RESEARCH

Land Use Changes and Net Primary Production in the Georgia, USA, Landscape: 1935–1982

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ABSTRACT / Land use since 1935 was quantified for Georgia, USA, and for a sample of 20 counties from the major physiographic regions within the state. Statistical data on crop production, pasture productivity, and forest growth were used to estimate net primary production. Appropriate harvest indices (ratio of crop yield to total plant production) were used to correct crop yield data for different decades. Net primary production (NPP) of the Georgia landscape increased from 2.5 to 6.4 tonnes/ha from 1935 to 1982, but varied considerably among land uses and physiographic regions. NPP in the piedmont and mountains reached a plateau between 1960 and 1982, but the upper and lower coastal plains showed a continued linear increase in NPP. In all regions, NPP rose most between 1960 and 1982, coinciding with increases in inputs such as fertilizer and irrigation. Natural ecosystem NPP for Georgia is approximately 16–18 tonnes/ha, and the estimated actual NPP is thus considerably less than the potential. Spatial and temporal patterns of NPP may be a useful basis for evaluating the biological performance of a landscape.

In natural landscapes, net primary production (NPP) provides the energetic and material basis for all heterotrophic life. In regions that are primarily agricultural or silvicultural, NPP also provides an important resource base for human economic activity. NPP has been calculated for landscapes for single years, and productivity profiles have demonstrated spatial variation in NPP of selected crops (Sharp and others 1975, Sharpe 1975). However, no studies have addressed how NPP changes temporally with landscape pattern. The redistribution of NPP among landscape elements represents an important functional aspect of a landscape and thus may be an essential feature of landscape ecology (Risser and others 1984).

The primary production of a landscape may be viewed as an output from a system driven by a series of inputs. NPP includes yield, or merchantable production; it includes all organic matter produced by plants less the amount respired. Productivity reflects the influence of a variety of inputs (Tangley 1986). Solar energy, of course, is a primary input, but other inputs, such as fertilizer and irrigation, may also be important.

In this study, I quantified land use patterns in Georgia, USA, from 1935 to 1982, estimated the annual net primary production associated with these patterns, and examined NPP in relation to selected inputs. My objectives were to answer four questions: (a) Does overall landscape NPP change with land use, or is it just allocated differently? (b) How do patterns of NPP vary by physiographic region? (c) How do patterns of NPP respond to changes in the patterns of human-controlled inputs to the landscape? (d) How does actual NPP compare with the natural rate of primary production?

KEY WORDS: Net primary production; Land use change; Georgia; Landscape ecology; Harvest index

The Georgia Landscape

Georgia encompasses three major physiographic regions, each of which has undergone substantial changes in land use during the past two centuries (Nelson 1957, Brender 1974, Healy 1985). These regions (Figure 1) include mountains (1,470,310 ha), piedmont (4,606,139 ha), and coastal plain (8,971,206 ha). The mountain region ranges in elevation from 183 to 1432 m, with mean annual temperature ranging from 12.8° to 16.1°C and annual rainfall ranging from 132 to 229 cm. The predominant forest types are oak–hickory (*Quercus–Carya*) and oak–pine (*Quercus–Pinus*). The Georgia piedmont consists of foothills underlain by acid crystalline and metamorphic rock. Elevation ranges from 152 to 457 m. Mean annual rainfall is 112–142 cm, and mean annual temperature ranges from 15.0° to 17.8°C. Major forest types are loblolly–shortleaf pine (*Pinus taeda* and *P. echinata*) and oak–pine. The large coastal plain region has gentle to moderate slopes and sandy soils underlain by marine sands, loam, and/or clays. Elevation ranges from 0 to 300 m; mean annual rainfall ranges from 112 to 135 cm, and mean annual temperatures range from 18.9° to 21.1°C. The dominant forest types are longleaf–slash pine (*P. palustris* and *P. elliotti*) and loblolly–shortleaf pine, with oak–gum–

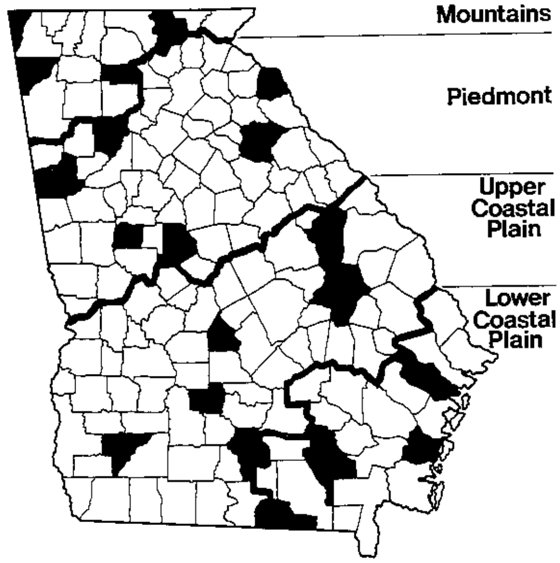

Figure 1. Map of Georgia, indicating physiographic regions and locations of sample counties.

cypress (*Quercus–Nyssa–Taxodium*) occurring along river floodplains. This region may also be divided into an upper coastal plain having rolling topography and a lower coastal plain which is relatively flat.

