BOREAL FORESTS AND TUNDRA

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Abstract. The circumpolar boreal biomes cover *ca.* 2 10^9 ha of the northern hemisphere and contain *ca.* 800 Pg C in biomass, detritus, soil, and peat C pools. Current estimates indicate that the biomes are presently a net C sink of 0.54 Pg C yr^{-1}. Biomass, detritus and soil of forest ecosystems (including *ca.* 419 Pg peat) contain *ca.* 709 Pg C and sequester an estimated 0.7 Pg C yr^{-1}. Tundra and polar regions store 60-100 Pg C and may recently have become a net source of 0.17 Pg C yr^{-1}. Forest product C pools, including landfill C derived from forest biomass, store less than 3 Pg C but increase by 0.06 Pg C yr^{-1}. The mechanisms responsible for the present boreal forest net sink are believed to be continuing responses to past changes in the environment, notably recovery from the little ice-age, changes in forest disturbance regimes, and in some regions, nutrient inputs from air pollution. Even in the absence of climate change, the C sink strength will likely be reduced and the biome could switch to a C source. The transient response of terrestrial C storage to climate change over the next century will likely be accompanied by large C exchanges with the atmosphere, although the long-term (equilibrium) changes in terrestrial C storage in future vegetation complexes remains uncertain. This transient response results from the interaction of many (often non-linear) processes whose impacts on future C cycles remain poorly quantified. Only a small part of the boreal biome is directly affected by forest management and options for mitigating climate change impacts on C storage are therefore limited but the potential for accelerating the atmospheric C release are high.

1. Introduction

The boreal forest biome consists of a broad complex of forested and partially-forested ecosystems which form a circumpolar belt through northern Eurasia and North America. Its southern boundary is formed with temperate deciduous forests where oceanic influences moderate climate, and with arid steppe, prairie or semi-desert in continental regions. Climatically, these regions are characterized by short growing seasons and low mean temperatures resulting in a forest cover dominated by coniferous vegetation. The boundary between the boreal and temperate forests is not sharp, instead there is a transitional zone with mixed species stands or a mosaic of temperate deciduous species established on favorable soils and boreal conifers on colder sites. To the north, the subarctic woodlands contain a patchwork of treeless patches and stunted forest stands

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which form the boundary between the boreal forest and tundra zones. The term 'boreal forest biome', as used in this paper, includes the closed-canopy boreal forests, the open canopy sub-arctic wood lands and the mixed hardwood-softwood forests which form the southern transition zone. Tundra zones include the wet (coastal) and moist (tussock) tundra (Shaver *et al.*, 1992). The polar deserts and semi-desert regions, covered by ice and stone barrens, contain negligible quantities of active biogenic C.

The objectives of this paper are threefold. First, estimates of the current C-pool sizes and fluxes for the boreal regions will be summarized. This C budget synthesis includes recent literature and results presented by the authors in this volume. Secondly, the processes which may be responsible for the current state of the C budget will be discussed with an emphasis on those which may be important in an enhanced-greenhouse future climate. This discussion will be followed by an assessment of future C budgets for the boreal region, considering climatic change and the potential for human influences, both positive and negative.

2. C in the Contemporary Boreal Region

2.1. ESTIMATES OF CURRENT CARBON POOLS

Primary C pools in the boreal forest biome are forest biomass, forest soils including litter and coarse woody debris, and organic soils associated with peat formation. Additional C stores are retained in undecomposed wood products and landfill material derived from forest biomass. Table 1 provides a summary of the estimated present sizes of these pools, separated into biospheric components and geographical regions. More detailed breakdowns may be found in the individual works cited in the table footnotes. The western coastal regions of Canada (Cordilleran) and the entire forests of Scandinavia have been included in the boreal forest biome (Fig. 1) for this assessment to facilitate global accounting of C pools and fluxes. The Cordilleran regions are shown separately in Table 1 because of their ecologically different character and higher biomass C density.

Estimates of live belowground biomass are included in Table 1 for the North American and Russian boreal forests, but these data are not available for Scandinavia. Root biomass is an important contribution to the total biomass and the paucity of data underlying the estimates in Table 1, together with other uncertainties in plant C allocation, poses a significant scientific challenge for forecasting future C budgets in a changing climate.

