

Carbon accumulation and distribution in a boreal mixedwood logged chronosequence near Wabowden, Manitoba



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The boreal forest, along with the mid-latitude temperate forests and equatorial tropical forests, is one of the world's dominant forest ecosystem, occupying 11% of global land surface. The boreal forest is important in the context of the global carbon cycle because of the potential for long-term carbon storage. Although the forest itself is arguably less productive than other forest types worldwide, the short frost-free period, cold temperatures, and generally high soil moisture levels suppress soil microbe and detritivore activity. The turnover time for carbon that is input into the soil or forest floor can therefore be extremely long, and these reservoirs can accumulate large stores of carbon.

Whether the boreal forest, or a region thereof, acts as a net carbon sink or source depends on the relative magnitudes of terrestrial carbon uptake versus its release to the atmosphere. Carbon flux into forest ecosystems from the atmosphere occurs via gross photosynthesis by primary producers such as trees, shrubs, herbs, and mosses, and is manifest both above and below ground. Carbon returns to the atmosphere primarily through root respiration, but also through mineralization in the soil, gaseous emission, and burning.

Historically, wildfire and pest outbreaks were the dominant disturbance regimes affecting the global boreal forest. Both types of disturbance impact the partitioning of carbon stores among ecosystem pools such as aboveground biomass, woody debris, forest floor/organic soil, and mineral soil. Specifically, insects affect rates of carbon input into the detrital stores through tree damage and mortality, while fires both drastically change the labile carbon pools and add charcoal to the pool of "inert" carbon. The recent advent of commercial timber harvesting has its own suite of effects on carbon dynamics, though these have not been a primary focus of study in the boreal forest. In Manitoba specifically, commercial harvesting is so young that few mature, harvest-originated stands exist and in general there are relatively few data pertaining to harvested areas. Except for a few areas in southern Manitoba, the boreal forest there is all primary forest and has never been harvested before. While the area of land in Manitoba that is subject to timber harvest is miniscule compared to that burned by wildfires every year, the total harvested area in the Province will only increase. Quantification of the effects of human-mediated disturbance on boreal forest carbon distribution is essential to understanding the implications of changes in land management in this region. Understanding how carbon stores are distributed among ecosystem pools after commercial harvest will become more important as more land area is subject to logging disturbance, and allows greater resolution for age-structure based carbon cycle models.

To quantify the effects of forest management on carbon storage in the boreal forest, we estimated the carbon stores in three stands near Wabowden, Manitoba, Canada that were harvested 11, 18, and 30 years ago. We also sampled a 65-year old fire-originated stand and estimated its carbon stores for comparison. We developed site-specific allometric equations for the four most abundant tree species: trembling aspen, balsam poplar, black spruce, and jack pine. The carbon stores sampled directly in this study were: 1) aboveground biomass in trees and understory herbs, 2) coarse woody debris

CWD), 3) forest floor and organic soil, and 4) mineral soil to a depth of 30 cm. Belowground biomass was accounted for indirectly as roots ≤ 2.5 cm in diameter were included in the forest floor samples but the coarse and fine root biomass was not incorporated into allometric equations.

Aboveground biomass at the harvested chronosequence increased with stand age at a faster rate than other boreal chronosequences of fire-originated black spruce and jack pine stands. This is primarily because regrowth at the harvested chronosequence consisted of faster-growing hardwood species such as aspen, paper birch, and balsam poplar. The fire-originated stands and the harvested stands were both stocked with conifers before their respective disturbance events, so harvesting appears to effect a substantial shift in species composition.

The coarse woody debris pool of carbon at the harvested stands was more similar in magnitude to jack pine stands in Saskatchewan than to black spruce stands to the north in Manitoba. Because wildfires vary so much in intensity, the amount of woody debris consumed or produced varies greatly and is not a wholly age-related function. Slash left on harvested sites, however, is determined by the wood end-product as well as environmental regulations and is therefore more predictable.