The presettlement vegetation of Georgia was primarily forest, with the exception of coastal salt marshes and grassy areas in the Okefenokee Swamp (Nelson 1957, Plummer 1975). The virgin forest was modified for centuries by the American Indians, (Stewart 1956), but more extensive modification of the landscape accompanied European settlement. Coastal plain forests were cut between 1866 and 1890, and by 1895, virgin pine timber was exhausted (Plummer 1975). During the 1800s, extensive clearing and farming also occurred on the Georgia piedmont (Brender 1952 and 1974), where the lands were worn out, abandoned, and new lands cleared almost continuously for more than a century (Hartman and Wooten 1935). By 1930, more than 80% of the lower piedmont region had been cleared at some time (Bond and Spillers 1935), and much of it had been cleared two or three times (Hartman and Wooten 1935). Most abandoned land reverted through natural succession to pine, primarily loblolly and shortleaf, and old-field pine comprised more than two-thirds of the total forest area in 1930 (Hartman and Wooten 1935). The rate of cropland abandonment has decreased substantially since the early part of the century and, although natural succession still contributes to the dynamics of Georgia's forest, the many processes associated with an urban–agricultural society predominate (Johnson and Sharpe 1976).

Table 1. Land use categories.

Softwood forest	Soybeans
Hardwood forest	Tobacco
Noncommercial forest	Wheat
Corn	Hay
Cotton	Pasture
Oats	Urban/developed
Peanuts	Water
Rye	Idle land
Sorghum	Wetlands

Table 2. Sample counties by physiographic region, Georgia.

Region	County	Area (ha)
Mountain	Chattooga	82,138
$n = 4$	Dade	43,530
	Pickens	58,214
	Union	80,039
Piedmont	Carroll	123,726
$n = 6$	Cobb	89,755
	Hart	59,802
	Monroe	103,229
	Oglethorpe	112,687
	Pike	59,595
Upper coastal plain	Baker	91,984
$n = 6$	Berrien	121,263
	Emanuel	177,749
	Jefferson	137,328
	Pulaski	65,632
	Turner	75,919
Lower coastal plain	Echols	110,121
$n = 4$	Glynn	109,154
	Liberty	133,182
	Ware	236,308

Methods

Land use since 1935 was quantified for Georgia and for a sample of 20 of its 159 counties (Figure 1) by categories representing the major land uses (Table 1). Counties were selected using a stratified random sample to assure adequate coverage of each physiographic region (Table 2).

To assess changes in landscape production patterns, data related to land use were required. Census data for agriculture and forests express the production of merchantable portions of NPP and can be converted to estimates of total NPP using appropriate conversion factors (Sharpe 1975). The general strategy was first to determine the area devoted to each land use category. The actual yield of food or fiber was then recorded and converted to net primary production for crops and forests, as explained in detail below.

Table 3. Data sources.

Forest data

The following are US Forest Service Research Bulletins:

- SE-1. Larson, R. W., and B. Spada. 1960. Georgia's timber.
- SE-19. Knight, H. A. 1971. Forest statistics for southwest Georgia, 1971.
- SE-21. Bellamy, T. R. 1972. Forest statistics for southeast Georgia, 1971.
- SE-22. Cathey, R. A. 1972. Forest statistics for central Georgia, 1972.
- SE-24. Knight, H. A. 1972. Forest statistics for north central Georgia, 1972.
- SE-25. Knight, H. A. 1973. Forest statistics for north Georgia, 1972.
- SE-27. Knight, H. A., and J. P. McClure. 1974. Georgia's timber, 1972.
- SE-69. Tansey, J. B. 1983. Forest statistics for Georgia, 1982.
- SE-73. Sheffield, R. M., and H. A. Knight. 1984. Georgia's forests.

Grant, B. F., and A. E. Patterson. 1946. Forest facts for Georgia. Agricultural and Industrial Development Board of Georgia, Forestry Bulletin 10.

McCormack, J. F. and J. W. Cruikshank. 1954. Forest statistics for Georgia, 1951–1953. USDA, Forest Service, Forest Survey Release 44.

Spillers, A. R. and I. F. Eldredge. 1943. Georgia forest resources and industries. USDA, Miscellaneous Publication 501 (data are for 1934–1936).

