provides a detailed analysis of carbon flow in a pine plantation on the Piedmont of North Carolina.

The carbon cycle is best understood if first considered within the context of the individual plant. Gross photosynthesis (*GP*), the total quantity of carbon fixed by the plant, is allocated according to Equation (1)

$$GP = R_a + \Delta B + L + G. \tag{1}$$

In this relationship R_a (autotrophic respiration) includes all maintenance and growth respiration, ΔB is the change in carbon mass, L represents carbon lost

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through litter fall, root turnover, and root exudates, and G represents carbon consumption by grazer and other consumer organisms. When this relationship is applied to an entire plant community, mortality is included in the L component. Net primary production (NPP) is expressed according to Equations (2) and (3)

$$NPP = GP - R_a, \tag{2}$$

$$NPP = \Delta B + L + G. \tag{3}$$

At the ecosystem level, we have the additional concern of heterotrophic respiration (R_h). With the inclusion of heterotrophic respiration in an expression for net primary production, we achieve a relationship for net ecosystem production (NEP)

$$NEP = GP - (R_a + R_h). \tag{4}$$

For this study, ecosystem boundaries have been defined to minimize the effects of carbon transport by wind, gravity, or water.

One primary objective of ecosystem analysis, and a major goal of this paper, is the quantification of subsystem roles in carbon pools and fluxes and the solution of these four defined equations. Through similar comparisons between different ecosystems, we will improve our understanding of carbon flow through the biosphere.

Materials and Methods

Site. The research site was located on a level unpland terrace on the Haw River in the Piedmont of North Carolina. The sandy loam soils, derived from acid igneous rock parent material, varied from 20 to 33 cm in thickness over friable sandy clay to clay subsoils (Ralston, 1973). The area had been in agricultural production prior to planting of loblolly pine (*Pinus taeda* L.) in 1958. Annual measurements of tree dimension have been made on 128 trees contained in a 0.0886 hectare plot since 1971 (Table 1). The forest canopy was considered to be closed before investigations were initiated on site.

Production Estimates. Using the biomass approach to productivity, net primary production is described by Equation (3). Neglecting consumption, due to a paucity of data, we modify Equation (3) as follows:

$$NPP = \Delta B + L. \tag{5}$$

In this study, the biomass approach was selected to determine ΔB. Twenty-six trees, selected to represent the range of size classes in the stand, were harvested. The foliage, branch, and stem components were oven-dried at 70° C and weighed. Roots systems of seven of these trees were excavated, separated into the below-ground stump component, lateral roots > 1 cm diameter, and lateral roots ≦ 1 cm diameter, which were also oven-dried and weighed. Regression equations were developed to predict component weight from measurements of height and diameter (Ralston, 1973). Additional information on root distribution by size class and on seasonal dynamics was obtained by coring with a 15-cm diameter stainless steel cylinder fitted with carbide teeth and attached to a gasoline-powered auger. Regression equations used to estimate biomass are presented in Table 2.

Selection of diameter at the base of live crown (*DBLC*) as the independent variable for estimation of canopy components not only provides a better estimate than does the use of diameter at breast height (*DBH*, measured at 1.37 m) but also provides better correspondence with field

Table 1. Average dimensions of trees within the plantation based on 128 trees on a 0.0886 ha plot for 1970 and 1971, 126 trees for succeeding years

	Diameter breast height (cm)	Diameter at base of live crown (cm)	Total height (m)	Height to base of live crown (m)
1970	16.07		10.80	
1971	16.75	10.94	11.85	6.01
1972	17.23	11.29	12.60	6.60
1973	17.47	11.09	13.85	7.27
1974	18.36	11.15	14.60	7.97

Table 2. Biomass estimation equations for loblolly pine

ln Stem wt (g) $= 1.9401 + 1.8625$ ln DBH (cm) $+ 1.3974$ ln Ht (m)

$r^2 = 0.979$; $s^2 = 0.00829$

ln Branch wt (g) $= 2.9721 + 2.4514$ ln $DBLC$ (cm)

$r^2 = 0.95$; $s^2 = 0.03791$

ln Foliage wt (g) $= 3.5707 + 1.9475$ ln $DBLC$ (cm)

$r^2 = 0.936$; $s^2 = 0.03264$

ln Root wt (g) $= 0.7637 + 3.0742$ ln DBH (cm)

$r^2 = 0.863$; $s^2 = 0.08984$

observations, which show that maximum canopy foliage biomass, on a stand basis, is reached at the time of crown closure. From this time on without thinning the stand, the canopy depth and foliage mass remain relatively constant with the lowest branches in a radiation regime that may be considered an annual light compensation point. As more foliage is added to the top of the canopy, foliage in a reduced radiation environment is lost from the bottom. Consequently the base of live crown moves up in height and $DBLC$ remains relatively constant over much of the stand's life. Stand estimates of foliage mass based on $DBLC$ allow the achievement of this steady-state condition, which the use of DBH as the independent variable would fail to do. A similar argument exists for estimation of canopy branch wood.