Forest floor carbon and carbon in the mineral soil (soil organic carbon) both decreased slightly with stand age in the harvested stands. In terms of overall magnitude, forest floor carbon stores were greater than those in more southern jack pine stands of comparable ages, though the mineral soil carbon data are less immediately comparable because of differences in sampling technique. The forest floor decrease following harvest has been documented repeatedly in temperate forests, and the explanations range from increased decomposition rates, to decreased litter inputs, to mixing of forest floor carbon into the mineral soil pool. The latter explanation is based on changes in logging technique over time from horses to tracked vehicles such as crawlers, to wheeled vehicles such as skidders. The decrease in forest floor carbon observed in the harvested stands in Manitoba is puzzling because the oldest stand is 30 years old. They were all harvested since the popularization of clear-cutting and the introduction of wheeled skidders, so the degree of forest floor/mineral soil carbon mixing should be relatively constant among the stands.

There is also no concurrent increase in carbon in the mineral soil, suggesting that perhaps other mechanisms are responsible. One proposed alternative is increased decomposition rates due to the effect of increased solar radiation on soil temperatures. The mineral soil carbon pool has the greatest turnover time compared to the other carbon pools, therefore the simultaneous decline in forest floor and mineral soil carbon warrants further scrutiny.

The harvested chronosequence differs from fire-originated stands primarily in the storage of aboveground carbon. In general, the aboveground biomass production rate is greater for the harvested sequence. Over the course of the chronosequence, the CWD and forest floor carbon pools decrease, but the increase in aboveground biomass more than compensates for this decrease. Still, CWD and forest floor carbon pools are greater than those in fire-originated stands, and contribute to overall elevated total ecosystem carbon values. It would seem, then, that harvesting increases ecosystem carbon storage outside of the living biomass pool. However, one issue that has not yet been discussed yet is the formation of charcoal by boreal forest fires. Charcoal is an inert form of carbon that may

be integrated into the mineral soil but is not released to the atmosphere. The carbon in the CWD and forest floor of the harvested stands will either be mineralized or integrated into the mineral soil, but in either case its release to the atmospheric carbon pool is only a matter of turnover time.

A major finding of this study is that even un-harvested stands in this area of Manitoba (i.e. the 1935 stand) have different carbon distributions than stands in other areas of the boreal forest. Harvested stands behave differently still, and the amount of harvested land relative to land affected solely by wildfire is only going to increase. There are two main uses for the data contained in this study. The first is to constrain existing and future models of carbon cycling on a landscape level. Once the carbon distribution pattern of a given category of land has been determined (for instance, harvested stands 10-15 years in age in the boreal forest) the areal extent of that land type can be calculated and the data can be scaled-up. Secondly, if certain site preparation or harvesting techniques are found to cause minimal soil and forest floor disturbance, land managers may be encouraged to employ those techniques in the interest of carbon sequestration.

Abstract

To quantify the effects of forest management on carbon storage in the boreal forest, we estimated the carbon stores in three stands near Wabowden, Manitoba, Canada that were harvested 11, 18, and 30 years ago. We also sampled a 65-year old fire-originated stand and estimated its carbon stores for comparison. We developed site-specific allometric equations for the four most abundant tree species: trembling aspen, balsam poplar, black spruce, and jack pine. Total ecosystem carbon, in t C ha^{-1} , was 78.7, 81.0, 83.1, and 109.3 for the 1990, 1983, 1971, and 1935 stands, respectively. Carbon in the living aboveground biomass increased from 10.7 t ha^{-1} in the 1990 stand to 55.6 t ha^{-1} in the 1935 stand. Forest floor/organic soil and mineral soil both decreased slightly from the 1990 stand to the 1971 stand. Coarse woody debris was most important in the 1990 stand, with the lowest mass per hectare in the 1971 stand. Total basal area increased from $5.4 \text{ m}^2 \text{ ha}^{-1}$ in the 1990 stand to $25.1 \text{ m}^2 \text{ ha}^{-1}$ in the 1935 stand, while the relative importance of deciduous species such as trembling aspen declined with stand age as conifer species, primarily black spruce, grew up to replace them.

