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Global model estimates of carbon and nitrogen storage in litter and soil pools: response to changes in vegetation quality and biomass allocation

By CHRISTOPHER S. POTTER* and STEVEN A. KLOOSTER, *Johnson Controls World Services Inc., NASA Ames Research Center, Mail Stop 242–4, Moffett Field, CA 94035 USA*

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ABSTRACT

Changes in plant production, structure, and tissue composition are primary drivers for terrestrial biogeochemistry under future environmental conditions. Consequently, there is a need for process-oriented assessment of the potential global importance of vegetation controls over extended periods of C and N sequestration in terrestrial ecosystems. In this study, plant litter quality (lignin content) and carbon allocation to woody tissues are used as surrogates for testing the hypothetical effects of vegetation change on C and N cycles. We tested the CASA (Carnegie-Ames-Stanford approach) biosphere model, which uses global gridded (1°) satellite imagery on a monthly time interval to simulate seasonal patterns in net ecosystem carbon balance and near steady-state C/N storage in detritus and soils. Under contemporary "reference" settings, combined organic matter storage (litter plus surface soil to ca. 30 cm depth) for C and N is estimated highest in tropical and boreal forest ecosystem zones, and in cultivated ecosystems. The worldwide C : N ratio (by weight) for standing litter plus surface soil organic matter (SOM) is estimated at 23. About 14% of the projected global pool of 1327 Pg (10^{15} g) soil C resides in "modern" form, in the sense that this proportion is in near-steady state exchange with plant production and decomposition on time scales of several decades. Likewise, about 12% of the projected global pool of 104 Pg soil N is in modern form. Sensitivity tests treated litter quality and allocation effects independently from other direct effects of changes in climate, atmospheric CO_2 levels, and primary production. For forested ecosystems, the model predicts that a hypothetical 50% decrease in litter lignin concentration would result in a long-term net loss of about 10% C from surface litter and soil organic matter pools. A 50% decrease in C allocation to woody tissues would invoke approximately the same net loss of C as a 50% decrease in litter lignin. With respect to nitrogen, the 50% downward adjustment in litter allocation to woody tissues may increase both the estimated net N mineralization rates and SLOW N pool by approximately 9% on a global basis. This pattern is consistent with an overall increase in N available for cycling, which is affected by the fraction of relatively N-poor to N-rich litter inputs. For comparison to the effects of these surrogate changes in vegetation tissue composition, model response to a globally uniform increase in surface air temperature of 1°C is a net loss of 5% C from litter and SOM pools.

1. Introduction

Ecosystem structure is dynamic. Climate and biogeochemical change can alter the composition of plant cover types and shift the dominance of relatively woody and herbaceous forms, with potentially important consequences for the storage of atmospheric carbon and other nutrients in terrestrial ecosystems (Emanuel et al., 1985). For example, loss of woody cover may increase CO_2

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* Corresponding author.

flux to the atmosphere, since within a given latitude zone, forests generally store more carbon in soils than grasslands (Post et al., 1985). In global terms, the amount of carbon in litter and soil pools comprises over two-thirds of total storage in terrestrial ecosystems (Potter et al., 1993; Schimel, 1995). Although much of this carbon is stored in relatively inert forms with residence times of thousands of years, a sizable amount is found in more liable pools that are susceptible to changes in both climate and land cover on the order of years and decades.

A major goal of modeling the terrestrial biosphere is to couple vegetation dynamics and disturbance regimes with biogeochemical cycling processes. There are, however, few (if any), extensively validated regional or global models, or definitive field studies to assess changes in whole ecosystem carbon and nitrogen balance under modified conditions of vegetation, climate, or atmospheric composition. Previous global modeling approaches (Emanuel et al., 1985; Peterson and Melillo, 1985; Prentice and Fung, 1990; Dai and Fung, 1993) have relied heavily on empirical flux relationships, single soil pools, and/or aggregated ecosystem representations, and therefore have not generally included mechanistic controls nor realistic feedbacks to vegetation and soil properties for prediction of terrestrial carbon cycling. Consequently, there is justification for testing surrogate variables for vegetation change effects on ecosystem structure and function through prognostic runs of existing process models. Fractional allocation of biomass and litterfall to woody versus non-woody tissues is one such surrogate factor. Altered leaf lignin content may reflect other species-specific effects on decomposition fluxes (Schimel et al., 1994). For example, Post et al. (1992) reported a strong positive relationship between species that exhibit drought tolerance and the lignin:nitrogen ratio of their respective leaf litter, which suggests important feedbacks between vegetation composition, climate controls on litter decomposition, and soil N availability.

We address two questions in this global modeling study: (1) how sensitive is long-term storage of C and N in litter and soil pools of terrestrial ecosystems to shifts in vegetation litter quality (leaf lignin content) and type (woody versus non-woody), and (2) how does this sensitivity to vegetation litter quality and type compare to the near steady-state effects of a hypothetical climate warming of 1°C over the entire globe? Schimel et al. (1994) presented global model tests to suggest that sensitivity of soil carbon storage is comparable for changes in air temperature and litter lignin content. Our paper expands on those tests in a fully gridded global analysis, using leaf lignin content and carbon allocation to woody tissues as independent surrogate factors for testing the hypothetical effects of vegetation change in simulation experiments with a modified version of the Carnegie-Ames-Stanford (CASA) Biosphere model described by Potter et al. (1993, 1994). CASA is a process-based formulation of coupled ecosystem production and soil carbon-nitrogen fluxes that is driven by gridded global data sets for climate, radiation, soils, and a remotely sensed vegetation index. Short of being truly predictive, the model provides a convenient prognostic framework within which to test the potential importance of surrogate variables for vegetation change effects on ecosystem biogeochemistry over continental areas. Although there may be substantial uncertainty in the possible response(s) of primary drivers (production, growth, and tissue allocation) for ecosystem C and N storage under future environmental conditions, results from our sensitivity analyses serve as a guide for assessment of the potential importance of several vegetation controls over extended periods of C and N sequestration in the terrestrial biosphere.

