

Changes in ecosystem carbon storage over 40 years on an old-field/forest landscape in east-central Minnesota

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Abstract

Organic carbon (C) storage in complex landscapes and its temporal change can be important in the global C budget. Change in C storage between 1938 and 1977 was estimated for a 2224 ha old-field/forest landscape in east-central Minnesota by coupling change in area of seven vegetation types (five forest and two non-forest) with vegetation-specific C densities (mg ha^{-1}). Carbon densities were based on sampling carried out between 1974 and 1990. Areas of vegetation types in 1938 and 1977 were determined from aerial photographs. Carbon density was greatest in forest overstory (60–100 Mg ha^{-1}) and organic and mineral soil (30–100 Mg ha^{-1} to 25 cm depth). Ecosystem C storage was approximately 212 000 Mg in 1938 and 225 000 Mg in 1977, an increase of ca. 13 000 Mg across the study area. This was due largely to an increase in upland forest at the expense of non-forest area. The largest proportional increase in C storage was in trees (a 13% gain), while mineral soil gained 4% and herbs gained 6%. C storage in O horizon and shrubs remained constant. For the 20% of the landscape originally occupied by cultivated fields, an empirical model based on chronosequence studies indicated a 40% increase in C storage over 40 years; C increased in mineral soil, O horizon and trees as both herbaceous succession and forest encroachment occurred. Uncertainties of the estimates, based on propagation of standard errors, were 5% to 19% for C storage and 6% to 1000% for change in C storage. Uncertainty was due primarily to sample variability, but included uncertainty in biomass equations and GIS processing. This uncertainty demonstrates the difficulties associated with expanding from point sample data to landscape-scale estimates of C storage.

Keywords: Plant biomass; Cedar Creek; Geographic information system

1. Introduction

Organic carbon (C) in forested ecosystems is an important reservoir of the world's total C (Houghton and Woodwell, 1989). Forests provide an important sink for CO_2 through photosynthesis, but may also

act as a large source of CO_2 through changes in land use such as burning or harvesting (Houghton et al., 1982; Harmon et al., 1990). Although harvesting may alter forest soil C (Covington, 1981), this has not been universally observed (Alban and Perala, 1990; Johnson et al., 1991). Changes in vegetation and soil C storage may also occur as a result of biomass accretion as forests grow or change through

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succession (Hall et al., 1991), or following abandonment of agricultural fields (Gleeson and Tilman, 1990; Zak et al., 1990). Tree and stand-level processes of C uptake and release have been extensively investigated (Eamus and Jarvis, 1989), and analyses of C storage have been made at regional (Burke et al., 1990; Grigal and Ohmann, 1992), national (Birdsey et al., 1993; Turner et al., 1995) and global (Woodwell et al., 1983; Detwiler and Hall, 1988) scales. However, landscape-level changes in C storage, incorporating data from separate species, vegetative strata, and soil horizons, have not been fully investigated.

The objectives of this study were to (1) quantify vegetation and soil C storage in a forest/old-field landscape and (2) estimate the change in C storage over a 40-year period. The study was carried out at the Cedar Creek Natural History Area (CCNHA) in east-central Minnesota. This area has been extensively studied, and a wealth of historic data are available on land use change (Pierce, 1954; Tester, 1989; Engstrom, 1992) and on successional change in vegetation and soil properties on abandoned agricultural fields (e.g., Inouye et al., 1987; Tilman, 1987). In addition, ecosystem-level data have been collected on soils (Grigal et al., 1974), nutrient cycling (Zak et al., 1990) and plant communities (Suhartoyo, 1991). Maps of soil type, forest cover type and water table surface have been digitized and incorporated into a geographic information system (GIS) database for CCNHA (Engstrom, 1992).

2. Methods

2.1. General

CCNHA is located approximately 50 km north of Minneapolis, Minnesota, USA (45° 35' N, 93° 10' W). The climate is continental, with a mean annual temperature of 6°C and a mean annual precipitation of 660 mm (Grigal et al., 1974). CCNHA comprises 2224 ha and is a mosaic of upland and wetland ecosystems. Plant communities occur across the landscape in response to water table depth, and include oak savanna, prairie, upland forest, marsh and swamp (Cushing, 1963). Upland soils were formed in glacial outwash and are primarily well-

drained fine and medium-textured sands; areas of organic matter accumulation occur where the surface is at or below the water table (Grigal et al., 1974; Hairston and Grigal, 1991).