Litter fall collections were made monthly from 12 1-m^2 traps in the plantation. Forest floor (litter standing crops) samples were collected in April 1971 and again in April 1973. Decomposition data were obtained from periodic weighings of litter bags constructed of fiberglass mesh. Branch mortality was determined by pruning the branches as they died at the base of the crown of 12 trees and drying and weighing them.

Root turnover, a below-ground litter component, was estimated for the period from June 1972 through May 1973 with the coring device described above. Soil-root samples from 0–20 cm provided an estimate of approximately 70 % of the lateral root biomass. Cores were taken at approximately monthly intervals, and roots were separated from the soil, washed, oven-dried (70° C), and weighed. These data provided temporal estimates of the standing crop of fine lateral roots (≤ 1 cm diameter), which constituted 40 % of the lateral root biomass. Estimates of net root production and turnover were obtained by summation of differences between seasonal maximum and minimum values.

Respiration. Autotrophic respiration was estimated for the plantation by measuring rates of CO_2 evolution in the field on intact tissue (Kinerson, 1975; Higginbotham, 1974) and in the laboratory on excised tissue (Kinerson, 1975). Relationships between CO_2 evolution rates, surface area, and temperature were used to quantify total and seasonal rates of autotrophic respiration.

Heterotrophic respiration was estimated on the premise that the predominant energy flow in forest ecosystems is through the detritus food chain (Reiners, 1968). Since the forest floor is the major zone of heterotrophic activity, litter decomposition data provide a measure of heterotrophic activity. Root turnover data provide estimates of heterotrophic metabolism within the soil profile.

Carbon Content. Needles, twigs, branches, and bark materials were analyzed for percent carbon by combustion in a high-frequency combustion furnace in which the evolved CO_2 is collected and weighed. No significant difference was found between plant components. Carbon content ranged from 45 to 54% of oven dry weight with a mean of 49% and a standard deviation of 2.3%.

Results and Discussion

The autotrophic standing crop at the end of the 1974 growing season was $7062 \, g \, C \, m^{-2}$ with a mean net annual increment over four growing seasons of $715 \, g \, C \, m^{-2} \, year^{-1}$. Data presented in Table 3 show marked annual variation in production but no evidence of decreasing production as a result of stand closure and increased intraspecific competition. An examination of the 4-year average compartmental allocation shows carbon distribution to stems 68%, branches 9%, foliage 4%, and roots 19%. Figure 1 illustrates carbon allocation to the identified system components and carbon transfer rates between components. The following discussion relates to these carbon transfers and their determination.

The autotrophic standing crop is a very dynamic entity with production and turnover occurring at all compartment levels. The dynamic nature of the foliage component is most readily appreciated as the canopy of a coniferous forest continually changes. Old foliage is shed throughout the year with the greatest loss in late autumn (November) and new foliage is added during the growing season (May through September). Total foliage biomass reaches its maximum when the current year and 1-year-old needles are in nearly equal proportions in the canopy. This maximum, 180% of foliage standing crop at the beginning of the growing season, decreases rapidly with the cessation of new growth and the acceleration of litter fall (Kinerson et al., 1974). Carbon return to the forest floor as needles in any given year is closely approximated by the carbon allocated to foliage production in the previous year.

The dynamic nature of the branch wood component has been examined by Kinerson and Higginbotham (1973). Those branches in the bottom of the canopy that fail to receive sufficient radiation for net photosynthesis to exceed metabolic demands, are unable to form buds and to produce foliage the following year. This branch turnover, estimated by pruning branches as they die each year, was equivalent to $330 \, g \, C \, m^{-2}$ in 1972 for a 4-year average turnover of $342 \, g \, C \, m^{-2} \, year^{-1}$.

The stem component is dynamic, because it increases biomass each year. The loss of two small trees in 1972 from the study plot provided stem mortality of only $2 \, g \, C \, m^{-2}$, the only negative increment in this component. As this transfer rate is less than $1 \, g \, C \, m^{-2} \, year^{-1}$ it is not included in Figure 1.

