Tellus (1999), 51B, 336–342
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TELLUS
ISSN 0280–6495

KEYNOTE PERSPECTIVE

Current perspectives on the terrestrial carbon cycle

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(Manuscript in final form 25 November 1998)

ABSTRACT

Over the last 5 or so years, there have been significant advances in the understanding of the current rôle of the terrestrial biosphere in the global carbon cycle, especially in terms of how pools and fluxes are affected by variations in climate (including interannual variability as well as longer-term climate change), increases in atmospheric CO_2 concentrations and changed rates of atmospheric nitrogen deposition. At the same time, significant advances have been made in terms of both direct measurement of ecosystem productivity and in an understanding of the key underlying mechanisms modulating carbon fluxes from terrestrial systems. A brief synopsis of these advances is the subject of this paper.

1. Background

It has long been known that the rate of increase in atmospheric CO_2 concentrations is less than than expected on the basis of estimated rates of anthropogenic emissions (including land-use change) and simulations of oceanic carbon uptake, the so-called "missing sink" problem (Broecker et al., 1979). However, prior to about 1992, that the terrestrial biosphere constituted a major component of this "missing sink", was still a matter of debate. For example, the first Intergovernmental Panel on Climate Change (IPCC) Scientific Assessment simply concluded that there was an unidentified net imbalance in the global carbon budget of 0.13 ± 0.11 Pmol C yr^{-1}, considering the existence of a terrestrial sink to be just one of several possibilities (Watson et al., 1990). However, by 1994, that view had already changed considerably with Schimel et al. (1995) even going as far as to provide specific estimates for net CO_2 uptake for the terrestrial biosphere due to forest regrowth (0.04 ± 0.04 Pmol C yr^{-1}), CO_2 fertilisation (0.04–0.17 Pmol C yr^{-1}), nitrogen deposition (0.02–0.08 Pmol C yr^{-1}) and climatic effects (0.0 ± 0.08 Pmol C yr^{-1}). This changed perspective, especially in terms of a greater confidence of the rôle of the terrestrial biosphere as a contemporaneous sink for atmospheric CO_2, has arisen from several sources. These are now considered.

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2. The atmospheric signal

Estimates of rates of fossil fuel emissions and measurements of spatial variations in the concentrations and isotopic abundances of atmospheric CO_2 have allowed specific inferences on the locations of terrestrial sinks to be made (Ciais et al., 1995; Enting et al., 1995). This information has also been complemented by similar inferences from global inversions in measured atmospheric O_2/N_2 ratios (Keeling et al. 1996). In addition to these studies, strong evidence for a terrestrial carbon sink has been inferred from an interpretation of long-term trends in atmospheric $\delta^{13}C$ (Francey

et al., 1995). Most recently, Rayner et al. (1999) have utilised long-term trends in $\delta^{13}C$ and O_2/N_2 ratios at Cape Grim in Tasmania with global observations of the temporal and spatial structure of atmospheric CO_2 concentrations, to infer the space–time structure of net surface fluxes of CO_2 over the period 1980–1995. As for the previous studies mentioned, once CO_2 emissions from changing land-use are considered, a significant terrestrial sink for CO_2 (but in this case with considerable interannual variation) is clearly inferred.

3. Simulations of the responses of terrestrial carbon fluxes to increases in atmospheric CO_2 concentrations

Over the last few years, several models simulating how fluxes into and out of the terrestrial biosphere should be changing in response to increases in atmospheric CO_2 concentrations have been constructed (Goudriann, 1992; Taylor and Lloyd, 1992; Polglase and Wang, 1992; Gifford, 1994; Friedlingstein et al., 1995). These studies follow from the work of Kohlmaier et al. (1987), and although varying in their estimate of the overall magnitude, they all suggest that only modest increases in net primary production, N_P, in response to elevated atmospheric CO_2 concentrations are required to produce a terrestrial carbon sink of order 0.1 Pmol C yr^{-1}. It is important to note that a terrestrial sink of 0.1 Pmol C yr^{-1} does not require that N_P be increasing by that amount. This is because, on average, there is an appreciable lag between the time that molecules are assimilated by an ecosystem (via photosynthesis) and their return via respiration. The mean residence time for carbon in an ecosystem, τ, can be simply calculated as M/N_P where M is the total (plant and soil) carbon density, and it turns out that for a simple linear increase in N_P, the rate of increase in M should be equal to the product $\tau\, dN_P/dt$ (Taylor and Lloyd, 1992).