2.2. Landscape analysis

Estimates of vegetative C densities (mg C ha^{-1}) were based on sampling carried out in 1990 (Suhartoyo, 1991). A total of 126 sampling points were randomly chosen from 235 points established at 50 m intervals along five transects distributed within CCNHA. At each sample point, tree stem diameter at breast height (dbh, 1.37 m above ground) was measured for trees 1–10 cm dbh on a 200 m² plot, and for trees > 10 cm dbh on a 400 m² plot. Tree seedling and shrub diameters in 0.25 cm classes at 15 cm above ground level were measured on four 1.5 m² subplots. Herb samples on five 0.25 m² subplots were clipped, oven-dried at 70°C and weighed.

For trees, species-specific equations based on diameter and height (Alemdag, 1983; Alemdag, 1984) were used to determine biomass. Tree height was not measured during field sampling but was based on a previously determined diameter-height relationship for the study site (D.F. Grigal, unpublished data). Tree root biomass was estimated from a general stem biomass/root biomass relationship reported by Whitaker and Marks (1975). Above- and below-ground biomass values were added for each tree, summed across trees on each plot, and converted to Mg ha^{-1} .

Above-ground shrub biomass was determined from allometric equations for species in Minnesota (Grigal and Ohmann, 1977; Roussopoulos and Loomis, 1979; Balogh, 1983; Connolly and Grigal, 1983; Buech and Rugg, 1989). Total (above- plus below-ground) biomass was assumed to be 2.5 times that of above-ground biomass, based on results from studies in northern North America and the Nordic countries (Reader and Stewart, 1971; Rencz and Auclair, 1978; Paavilainen, 1980; Vasander, 1982; Grigal et al., 1985; Backeus, 1990). Total biomass was summed across all shrubs on each subplot and converted to Mg ha^{-1} . Tree seedling biomass was assumed to be constant for all seedlings less than 30 cm in height; biomass per seedling was 0.008 kg for coniferous species (Alemdag, 1983) and 0.009 kg for hardwood species (Alemdag, 1984).

Above-ground herb biomass was determined by clipping, drying and weighing all herbaceous material on five 0.25 m² subplots within each plot. Values were averaged among the five subplots and expressed as Mg ha⁻¹. Total herb biomass was assumed to be five times that of above-ground biomass, based on work carried out at CCNHA (Gleeson and Tilman, 1990). Carbon concentration of biomass in this study and other studies used for comparison was assumed to be 47.5% (Raich et al., 1991), expressed on an oven-dry basis.

Point estimates of vegetative C were applied to the CCNHA landscape using GIS. Vegetative cover types were digitized from aerial photographs taken in 1938 and 1977 and converted to map layers (Engstrom, 1992). The 20 original cover types proved unwieldy for this study and were grouped into seven vegetation types (Table 1). Upland deciduous species were divided into those with wood of high density (UDH) and those with wood of low density (UDL). A map of the sample points was overlain with the

digitized 1977 vegetation type map, indicating the identity of the sample points with respect to each of the vegetation types. The observed vegetation for each point and the vegetation type assigned by the map agreed in all cases. Carbon densities were averaged within vegetation types, resulting in a mean C density for herbs, shrubs and trees for each type. C density of the lowland O horizons (0–25 cm depth) was taken from Grigal et al. (1974) and assumed to be equal across the three lowland vegetation types. C densities of the O horizon and mineral soil (0–25 cm depth) for each of the four upland vegetation types were determined from other CCNHA studies (Grigal et al., 1974; Tester, 1989; Zak et al., 1990; Hairston and Grigal, 1991; Bouabid, 1992; Grigal and Homann, 1994; Homann and Grigal, in press). The GIS was used to determine the area of each vegetation type and the change in area between 1938 and 1977; the change in area multiplied by the mean C density indicated the change in C content for each ecosystem component within each vegetation type.