INTRODUCTION

The boreal forest matches the mid-latitude temperate forests and equatorial tropical forests in being one of the three dominant forest ecosystems on earth. Its northern circumpolar band encompasses the mostly coniferous forests of subarctic Russia, Scandinavia, and North America (Figure 1) and comprises 11% of the global land surface. It therefore covers almost one quarter of the world's closed canopy forest as well as vast expanses of open transitional forest (Natural Resources Canada, 2001). The boreal forest is an important biome in the context of the global carbon cycle and in light of projected climate change. During the most recent warming period (1976 to 1999), mid- and high-latitudes of the continental Northern Hemisphere experienced larger temperature increases than other regions of the globe (IPCC WG-1, 2001). Fire frequency in the North American boreal forest is expected to increase, and the structure of high-latitude vegetation is predicted to change due to climate warming (Apps and Price, 1996). The so-called missing carbon sink—the biotic uptake unaccounted for in the global carbon budget—may be accounted for at least partially in high-latitude terrestrial areas (Fan et al. 1998). Accurate measure of carbon distribution and storage in the boreal forest not only sheds light on intraecosystem functions but also provides much-needed data on which to base regional and global models of carbon cycling.

In this study we examined a chronosequence of three logged stands in northern Manitoba, Canada to see how commercial harvesting affects total ecosystem carbon and its distribution. We therefore measured aboveground biomass, woody debris, organic soil and mineral soil in each of the study stands, as well as vegetation density and relative species abundance. We compared the logged chronosequence to a mature unlogged stand

to determine changes in carbon pools, and then compared our data to values reported in the literature for fire-originated chronosequences.

Historically, wildfire and pest outbreaks were the dominant disturbance regimes affecting the global boreal forest. Both types of disturbance impact the partitioning of carbon stores (Volney, 1996). The recent advent of commercial timber harvesting has its own suite of effects on carbon dynamics, though these have not been a primary focus of study in the boreal forest. In Manitoba specifically, commercial harvesting is so young that few mature, harvest-originated stands exist and in general there are relatively few data pertaining to harvested areas. While vast tracts of non-harvested boreal forest remain, the interactions between harvest effects and projected climate change, while not the specific subject of this study, certainly justify research on human-mediated disturbance in the boreal forest.

The boreal forest is important in the context of the global carbon cycle because of the potential for long-term carbon storage. Although the forest itself is arguably less productive than other forest types worldwide, the short frost-free period, cold temperatures, and generally high soil moisture levels suppress soil microbe and detritivore activity. The turnover time for carbon that is input into the soil or forest floor can therefore be extremely long, and these reservoirs can accumulate large stores of carbon. As an illustration, Houghton (1996) calculated changes in the areal extent of major terrestrial ecosystems and the associated changes in vegetation and soil carbon content (Table 1). While the boreal forest experienced the least amount of areal change, its ratio of carbon loss to areal change is extremely high for both the vegetation and soil categories. It is this quality of the boreal forest that makes it particularly important in the

context of a changing global climate. Quantification of the effects of natural and human-mediated disturbance on boreal forest carbon distribution is essential to understanding the implications of changes in land management in this region. Understanding how carbon stores are distributed among ecosystem pools after commercial harvest will become more important as more land area is subject to logging disturbance, and allows greater resolution for age-structure based carbon cycle models.

ECOSYSTEM CHARACTERISTICS

Paleoecology

The North American boreal forest is geologically young, having developed in Alaska and western Canada during the early Holocene, and more recently in eastern Canada (Payette, 1992; Roberts, 1998). At the time of the last glacial maximum, approximately 20,000 years ago, the Laurentide Ice Sheet extended south of the Great Lakes (COHMAP members, 1988). It covered virtually all of Canada east of the Canadian Rockies. A spruce parkland, as identified by spruce pollen concentrations greater than 20% and sedge pollen values above 5%, was reduced to a small area in what is currently central/Midwestern United States. As the glacier retreated, spruce populations spread to the eastern seaboard and then became reduced in numbers before migrating north by the mid-Holocene. The current extent of the North American boreal forest is the greatest it has experienced since the last glacial maximum (Roberts, 1998, p. 102).