2. Model description

The CASA-biosphere model (Potter et al., 1993 and 1994) includes interactions of several controls on storage of soil organic matter, trace gas flux, nutrient substrate availability, soil moisture, temperature, soil texture and microbial turnover (Fig. 1). The model runs on a monthly time interval to simulate seasonal patterns in carbon uptake, nutrient allocation, litterfall, soil nitrogen mineralization and CO_2 emissions. The Normalized Difference Vegetation Index (NDVI) from the Advanced Very High Resolution Radiometer (AVHRR) is used to calculate net primary production (NPP) at monthly intervals, based on the concept of light-use efficiency described by Monteith (1972, 1977). The coupled plant produc-

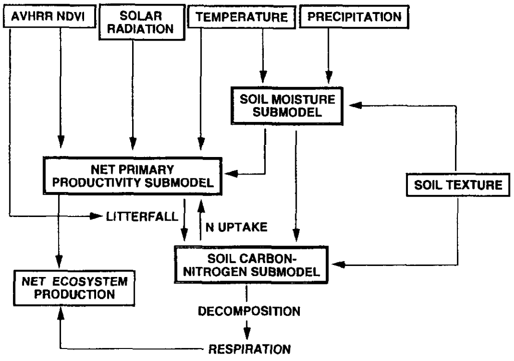

Fig. 1. Framework for input variables and submodel coupling in the CASA-Biosphere model.

tion and soil respiration components of the model are regulated by a common soil moisture submodel. The soil moisture submodel in the original version of the CASA model (Potter et al., 1993) is a one-layer "tipping bucket" formulation that resembles previous simulation models used in regional and global surface hydrology (Mintz and Serafini, 1981; Vörösmarty et al., 1989; Bouwman et al., 1993).

Allocation of available C among plant tissues in forest vegetation types (Fig. 2) is treated as a fixed partitioning ratio of 1:1:1 among leaf, fine roots and wood (Running and Coughlan, 1988). For grasslands, carbon is allocated 1:1 between leaf and root pools. Litter inputs from these tissue allocation pools are transferred each month to the soil according to algorithms that again use the AVHRR-NDVI driver (Potter et al., 1993). Allocation of N among litter pools is calculated so as to first satisfy fixed pool C-to-N ratios of *structural* (slowly decomposing cellulose plus lignin) leaf and fine root (C:N 150) and woody pools (C:N 260); residual N is partitioned equally between *metabolic* (rapidly decomposing cytoplasmic constituents and nucleic acids) leaf and fine root pools.

The soil submodel in CASA (Fig. 2) simulates carbon and nitrogen cycling using a set of compartmental difference equations based on a simplified version of the CENTURY model (Parton et al., 1987, 1988). Carbon and nitrogen fluxes are controlled using series of non-dimensional indices related to air temperature, soil moisture, litter substrate quality (N and lignin contents), and soil texture. Nitrogen transformations are stoichometrically related to C flows. Carbon and nitrogen in soil organic form is represented by two surface storage pools: the SLOW pool, which is thought to contain chiefly chemically protected C and functionally defined as having a C residence time of several decades, and the OLD pool (also called the passive pool in CENTURY; Parton et al., 1987), which is thought to contain mainly physically protected C and functionally defined as having a C residence time of hundreds of years. Fluxes from litter and soil to microbial pools and from microbial pools back to soil pools occur in proportion to C assimilation rates so that prescribed C-to-N ratios for the various recipient organic matter pools are maintained (Parton et al., 1987). Litter decomposition is slower where substrate lignin-to-nitrogen ratio is high. Soil texture controls microbial turnover rates (lower in fine textured soils), and regulates the fraction of carbon lost as CO_2 from soil microbes during transfer to the SLOW pool, which decreases as the soil silt plus clay content increases.

In order to include human-altered land cover, two modifications are made for grid cells identified as cropped agricultural systems, as identified in the NDVI-derived land cover classification of DeFries and Townshend (1994). First, plant residue lignin concentrations are set at 5% and the minimum C:N ratio of litter is 15. Second, turnover rates of soil microbial and organic carbon (SLOW and OLD) pools (Fig. 2) are increased by 25% and 50%, respectively to account for potential effects of tillage (Tisdale and Oades, 1982; Parton et al., 1987). For this model version, we assumed that 100% of crop residue is returned to the soil annually with no losses of litter carbon due to harvesting. Future model tests will include irrigation effects and nitrogen fertilizer amendments.

We have made several adjustments in the CASA model version described by Potter et al. (1993) to improve calculations of soil C cycling and total ecosystem N availability in relation to plant uptake demand. First, we set constant lignin and nitrogen contents for non-woody litterfall by ecosystem type (Fig. 3), using values for new plant production reported by McGuire et al. (1992). In addition, the SLOW soil organic pool was uniformly initialized at zero, whereas in the original version of the model (Potter et al., 1993), a constant fraction (30%) of the soil C content

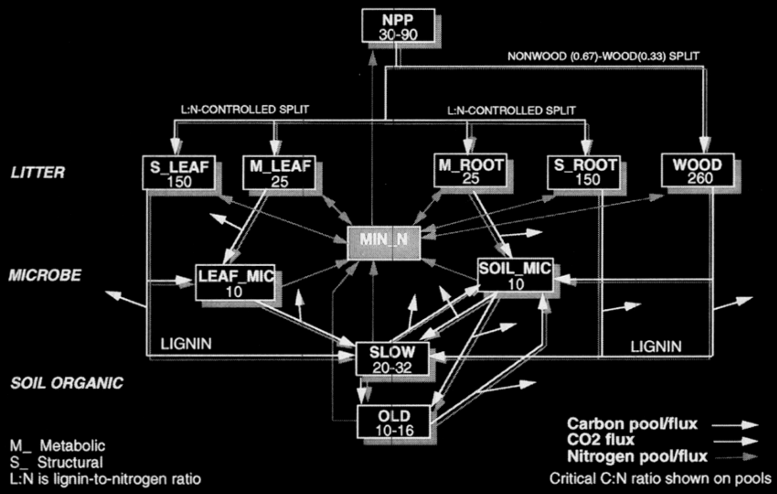

Fig. 2. Litter and soil C and N transformations which lead to substrates for trace gas production. Carbon pools are outlined in black and labeled with C-to-N ratios, C fluxes in solid arrows, CO_2 production in stippled arrows; Nitrogen pools in gray, N fluxes in gray arrows. NPP is split between woody and non-woody litter fractions. Litter, microbe (MIC) and soil organic (SLOW and OLD) pools make up the non-plant storage of ecosystem C and N. Structural (S) and metabolic (M) pools are shown for leaf and root litter.