Crop data

USDA, Census of Agriculture for the years: 1935, 1945, 1954, 1959, 1972, 1982. (Primary source of data.)

Georgia Crop Reporting Service. Georgia agricultural facts. (Data from these volumes were used occasionally to complete information not available in the Census.)

1976 land use, especially urban and water

Georgia Department of Natural Resources, 1979. Georgia statewide Landsat classification statistics by counties. Environmental Protection Division, Resource Assessment program. Unpublished.

For other land uses, average primary production values were estimated from the literature and multiplied by the area. The production across all land use categories was then totaled. Sources of the data used in this study are listed in Table 3.

Conversion of Data to Net Primary Production

A major challenge in all productivity profiles is the conversion of crop yield and net annual tree growth to NPP values (Sharpe 1975). For crops, the unharvested portions of the plants must be included. For example, the yield data for oats only include the grain, but the percentage of dry weight of different shoot components at maturity are: leaves, 7%; upper stem, 20%; lower stem, 14%; vegetative tiller, 3%; chaff, 15%; and grain, 41% (Singh and Stoskopf 1971). Similarly, for forest production, growth in roots, foliage, and unharvestable branches must be included.

Data upon which to base conversion factors are sparse, and temporal changes add to the difficulty of estimation. The harvest index (HI), or proportion of aboveground plant material in the harvestable component, has increased substantially and progressively in many crops (Austin and others 1980, Evans 1980). Selection for an increasing harvestable proportion of the crop has resulted in larger yields (Evans 1980), even though there has been no increase in the rates of photosynthesis and growth (Donald and Hamblin 1976). Thus, 100 bushels (3524 liters) of corn recorded in 1935 and 1985 probably indicate different rates of primary productivity.

Cropland

Crop yields were first converted from the units in which they were reported (bushels, bales, tons, pounds) to their mass in kilograms (USDA 1984). This mass was then corrected for moisture content assuming a 12% water content (Sharp and others 1976). The dry mass of crop yield was then multiplied by the inverse of the harvest index to give total aboveground plant production. Finally, belowground production was included by assuming that 10% of the plant production is belowground, a reasonable root–shoot ratio for annual plants (Monk 1966). The resultant total NPP can also be divided by the area planted to obtain productivity rates (kg/ha).

Different harvest indices were used for different decades based on changes in harvest indices reported in the literature (Table 4). During this century, the HI of wheat has increased from 34% to 40% in the Netherlands (Van Dobben 1962), from 28% to 36% in Australia (Sims 1963), and from 32% to 38% in eastern Washington (Vogel and others 1963). Increases in the HI from 33% to 41% have also been reported for oats

Table 4. Conversion factors for crop data.

Crop (unit[e])	To kg	To dry wt	Harvest index 1935	1945	1954	1959	1974	1982	Overall conversion factors[f] 1935	1945	1954	1960	1972	1982
Corn (bu)	30.8	.88	.35	.37	.40	.415	.43[a]	.47	88.84	84.04	77.73	74.92	72.31	66.16
Cotton (bales)	218	1	.45	.46	.47	.475	.481[b]	.49	591.6	579.8	568.6	563.2	556.9	547.6
Oats (bu)	14.5	.88	.38	.39	.41	.41	.41[c]	.42	37.31	36.35	34.58	34.58	34.58	33.76
Peanuts (lb)	0.45	.88	.53	.53	.53	.54	.558[b]	.56	0.838	0.838	0.838	0.823	0.796	0.794
Rye (bu)	25.4	.88	.23	.235	.25	.26	.27[c]	.28	108.0	105.7	99.34	95.52	91.98	88.70
Sorghum (bu)	25.4	.88	.45	.45	.47	.47	.49	.50[d]	55.1	55.1	52.79	52.79	50.63	49.62
Soybeans (bu)	27.2	.88	.24	.24	.24	.245	.25[b]	.255	110.8	110.8	110.8	108.5	105.9	104.3
Tobacco (lb)	0.45	.88	.55	.55	.55	.556	.559[b]	.56	0.808	0.808	0.808	0.799	0.796	0.794
Wheat (bu)	27.2	.88	.27	.28	.295	.30	.31[b]	.32	98.5	94.9	90.1	88.6	85.8	83.1

[a] From Scarsbrook and Doss (1973).
[b] From Sharp and others (1971).
[c] From Singh and Stoskopf (1971).
[d] From P. Hendrix, data for Georgia piedmont (personal communication).
[e] bu, bushel; and lb, pounds.
[f] Also included is a 10% root/total plant organic matter conversion.

in Australia (Sims 1963), from 36% to 53% for rice in Taiwan (Chandler 1969), and from 40.1% to 57.1% for barley in the United Kingdom (Cannell 1968). No values were available for crops actually grown in Georgia. Based on the magnitude of these changes elsewhere, estimates of historical harvest indices for the crops in this study were assigned (Table 4).