The magnitude of root system dynamics has only recently been appreciated. On the basis of excavated root systems, 50% of the biomass was apportioned to

Table 3. Standing crop of carbon by component at the end of four growing seasons

Component	1971	1972	1973	1974
		$(g\,m^{-2})$		
Stem	3154	3698	4285	4992
Branch	484	537	505	520
Foliage	256	275	262	266
Root	984	1065	1148	1284
Total	4878	5570	6200	7062

GROSS PRODUCTION

4124

RESPIRATION

657

FOLIAGE
265

265

618

264

LIVE
BRANCHES
510

342

12

DEAD
BRANCHES
300

307

1084

STEMS
4032

1697

613

35

LITTER
904

72

63

ROOTS
1120

629

466

100

694

KEY:

COMPONENT
SC
ΔB

X

X

SC = STANDING CROP
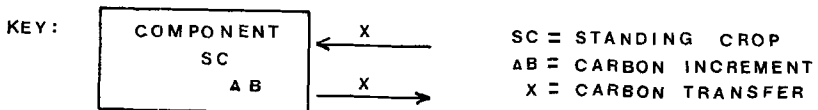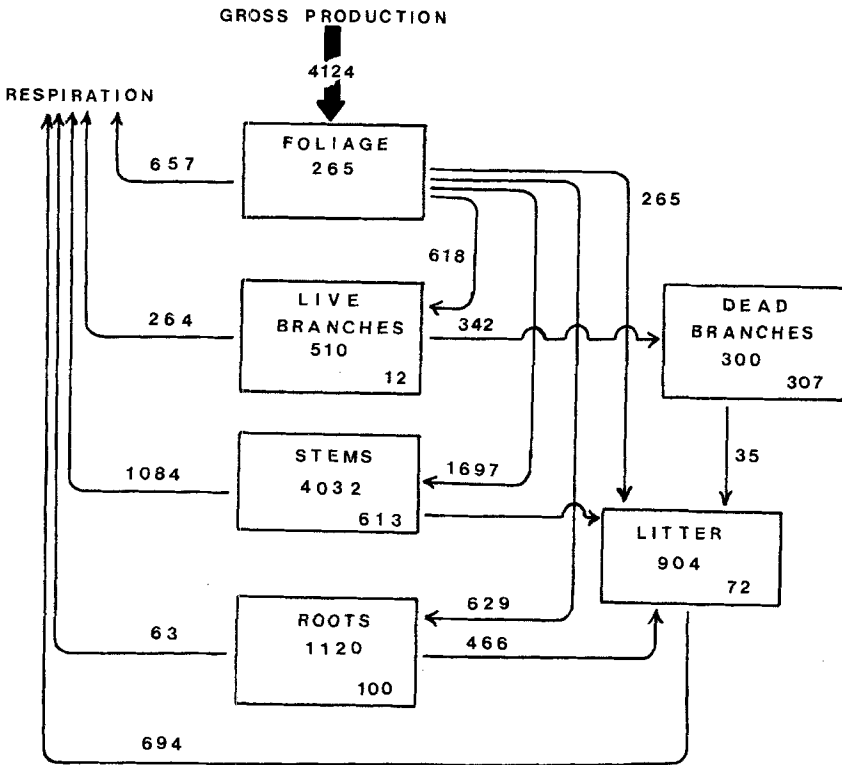ΔB = CARBON INCREMENT
X = CARBON TRANSFER

Fig. 1. Compartmental allocation of foliage, living and dead branches, stems, roots, and litter $(g\,C\,m^{-2})$ and transfer rates between system components $(g\,C\,m^{-2}\,year^{-1})$ for the loblolly pine plantation

the below-ground stump component and the remainder to the lateral roots. Of the laterals, approximately 40% were $\leqq 1$ cm in diameter. Seventy-five % of lateral root biomass was located in the top 20 cm of soil. These fine roots were examined in 1972 and annual root turnover was estimated at 900 g of organic matter per m^2, equivalent to $441\,g\,C\,m^{-2}\,year^{-1}$. The 4-year average turnover rate was $466\,g\,C\,m^{-2}\,year^{-1}$.

Litter standing crop on the forest floor was estimated as $760\,g\,C\,m^{-2}$ in April 1971 (immediately prior to initiation of new growth). During the next 2 years the litter input of needles, branches, and debris amounted to $597\,g\,C\,m^{-2}$. When the forest floor was remeasured in April 1973, there were $735\,g\,C\,m^{-2}$ present. These data suggest a decomposition rate of $311\,g\,C\,m^{-2}$ $year^{-1}$ and a net loss of carbon from the forest floor. In another study in the area, the forest floor accumulation rate between ages 13 and 16 was about $200\,g\,C\,m^{-2}\,year^{-1}$. The reason for the apparent lack of forest floor accumulation in this plantation is not known (Wells and Jorgensen, 1975). Because of large, within-plot variation of the forest floor standing crop, resulting largely from litter accumulations between ridges left from prior agricultural use, an independent estimate of decomposition was made from litter bag studies. Twenty-five litter bags of 26.6 cm^2, each with about 25 g of freshly fallen needles, were placed in each of 2 plots. Five litter bags were removed from each plot after each of 3 years to determine decomposition rate.