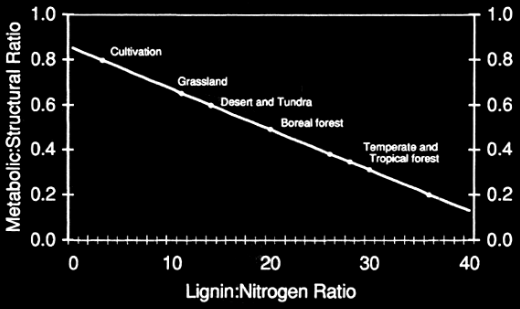

Fig. 3. Settings by ecosystem type for the split between structural and metabolic constituents as a function of lignin:nitrogen ratio of non-woody litterfall.

reported by Post et al. (1985) was used to intialize. The SLOW pool was also assigned a minimum C-to-N ratio between 20 and 32 (depending on soil texture of fine to coarse) for transfer of N from litter and microbial pools. Hence, it is assumed that the SLOW pool C-to-N ratio can be considerably higher than the microbial pool and is not equal to total soil organic matter, which is more consistent with experimental findings (Hadas et al., 1992). The sensitivity of litter decomposition to temperature was set at a revised Q_{10} value of 1.5 to reflect the use of air temperature data rather than direct estimation of soil temperature (Raich and Potter, 1995).

A model version adjusted to these reference settings was applied using global data inputs at over 14000 non-ice terrestrial grid cells. Monthly drivers for climate, radiation, and net primary production (NPP) reflect average contemporary conditions. The global total for annual NPP in the reference case is 48 Pg C (where $Pg = 10^{15}$ g). Reference settings for leaf litter lignin content were 20% and 10% lignin for forest and grassland litter, respectively. For input settings of litterfall pools, one-third of annual NPP was allocated to each litterfall flux of leaf, fine root, and woody tissues in forests; 50% to both leaf and fine root litterfall fluxes in grasslands. For all simulations, the model was run for 300 years to reach near-steady state conditions for litter and SLOW soil pools. Results were aggregated by ecosystem types (Leemans, 1990) for global level analysis.

3. Modeling results and discussion

3.1. *Contemporary reference case*

Under the reference settings described above, the combined organic matter storage including all litter and microbial pools together with the SLOW pool (as shown in Fig. 2), abbreviated henceforth as LMS, is estimated highest for both C and N in tropical and boreal forest ecosystem zones (Table 1), along with the zone broadly defined as *cultivation* . This cultivated class is adopted from the system of Dorman and Sellers (1989); it covers many areas that are not intensively cropped and therefore includes some grid cells with a woody vegetation component. The global totals (286 Pg C and 12.6 Pg N) estimated for LMS storage are 30–50% lower than those estimated using the model version described by Potter et al. (1993 and 1994). Adjustments of pool C:N ratios and initialization of the SLOW pool at zero (as described above) are responsible for these revised projections of total LMS storage of carbon and nitrogen.

On a world-wide basis, the estimated SLOW pool contains 65% of total LMS storage of C and 96% of the total LMS storage of N, a pattern that is consistent with previous studies that show surface soil layers as an important component for carbon storage, but is by far the major ecosystem storage reservoir for nitrogen (Soderlund and Rosswall, 1982). Estimated storage in the SLOW pool averages 1.5 kg C m^{-2} and 79 g N m^{-2} in boreal forests, 0.7 kg C m^{-2} and 39 g N m^{-2} in temperate grasslands, 2.0 kg C m^{-2} and 133 g N m^{-2} in temperate deciduous forests, and 3.4 kg C m^{-2} and 242 g N m^{-2} in tropical evergreen forests. On a global basis, the estimated C:N ratios for the various pools are: 148 for non-woody litter, 338 for woody litter, and 15 for SLOW, which result in a composite C:N value of approximately 23 for LMS storage worldwide

Table 1. *Carbon and nitrogen storage in litter and soil pools of global ecosystem classes (Pg (10^{15} g))*

Ecosystem class[a]	Land area (10^6 km^2)	Non-wood[b] C	N	Wood C	N	Slow C	N	Total C	N	C:N ratio
tundra	6.7	3.95	0.036	2.01	0.005	5.25	0.271	11.21	0.312	36
forest tundra	8.2	2.45	0.006	3.36	0.009	9.85	0.515	15.66	0.531	30
boreal forest	17.4	5.80	0.023	7.79	0.023	23.75	1.289	37.34	1.335	28
cool desert	3.7	0.68	0.000	0.39	0.001	0.82	0.050	1.89	0.051	37
hot desert	21.0	1.11	0.001	1.42	0.001	4.11	0.223	6.64	0.225	29
temperate grassland	7.5	0.60	0.004	0.00	0.000	2.36	0.142	3.25	0.147	22
cultivation	14.7	8.32	0.067	7.75	0.023	32.28	2.198	48.35	2.289	21
chaparral	5.3	0.57	0.004	0.53	0.002	2.39	0.157	3.48	0.163	21
cool temperate forest	10.3	2.54	0.017	3.12	0.010	10.73	0.673	16.39	0.699	23
warm temperate forest	3.0	0.72	0.005	0.92	0.003	3.35	0.315	4.99	0.323	15
tropical semi-arid steppe	9.6	1.40	0.008	1.01	0.002	5.68	0.393	8.09	0.402	20
tropical savanna	14.5	4.96	0.040	6.59	0.020	23.18	1.731	34.72	1.791	19
tropical seasonal forest	15.0	6.96	0.051	10.86	0.034	35.24	2.334	53.06	2.419	22
tropical rain forest	10.8	5.46	0.044	8.41	0.027	27.61	1.889	41.49	1.960	21
total		45.51	0.307	54.15	0.160	186.60	12.178	286.26	12.616	
C:N ratio		148		338		15		23		

[a] Based on global map distributions provided by Leemans (1990), with addition of the cultivation class from Dorman and Sellers (1989).

[b] Litter and soil microbial pools are included.