Forests

Acreage and net annual growth of growing stock were recorded for hardwood and softwood forests. The growth rate per acre was calculated, then converted to NPP as follows:

$$\frac{\text{growth/acre}}{0.4046 \times 35.3} \times \text{specific gravity} \times \text{CF} = \text{NPP (t/ha)}$$

where 0.4046 converts acres to hectares
35.3 converts cubic feet to metric tons
specific gravity = 0.43 (softwood) or 0.52 (hardwood)
CF = a correction factor which accounts for nonmerchantable plant production, including leaves, branches, and roots

For softwood, CF = 3.2 (based on Sharp and others 1976; data from Nemeth 1973, Gholz and Fisher 1982; and H. Lieth personal communication). For hardwood, CF = 4.0, accounting for greater understory production (based on Harris and others 1980, Boring and Swank 1984). These factors closely agree with those reported for hardwood and softwood species by Stearns and others (1971).

Hay, Pasture, and Idle Land

Production of hay (dry weight) was converted to kilograms then multiplied by 1.5 to include an assumed 40% below-ground production for herbaceous perennials (Monk 1966).

Yield data were not available for pastures. NPP of pastures was determined by multiplying pasture acreage by one-half of the rate of hay production (Sharp and others 1976), assuming lower production rates on unimproved, unfertilized grazed lands. The rate of pasture production was also applied to idle or failed cropland.

Urban

The productivity of urban areas was estimated to be 3.5 tonnes/ha, half the productivity of lawns in the temperate zone (Falk 1980). The rate is reduced because of the area covered by buildings and pavement

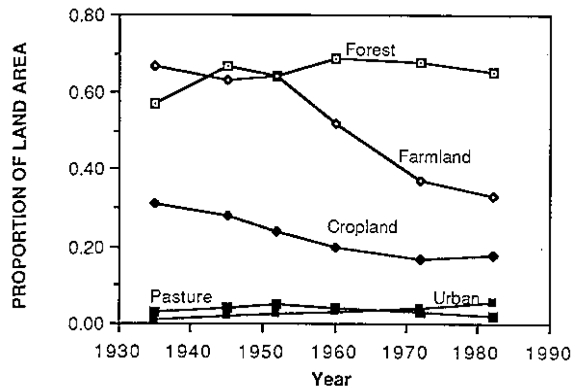

Figure 2. Major land uses in Georgia as a proportion of the total land area, 1935–1982.

and because not all developed areas in Georgia are fertilized and irrigated.

Wetlands

Productivity of coastal marshes has been well studied, and is approximately 20 tonnes/ha (Pomeroy and others 1980).

Water

Water other than wetlands occupies a small proportion of Georgia, and productivity rates comparable to tonnes/ha are not available. Thus, water was not included in the analysis.

Results

Land Use

Land use has changed in Georgia from 1935 to 1982. Cropland and total land in farms have declined, while forests and urban areas have increased (Figure 2). Farms represented 68% of the state in 1935 but only 33% of the area in 1982. Cropland decreased from 32% to 20% during the same interval. Forests increased by almost 10% since 1935 and presently include 66% of Georgia. The proportion of land in pastures has remained relatively constant, at approximately 4%. Urban area has increased to approximately 5% of the total land area.

Changes in the three major categories of land use (farms, cropland, forest) differed by physiographic region (Figure 3). All regions show a decrease in the proportion of land in farms from 1935 to 1982, but the piedmont and mountains had the largest declines. Cropland declined most in the piedmont, from 42% in 1935 to 19% in 1982, but there was little change in the upper and lower coastal plain. Forest area increased between 1935 and 1960 in each region except the