Range

Currently the North American boreal forest ranges from Alaska east and south through the Yukon Territory, northern British Columbia, the central and northern areas of Alberta, Saskatchewan, Manitoba, Ontario, and Quebec as well as northern New Brunswick and the Maritime Provinces. The northern limit is defined by the transition to tundra, while to the south the forest becomes more and more dominated by northern hardwoods and white pine. Pare and Bergeron (1995) define the southern boreal forest as bordered by the northern hardwood forest to the south and the black spruce forest to the north, an area of approximately 375,000 km². For the purposes of the study we are considering only those regions commonly referred to as forest. While canopy openness is considered a trademark characteristic of forest-tundra, taiga, and other boreal zones, these zones are not included, in part because they tend not to be areas subject to commercial logging.

Annual mean temperature hovers below 0°C (Canadian Soil Information System, 2001). Winters are long and harsh, and the summer growing season is short: at the Boreal Ecosystem Atmosphere Study (BOREAS) Northern Study Area north of Thompson, Manitoba, the average frost-free period is 120 days (Steele et al. 1997).

Vegetation Characteristics

The arboreal species diversity in the North American boreal forest is relatively depauperate compared with more southern ecoregions. With cold climates developing only since the Eocene, 50 million years ago, the flora adapted to growing in cold regions has had less time to evolve than tropical and temperate floras. Tree species include paper

birch (*Betula papyrifera* Marsh.), larch (*Larix laricina* (Du Roi) K. Koch), black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss), jack pine (*Pinus banksiana* Lamb.), balsam poplar (*Populus balsamifera* L.), quaking aspen (*Populus tremuloides* Michx.), and northern white cedar (*Thuja occidentali* L.) (Fowells, 1965). Herb and understory species include Labrador tea (*Ledum* spp.), blueberry and cranberry (*Vaccinium* spp.), bog rosemary (*Andromeda polifolia* L.), bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.), American red raspberry (*Rubus idaeus* L. var. *strigosus* (Michx.) Maxim.), wild roses (*Rosa* spp.), alders (*Alnus* spp.), and willows (*Salix* spp.) (Viereck and Little, Jr., 1975). The classic species assemblage in the central Provinces is black spruce-balsam fir-trembling aspen-paper birch, which arose only 6000 years ago in North America (Webb III et al. 1983). Manitoba specifically is also host to jack pine, larch, and balsam poplar. Local species composition varies with latitude, drainage, soil quality, and microclimate effects. Black spruce is typically found in poorly drained lowland soils and upland mineral soils, jack pine in well-drained sandy uplands. Aspens, along with other broadleaf species such as balsam poplar and white birch, prefer finely textured upland soils but are also among the first colonizers of disturbed sites (Gower et al. 1997) and therefore tend to be more prevalent at younger stands (Table 2).

THE COMPONENTS OF CARBON STORAGE IN THE BOREAL FOREST

Whether the boreal forest, or a region thereof, acts as a net carbon sink or source depends on the relative magnitudes of terrestrial carbon uptake versus its release to the atmosphere. Influx of carbon into forest ecosystems from the atmosphere occurs via gross photosynthesis by primary producers such as trees, shrubs, herbs, and mosses, and

is manifest both above and below ground. Carbon returns to the atmosphere primarily through root respiration, but also through mineralization in the soil, gaseous emission, and burning. Carbon is also removed when timber is harvested and transported off-site.

To measure carbon storage within the boreal forest, ecologists and foresters commonly partition the carbon among aboveground biomass, belowground biomass, forest floor/soil organic matter, mineral soil stores, and dead and decomposing organisms. In this study we measured aboveground biomass, forest floor/organic soil, mineral soil, and coarse woody debris. These stores, and techniques for measuring them, are described in the following subsections.