Estimates of C stored in harvested forest biomass do not appear to have been previously estimated at a national scale for boreal systems except for Canada (Kurz *et al.*, 1992), although global estimates cited by Vitousek (1991) are consistent with the estimates in

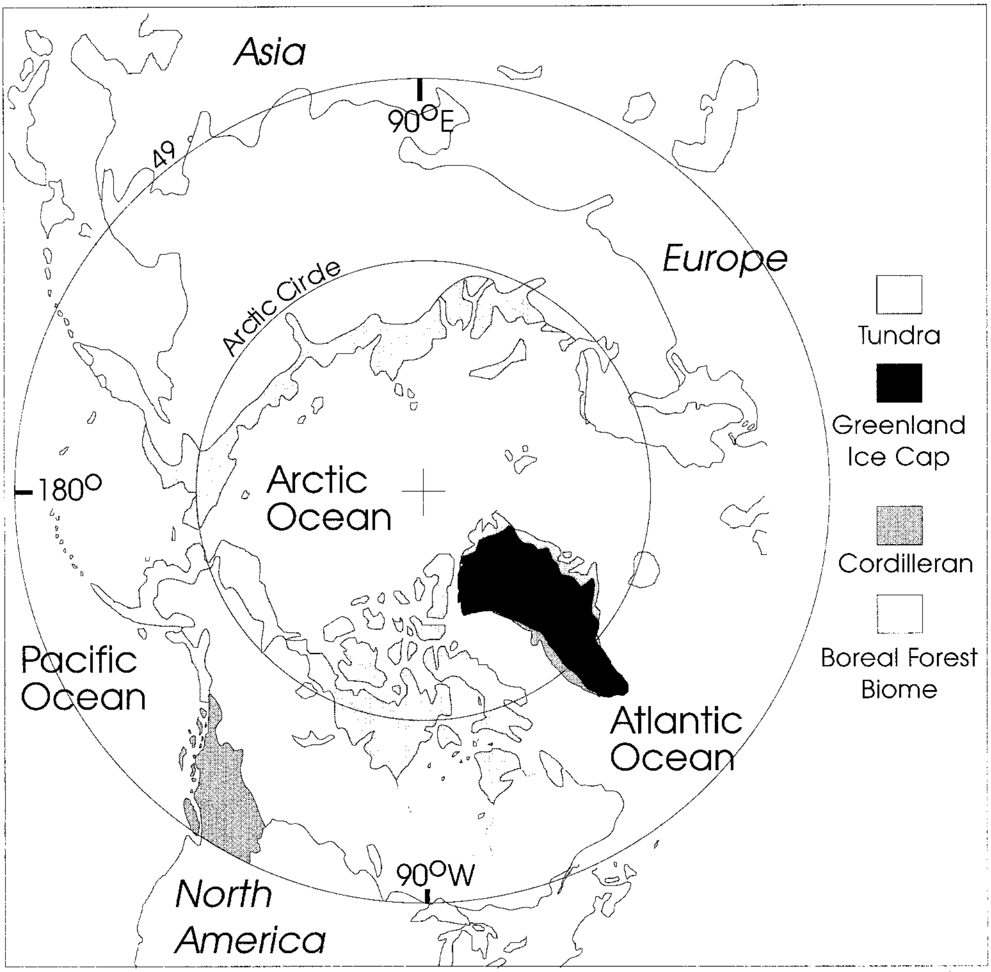

Figure 1. A polar view of the circumpolar boreal regions.

pools, but the annual net storage in these pools plays a potentially important part in the annual forest sector C budget (Apps and Kurz, 1991).

The estimates for boreal peatlands shown in Table 1 for North America (see Kurz *et al.*, 1992) and Scandinavia were derived from Gorham's (1991) estimates, while the values for Russia are based on area estimates by Botch and Masing (see Kolchugina and Vinson, this volume). Gorham (1991), whose estimate of global northern peatlands (342 Mha and

Table 1: Contemporary boreal forest biome areas and C pools. (Totals may not agree due to rounding errors)

	AREA (Mha)		CARBON POOLS (Pg C)					
	Area	Peat-land	Plant Biomass	Plant Detritus	Forest Soil	Peat	Forest Products	Total
Alaska	52[1]	11[6]	2[10]	1	10	17[17]	<0.1	30
Canada (Boreal Forest Biome)	304[2]	89[7]	8[11]	N/A[14]	65	113[18]	0.2[21]	186
Canada (Cordilleran)	72[3]	3	6	N/A[14]	16	4[18]	0.3	27
Russia	760[4]	136[8]	46[12]	31[15]	100[16]	272[19]	2.9[22]	451
Scandinavia	61[5]	20[9]	2[13]			13[20]		15
Total	1249	260	64	32	199	419	3.4	709