Although we are now in a position to say that a terrestrial carbon sink of order 0.1 Pmol C yr^{-1} in response to CO_2 fertilisation is a most reasonable proposition, attempts to use a modelling approach to ascertain the general geographic location of such a sink or to obtain a more concise indication of its magnitude, are fraught with problems. For example, both Goudriann (1992) and Lloyd and Farquhar (1996) showed that the level of aggregation chosen within models can drastically affect the magnitude of the modelled sink in response to CO_2 fertilisation. Furthermore, other uncertainties exist in terms of appropriate values for the sensitivity of plant productivity to changes in CO_2 concentrations, and the extent to which interactions between the carbon cycle and the nitrogen and phosphorous cycles need to be considered.

Nevertheless, when considered on a per unit area basis, almost all models attempting such simulations have shown that tropical and temperate forests should be the biomes dominating the rate of CO_2 sequestration in direct response to atmospheric increases (Taylor and Lloyd, 1992; Polglase and Wang, 1992; Friedlingstein et al., 1995; Lloyd and Farquhar, 1996). This has been explained from a theoretical viewpoint, the rate of ecosystem carbon sequestration being dependent not only on the rate of increase in N_P, but also increasing with the mean residence time (Taylor and Lloyd, 1992; Thompson et al., 1996).

4. Simulations of the effects of increased rates of atmospheric nitrogen deposition on terrestrial carbon fluxes

The crucial rôle of nitrogen availability in influencing plant productivity has long been beyond doubt (Lawes and Gilbert, 1855), and it is now well documented that industrial activity in recent decades has caused a considerable increase in emissions of reactive N to the atmosphere (Galloway et al. 1995). Much of this is deposited back onto the land surface and some plant growth stimulation in response to these increased rates of N deposition should therefore be occurring. There have been several studies in recent years taking the spatial variability in modelled rates of terrestrial nitrogen deposition from atmospheric chemistry models and making assumptions about their historical pattern, estimating rates of carbon sequestration in response to these increased rates of N deposition (Townsend et al., 1996; Holland et al., 1997). These studies have suggested that large rates of carbon sequestration could be occurring in polluted areas of the northern hemisphere, subject to high rates of N deposition, particularly temperate forests in Central Europe and the

Eastern United States. As for modelled responses to increasing carbon dioxide concentrations, the rates of C sequestration implied by these studies are globally significant, of order 0.1 Pmol C yr^{-1} (Townsend et al., 1996; Holland et al., 1997). However, the accuracy of such estimates is currently constrained by uncertainties in source fields for rates of N input into the terrestrial biopshere, especially in terms of ammonia deposition (Holland et al., 1997).

A further problem is that a mechanistic linking of soil nitrogen with plant photosynthetic rate and plant growth rate via rates of plant nutrient uptake and changes in plant allocation patterns has yet to be made, even at the individual plant level. This has required ecosystem responses to changes in soil N status to be modelled using notions of constant C/N ratios. However, it is clear that, unlike aquatic systems, C/N ratios vary considerably with both nitrogen availability and plant size (Wong et al., 1992; Lloyd and Farquhar, 1996). Thus, advances in understanding the rôle of N deposition in stimulating carbon stocks will partially be dependent on conceptual advances made at the more fundamental level of the physiological mechanisms of plant responses to changes in N availability and their interaction with plant carbon supply. Even when such advances have been made at the whole plant level, combining them with soil chemistry models and scaling them to the ecosystem in a realistic manner will remain a major challenge for terrestrial biogeochemistry over the next decade.

5. Variability in climate

Over this century, there has been a significant increase in average temperatures (Hansen and Lebedeff, 1987) as well as significant regional variations in precipitation (Rasmusson and Arkin, 1993). Over recent years, the carbon cycle community has become increasingly aware that climate variability could contribute to changes in plant productivity and hence in the amount of carbon stores in the terrestrial biosphere.

This possibility was first investigated by Dai and Fung (1993) who, in a landmark paper, investigated the potential importance of climate variability and concluded that climate variability could account for about 50% of the terrestrial carbon sink, with most of this in the northern hemisphere. However, that analysis relied on very crude representations of the dependence of plant growth and soil respiration upon precipitation and temperature. Furthermore, Dai and Fung (1993) used a climate dependence of soil respiration that also included respiration by plant roots (Raich and Schlesinger 1992). They took the ratio of N_P to (soil + root) respiration for boreal forests to be 1.2 to 1.5 in the steady state. Even allowing for some herbivore consumption, this means that their model had boreal forest roots which were photosynthesising. This is an unlikely possibility which may have lead to an overestimate of positive effects of increasing temperatures on boreal forest carbon balance.