(Table 1). Differences in C:N ratio of total LMS among ecosystem classes result from the combined effects of litter quality settings and soil texture (e.g., higher C:N ratio in more sandy soils).

For comparison of CASA model results to total below-ground storage of C and N, we independently generated global maps for total C and N content to 1 m soil depth by assigning average measured values ($\mathrm{g\,m^{-3}}$) from Post et al. (1985) to ecosystem classes in the global data set produced by Leemans (1990). The data were interpolated from 0.5° to 1° latitude/longitude grid cell resolution using a bi-directional splining procedure, preceded by nearest-neighbor fill to conserve land/water boundary elements. These "total storage" maps were assumed to accurately represent the aggregate accumulation of C and N in surface profiles over centuries of soil development. This "total storage" derivation is completely independent from CASA model results. Comparison of estimated SLOW pool sizes from the model to total storage maps derived from Post et al. (1985) would therefore provide an index of the proportion of total soil C and N that is "modern", i.e. defined as the amount in near-steady state exchange with plant production and decomposition on time scales of several decades. While most modern SOM is generally found to reside in surface soil layers (Schimel et al., 1994), the SLOW pool does not necessarily exclude SOM below 20–30 cm depth and therefore the comparison to total C and N stocks is a valid one for initial assessments.

The size of the global SLOW C pool (187 Pg C) is equivalent to about 14% (Fig. 4a) of the global pool of 1327 Pg soil C that was computed from the data set of Post et al. (1985) . Likewise, the global SLOW N pool of about 12 Pg (Fig. 4b) is equivalent to about 12% of the total global storage of 104 Pg N. There are notable differences in the relative size of the modern fraction among ecosystem classes. In tropical zones, 25–45% of both total soil C and N is typically in the modern state. In contrast, higher latitude forests appear to contain a greater percentage of total soil C and N in the more inert state (i.e., not cycling actively among plant-soil-atmosphere pools). Over temperate and boreal forest zones, our comparison suggests that only 5–20% of both total C and N stored to 1 m soil depth is typically in the modern state. Model results suggest that nearly 60% of the carbon and 50% of the nitrogen contained in the total global pool of inert soil organic matter are stored in ecosystems located north of 30 latitude.

Our analysis also shows that the mean residence time (MRT, defined as the pool size divided by the annual loss rate by decomposition fluxes) of carbon in the various litter and soil pools decreases exponentially as a function of latitude zone change from the poles to the equator (Fig. 5). MRT of the SLOW C pool approaches 30 years at the highest northern latitudes; in the zone between about 12°N to 20°S, MRT for carbon in this pool is estimated to be less than 10 years. Together with seasonal CO_2 fluxes from terrestrial ecosystems, these spatially resolved estimates on MRT of carbon in the various litter and soil pools can be useful additions to models of atmospheric transport that include $\delta^{13}C$ deconvolution for partitioning sources and sinks of CO_2 among ocean and terrestrial components (Ciais et al., 1995).

3.2. *Evaluation of litterfall settings*

Because of the inherent mismatch in scales between the model grid resolution of about 100 km and measurements of litter pool sizes, most of which are made over one to several square meter areas, validation for the model estimates of litter pool storage is difficult to achieve. Moreover, the net storage in litter and soil pools is a function of both input rate (litterfall) and decomposition rate, which means that comparison of estimated and observed litterfall rates alone cannot provide a complete evaluation of the model predictions for LMS storage of carbon. There are, nevertheless, a select number of synthesis studies for standing litter and annual litterfall in ecosystems distributed world-wide that are useful for comparison to model results in an effort to uncover systematic discrepancies.

Comparison of C storage estimates from reference model settings to measurements of leaf litter pools compiled by Vogt et al. (1986) for selected forest ecosystems suggests that the model underestimates C litter storage on the forest floor in boreal and certain temperate ecosystems (Table 2). This pattern is supported by comparison of observed and predicted estimates for annual leaf litterfall. Measured values of litterfall compiled by Vogt et al. (1986) are consistently higher across