1. From Birdsey (1992).
2. Areas in boreal, arctic, and subarctic ecoclimatic provinces that have biomass data in the national inventory (Kurz *et al.*, 1992)
3. See text for explanation.
4. Forest area of Russia, *ca.* 95% of Former Soviet Union forests (Kolchugina and Vinson, this volume).
5. Area estimates from UN-ECE/FAO (1992), Table 11.
6. From Kivinen and Pakarinen (1981), including only thick peat soils, excluding 38.0 Mha of tundra bog soils.
7. Canadian Wetlands Working Group (1986) and Kurz *et al.* (1992).
8. From USSR State Forestry Committee, 1990 (See Kolchugina and Vinson, this volume).
9. From Kivinen and Pakarinen (1981).
10. From Birdsey (1992), above and belowground live biomass.
11. From Kurz *et al.* (1992); revised Kurz and Apps (in prep), above and belowground live biomass.
12. From Kolchugina and Vinson (this volume), above and belowground phytomass, understory vegetation and grasses.
13. Pekka Kauppi, pers. com. (1993), range 1.5-1.9 Pg C.
14. Plant detritus estimates are included in soil C pool.
15. From Kolchugina and Vinson, pers. com. (1993), litter (10.6 Pg C) plus necromass (20.2 Pg C).
16. From Kolchugina and Vinson (this volume). Forest ecosystems only, excluding peat.
17. Based on Gorham (1991), mean depth 2.5 m, mean bulk density 0.112 g cm^{-3}, 51.7% C content.
18. See note 17, mean depth 2.2 m.
19. Area, density (2,000 Mg C ha^{-1}), T. P. Kolchugina, pers. com.
20. See note 17, mean depth 1.1 m.
21. Residual C content of materials harvested from this region (1940-1980) (Kurz *et al.*, 1992, Apps and Kurz, 1991).
22. From Sinitsin (1990).

455 Pg C) is comparable with the values shown in Table 1, discusses the major uncertainties associated with peatland C on a global scale. Broadly speaking, the largest uncertainties are associated with the areal extent of the different types of peatlands and their depth. Estimates of combined forest and peatland C pools introduce additional uncertainty because of the unknown degree of overlap between forest inventories and peatland inventories from which soil C pools and peatland pools are calculated. The potential double-accounting for the overlapping parts of the land-base is probably small relative to the other uncertainties in these pool estimates. The overlap, however, tends to confound separation of flux estimates from forest and peatland systems.

Two different sets of estimates of area and C pools for arctic tundra are provided in Table 2. The first is based on area estimates and average C densities following Kolchugina and Vinson (this volume). The second is based on the C pool estimate of Shaver *et al.*, (1992) spatially distributed according to the BIOME model of Prentice *et al.* (1993) (36% in North America, 53% in Asian Russia, and 5.4% in western Europe, with the remaining 6% in scattered pockets). Because of the difficulties in scaling to the biome, both these estimates must be considered very uncertain. Previous estimates of C stores in the tundra and polar regions exhibit even higher ranges, from 55 Pg C (Post, 1990) to 256 Pg C (Prentice *et al.*, 1993). The wide range of estimates arises partly from differences in definitions of the C pools involved (and their geographical distribution) and partly because of the way in which areal estimates are scaled up to the biome level.

Table 2: Summary of estimates of contemporary tundra areas and C pools.

	AREA (Mha)	CARBON POOL (Pg C)
North America	240[1] to 420[2]	41[1'] to 22[3]
Russia	226[4] to 624[2]	59[4] to 32[3]
Scandinavia	63[3]	3[3]
Other	70[3]	4[3]
Total	600 to 1180	107 to 61

1. Area of arctic regions, C density (17 ± 5 kg C m^{-2}) from Kurz *et al.* (1992).
2. Area estimates based on BIOME model (Prentice *et al.*, 1993; Rik Leemans, pers. com.).
3. C density from Shaver *et al.* (1993), apportioned to areas from note 2.
4. From Kolchugina and Vinson (this volume) and Tatyana P. Kolchugina (pers. com.).