In the calculation of decay we equated the change in litter on the forest floor over some time period to litter fall minus decomposition. Expressed in equation form this becomes

$$\frac{\Delta X}{\Delta t} = L - D. \tag{6}$$

As shown by Olson (1963), if L is a steady input of litter and X is the amount of litter present, the constant instantaneous rate of decay k is

$$\frac{dX}{dt} = L - kX. \tag{7}$$

If litter can be assumed to be continuously added at a constant rate, this equation has the solution

$$X_t = \left(\frac{L}{k}\right)(1 - e^{-kt}). \tag{8}$$

In the litter bag studies, k is determined by eliminating L with the resulting Equation

$$\frac{dX}{dt} = -kX. \tag{9}$$

Solving Equation (8) for X_t yields

$$X_t = X_0 e^{-kt}$$

$$\ln \left(\frac{X_t}{X_0}\right) = -kt$$

$$k = -\frac{\ln \left(\frac{X_t}{X_0}\right)}{t}. \tag{10}$$

Litter bag data used with Equation (10) indicate a slightly higher decomposition rate the first year after litter fall ($k = -0.282$) than the average rate for 3 years ($k = -0.217$). This is to be expected, due to the loss of the more readily decomposable material passing through the detrital food chain and leaving behind those components that are more resistant to decomposition such as lignin, resins, and similar materials. The value of k appropriate to the total decomposition time required for pine litter may be slightly lower than that found over a 3-year period. Nevertheless, we use the value of $k = -0.217$ in our calculations with Equation (9).

Litter dynamics on the forest floor depends upon quantity and periodicity of organic input. Of the 760 g C m^{-2} on the forest floor at time of sampling in 1971, 430 g C m^{-2} would remain in 1973 with no additional inputs ($k = -0.217$). The bulk of the needles are shed in October and November, approximately 0.5 year from the time of evaluation of the forest floor standing crop. Litter fall during the 1971–1972 period (273 g C m^{-2} year^{-1}) would have been on the forest floor 1.5 years by the time the forest floor was again sampled in 1973. During this time 89 g would have passed through the detrital pathway leaving an accumulation of 184 g. Litter fall during the 1972–1973 period (325 g C m^{-2} year^{-1}) would have been on the forest floor 0.5 year prior to sampling in 1973 during which time 35 g would have passed through the detrital system and 290 g would have accumulated. The forest floor standing crop in 1973 is then $430 + 184 + 290 = 904$ g C m^{-2} for an increase of 72 g C m^{-2} year^{-1}. These data are taken as being representative of the 4-year average conditions.

Autotrophic respiration was estimated by gas exchange techniques. Calculations based on average component mass provided values of 657, 264, 1084, and 63 g C m^{-2} year^{-1} for foliage, branches, stems, and roots, respectively, for a total of 2068 g C m^{-2} year^{-1}. Quantification of changes in the forest floor provided an heterotrophic respiration estimate of 694 g C m^{-2} year^{-1}.

Carbon increment and litter data for each year (1971 through 1974) are presented in Table 4 for each system component. Using the 4-year averages of these data we calculate net primary production, from Equation (5), as

$$NPP = \Delta B + L$$
$$= 976 + 1080$$
$$= 2056.$$

Gross production is obtained from Equation (2) as follows

$$GP = NPP + R_a$$
$$= 2056 + 2068$$
$$= 4124$$

Table 4. Annual carbon increment in total above-ground net primary productivity (AGNPP) and total below-ground net primary productivity (BGNPP) and by component

Year	AGNPP =	B_{fol} +	B_{bra} +	B_{stem} +	L_{fol} +	L_{bra}[a] +	L_{debris}[b]
1971	1398	256	18	548	234	330	12
1972	1462	275	48	544	247	330	18
1973	1491	262	−26	587	291	362	15
1974	1607	266	15	707	260	344	15

Year	BGNPP =	B_{root} +	turnover
1971	517	103	414
1972	522	81	441
1973	558	83	475
1974	668	136	532

[a] L_{bra} represented as branch mortality data, not (g C m^{-2}) branches in litter fall
[b] L_{debris} represents all litter components not identified as either foliage or branch material (i.e., bark, flower and fruit parts, etc.)

while net ecosystem production from Equation (4) is

$$NEP = GP - (R_a + R_h)$$
$$= 4124 - (2068 + 694)$$
$$= 1362.$$

These production data and other system relationships are compared (Table 5) with two other forest ecosystems for which carbon cycles have been examined. The high productivity of this system is a function of the forest's age and the highly productive nature of the species.