Aboveground biomass

Aboveground biomass encompasses the carbon in living plants and is sometimes equated with commercial productivity or board footage because trees make up the greatest portion by far. The amount of carbon in aboveground biomass depends on the time since last disturbance and the successional stage of the forest in question. It is therefore highly variable because it is susceptible to short-term disturbance events such as catastrophic fires as well as to long-term climatic shifts. After a disturbance event, forests experience an initial aggradation phase, in which the total biomass of the vegetation increases and the system acts as a carbon sink. After this initial phase, many forests level off and eventually show a decline in total aboveground biomass. In a study of the southern boreal forest in Quebec, total living aboveground biomass increased after fire until year 75, then plateaued at 144 years (Pare and Bergeron 1995). Amiro et al. (2000) report that in the Boreal Plains ecozone of Alberta, net primary productivity levels

off after 20 to 30 years following fire, and remains constant for 60 years. The factors leading to this slowdown in growth and eventual biomass loss are a subject of great debate for all of the forests in which they are observed (Gower et al. 1996). Some postulate that the loss of biomass is caused by nutrient limitation as living vegetation draws down the soil nutrient stores (Binkley et al. 1995, Pastor et al. 1987). Others have shown that in some cases the biomass loss is a function of succession, i.e., that later-successional species may not amass as much biomass as early-successional species (Pare and Bergeron 1995). In any case, the time since disturbance as well as the kind and intensity of disturbance, influence carbon storage in aboveground biomass. The trends for aggradation and biomass loss have been modeled in some cases to help landowners and foresters manage their forests for higher carbon accumulation (Rowland, 2001). Finding sites old enough to display this trend is difficult northwards within Canada, however, because the disturbance frequency is so high (Johnson 1992, Payette 1992).

Belowground biomass

Belowground biomass consists of coarse and fine roots, and is inherently more difficult to assess because of the process of digging up roots, and the disturbance involved. One approach is to include belowground biomass in allometric equations developed for boreal species, but accurately surveying fine roots in the first place still presents difficulty. In addition, fine root mass may correlate directly with various soil qualities such as forest floor nutrient levels, and therefore vary significantly between sites. Another approach is to assume that root respiration occurs in proportion to belowground biomass and to measure carbon dioxide efflux from the soil (Raich and

Nadelhoffer, 1989). Estimating fine root biomass is further complicated by high annual turnover rates. Even if an area is sampled directly, the roots present at any one time are only a portion of the roots produced in a growing season. Fine root production may occur in proportion to annual litter production. For instance at Hubbard Brook Experimental Forest, production of fine roots was found to be almost double that of leaves (Fahey and Hughes 1994). However, the nature of the relationship appears to vary with forest type (Raich and Nadelhoffer 1989).

Forest floor

For the purposes of this study, forest floor was defined as encompassing the following materials: woody debris ≤ 2.5 cm at center diameter, differentiable litter and debris, litter which is partially decomposed, and the Oa soil horizon consisting of completely undifferentiable organic matter. We did not include the “A” soil horizon because of the difficulty in determining its lower boundary in the field. Carbon in the forest floor (the soil organic layer) originates from annual litterfall, herb senescence, root turnover, and coarse woody debris. Species and stand type (pure versus mixed) affect both rates of litterfall and leaf litter decomposition rates (Cote and Fyles 1994). Williams and Gray (1974) estimate annual litterfall at 0.6-1.5 T/ha/year for arctic regions, 1.0-6.9 for cool temperate forests, 2.9-8.1 for warm temperate forests, and 5.5-15.3 for equatorial rainforests.

The carbon and nutrients from these various sources are taken up by living plants, decomposed to CO₂, or leached down into the mineral soil. The rate at which carbon is released depends on the activity level of detritivores, which in turn depends on abiotic

factors such as nutrient availability, moisture levels, and temperature. The quality of leaf litter may be referenced by the ratio of carbon to nutrients therein, notably carbon to nitrogen. In the case of leaf litter, the ratio of carbon to nitrogen is negatively correlated with the rate of decomposition. Forest floor nutrient levels are important to whole-system productivity since relatively little new nutrients enter the system each year (Reuss et al. 1996). Differences in carbon quality also affect rates of litter decomposition (Aber and Melillo 1991, p. 175). Moisture content directly affects aeration and gaseous diffusion. Williams and Gray (1974) point out that waterlogging to the point where leaf litter becomes an anaerobic environment for detritivores is not a common situation. In the context of a boreal forest, however, it is a seasonal reality. The forest floor dries progressively throughout the summer but for much of the year in the southern boreal forest it is poorly aerated.