Adams *et al.* (1990) estimate an accumulation over the last 18 kyr of 240 Pg C in the closed-canopy boreal forest (soils and vegetation biomass), with an additional 190 Pg C uptake in open-canopy woodlands and tundra. In contrast, Prentice and Fung (1990) estimate an uptake over the same time frame of only 80 Pg C in boreal forests (50 Pg C in soils and 30 Pg C in biomass) and a decrease of 1-2% in tundra C storage (which they estimate presently to be 91 - 133 Pg C). Direct comparisons of these previous estimates with Tables 1 and 2, which are primarily based on synthesis of national-scale databases, are complicated by differences in definitions used to delineate boreal forest and boreal biome distributions. The discrepancies illustrate the divergence in different scaling assumptions - a challenge which also faces flux estimates.

2.2. ESTIMATES OF CURRENT CARBON FLUXES

The estimates of fluxes presented in Table 3 are inferred from estimated annual changes in the biospheric C pools. To be meaningful, this inference requires that all significant changes in these pools be accounted for (Apps and Kurz, 1993); bias and errors will result if significantly changing pools (or processes) are ignored. Comprehensive analyses of C fluxes have been performed for both the Russian and Canadian forest biomes which between them (including their peatlands) account for 91% of the circumpolar northern forest area, 90% of its C stores, and account for 90% of it's net atmospheric C exchange (Tables 1 and 3). Discussion of the forest sector portions are provided in the cited references (see also section 3 below) but peatland and tundra estimates require comment here.

Table 3 indicates that peatlands have been a significant sink of atmospheric C throughout the boreal region. These estimates are based on the historically-observed rate of peat accumulation (for references, see Kolchugina and Vinson & Kurz and Apps, this volume). These estimates have two sources of uncertainty; the areal extent of peatlands (which also affects the estimates of pool size) and the estimate of net ecosystem productivity (NEP) for these peatlands. The widely accepted value of 23 g C $m^{-2}yr^{-1}$ (Gorham, 1991) falls in the middle of the range measured by Zoltai (1991) for boreal forest and subarctic peatlands of central Canada. The challenges of scaling to the biome with such an 'average' NEP have been previously noted (section 2.1, and Apps, 1993) and apply to both these sources of uncertainty. The apparent difference in peatland NEP between North American and Russian peatlands is almost certainly an artefact of the difference in procedures between the Russian and North American estimates; it is likely that the Russian forest soil estimates include some peat deposition fluxes which result in a decreased peat NEP and a corresponding increased forest ecosystem NEP (relative to the North American estimates in which a greater degree of separation has been attempted).

Table 3: Summary of present C fluxes in the circumpolar boreal regions. Net transfers from the atmosphere (+), net releases to the atmosphere (-).

	Ecosystem[1] ($Tg\ C\ yr^{-1}$)	Peatland ($Tg\ C\ yr^{-1}$)	Products ($Tg\ C\ yr^{-1}$)	Net Flux ($Tg\ C\ yr^{-1}$)
Boreal Forest Biome	+605	+45	+57	+707
Alaska	+6[2]	+3[7]	<+1	+9
Canada (Boreal)	+62[3]	+25[8]	+8[10]	+95
Canada (Cordilleran)	+1[3]	+1[8]	+11[10]	+13
Russia	+493[4]	+11[9]	+26[11]	+530
Scandinavia	+43[5]	+5[7]	+12[12]	+60
Tundra				
moist (Tussock)	-140[6]			-140[6]
wet (coastal)	-30[6]			-30[6]
Total	+435	+45	+57	+537