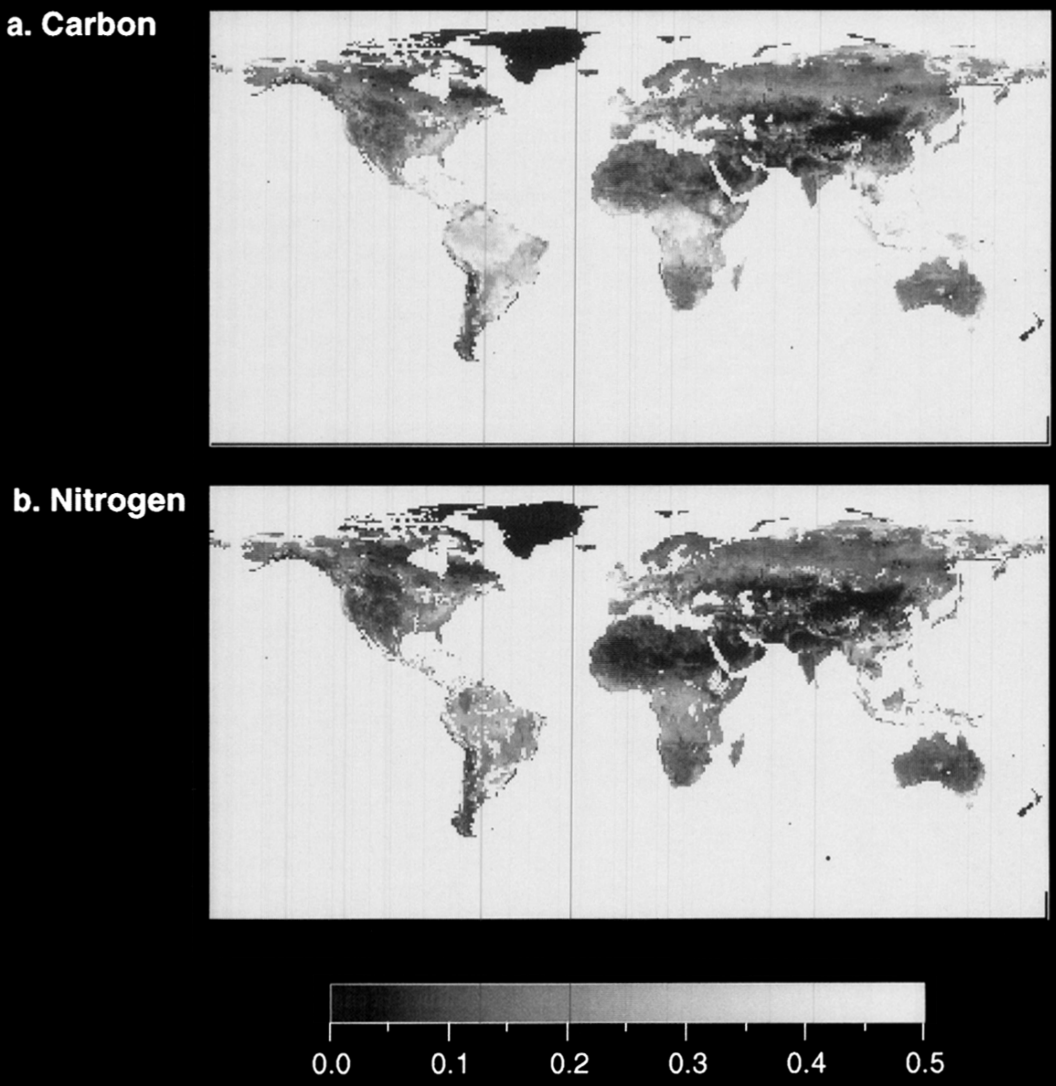

Fig. 4. Proportional size of SLOW C and N pools from CASA reference case settings in comparison to estimated total storage in soils to 1 m depth.

all ecosystem classes than those projected according to reference settings of the model. In addition, woody litterfall rates reported by Vogt et al. (1986) are consistently lower across all ecosystem classes than the model's leaf-equivalent rates for woody litterfall under reference settings. However, leaf litterfall rates derived from the regression analysis of Meentemeyer et al. (1982) match closely with reference model estimates for mean ecosystem fluxes. Although these comparisons are not conclusive, it appears that use of a greater fractional allocation of annual NPP to non-woody litterfall in subsequent model runs could be supported by the available field data sets.

Whereas the generalized CENTURY model design, upon which our computations of litter stocks are based, treats dead leaf material as a combination of structural and metabolic fractions with different turnover times, standing litter pool estimates from the literature are based on whole

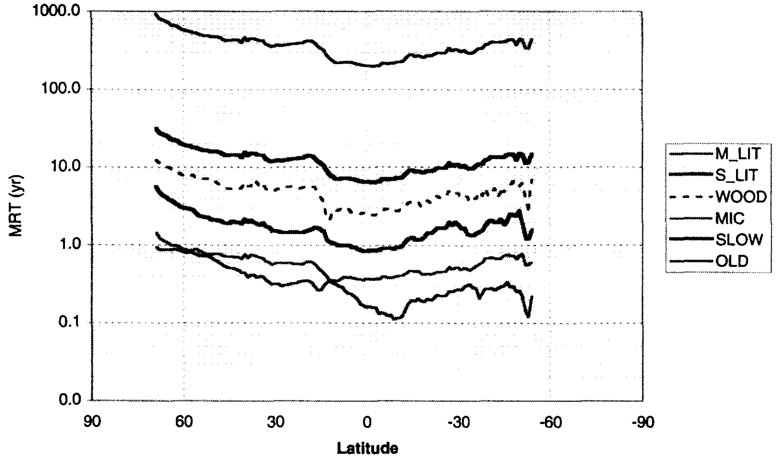

Fig. 5. Mean residence time (MRT) of carbon in litter, microbial, and soil organic pools estimated with CASA reference case settings. Latitude labeling is north as positive and south as negative.

leaf mass with no discrimination among biochemical components. Evaluation of discrepancies in reference model estimates to field measurements of leaf litter pools is further complicated, therefore, by uncertainties associated with the global applicability of both the CENTURY algorithm for lignin : nitrogen (L : N) ratio control over the structural-to-metabolic split in non-woody litter (Parton et al., 1987), and static ecosystem settings for L : N content of litter (Fig. 3). There is a need to further validate this generalized linear relationship, particularly at relatively high L : N levels.

3.3. Sensitivity tests

3.3.1. Test 1. Litter quality and tissue type. Model runs were designed to test the sensitivity of projected storage of C and N in litter and soil pools to changes in vegetation litter quality (leaf lignin content) and type (woody versus non-woody). In separate simulation runs to near-steady state, settings for non-woody litter lignin content and allocation to woody tissues (relative to non-woody tissues) were adjusted up or down, each by 50%, for comparison to results from our reference case settings for these same variables. These tests were aimed mainly at evaluation of sensitivity to internal model settings. Although there may be a wide range (ca. 15–60%) in structural (lignin + cellulose) content for a variety of grassland, forest, and crop leaf litters, our choice of ±50% of reference settings applied globally should not be interpreted as predictive of the magnitude of changes in litter quality or type under any specific cause of altered environmental conditions.

As an example of model response, 50% adjustment downward of either settings for non-woody litter lignin and allocation to woody tissues leads to a decrease in total LMS storage (equivalent to 25–28 Pg C, world-wide) of about 10% LMS-C for most ecosystem types, compared the reference case level (Fig. 6a). Adjustment upward of 50% in either of these variable settings shows the same magnitude of change in the opposite direction (i.e., increase in total LMS storage of about 10% C). The model response is different, however, between the two variable adjustments in that alteration up or down of litter lignin content does not change the proportions of total LMS storage of carbon among non-woody, woody, and SLOW pools (compared the reference case), whereas the decrease in litter allocation to woody tissues results in a substantial shift in LMS storage percentage among the three C pools. Furthermore, under conditions of altered lignin content (either up or down), absolute changes in C storage are greatest for the SLOW pool, whereas under altered woody litter allocation, the SLOW pool size is practically unchanged from reference levels. There is little difference among ecosystem classes with

Table 2. *Comparison of measured leaf litter pools and litterfall fluxes to reference model estimates*

Ecosystem class	Leaf litter mass ($g\ C\ m^{-2}$)		Leaf litterfall ($g\ C\ m^{-2}\ yr^{-1}$)			Woody litterfall ($g\ C\ m^{-2}\ yr^{-1}$)
	measured[a]	predicted CASA	measured[a]	predicted[b] regression	predicted CASA	measured[a]
tundra	NA	382	NA	33	24	NA
boreal forest	2235	682	121	66	65	50
high latitude deciduous forest	695	772	180	58	68	NA
temperate grassland	NA	102	NA	87	55	—
cropped	NA	112	NA	151	113	—
temperate mixed forest	2228	953	157	137	137	30
temperate deciduous forest	574	838	212	177	154	45
savanna and wooded grassland	440	955	472	247	224	NA
tropical evergreen forest	1128	1300	468	348	370	311

[a] Average forest ecosystem values from Vogt et al. (1986), who defined woody litterfall as greater than 1 cm diameter. Reported mass values were multiplied by 0.5 to adjust for carbon content (Schlesinger, 1977).