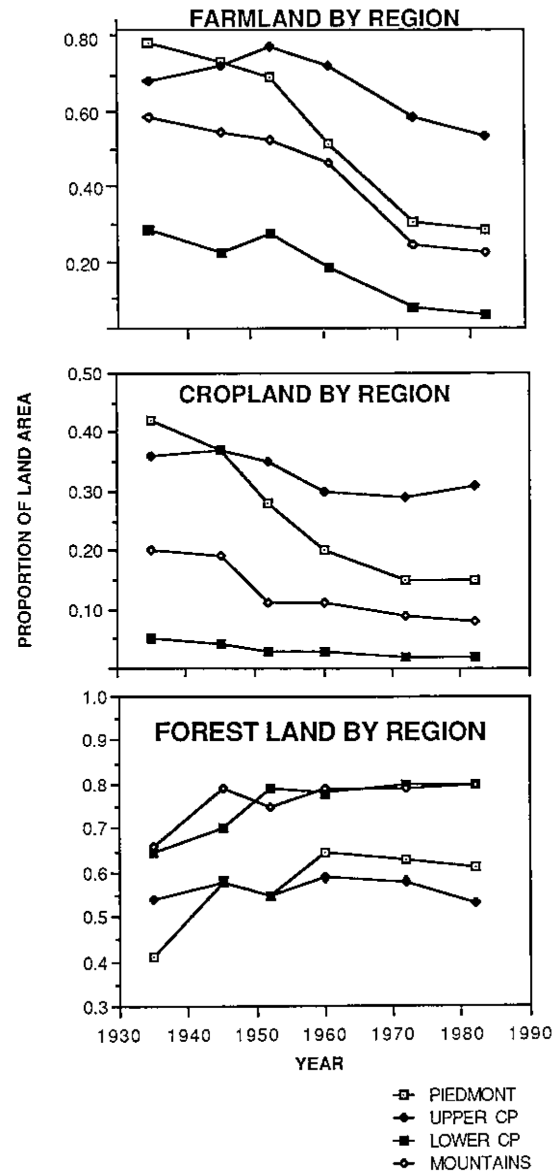

Figure 3. Mean proportion of land in farms **(top),** crops **(center),** and forest **(bottom)** by physiographic region in Georgia, 1935–1982.

upper coastal plain. Between 1960 and 1982, forest area remained relatively constant in the lower coastal plain and mountains, and declined slightly in the piedmont and upper coastal plain. Variation in the mean proportion of land in forests and crop was highest in the piedmont, reflecting the diversity of land use in the region. The piedmont is presently undergoing substantial changes, including extensive urbanization around the Atlanta metropolitan area and smaller cities.

Net Primary Production

The data compiled for the whole state of Georgia

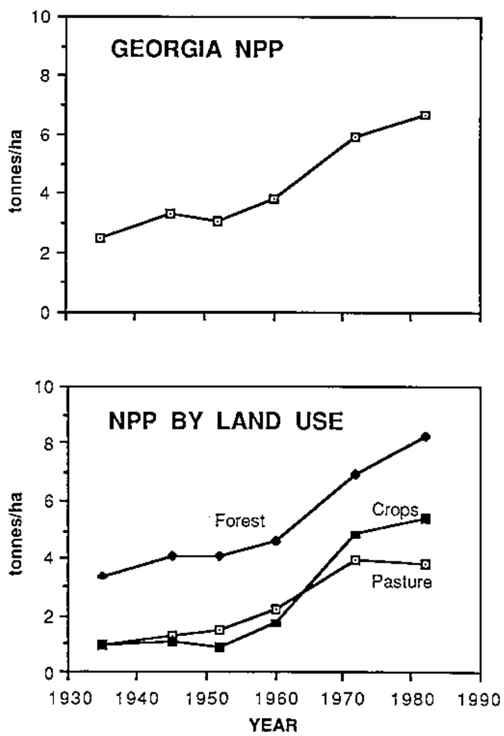

Figure 4. Net primary production in Georgia, 1935–1982, overall **(top)** and by land use **(bottom).**

indicate that NPP has increased from 2.5 to 6.4 tonnes/ha from 1935 to 1982 (Figure 4, top). This trend was gradual until 1960 then almost expontential from 1960 to 1982. The increase is largely attributable to changes in forest and agricultural productivity rates (Figure 4, bottom), both of which increased from 1960 to 1982. The importance of components of these categories has also changed. For example, the total production of cotton in 1935 was considerably greater than in 1985, whereas the total production of soybeans was much less (Table 5). For the forests, the area in softwoods decreased but production increased by 300%, while hardwood forest doubled in area but production increased by less than 100% (Table 5).

The total NPP by region was similar to the statewide pattern (Figure 5). The increase in total NPP since 1935 varied from approximately 50% (mountains) to 300% (upper coastal plain). Between 1972 and 1982, NPP in the piedmont and mountains reached a plateau, but in both the upper and lower coastal plains it continued to rise rapidly. There was also a trend of increasing NPP from the mountains to the coastal plain, also reported for North Carolina (Sharp and others 1976), which has become more apparent in recent years.