However, more sophisticated models of global scale responses to climate variability have been developed in recent years and these models seem to be able to reasonably reproduce observed inter-annual variation in plant production (Malmström et al., 1997). Yet, a key limitation to these models is the reliability of the satellite-derived normalised-difference vegetation index, NDVI (Malmström et al., 1997). This is especially the case for tropical rainforests where persistent cloudiness can often obstruct the derivation of meaningful NDVI values (Los et al., 1994). However, tropical forests have the highest productivities and their reasonably long turnover times mean that they could be key contributors to any changes in global carbon storage due to short-term or long-term climatic variability. What little high frequency and reasonably long-term growth data that is available for tropical rainforest trees indicates substantial interannual variability, perhaps related more to changes in photosynthetically active radiation than to changes in temperature or precipitation (Clark and Clark, 1994). However, there are also clear indications of effects of soil water deficit on tropical rain forest carbon exchange, even in relatively moist regions (Malhi et al., 1998), and this seems likely to be causing considerable inter-annual variability in continental-scale carbon fluxes in the tropics (Tian et al., 1998; Prentice and Lloyd, 1998).

Analysis of long-term changes in the seasonal patterns of NDVI have also been taken to indicate an extension of the length of the growing season in the mid-to-high northern latitudes, attributable to a marked warming in spring temperatures (Myeni et al., 1997), and that analysis is consistent with changes in the seasonal cycle of CO_2 at high northern latitudes (Keeling et al., 1996). However, on

what evidence is available to date, enhanced thawing of soil in boreal ecosystems may result in substantial increases in soil carbon efflux and hence a decline in ecosystem carbon stocks (Goulden et al., 1998). However, as was shown by Braswell et al. (1997), effects of interannual variations temperature on ecosystem productivity are complex, with short-term responses (less than one year) often of opposite sign to statistically significantly longer-term lagged correlations. Furthermore, that analysis shows that tropical systems show very different apparent responses to temperature fluctuations than do temperate or boreal systems.

6. Does forest regrowth constitute a significant sink for CO_2?

Over the last few years, some workers have proposed that an increase in northern hemisphere forest stocks, mostly as a consequence of afforestation of previously cultivated areas, constitutes a significant source of carbon sequestration by the terrestrial biosphere (Sedjo, 1992; Dixon et al., 1994; Kolchugina and Vinson, 1995). Yet, as has been pointed out by Houghton (1993), some of these studies do not account for all fluxes associated with timber harvesting and different patterns of land use. Furthermore, the temporal pattern of the terrestrial CO_2 sink this century implied by the historical record and ocean carbon exchange models is not consistent with forest regrowth accounting for a substantial proportion of the terrestrial carbon sink (Craig and Holmén, 1995). Furthermore, even for the same region current, estimates vary widely. For example, Kolchugina and Vinson (1993) estimate a net carbon sink due to changes in forest carbon stocks in Russia of 0.04 Pmol C yr^{-1} but for about the same period, Krankina et al. (1996) estimate that the Russian forest sector was a net source of CO_2 to the atmosphere of 0.004 Pmol C yr^{-1}. A further complication is that some of the carbon accumulation modelled to occur in these studies might actually be a consequence of nitrogen deposition and CO_2 fertilisation (Schimel et al., 1995). For both Canada (Kurz et al., 1995) and the USA (Turner et al., 1995), modelled increases in carbon sequestration by the forest sector are quite low (less than 0.01 Pmol yr^{-1}). Kauppi et al. (1992) estimated that the European forest sector was accumulating about 0.01 Pmol C yr^{-1}, but also noted that much of this was probably attributable to increased nitrogen deposition. More recently, Martin et al. (1998) have estimated a somewhat higher number for forests in the European Union: 0.015 to 0.03 Pmol C yr^{-1}. However, that estimate ignores removals of wood by harvesting and subsequent decay off-site. When such losses to the atmosphere are also considered, that estimate becomes similar to Kauppi et al. (1992) and other recent studies (Nabuurs et al., 1997).

This is not to say that changes in land-use in the temperate and boreal regions have not resulted in some sequestration of atmospheric carbon, but it is likely to be towards the lower end of the 0.04 ± 0.04 Pmol C yr^{-1} quoted by Schimel et al. (1995).