Table 1

Vegetation types and dominant species at Cedar Creek Natural History Area (nomenclature follows Gleason and Cronquist, 1963)

Vegetation type	Code	Dominant species
Lowland conifer	LC	<i>Larix laricina</i> (Du Roi) K. Koch <i>Thuja occidentalis</i> L.
Lowland deciduous	LD	<i>Betula papyrifera</i> Marshall <i>Fraxinus nigra</i> Marshall <i>F. pennsylvanica</i> Marshall <i>Salix</i> spp. <i>Ulmus americana</i> L.
Lowland non-forest	LNF	<i>Typha latifolia</i> L. <i>Carex</i> spp.
Upland conifer	UC	<i>Pinus resinosa</i> Sol. ex Aiton <i>Pinus strobus</i> L.
Upland deciduous high density	UDH	<i>Quercus alba</i> L. <i>Q. ellipsoidalis</i> E. Hill <i>Q. macrocarpa</i> Michaux <i>Q. rubra</i> L.
Upland deciduous low density	UDL	<i>Acer rubrum</i> L. <i>A. saccharinum</i> L. <i>Betula alleghaniensis</i> Britton <i>Populus tremuloides</i> Michaux <i>P. grandidentata</i> Michaux <i>Prunus serotina</i> Ehrh. <i>Tilia americana</i> L.
Upland non-forest	UNF	<i>Andropogon scoparius</i> Michaux <i>Panicum xanthophysum</i> A. Gray <i>Poa pratensis</i> L.

Uncertainty was propagated through all estimates using standard methods (Freese, 1962). Uncertainty associated with estimates of C storage was made up of three components: sample variability, uncertainty in biomass equations, and uncertainty introduced by GIS processing. For vegetative C density, uncertainty combined the standard error of samples within a vegetation type and the standard error of the estimate for the tree, shrub and herb biomass equations. For O horizon and mineral soil C density, the uncertainty was the standard error. The GIS-related uncertainty, which resulted from line width and 'rubber sheeting' (Engstrom, 1992), was $\pm 1 \text{ m}^2$ of polygon area per meter of polygon boundary.

2.3. Field analysis

For the fields with known histories (Table 2), C density and its change were estimated with an empirical model. The model accounts for change in C in above- and below-ground vegetation, O horizon, and mineral soil as abandoned fields undergo herbaceous succession (Inouye et al., 1987) or encroachment by forest (Engstrom, 1992).

The model used data collected at CCNHA, except for C density of encroached forest vegetation, which was based on biomass of a 29-year-old red oak (*Quercus rubra* L.) plantation (Gower and Son,

Table 2

Area of forest and non-forest vegetation types in 1938 at Cedar Creek Natural History Area included in the landscape and old-field analyses

Vegetation type	Area (ha)	Area (% of total)
<i>Upland</i> ^a	1257	57
UC	2	0
UDH	458	21
UDL	38	2
UNF	759	34
Uncultivated non-forest	257	12
Fields of unknown history	51	2
Fields of known history ^b	451	20
Cultivated in 1938	434	20
Abandoned before 1938	17	1
<i>Lowland</i> ^a	797	36
LC	236	11
LD	138	6
LNF	423	19
<i>Excluded from analysis</i>	170	8
Water	141	6
Industrial, residential, other	29	1
Total area	2224	

^a Included in landscape analysis.

^b Included in old-field analysis.