[b] Litterfall based on regression analysis of Meentemeyer et al. (1982) using actual evapotranspiration as the independent variable; for leaf litter measured at 53 data sites worldwide. Predicted mass values were multiplied by 0.5 to adjust for carbon content (Schlesinger, 1977).

NA: data not available.

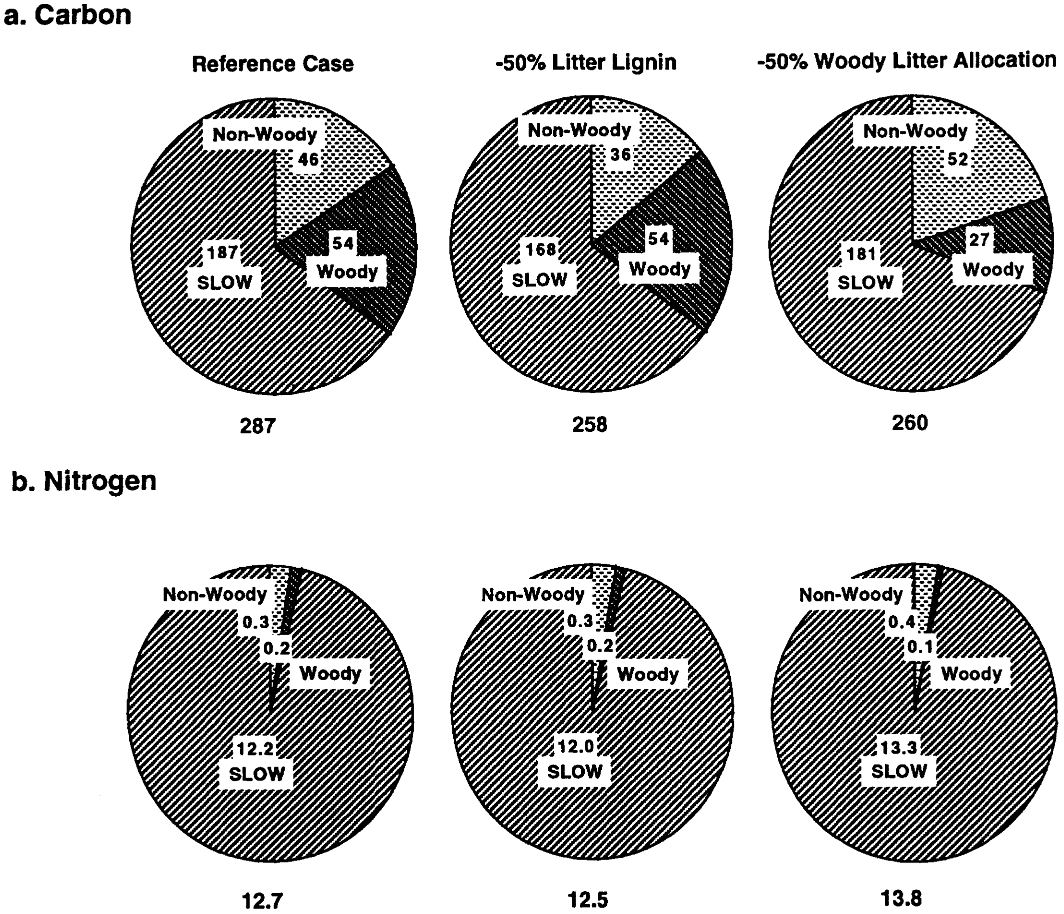

Fig. 6. Changes in global litter and soil C/N storage in response to shifts in CASA litter quality and tissue type settings. Units for all number labels are Pg C or N, total storage amount shown under each.

respect to the estimated magnitude of change in LMS storage of C in response to altered lignin content (specific data not shown). Differences among ecosystem classes are more notable in response to adjustment in allocation of NPP to woody litter tissues, with slightly greater than 10% change from reference LMS storage of C for hot desert, tropical forest, and boreal forest zones, and slightly less than 10% change from reference LMS storage of C for cool desert, tundra, and temperate forest zones.

Whereas changes in estimated LMS storage of C are substantial with respect to altered litter quality and type, estimated response of LMS storage of N to these same sensitivity settings reflects the closed formulation of the model regarding N cycling among ecosystem pools. Owing both to lack of process-based data inputs and issues of scale, neither biological N fixation, atmospheric inputs, nor leaching of N in soils is included in the closed *CASA-biosphere* scheme. Therefore, the potential effects of these sensitivity tests on N cycling is to demonstrate either: (1) a redistribution of N among the various litter, soil, and mineral pools, or (2) in the case of changes in allocation to woody tissues, alteration in the percentage of relatively N-poor to N-rich litter supplied to soil microbes. Moreover, because over 90% of total LMS storage of N is in the SLOW pool (as shown previously in Fig. 4b), changes in litter quality and type do not manifest themselves as quickly as they do for carbon cycles.