Age considerations are of paramount importance in productivity comparisons between forest ecosystems. The relationship between standing crop and time is the same sigmoid curve form as used by the population biologist. The slope of the curve expresses the growth rate [ΔB of the net production relationship, Eq. (3)]. Four years of data for the loblolly plantation (Table 4) show a slight increase in NPP placing this system on the nearly linear portion of the growth curve, but to the left of the inflecting point (at which the 2nd derivative of the growth function is zero). While data are not available to examine year to year trends for the *Liriodendron* and *Pinus-Quercus* systems, calculated relative production ratios of 9% and 10% (Table 5) place these systems on the upper portion of the growth curve. This positioning is further supported by the ratios of ecosystem respiration to gross production, which would equal 1.0 for a steady-state system.

Examination of autotrophic respiration rates and mean annual temperatures suggests that much of the difference between the *Pinus-Quercus* system and the other two systems may simply be a temperature effect. Comparison of data

Table 5. Comparison of structure, metabolism, and climate of three forest ecosystems

Parameter	Units	*Pinus taeda*	*Liriodendron*[a]	*Pinus-Quercus*[b]
Total standing crop (TSC)	($g m^{-2}$)	7062	8760	5960
Net primary production (NPP)	($g m^{-2} year^{-1}$)	2056	730	600
Relative production (NPP/TSC)	%	29.1	8.9	10.1
Autotrophic respiration (R_a)	($g m^{-2} year^{-1}$)	2068	1440	680
Ra/TSC	($year^{-1}$)	0.29	0.16	0.11
Heterotroph respiration (R_h)	($g m^{-2} year^{-1}$)	694	670	290
Ecosystem respiration ($R_e = R_a + R_h$)	($g m^{-2} year^{-1}$)	2762	2110	970
Net ecosystem production ($NEP = GP - R_e$)	($g m^{-2} year^{-1}$)	1362	60	310
Annual decay	($g m^{-2} year^{-1}$)	694	700	360
Gross production (GP)	($g m^{-2} year^{-1}$)	4124	2170	1280
Production cost (R_a/GP)		0.50	0.66	0.53
R_e/GP		0.67	0.97	0.76
Age	(year)	16	48	43
Mean annual temperature	(°C)	15.6	13.3	9.8
Mean annual precipitation	(mm)	1150	1265	1240
Length of growing season	(days)	231	220	—
Mean temperature during growing season	(°C)	20.3	19.5	—
Mean precipitation during growing season	(mm)	749	705	—

[a] Harris et al. (1975)
[b] Woodwell and Botkin (1970), as presented in Harris et al. (1975)

presented by Woodwell and Botkin (1970) and Kinerson (1975) show similar patterns and magnitudes and lend credence to this hypothesis. Stem and branch respiration rates (Kinerson, 1975) were expressed on a unit mass basis ($g CO_2 g$ biomass$^{-1} h^{-1}$) and plotted against temperature (°C) and fitted with the resulting equation:

$$resp = 0.1134 E - 05 - 0.2810 E - 06 \, temp + 0.2213 E - 06 \, temp^2. \tag{11}$$

Using mean annual temperatures for the three forest systems, respiration rates were calculated as $0.196 E - 04$, $0.365 E - 04$, and $0.506 E - 04 \, g g^{-1} h^{-1}$ for *Pinus-Quercus, Liriodendron,* and *Pinus taeda,* respectively. The temperature effect upon respiration in these systems is elucidated by comparing ratios of both calculated and measured rates between systems. Since Equation (11) is from the loblolly system, this becomes our basis of comparison. The *Pinus taeda: Pinus-Quercus* calculated ratio of $0.506/0.196 = 2.6$ compares favorably with the measured ratio of $2068/680 = 3.0$, as do the *Pinus taeda: Liriodendron* ratios of $0.506/0.365 = 1.4$ and $2068/1440 = 1.4$. The observed differences in rates of autotrophic respiration between these systems are unequivocally due to regional climate.

Through quantification of major subsystem roles in carbon cycling and through solution of Equations (1)–(4), we have seen the necessity of carefully

examining individual systems when making broad intersystem comparisons. Marked differences in magnitudes of pools or fluxes may lead to greater insight into the properties of the respective systems. Age or relative position along a growth curve and differences in regional climate have been shown to have a strong influence on rates of production and respiration.

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