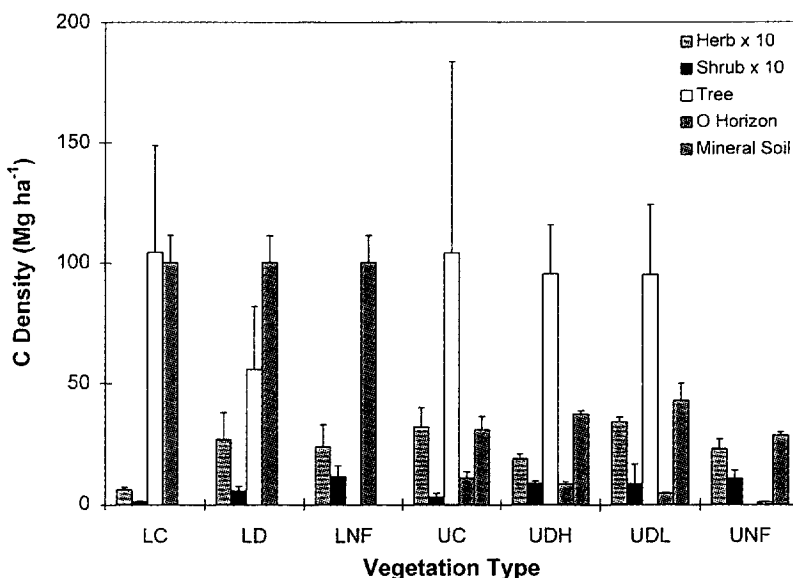


Fig. 1. Carbon densities for five ecosystem components in seven vegetation types at CCNHA. Error bars indicate uncertainty associated with each estimate. See text for explanation of uncertainty. Note the value for herb and shrub C are plotted at ten times their actual value.

1992). Vegetative C density of abandoned fields was from Gleeson and Tilman (1990) and of cultivated fields from Bray et al. (1959), adjusted for temporal changes in productivity due to agronomic practices, including genetic and land management changes (Cardwell, 1982). O horizon C density was from a chronosequence of abandoned fields ($n = 8$) and young forest stands bordering them (Homann and Grigal, in press). Mineral soil C density of 0–10 cm depth for encroached forest was taken from the latter stands, and for abandoned fields from the chronosequence of Zak et al. (1990), corrected for fine-root mass and bulk density associated with changes in C (Bormann et al., 1995). Mineral soil C density of 10–25 cm depth was taken from Homann and Grigal (in press).

To apply the C-density model to fields, a map of original field boundaries from the CCNHA archives (John Tester, personal communication, 1992) was digitized into the GIS. The map identified 99 individual fields, of which 85 had known dates of abandonment. Vegetation type (field or forest) within each original field boundary was determined for 1938 and 1977 by overlaying vegetation maps from the landscape analysis (see above). For each field of known history, C content (mg C) was calculated by multiplying field or encroached forest area by appropriate values from the C-density model. Uncertainties were propagated through calculations by standard formulas (Freese, 1962). Uncertainties of C densities were based on standard errors (Gleeson and Tilman, 1990; Gower and Son, 1992; Homann and Grigal, in press).

3. Results and discussion

3.1. Carbon densities

Carbon density was highest in the tree and organic soil components and lowest in the shrub component (Fig. 1). Total C density across all ecosystem components was highest in the Lowland Conifer vegetation type (205 Mg ha^{-1}) and lowest in the Upland Non-Forest vegetation type (33 Mg ha^{-1}).

The C densities of CCNHA forests are generally similar to those of other forested areas of the Lake States. Pastor and Bockheim (1981) found that total tree C in a northern Wisconsin mixed hardwood

stand was 95 Mg ha^{-1} , similar to that of the tree component at CCNHA. Grigal and Ohmann (1992) estimated C density along a transect through 169 upland forest stands in Minnesota, Wisconsin and Michigan. They found that O horizon C ranged from $10\text{--}20 \text{ Mg ha}^{-1}$, higher than we measured. Mineral soil C (to 25 cm) was between 30 and 50 Mg ha^{-1} , similar to the levels we found at CCNHA. Total tree C was $50\text{--}100 \text{ Mg ha}^{-1}$, also similar to the values at CCNHA. Ohmann and Grigal (1985) determined above-ground biomass of 13 upland forest communities in northern Minnesota. If their estimates are converted to total vegetative C, herb C was $0.5\text{--}1.0 \text{ Mg ha}^{-1}$, somewhat lower than our estimates for CCNHA; total shrub C was $1.2\text{--}3.8 \text{ Mg ha}^{-1}$, somewhat higher than our estimates; and tree C was 57 to 95 Mg ha^{-1} , very similar to the range of values we found at CCNHA. In addition, their *Thuja occidentalis* L. community type yielded C densities similar to those in our Lowland Coniferous vegetation type. Botkin et al. (1993) recently estimated C density for temperate deciduous forests in the eastern US. They reported a mean C density of 36 Mg ha^{-1} in the tree plus shrub component, considerably lower than that at CCNHA and at several other study sites.