7. How important are interactions between the phoshorous and carbon cycles?

Phosphorus levels are often low in tropical and sub-tropical soils, particularly in rain forests (Vitousek and Sandford, 1986), and using the "law of limiting factors", it has been assumed that this low level of phosphorous availability should constrain tropical forest CO_2 responses (Friedlingstein et al., 1995). However, recent evidence suggests that improved carbohydrate status under conditions of increasing atmospheric [CO_2] should help plants actively acquire phosphorous.

Firstly, mycorrhiza (associations between fungi and plant roots) play a key rôle in phosphorous acquisition, especially in the tropics (Harley and Smith, 1983). However, phosphorous acquisition by this source is expensive in terms of its energy (i.e., carbon) requirements (Eissenstat et al., 1993). Increased carbon availability in plants growing at high atmospheric [CO_2] should enhance mycorrhizal colonisation and thus help plants overcome phosphorous limitations. This has been generally observed (Lewis et al., 1994; O'Neil, 1995; Hodge, 1996; DeLucia et al., 1997).

Secondly, both mycorrhizal and non-mycorrhizal roots produce enzymes known as phosphatases. These hydrolyse ester linkages on soil organic-P compounds (Duff et al., 1994) and contribute to improved plant phosphorous nutrition (Tarafdar and Claassen, 1988). Importantly, for some species such as the native Australian

grass, *Danthonia richardsinii* (Gifford et al., 1996) or in wheat (Barrett et al., 1998), increases in atmospheric [CO_2] stimulate phosphatase production leading to increased phosphorus uptake and carbon gain at higher [CO_2].

Thirdly, roots can also exude organic acids such as citrate and oxalate which can directly help liberate phosphorous from bound forms within the soil and increase availability of inorganic phosphorous in the soil solution (Bolan et al., 1994). As is the case for mycorrhizal associations and phosphatase production, this is energetically demanding and tends to increase with improved plant carbohydrate status (Gifford et al., 1996; DeLucia et al., 1997). However, on a root length basis, there can be no effect of elevated [CO_2] on citrate efflux, even though ontogenic patterns may be altered (Watt and Evans, 1999).

Thus, plants have several means by which to increase the rate of phosphorus mineralisation and/or the rate of phosphorus uptake from the soil solution when available soil phosphorous levels are low, and there is some evidence that these mechanisms are enhanced when plant carbohydrate status is increased, as should be the case when atmospheric [CO_2] is increasing. We are not yet in a position to determine the magnitude of this effect in natural ecosystems since preindustrial times, but it does not seem appropriate on the basis of the evidence to date to assume that where organic sources of phosphorous are available, as is the case in natural ecosystems, that low phosphorous availability will reduce the magnitude of the CO_2 growth response.

Indeed, perhaps the opposite is actually the case, and evidence for significant rates of carbon sequestration by nutrient poor Amazonian forest has recently come from two studies using the eddy covariance techniques (Grace et al., 1994; Malhi et al., 1998). Although these two studies could be criticised on the grounds that they considered only a limited region of forest, recent evidence from large scale forest inventory data also suggest that the phosphorus-poor forests of the Amazon basin constitute a significant component of the terrestrial sink for atmospheric CO_2 (Phillips et al., 1998).

8. Concluding comments

Over the last few years, evidence from atmospheric inversions, eddy covariance studies of undisturbed ecosystems, forest inventory data as well as modelling studies of effects of increases in atmospheric carbon dioxide concentrations and increased rates of atmospheric N deposition, have all combined to improve our confidence in the notion that that there is currently a significant terrestrial sink for anthropogenically released CO_2. However, especially in relation to the spatial distribution and temporal variation of such a sink, there is still considerable controversy. Most modelling studies of a direct CO_2 effect on terrestrial carbon sequestration put a significant component of the terrestrial sink in the tropics. Although such a notion is also supported by direct measurements, it is in direct conflict with some (but not all) inversion studies, especially those which conclude that the northern hemisphere is the dominant location of the terrestrial carbon sink. But that latter notion is consistent with some high modelled rates of carbon sequestration in relation to atmospheric N deposition.

Most likely, both mechanisms are operating at the current time: N deposition effects on productivity dominating in the temperate regions and direct effects of CO_2 on plant productivity in the warmer tropical regions. More accurately defining the nature and location of these terrestrial sinks for CO_2, especially in terms of understanding how they may be modulated by future changes in climate and atmospheric CO_2 concentrations, remains a major challenge for globally-scaled terrestrial biogeochemistry.

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