In the case of altered litter lignin settings, the global SLOW N pool changes little (less than 2%) from the reference case level (Fig. 6b), although total N storage in non-woody litter pools decreases by 10 to 50% for tundra, boreal forest, and other cool temperate zone ecosystems. This redistribution pattern is consistent with a closed N cycle formulation. The 50% downward adjustment in litter allocation to woody tissues, however, has a more conspicuous effect on LMS storage of N; i.e., both net N mineralization rates and SLOW N content are increased by approximately 9% on a global basis. This pattern is consistent with an overall increase in N available for cycling that is generated through alteration in the fractions of relatively N-poor to N-rich litter. On a global basis, this elevated level of available mineral N could support a 2–6 Pg C increase in annual NPP, under the unverified assumptions that new production occurs with a C:N ratio (by weight) ranging from 30 to 90 (McGuire et al., 1992), and that plants are able to capture and retain all the additional mineralized N. The increased N mineralization effect under hypothetical conditions of lower woody litter is most notable (at between 10–15% increase) in tropical and warm temperate ecosystem zones. Model response also suggests that increased net N mineralization rates could be particularly important in forest tundra zones. Feedback effects of N on plant production potential in those areas should be the topic of further modeling experiments. It is worth noting, nevertheless, that increased rates of ecosystem N cycling could lead to greater N losses due to leaching and N trace gas emission, which might limit the potential for long-term system C storage (Davidson, 1995).

3.3.2. Test 2. Climate warming To further observe model response between surrogates for vegetation cover and changes in climate, we conducted sensitivity analysis of relationships between predicted LMS storage of C/N and a hypothetical change in surface air temperature (ΔT). In an additional model run to near-steady state, we increased average reference values for monthly air temperature (Leemans and Cramer, 1990) everywhere by 1°C. Although climate models may predict greater or lesser degrees of warming under conditions of increased greenhouse gas concentrations, our main objective was to determine the derivative of near-steady state LMS storage with respect to T as a standard for comparison to other soil carbon models (those of Jenkinson et al., 1991; Friedlingstein, 1992; Melillo et al., 1993; and others reviewed by Schimel et al., 1994). We note that short-term (year-to-year) changes in response to variable climate conditions cannot be evaluated with this type of steady state response design; nor have we considered the potential feedback effects of enhanced N mineralization on NPP under warmer transient conditions.

Under a hypothetical global warming scenario of $\Delta T_{(+1)}$, the annual NPP driver for CASA decreases by less than 1 Pg C. This suggests that any major deviations in LMS storage of C from the reference case levels in this test would be due almost entirely to estimated warming effects on soil decomposition and mineralization fluxes. We find that a global setting of $\Delta T_{(+1)}$ leads to a decrease in total LMS storage equivalent to 13 Pg C world-wide, which represents about 5% change in LMS storage of C over most ecosystem classes, measured against the reference case level (Table 3). Ecosystems most strongly contributing to the net transfer of C from land to atmosphere under this warming scenario are those that cover relatively vast regions and contain the largest pools of modern LMS for carbon, namely boreal forests, cultivated areas, and tropical forests. Country-by-country comparison suggests that the greatest C losses in LMS under conditions of $\Delta T_{(+1)}$ are estimated from land masses of the former Soviet Union and Brazil, followed by the United States, Canada, and China. As expected in the closed system formulation, changes in LMS storage of N and mineralization are minor under the near steady-state conditions of $\Delta T_{(+1)}$. Consequently, feedback effects of higher N availability on potential plant production are also lacking in the model $\Delta T_{(+1)}$ response.

A comparsion of various model $\Delta T_{(+1)}$ responses for soil C storage was presented by Schimel et al. (1994), ranging from -11 Pg C to -34 Pg C. Results from the original version of CASA (Potter et al., 1993) were reported at twice the level of reduction (-27 Pg C) in total LMS storage as we report with our revised version. It appears that lower model sensitivity to warmer temperature is explained chiefly by initialization

Table 3. *Change in total carbon storage of litter and soil pools under conditions of hypothetical climate warming*

Ecosystem class[a]			Country[b]		
	Pg C	(%)		Pg C	(%)
tundra	1.5	13	former USSR	1.4	3
forest tundra	0.7	4	Brazil	1.3	3
boreal forest	1.3	4	USA	0.8	4
cool desert	0.1	7	Canada	0.6	3
hot desert	0.2	3	China	0.5	3
temperate grassland	0.1	4	Indonesia	0.5	5
cultivation	2.3	5	Zaire	0.4	3
chaparral	0.2	5	Argentina	0.3	4
cool temperate forest	0.6	4	Australia	0.3	3
warm temperate forest	0.3	6	Burma	0.3	9
tropical semi-arid steppe	0.1	2	Bolivia	0.2	4
tropical savanna	1.2	4	Columbia	0.2	5
tropical seasonal forest	2.3	4	India	0.2	5
tropical rain forest	2.2	5	All others	6.2	5

Units are in Pg C (10^{15} g) lost and % decrease, compared to reference case settings.

[a] Based on global map distributions provided by Leemans (1990), with addition of the cultivation class from Dorman and Sellers (1989).

[b] Boundaries in 1° country map provided by Lerner et al. (1988).

of the SLOW pool at zero (as described in Section 2 above), which now allows the model to converge unambiguously on a steady-state between annual NPP and LMS storage of "modern" carbon. Initial conditions therefore influence model response to a ΔT test, and should be accounted for in any subsequent comparsions of model $\Delta T_{(+1)}$ responses in soil C storage.

4. Remarks on coupled modeling of vegetation change and global biogeochemistry

Improved model prediction for biogeochemical consequences of altered ecosystem distribution and structure is a high priority in climate change research (Melillo et al., 1995). There are, nonetheless, many fundamental uncertainties in our ability to predict the possible shifts in natural vegetation structure due to interactions of changing climate and atmospheric trace gas concentrations. Several ecological modeling approaches have been developed to address these issues, including those by Emanuel et al. (1985), Woodward (1987), Overpeck et al. (1990), Stephenson (1990), Neilson et al. (1992), Solomon and Bartlein (1992), Prentice et al. (1992), Neilson (1996), and Woodward et al. (1995). None of these models were designed, nor have they been sufficiently modified, to expressly account for the transient effects of natural and human-driven disturbance on plant succession, change in ecosystem structure, and carbon cycling at global levels.

As general strategies for progress are advanced, we anticipate that the dynamic linkage of biogeochemical cycling and vegetation disturbance formulations will involve (1) more mechanistic connections between production, growth, tissue allocation, litter quality, and nutrient availability feedbacks, and (2) better understanding about the scale dependency of these potential connections. Results from our present study of global soil C/N storage highlight a number of unresolved questions concerning the coupling of vegetation change and global biogeochemical cycles; these issues are difficult to resolve using the current generation of global models and data sets generated in localized field experiments.