Changes in carbon densities of the fields between 1938 and 1977 varied considerably and depended on time of field abandonment and successional trajectories (Fig. 2). For fields that remained cultivated, changes in agronomic practices (Cardwell, 1982) greatly enhanced vegetative C density (Fig. 2). For abandoned fields, vegetative C density increased slowly during herbaceous succession following an initial decrease, and it increased substantially via forest encroachment. Because of the young age of the encroached forest, its C density is less than half that of the mature forest at CCNHA (Fig. 1). The O horizon C density increased moderately during herbaceous succession and substantially from forest encroachment. Surface (0–10 cm depth) mineral soil C initially decreased after field abandonment, then increased during herbaceous succession (Zak et al., 1990) and forest encroachment. Because organic C deeper in the profile is not well-related to recent land-use/vegetation history (Homann and Grigal, in press), mineral soil C density of the 10–25 cm depth was considered constant. The uncertainties of the C densities, based on standard errors, were equivalent

Table 3

Area and C storage in ecosystem components for seven vegetation types at CCNHA in 1938 and 1977. C storage in O Horizon and Mineral Soil to 25 cm depth. Uncertainties were calculated by propagation of standard errors (see text) and are presented for the total area

Year	Vegetation Type	Area (ha)	C storage (Mg)					Total
			Herb	Shrub	Tree	O Horizon	Mineral soil	
1938								
	LC	236	140	26	24 700	23 700	0	48 600
	LD	138	370	79	7 700	13 900	0	22 000
	LNF	423	1020	500	0	42 500	0	44 000
	UC	2	6	0	210	20	62	300
	UDH	458	870	400	43 800	3 900	17 100	66 100
	UDL	38	130	33	3 600	180	1 600	5 500
	UNF	759	1 750	830	0	760	21 600	24 900
	Lowland subtotal	797	1 530	610	32 400	80 100	0	115 000
	Upland subtotal	1 257	2 760	1 260	47 600	4 800	40 400	97 000
	Total	2 054	4 290	1 870	80 000	84 900	40 400	212 000
	(Uncertainty)		(530)	(330)	(15 000)	(6 500)	(1 800)	(15 000)
1977								
	LC	173	100	20	18 100	17 400	0	35 600
	LD	183	490	100	10 200	18 400	0	29 200
	LNF	441	1 060	520	0	44 300	0	45 900
	UC	34	110	10	3 500	400	1 000	5 000
	UDH	488	930	430	46 700	4 100	18 200	70 400
	UDL	124	420	110	11 800	600	5 300	18 200
	UNF	611	1 410	670	0	610	17 400	20 100
	Lowland subtotal	797	1 700	640	28 300	80 100	0	110 000
	Upland subtotal	1 257	2 900	1 200	62 000	5 700	41 900	114 000
	Total	2 054	4 600	1 800	90 300	85 800	41 900	225 000
	(Uncertainty)		(540)	(310)	(14 500)	(6,500)	(2 000)	(16 000)
Net Change								
1938–1977								
	LC	–63	–40	–6	–6 600	–6 300	0	–13 000
	LD	45	120	20	2 500	4 500	0	7 200
	LNF	18	40	20	0	1 800	0	1 900
	UC	32	100	10	3 300	380	900	4 700
	UDH	30	60	30	2 900	200	1 100	4 300
	UDL	86	290	80	8 196	413	3 689	12 664
	UNF	–148	–340	–160	0	–150	–4 200	–4 800
	Lowland subtotal		120	30	–4 000	0	0	–4 000
	Upland subtotal		110	–40	14 400	900	1 500	17 000
	Total		230	–12	10 300	900	1 500	13 000
	(Uncertainty)		(48)	(114)	(3 400)	(2 600)	(400)	(4 300)
Area-weighted C density (Mg ha ⁻¹)								
1938	Lowland	797	1.9	0.8	40.7	100.5	0.0	144.3
	Upland	1 257	2.2	1.0	37.9	3.8	32.1	77.2
	Total	2 054	2.1	0.9	38.9	41.3	19.7	103.2
1977	Lowland	797	2.1	0.8	35.5	100.4	0.0	138.8
	Upland	1 257	2.3	1.0	49.4	4.6	33.4	90.5
	Total	2 054	2.2	0.9	44.0	41.8	20.4	109.5
Net change Lowland								
			0.2	0.0	–5.1	0.0	0.0	–5.0
1938–1977 Upland								
			0.1	0.0	11.5	0.7	1.2	13.5
	Total		0.1	0.0	5.0	0.4	0.7	6.3