1. Annual net flux from ecosystem C pools includes all biomass and soil C pool dynamics, disturbance releases, and harvest removals. Where calculations were available, peatland fluxes are shown separately in column 3.
2. Flux estimate for Alaska assumes that the per ha fluxes on average are equal to those in the Canadian Yukon Territories (Kurz *et al.*, 1992, revised in Kurz and Apps, in prep.).
3. Net change in ecosystem C (biomass plus soil and detritus C pools) from Kurz *et al.* (1992), revised in Kurz and Apps (in prep.).
4. From Kolchugina and Vinson (this volume and pers. com.), calculated from average NEP (1.05 Mg C ha^{-1} yr^{-1}) and area, minus fire release (199 Tg C yr^{-1}), harvest (152 Tg C yr^{-1}), and burned peat (100 Tg C $^{-1}$).
5. From Pekka Kauppi (pers. com.), range of estimates for ecosystem C sink, 29.7 to 56.6 Tg yr^{-1}.
6. From Oechel *et al.*, 1993. Note, however, that Kolchugina and Vinson (this volume) and others consider tundra to be a sink, not a source. See text.
7. Assuming a net sink of 23 g C m^{-2} yr^{-1} (Gorham 1991).
8. Assuming a net sink of 28 g C m^{-2} yr^{-1} (Kurz et al., 1992; Gorham, 1991; Stephen Zoltai, pers. com.).
9. Assuming a net sink of 30 g C m^{-2} yr^{-1} and release of 30 Tg C yr^{-1} from peat burning (Tatyana P. Kolchugina, pers. com.).
10. Net balance between oxidation of stored forest products (including landfills), production emissions, and harvest input (from Kurz *et al.*, 1992; Apps and Kurz, 1991).
11. Difference between forest product accumulation (statistical data 277 Mm^3 yr^{-1} and multiplier 0.26 to convert volume to C) and product decomposition (46 Tg C yr^{-1}) from Melillo et al. (1988).
12. Annual harvest from Pekka Kauppi (pers. com.), and assuming 50% C retention in forest products.

There have been several recent, but conflicting, estimates of atmospheric C exchange (CO_2 and CH_4) in the tundra and polar regions. The estimates in Table 3 are based on a 200 km transect study through moist and wet tundra of the North Slope of Alaska (Oechel *et al.*, 1993) which indicate that a lowering of the water table and increased decomposition may already be occurring in response to warmer conditions. In contrast, however, Schell and Barnett (1993) have reported that production exceeds respiration; even where drainage may lead to aeration and increased respiration of peat, C continues to accumulate in valleys and low-lying foothill tundra of arctic Alaska at rates of up to 20 g C m^{-2}. Harden *et al.* (1992) also make the point that northern systems still continue to accumulate C; they are still responding to post glacial warming and although the response has slowed, they may not yet have reached a steady state. They have also shown that there are significant variations in the soil dynamics of northern continental North America following the retreat of the Laurentide ice-sheet. Because these deglaciated systems have a distinct spatial pattern, there is considerable danger in the extrapolation of site-specific average results to the global scale and for this reason the results shown for tundra in Table 3 must be considered very uncertain.

3. C in the Future Boreal Region

The boreal forests are not static ecosystems and can not be assumed to be in equilibrium in terms of C exchange. In these systems, the current C cycle is strongly influenced by their past history over several time scales. The boreal forest is still evolving since the last glaciation on a time scale of millennia (e.g., Davis, 1969); species migration may still be occurring at the biome level. Recent evidence points at shorter-term disequilibria on the scale of decades and centuries which must be superimposed on these longer-term changes. Continuing responses to recent climate fluctuations such as the little ice-age (1250-1850 AD, Ian Campbell, pers. com.) and to changes in historical disturbance regimes have shaped the structure and function of the contemporary boreal forests on these shorter time and finer spatial scales (Apps, 1993; Kurz and Apps, this volume).

While the global boreal forests is presently estimated to be a sink for atmospheric C, can it be assumed that the mechanisms which are responsible for this sink will continue to function at their present strength? This does not appear likely. Even in the absence of climate change, the major sink mechanisms identified previously will become saturated over time and switches from C-sinks to C-sources are likely to occur at different parts of the biome over the coming decades. These transient phenomena will likely be amplified by changes in the global environment and in the discussion that follows, a distinction is made between long-term projections where equilibrium conditions (in both climate and ecosystem response) are assumed to have been achieved and short term (50 to 100 yr) C-cycle projections, where transient behavior is expected to dominate.

Kurz and Apps (this volume) argue that in the absence of other environmental changes (including changes in the disturbance regime) the forest ecosystem C sink associated with a shifting age-class structure will diminish, and eventually vanish, in the coming decades. Aging of the global boreal forest cannot continue indefinitely. If in addition, disturbance regimes (fire, insect-induced mortality, windthrow, and harvesting) increase in intensity and frequency, they will be accompanied by transient C-releases followed by longer-term response by younger forests whose spatial structure and growth characteristics will depend on the then-prevailing climatic and environmental conditions. Thus in the short-term, it is likely that the present C sink will vanish and be replaced by a transient C source even if the over the longer -term the new biome becomes an eventual sink for atmospheric C.