Table 5. Contribution of land use categories to net primary production estimate for Georgia, 1935 and 1982.[a]

Land use	1935 Area (ha)	1935 Yield[b]	1935 Production[c] (t)	1935 NPP[c] (t/ha)	1982 Area (ha)	1982 Yield[b]	1982 Production[c] (t)	1982 NPP[c] (t/ha)
Softwood forest	5,649,473	449,300,000 ft³	16,419,178	2.90	4,631,141	1,189,564,000	43,471,319	9.39
Hardwood forest	2,866,923	193,700,000 ft³	8,560,113	2.98	4,977,637	566,689,000	25,043,480	5.03
Noncommercial forest	160,728	NA	471,431	2.93	205,973	NA	1,468,680	7.13
Corn	1,780,833	38,036,900 bu	3,379,198	1.9	319,152	60,031,900	3,971,711	12.4
Cotton	873,319	971,400 bales	574,680	0.66	53,157	235,000	128,686	2.4
Oats	31,323	1,428,700 bu	53,304	1.7	36,437	5,490,000	185,342	5.1
Peanuts	189,068	338,575 × 10⁶ lb	283,725	1.5	178,300	1,379,318 × 10³	1,095,179	6.1
Rye	8,330	117,320 bu	12,670	1.5	28,340	1,470,000	130,389	4.6
Sorghum	885	29,875 bu	1,646	1.9	38,068	3,984,900	197,730	5.2
Soybeans	2,834	42,000 bu	4,654	1.6	819,314	51,993,100	5,422,881	6.6
Tobacco	20,556	31,671,000 lb	25,590	1.2	18,117	95,134,000	75,536	4.2
Wheat	68,230	1,430,600 bu	140,914	2.0	403,223	31,864,400	2,647,932	6.6
Hay	377,650	516,889 tons	469,899	1.4	195,319	1,090,697	991,543	5.1
Pasture	671,520	NA	626,665	0.93	888,258	NA	3,381,950	3.8
Urban	100,000	NA	350,000	3.5	600,381	NA	2,101,334	3.5
Wetlands	260,076	NA	5,201,520	20.0	260,076	NA	5,201,520	20.0
Idle	2,083,820	NA	1,937,953	0.93	260,076	NA	740,322	3.8
Total[d]	15,216,194	NA	38,513,140	2.5	15,047,658	NA	96,255,534	6.4

[a] Conversion factors are discussed in the *Methods* section.

[b] bu, bushels; ft, feet; and lb, pounds.

[c] Total production is in metric tonnes (t), NPP is in t/ha.

[d] Total area is for the whole state, not a sum of the above.

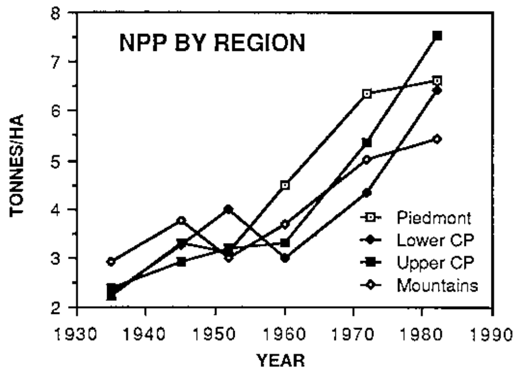

Figure 5. Mean net primary production by physiographic region in Georgia, 1935–1982.

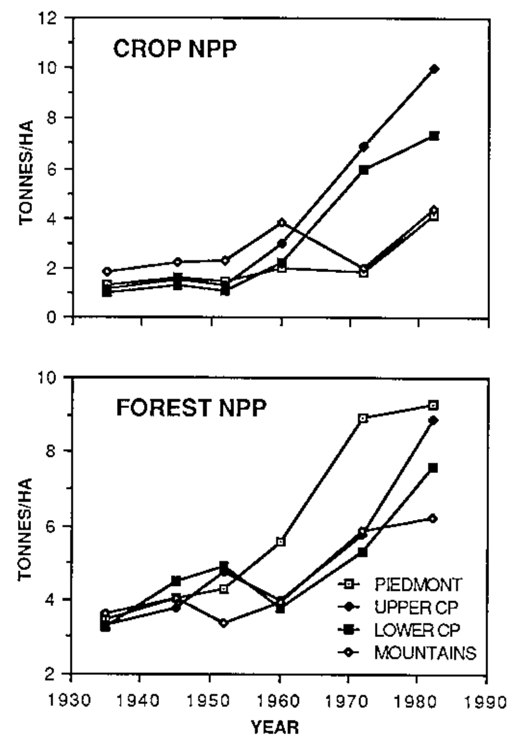

Figure 6. Mean net primary production of cropland **(top)** and forest land **(bottom)** by physiographic region in Georgia, 1935–1982.

The rate of forest and agricultural production varied among physiographic regions (Figure 6). Between 1935 and 1960, forest production showed little change in all four regions. Between 1960 and 1972, production almost doubled in the piedmont, and then reached a plateau. The mountains followed a similar pattern, although production only increased by about 30%, since slower-growing hardwood species are predominant. In both the upper and lower coastal plain, forest production increased steadily between 1960 and 1982, and has not reached a plateau.