4.1. *As climate changes, how will ecosystem biogeochemistry be affected during relatively rapid transition from one type of plant cover type to another?*

The fossil pollen record demonstrates vegetation response to climate change as individual taxa. Consequently, the next generation of global models will be based on more mechanistic understanding of environmental tolerances of different plant forms (Prentice et al., 1992; Neilson, 1996). Constraints such as number of growing degree days and annual moisture deficits can produce reasonable biome distributions compared to present vegetation maps, although questions remain as to whether the assumptions underlying model applications (Leemans and van den Born, 1994) are valid under conditions of relatively fast (one to several decade) changes in ecosystem boundaries that could occur in the near future. For example, we cannot assume with much certainty that a dominance hierarchy implicit in certain existing models will be maintained through any projected shift from one forest type to another, or whether an intermediate, largely herbaceous ecosystem will possibly form for several years as a transient stage. Our CASA simulation results imply that carbon storage in soils would be overestimated if low-wood intermediate stages were ignored, although the CASA model is, like many ecosystem distribution models, designed to predict steady state patterns over several decades rather than short-term changes. Nevertheless, our general observations are consistent with the potential for a "CO_2 spike" resulting from transient, relatively low carbon, vegetation types (King and Neilson, 1992; Smith and Shugart; 1993).

One hypothesis to account for effects of altered plant cover on LMS storage of C is that increased structural (lignin) content of leaf litter and/or lower carbon allocation to woody tissues may develop as a consequence of increased environmental stress, particularly changes in seasonal moisture deficit or supply. Research in plant biogeography (Stephenson, 1990; Lauenroth et al., 1993) and a few experimental studies (Post et al., 1992) lend some support to this theory. Nevertheless, complex reproductive and community-level interactions among plant forms are conceivable under warming conditions (Harte and Shaw, 1995). Moreover, evidence from studies of continental climate-forest distributions suggest that moisture deficits may not be the most important factor in determining dominance of coniferous over deciduous species (Stephenson, 1990); length of growing season must also be considered a significant factor (Arris and Eagleson, 1994). If so, changes in litter quality and tissue allocation within a vegetation type (as defined by subtle shifts in leaf form or longevity) could be as important as those among cover types. Algorithms that relate litter quality to C storage must therefore be well supported by field measurements in the next generation of ecosystem production models.

It is important to note that changes in litter quality could be accompanied by significant changes in litter amount; the latter in turn is a function of NPP and ultimately, climate (Solomon and Bartlein, 1992; Field et al., 1996). In a model like CASA, long-term storage of carbon in the SLOW pool is directly proportional to annual litter amount at an approximate rate of 3 g C m^{-2} increase per additional 1 g C m^{-2} in annual NPP ($r^2 = 0.83$; specific data not shown). Any environmental factor or combination of factors (e.g. climate, pollution, pests, pathogens, human management) that reduce ecosystem production will have a significant long-term effect on storage of carbon in terrestrial biomes. It has been suggested, for example, that rapid climate change brought on by elevated CO_2 and other trace gases could increase tree mortality and speed forest decline, further increasing fire fuels and biomass burning losses from ecosystems (Overpeck et al., 1990). Furthermore, high fire frequency associated with drought has been shown to restrict regrowth of woody plant forms (Simms, 1988).

4.2. *Will elevated CO_2 in the atmosphere affect the long-term partitioning of biomass between leaves, roots and woody tissues with feedbacks on decomposition and storage of soil organic matter?*

Increased below-ground allocation of fixed carbon under conditions of elevated CO_2 has been observed (Norby et al., 1992; Rogers et al., 1994), but it is not known how this response is restricted under certain ecosystem conditions. Although many mechanisms and resource interactions are not well understood, several lines of experimental evidence suggest that ecosystem production response to increasing atmospheric CO_2 concentrations is greatest in areas where nutrients are not severely limiting to photosynthesis (Bazzaz, 1990 and Rogers et al., 1994). Potential areas of high N availability are fertilized agricultural systems (Matthews, 1994) and moist forest zones. An alternate hypothesis is that production response to elevated CO_2 is greatest where moisture stress is relatively high, owing to increased water use efficiency (WUE) during periodic water shortage (Morrison and Gifford, 1984; Allen, 1989). One of the main unresolved theoretical issues in this area is whether plant production, growth, allocation, and acclimation functions that have been measured at the leaf level under controlled laboratory conditions of elevated CO_2 can be scaled up through plant level processes of dynamic allocation to different tissues and stand level attributes of competition for resources and succession.

Assuming however that increased below-ground allocation becomes a prevalent response to elevated CO_2, the implications of increased carbon allocation to more labile fine root tissues over more recalcitrant woody tissues would be to increase decomposition and accelerate ecosystem nutrient cycles. As demonstrated in our model sensitivity results, soil and litter carbon storage would decline under these conditions, although long-term responses to altered nutrient availability and uptake feedbacks cannot be ignored in model designs and predictions. For example, if root N content and transport to stems decreases while carbon allocation from photosynthate increases, enhancement effects on decomposition could be neutralized. Advanced model designs should also include potential changes in biological N fixation under elevated CO_2.

4.3. What is the nature of inert soil carbon and could it become more active with warming in areas that are now relatively unproductive because of cold temperature effects?

A definitive answer to this question will depend upon more complete understanding of the chemical nature of relatively passive C and N pools in the soil (Trumbore, 1993), and how stabilization/decomposition controls change with soil depth or plant rooting patterns. If stabilization processes and resistance to microbial breakdown of organic matter with long residence time is chiefly due to biochemical composition rather than to physical protection from degradation, then both shifts in litter quality and warmer temperatures could further activate decomposition. If instead passive organic matter is chiefly protected from decomposition by characteristics of the mineral soil such as texture, drainage, acidity, or redox conditions, then the combined effects of climate, natural fire regime, and human-driven land cover change and soil management (Cambardella and Elliot, 1992) will more likely drive any major changes belowground environment for C storage. More definitive assessments await mechanistic model couplings between climate, net primary production, tissue allocation, litter quality, and nutrient availability feedbacks over scales from local to global.

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