Kauppi *et al.* (1992) have suggested that several other factors may have also contributed to the net C uptake of European forests through enhancements of biomass growth at the tree and stand level. Site-specific studies in Europe have generally indicated a slight increase in tree growth which may reflect improved climate conditions and nitrogen deposition associated with air pollution. In particular they suggest that fertilization response to air pollution may have obscured detectable adverse effects of soil acidification. Experimental evidence for a fertilization mechanism has been provided by Nilsson (this volume). These authors are careful to point out that such increased forest productivity is unlikely to be sustainable in the medium-to-long term; soil acidification and decreasing availability of base cations will eventually lead to nutrient imbalances and site degradation. Nilsson also emphasizes the importance of soil water availability to the net C accumulation rates in such circumstances.

Because CO_2 doubling experiments with seedlings of boreal forest species have shown an average increase in growth of 38% (Wullschleger *et al.*, in press), some authors suggest that the 25% increase in atmospheric CO_2 over the last 100 years may have contributed to a forest C sink. There is no evidence, however, that trees growing under boreal field conditions have responded to this increase. Although some unexplained increases in tree growth have been reported, Graumlich (1991) has shown that similar unexplained increases in tree growth have occurred prior to industrialization, and, further, the increases often exceed the response that can be expected from CO_2 enrichment (Luxmoore *et al.*, this volume).

It is possible that boreal forests will respond to increasingly elevated CO_2 with increased root growth. This is expected on nutrient poor sites and under drier conditions; however, no observations of such root response to the historical rise in atmospheric CO_2 have yet been reported. Forecasting a boreal forest response to CO_2 fertilization suffers from difficulties of scaling. Small-scale physiological models generally predict increases in growth rate at elevated CO_2 levels, while plot-level succession models do not show much response to CO_2 after several decades, even when increased water-use efficiency is included. Biome-scale models generally show increased NEP with elevated CO_2, although the predicted response for the boreal biome can be small. One reason for the differing model predictions relates to model structure. In the case of physiological and biome models, the CO_2 response is not overridden by other processes, but this is not the case for succession models. The stochastic representation of mortality of old trees and ingrowth of new individuals introduces variability in stand biomass in succession models that masks detection of a CO_2 growth stimulation (Luxmoore *et al.*, this volume).

Peat C accumulation rates are determined by the difference between net primary productivity (NPP) and decomposition, both of which are strongly influenced by site-specific hydrologic and nutrient conditions (Zoltai, 1991). Zoltai and Vitt (1990) have shown that large scale climatic and hydrologic changes - which vary considerably across the circumpolar boreal zone - can substantially influence the rate of peat accumulation. The range of accumulation rates reported by Zoltai (1991) reflects the role of permafrost and the age of deposition. Vegetation development plays a secondary role to hydrological and nutrient-cycling processes and is largely controlled by these other factors (Gignac *et al.*, 1991).

The role of boreal peatlands under a warmer, but stable, future climate is also difficult to predict with certainty but these regions hold the potential for significant C-feedbacks to the climate system (Gorham, 1991). Distributions (and therefore C uptake) of boreal peatlands will shift northward in response to global warming with the consequent northward movement of the zones of continuous and discontinuous permafrost (Zoltai and Vitt, 1990; Zoltai, 1993a). Zoltai (1993b) has hypothesized that, when integrated across the entire expanse of Canadian peatlands, positive feedbacks (e.g., increased release of CH_4 in the warmer north and CO_2 in the drier south) may nearly balance negative feedbacks (e.g., increased C-uptake in the north and reduced CH_4 efflux in the south), thereby cancelling any significant changes. Kolchugina and Vinson (1993) have examined the future C cycle within the permafrost zone of Russia under a climate warming scenario and conclude that an additional 0.46 to 0.72 Pg C yr^{-1} may be gradually released to the atmosphere from increased decomposition of litter and coarse woody debris. They point out, however, that this efflux may be concurrently balanced by increased NPP and forest expansion into these regions thus moving towards a new equilibrium in the C cycle (albeit at a higher rate of C turnover); transient effects are likely to be more significant than long-term, equilibrium changes in C-storage.