Note: Some columns and rows do not sum to total, due to rounding of values.

to 33% of the C density for field vegetation, 56% for forest vegetation, 12% for O horizon, 12% for 0–10 cm mineral soil, and 5% for 10–25 cm mineral soil.

3.2. Change in area

Shifts occurred in the areal distribution of vegetation types between 1938 and 1977 (Table 3). There was a net change of 211 ha from one type to another, equivalent to ca. 10% of the study area. The net increase in upland forests (Upland Coniferous, Upland Deciduous High Density, Upland Deciduous Low Density) was balanced by a decrease in Upland Non-Forest, while the increase in Lowland Deciduous and Lowland Non-Forest was balanced by a decrease in Lowland Conifer. The largest change in area was an decrease of 148 ha in Upland Non-Forest, representing ca. 7% of the study area.

The field analysis encompassed the area occupied by fields of known history and represented one-fifth of the landscape (Table 2). Between 1938 and 1977, this area changed from 96% cultivated fields and 4% recently abandoned fields to 6% cultivated fields, 74% abandoned fields, and 20% forest. The GIS-related uncertainty was equivalent to an average of 2% of field area.

3.3. Carbon storage

Our estimates indicate C storage on 2054 ha of the CCNHA landscape was 225 000 Mg in 1977, an

increase of 6% over that of 1938. The increase in C storage over the 40-year period was due principally to the conversion of Upland Non-Forest to Upland Conifer, Upland Deciduous High Density, and Upland Deciduous Low Density, which have much higher C densities for trees and somewhat higher C densities for O horizon and mineral soil (Fig. 1). This was partially offset by a decrease in C storage in lowland, as Lowland Conifer, with its high tree C density (Fig. 1), shifted to Lowland Deciduous and Lowland Non-Forest. Of the net increase in storage, 80% was in trees and 13% in mineral soil. These are equivalent to a 13% increase in tree C and 4% increase in mineral soil C. For other ecosystem components, uncertainty greatly exceeded calculated net changes, and no change in O horizon, shrubs, and herbs can be assigned. Relative uncertainties for C storage of individual ecosystem components ranged from 5% to 19% of the C storage estimates, and from 20% to nearly 1000% of change in C storage. Absolute uncertainty was lowest in shrubs and highest for trees. Among all ecosystem components, nearly all (85 to 99%) of the uncertainty was related to sample variability, with the remainder due to the uncertainties of biomass equations and GIS processing.

The field analysis indicated an increase in ecosystem C storage of 40% between 1938 and 1977 on 451 ha of the CCNHA landscape, as herbaceous succession and forest encroachment took place in

Table 4
Change in C storage and C densities from 1938 to 1977 in areas occupied by fields of known history in 1938

Year	Vegetation type	Area (ha)	C storage (Mg)			
			Vegetation	O Horizon	Mineral soil	Total
1938	Field = Total	451	940	43	11 500	12 500
	(Uncertainty)		(310)	(5)	(610)	(680)
1977	Field	363	1130	380	9300	10 800
	Encroached forest	88	3480	410	2700	6600
	Total	451	4600	790	12 000	17 400
Change 1938–1977	(Uncertainty)		(2000)	(65)	(560)	(2100)
	Field	–88	190	340	–2200	–1700
	Encroached forest	88	3480	410	2700	6600
	Total	0	3700	750	500	4900
	(Uncertainty)		(2000)	(63)	(260)	(2000)
			Area-weighted C density (Mg ha ⁻¹)			
	Total 1938		2.1	0.1	25.5	27.7
	Total 1977		10.2	1.8	26.6	38.6
	Change 1938–1977		8.2	1.7	1.1	10.9

Note: Some columns and rows do not sum to total, due to rounding of values.