Net primary production of crops also increased only slightly in all regions between 1935 and 1960 (Figure 6). After 1960, crop NPP increased from 2.5 to 10 tonnes/ha on the upper coastal plain and from 1.9 to 6.9 tonnes/ha on the lower coastal plain. In contrast, NPP of crops in the piedmont and mountains declined between 1960 and 1972, and then doubled between 1972 and 1982, from approximately 1.7 to 3.5 tonnes/ha.

Sensitivity Analyses

To assess the sensitivity of the NPP estimates to the conversion factors and to determine what factors were most important, sensitivity analyses were conducted. Harvest indices and forest conversion factors were altered and new NPP estimates were calculated. The percentage change in NPP was then determined.

The NPP estimates were not particularly sensitive to the harvest index values. When harvest indices were held constant at their 1972 values, which were obtained from the literature, NPP by county changed from −1% to +4%. However, half of the values did not change at all. A 10% increase in the harvest indices brought about increases in NPP ranging from 0 to 5%, but over half the values showed no change. Since numerous crops contribute to agricultural production, the harvest index of a particular crop has little effect on overall NPP.

In contrast, the conversion factors for forests strongly affect the NPP determinations. When the conversion factors accounting for nonmerchantable forest production were increased by 10%, NPP values increased by 5%–10%. When the conversion factors were decreased by 33%, NPP values declined by 15%–42%. Forests are the single largest contributor to NPP, and a percentage change in the forest conversion factor may cause an even greater percentage change in the NPP estimate for a county.

Inputs

Fertilizer and water represent two major human inputs to agricultural lands. Both have increased in Georgia from 1935 to 1982 (Figure 7). Use of nitrogen fertilizer has increased almost eight times since 1935, and much of this increase is since 1960. This corresponds to the large increases in crop NPP during the same time period. Irrigation has become more extensive only in the past 15 years, and accounts presently for 9% of the cropland in Georgia. Other inputs include pesticides, herbicides, and the energy of planting, all of which contribute toward an increased output of organic matter.

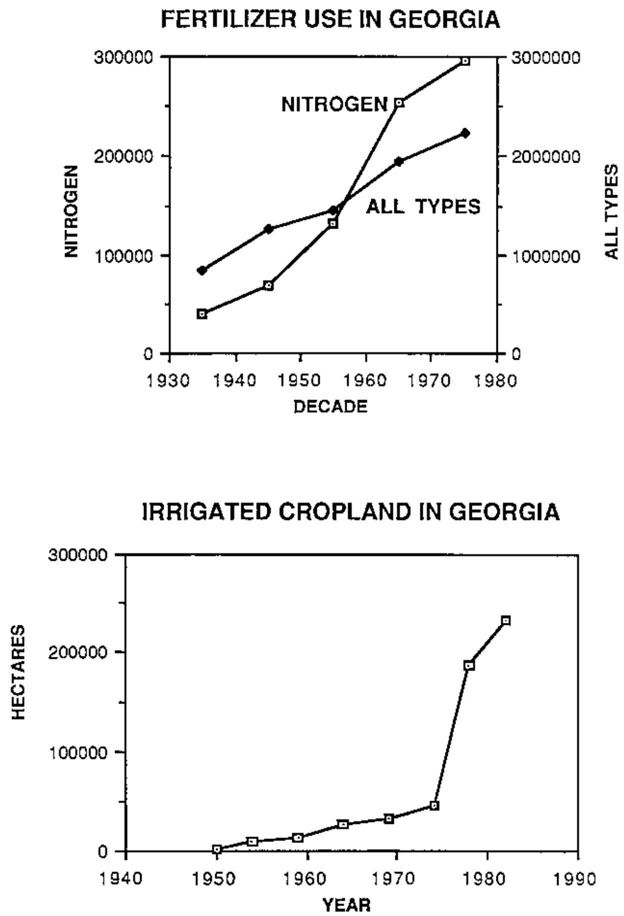

Figure 7. Inputs to agricultural lands in Georgia: nitrogen fertilizer, 1935–1983 **(top)**, and irrigated area, 1950–1982 **(bottom)**.

Actual and Predicted NPP

The net primary production estimated for Georgia can be compared with natural rates of NPP. Predictions from several world models suggest a range of annual NPP for Georgia from 10 to 22 tonnes/ha (Table 6), with 16–18 tonnes/ha most likely (Olson 1975, Waring and Schlesinger 1985, E.O. Box personal communication). My analysis suggests that although annual NPP in Georgia has increased during the past 50 years, it remains considerably below the predicted natural rates. The average NPP of forests in Georgia was 8.3 tonnes/ha in 1982, approximately two-thirds of the predicted natural rate. The production of cropland averages about 5.1 tonnes/ha, but tremendous variation was observed by physiographic region. The highest estimate of crop productivity in this study was 15.2 tonnes/ha in Emanuel County, which approximates the predicted natural rate.