3.1. EQUILIBRIUM FUTURE BOREAL C-POOLS AND FLUXES

Some equilibrium projections (eg., Smith *et al.*, this volume) suggest that future boreal forest regions will contain more C than they do today (i.e., when averaged over a long enough time, they will act as a net sink). These projections are based on potential vegetation and to be achieved, require that the forest ecosystems reach equilibrium with the new (and assumed stable) climate system - a process that will take millennia (Schlesinger, 1990). There are two principal reasons for expecting eventually enlarged boreal forest C pools: 1) increased temperatures result in increased forest productivity and 2) unimpeded migration of the boreal forest into the presently unforested tundra regions.

The equilibrium picture for boreal forests is, however, far from well-established. Prentice and Fung (1990) point out that the global C implications of these projections of potential vegetation are most sensitive to misclassifications in areas having a strong gradient in C density and cite the transition through the boreal forest, tundra and polar regions as a particular case in point. It is noteworthy that a slightly different approach by Nielson (this volume) suggests that increased drought stress will result in the boreal region losing a significant quantity of C - that is, the boreal forest will act as a long-term source of atmospheric C. Although C analyses have not yet been performed, the projections of Rizzo and Wiken (1992) for Canadian ecosystems suggest similar trends to those of Nielson - warmer and drier mid-continental conditions will favour encroachment of grasslands into the present boreal regions more strongly than migration of these forests into the present arctic tundra, resulting in a net loss of area having high C stores.

3.2. TRANSIENTS

Under projected climate change scenarios, the climate system is expected to undergo warming at a much faster rate than records show that species and ecosystems have had to respond in the past 20 kyr. Even if the climate conditions were to stabilize at the doubled-CO_2 scenario projections, the rapidity of these changes will produce transient and non-linear responses as ecosystems lose synchronization with their environment (Holling, 1992). Because of the stand-replacing role that disturbances play in boreal ecosystem dynamics, C storage and exchanges during such transients cannot be assumed to vary linearly between two steady-state or equilibrium states (Apps, 1993). Thus, projections based on observations of the relatively slow changes in prior times could be misleading and result in underestimates of short-term C fluxes.

On a regional scale, the transient C fluxes from forest ecosystems could be either positive or negative, depending upon differences in response times associated with NPP, respiration, disturbance regimes, and the changes in the regional environment (King and Nielson, 1992; Townsend *et al.*, 1993). At the biome scale, the transient behavior (250 year period) of Canadian forests has been simulated by Nielson *et al.* (1993). In nearly every scenario that these authors examined, short-term (50-100 year) transients resulted in C release from forest ecosystems, even in cases where these same ecosystems showed net C uptake in longer term (100-250 year) projections.

Succession models suggest that large changes in ecosystem distribution could result from warming due to changes in soil water availability. Smith and Shugart (1993) used simulation of global warming effects on terrestrial ecosystems to show that transitions from one ecosystem to another occurring over a 50 to 100 year time frame could result in a significant release of CO_2 to the atmosphere. Much of the CO_2 release was due to transient changes in tundra and boreal ecosystems.

One of the most significant factors influencing the transient response of boreal regions to global change is the potential for dramatic changes in disturbance regime intensity and frequency (Apps, 1993; Overpeck *et al.*, 1990). Disturbance regimes have an influence on both the immediate and the medium-term C cycle of boreal forests. A three-fold difference in Canadian wild fires between a high-fire year (1989) and a reference year (1986) resulted in an 86% reduction in the net ecosystem C sink (Kurz *et al.*, 1992). Moreover, an additional 0.08 Pg C were transferred from aboveground biomass to the soil pools and will decompose in subsequent years. With increased decomposition rates accompanying a warming climate (Townsend *et al.*, 1993), such transfers of aboveground biomass to forest-floor detrital pools may contribute to an increasingly important forest floor C efflux. Carbon transfers associated with disturbances must be balanced against the uptake from the regenerating forests and their potentially enhanced productivity.

Where soils permit, forests at the northern margin will expand into the present tundra and modest vegetative cover will develop as slumping and exposure of mineral soils accompanies permafrost melting. Losses of organic soil C in some areas will be balanced by increased aboveground C storage. Forests at the southern margin will likely suffer dieback as temperate forests and grasslands invade. The rate of dieback may exceed the rate of incursion in some areas, particularly where soil moisture is reduced. Forests in the middle of the boreal biome may exhibit small to modest increases in biomass in response to the generally more favorable growing conditions associated with the warming, provided that available soil water is not reduced.