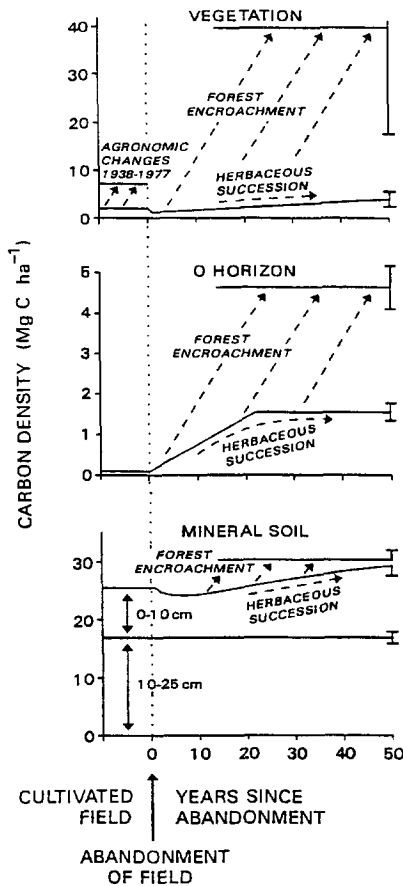


Fig. 2. Model of change in C density following abandonment of agricultural fields at CCNHA. Uncertainty is proportional to values; error bars indicate uncertainty for values at Year 50.

abandoned fields (Table 4). The increase in C storage was principally due to tree C associated with forest encroachment, but C storage also increased in O horizon, mineral soil, and field vegetation. Of the net increase in storage, 71% was in trees, 14% in the O horizon, and 11% in mineral soil. Relative uncertainties of individual ecosystem components ranged from 5% of C storage for mineral soil to 42% for vegetation and 8% to 54% of change in C storage. Among all ecosystem components, 70 to 99% of the uncertainty was related to C densities (Fig. 2), with the remainder associated with GIS processing.

Both the landscape and field analyses indicate an increase in C storage over a 40-year period, largely through the invasion of forest into non-forest area in the uplands. Trees dominate the enhanced C storage, but smaller increases in C are also associated with O

horizon and soil. Refinements in estimates of C storage and its changes could be made for CCNHA by additional measurements and long-term studies that focus on specific assumptions made in our analysis. (i) The landscape analysis assumed that C densities for ecosystem components for each vegetation type are constant over time. Currently we have no direct way to test this assumption for CCNHA. The tree C density for an oak stand at CCNHA was 86 Mg ha⁻¹ in 1959 (Ovington et al., 1963), which is slightly lower than our mean but well within our range of values measured in 1990 (Fig. 1). We have established permanent plots (Grigal and Homann, 1994) to monitor ecosystem function, including C storage, at CCNHA in the future. (ii) The landscape analysis did not account for potential changes in O horizon in lowlands because of lack of relevant data, although accretion or decomposition could increase or decrease C storage in this ecosystem component. (iii) The field analysis used C density for young oak forests from another site. On-site measurements at CCNHA could reduce uncertainty associated with this ecosystem component.

4. Conclusions

We quantified C storage on a complex landscape using a combination of plot data, allometric biomass equations and GIS analysis. Our estimates indicate an increase in C storage of about 6% across the 2224 ha study area. Much of the increase was caused by encroachment of forest onto abandoned agricultural fields. Vegetation (especially trees), O horizon, and mineral soil all contributed to this increase. Uncertainty was due mainly to sample variability, with smaller contributions from biomass estimation equations and GIS processing. In spite of this uncertainty, our study indicates the feasibility of assessing subtle changes in C storage on complex landscapes. This can be important at regional scales and help answer current questions about 'missing carbon' in global C budgets (Detwiler and Hall, 1988).

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