Table 6. Natural annual net primary production of Georgia.[a]

Model	Predicted annual NPP (tonnes/ha)
Innsbruck	10–16
Miami	14–20
Montreal	15–22
GPP-R	16–18

[a] The Innsbruck map is estimated actual net primary productivity (Lieth 1972), the Miami model predicts NPP from temperature and precipitation (Box and others 1971), the Montreal model predicts NPP from actual evapotransipiration (Lieth and Box 1972), and the GPP-R uses gross primary production minus dark respiration to estimate NPP (Box 1978).

Discussion

The low NPP observed from 1935 through 1960 may be due to poor agricultural practices which had caused the fertility of the land to decline. In the piedmont, for example, nearly all the original topsoil was lost from 47% of the land (Hartman and Wooten 1935). Thus, it is not surprising that net primary production was low in 1935, and that increases were slight during the next 25 years. However, as the agricultural area shrank, the least productive lands were abandoned first (Clawson 1981). Particularly in the south, some of these lands have formed relatively productive bases for forestry (Clawson 1981).

Improvements in both agriculture and silviculture began to yield results during the 1960s. Both fertilization and irrigation of cropland began to increase, with irrigation being particularly important in the upper coastal plain. Double cropping also contributed to the increase in annual primary production. The National Resource Inventory for 1982 indicated that 31% of the total cultivated cropland in Georgia was double cropped (USDA SCS 1984). Similarly, intensive forest management and a relatively constant rate of removal resulted in increased forest growth throughout the entire southeast during the past few decades (USDA FS 1978).

Estimates of present NPP are still far below the predicted rates, and this is probably due to several factors. The past land abuses may still influence NPP, as on the notably poor soils of the Georgia piedmont. In addition, my overall NPP estimates may be low because: (a) certain land uses, such as orchards and vegetable fields, were not included because data were not available for the study period; (b) weed production was not included in the analysis but may sometimes account for up to 50% of the above-ground primary production on cropland (P. Hendrix, personal communication); and (c) conversion factors are generally conservative and would certainly be improved with additional local data.

This study supports Melillo's (1984) conclusion that it is difficult to predict agricultural production from the rate of production of the natural vegetation. Claims of agricultural production exceeding natural production may involve comparisons of crops given subsidies of nutrients or water or both with adjacent communities that are not subsidized (Mitchell 1984). However, increasing fertilizers or other inputs will not result in raising yields indefinitely because of the biological principle of diminishing returns with increasing quantities of inputs (Pimentel 1984). Furthermore, although yields have increased, they are sometimes less stable, since the effort devoted to sustaining the yields must also increase (Plucknett and Smith 1986).

Several costs are associated with increases in agricultural production. The conversion of a "natural" ecosystem to an agricultural system involves a change in the mode of exploitation, especially on the nutrient cycles in the system (Melillo 1984). Soil erosion diminishes the productivity of agricultural land, and is still a serious threat to sustainable agriculture (Larson and others 1983, Pimentel 1984). Loss of soil may reduce plant nutrient-holding capacity, reduce water-holding capacity, increase water runoff, and restrict rooting depth (Pimentel 1984). Yield reductions of 25%–50% for various crops in the southern United States have been attributed to soil erosion (Adams 1949, Buntley and Bell 1976, Langdale and others 1979). Eutrophication of water bodies is another associated cost of high NPP. Losses from agricultural areas may flow across the landscape and become inputs to other components.

An extension of the effect of changing land use on NPP is the effect on carbon storage. Patterns of carbon storage have been described for the southeast (Delcourt and others 1981, Delcourt and Harris 1980) and for the upper piedmont of Georgia (Sharpe and Johnson 1981). Secondary forests in the southeast today store 75% of the total carbon within the terrestrial biota; another 20% of the organic carbon is in cropland, and less than 5% remains in virgin forest (Delcourt and Harris 1980). Southeastern forests are now serving as a sink for CO_2 at a rate of 7×10^7 tonnes/year over an area of 1.4×10^6 km^2 (Delcourt and Harris 1980). During the next 10–20 years, old field succession and reforestation of the piedmont in Georgia and the Carolinas should result in a net increase of biomass and carbon in secondary forests of that region, whereas southeastern bottomlands are expected to be converted largely to cropland before 1990 (USDA FS 1979).

Conclusion

NPP increased in Georgia between 1935 and 1982, and this was associated with changing land use. Forests now produce an average of two-thirds the predicted natural NPP, and some agricultural areas approximate the natural rates, but with large inputs. The pattern of abandoned cropland reverting to forest was common in many areas, and the associated trends in NPP are likely to be widespread. Spatial and temporal patterns of NPP may be a useful basis for evaluating the biological performance of a landscape.

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