Soil warming experiments have shown increased nutrient availability due to greater rates of organic matter decomposition and N mineralization (Van Cleve *et al.*, 1990). Increased air and soil temperatures will result in enhanced soil respiration (Raich and Schlesinger, 1992) but it is uncertain if the enhanced growth from greater N mineralization will offset the loss of soil C through respiration as suggested by Townsend *et al.* (1993). Townsend *et al.* (1993) examined the transient behaviour of forest soils under global warming scenarios. They point out that if only warming occurs (i.e. without considering changes in soil water conditions), heterotrophic respiration (decomposition) will rise considerably more rapidly (exponential) than will NPP (linear) resulting in an approximately linear release of extant soil C. Townsend *et al.*'s analyses suggests that transient phenomena in soil processes will have a major impact on the C cycle of northern systems but the transient may play out over a relatively long time scale (100 years and beyond).

Transient behaviour in boreal peatlands may also be much more significant than the net changes in equilibrium storage might indicate (Gorham, 1991). While increased temperatures will likely enhance vegetation productivity, larger impacts are expected with changes in water table that will alter the balance between aerobic (CO_2 release) and anaerobic (CH_4 release) decomposition pathways. Hydrological and landscape changes in the patterns of bogs and fen formations with global change will be expected. In the north, melting of permafrost will likely favour an areal expansion of active wetlands, while drier conditions in southern regions will likely lower water tables changing the function and distribution of extant wetlands. Periodic severe droughts and increased incidence of forest fires that spread to the dry surfaces of peatland formations throughout the biome will accelerate reduction in C storage and increase the release of CO_2 (Post, 1990; Zoltai, 1993).

There have been few attempts to forecast climate-induced changes in the future tundra and polar regions. It has been estimated, however, that under a 5^0 C warmer climate the northern tundra and polar regions could release an additional 1.3 - 1.6 Pg C yr^{-1} as CO_2 and 0.1 Pg C yr^{-1} as CH_4, depending on the assumptions made about future moisture conditions (Post, 1990). The observations by Oechel *et al.* (1993) that arctic ecosystems may presently be a CO_2 source may already be an indication that transient C-releases associated with ecosystem readjustment to the slight warming trends of the last few decades are taking place.

4. Conclusions

The circumpolar boreal region is one of the largest biomes in the world and contains significant pools of biogenic C that are sensitive to changes in the global environment. Although conflicting evidence exists, there are indications that the tundra regions may already act as a source of atmospheric C (0.17 Pg C yr^{-1}). The contemporary boreal forests are, however, believed to presently taking up *ca.* 0.7 Pg C yr^{-1}. The principal mechanisms responsible for this present sink are believed to be continuing responses to: post-glacial warming; climatic perturbations such as the little ice-age (1250-1850); changes in disturbance regimes over the past two centuries; and more recently, nutrient inputs associated with air pollution.

Although the circumpolar boreal forest is presently be a sink for atmospheric C, the mechanisms believed responsible for this sink are not likely to be sustained, even if there is no change in climate. One of the principal mechanisms appears to be an aging and aggrading boreal forest, primarily due to changes in past and present disturbance regimes, a structural phenomenon which cannot be maintained indefinitely. Forest protection measures, such as fire suppression for example, must take into account both the biological role of such disturbances and the geographical reality of lack of access to vast forest areas. Other possible mechanisms, such as nutrient inputs associated with low-level, but wide-spread air pollution, may yield short-term increased C uptake but may lead to future forest decline.

How the C cycle in the boreal biome will be affected by climate change (and whether it has already been) is a challenging problem. There has been no compelling evidence, at the biome level, for an increase in boreal forest productivity due to recent changes in climate (temperature and precipitation) or to ambient CO_2 levels. There seems to be a clear consensus, however, that both the structure and function of boreal regions will be drastically altered by the climate changes projected by present global circulation models. It is also expected that non-linear, transient ecosystem responses will dominate the C dynamics during a period of rapid climate change.

Can boreal forest nations do anything to mitigate against increasing atmospheric C? Apart from Northern Europe, much of the circumpolar boreal forest remains in a wilderness state in that silviculture and timber harvesting directly influence only a relatively small fraction of the area. Improved management practises have the potential for significantly increased biomass yields at the regional level but it is hard to see how these could be applied at the biome scale in North America and Russia. Non-sustainable development practises, on the other hand can adversely affect C-storage capacity and pools in a significant way. Even in the absence of such human intervention, however, transient response to climate change has the potential for significant positive feedbacks to the climate system by releasing large quantities of C to the atmosphere.

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