Mineral Soil

For the purposes of this study, we considered soil to be the mineral layers below the Oa horizon. Senescent roots and dissolved organic carbon (DOC) leached from the forest floor constitute the two major inputs into the soil carbon pool, while the decomposition of soil organic matter to CO₂ represents the primary efflux. As is the case with the forest floor, waterlogging and cold temperatures inhibit soil microbe activity at least in the organically active A horizon, and in most cases the mineral soil is the largest carbon reservoir in the boreal forest. For instance, in sites dominated by black spruce at the northern and southern BOREAS study areas, 87-88% of ecosystem carbon was in the

soil (Gower et al, 1997). Soil carbon is also difficult to sample completely because the bedrock is often so far beneath the soil surface that not all the soil can be sampled.

Coarse Woody Detritus

Coarse woody detritus, or CWD, is defined as woody material that is not small enough or has not yet broken down to the point of inclusion in the forest floor pool, though the cutoff point is somewhat arbitrary; here, 2.5 cm. CWD can take the form of standing dead wood, snags, and fallen wood at various degrees of contact with the ground and in various stages of decomposition. It is a carbon pool that has been largely overlooked or underestimated until fairly recently (Harmon and Sexton, 1996). Inputs occur via self-thinning of branches and blow-downs of living and already-dead trees, as well as from violent disturbance events such as windstorms, wildfire, and timber harvesting. CWD is eventually assimilated into the forest floor and then the soil but is in many cases a significant carbon pool in its own right, depending on turnover times. CWD is often described as showing bimodality as the forest grows up after disturbance. At first the amount of dead and/or downed wood increases sharply due to the direct effects of the disturbance. As time passes that wood decomposes and is assimilated into the forest floor, and the mass of CWD declines. Eventually the stand ages to the point of tree senescence, and as mature trees die or lose branches, the pool of CWD increases again. In the case of timber harvest, CWD comes from slash, whose amount and distribution is determined by logging practices and the intended use of the lumber (i.e. pulpwood versus finishing wood). Because CWD is a major pathway for long-term

carbon storage in the soil, characterizing and quantifying this carbon pool is especially important.

DISTURBANCE IN THE BOREAL FOREST

Lightening-started wildfires, insect outbreaks, and timber harvest are the major disturbances in the boreal forest of North America. Insect outbreaks, such as spruce budworm, affect a greater total acreage than wildfires (Natural Resources Canada, 2001) and are certainly important from a commercial perspective: nearly 182,000 hectares were defoliated in 1997 (Johnston 2000). However, the effects of insect outbreaks differ from those caused by wildfire and harvest in terms of tree mortality, forest productivity, and long-term successional changes. Insect defoliators typically target conifers and may or may not cause damage sufficient to induce mortality. Insects can affect large areas, but an outbreak does not necessarily result in an even-aged forest. Because insect damage was not a major factor in the stands that we studied, I will not discuss this type of disturbance further.

In Manitoba, forested land accounts for 26.3 million hectares, out of 54.8 million hectares of total land. Approximately 60% is stocked with softwood species, and 20% each mixedwood and hardwood. In 1997 almost 42,000 hectares were burned in wildfires (Johnston, 2000), more than twice as much land area as the 15,544 hectares that were harvested. However the comparison is misleading because for the period 1990-2000 the average annual burned area was much greater, approximately 337,000 hectares. Spatially, burned and harvested areas tend to be rather disparate in Manitoba. Maps of fire frequency reveal a high concentration of firestarts in the northern half of the

province, while the area licensed to timber companies is predominantly in the central/western area. The forests we studied are within the overlap zone of the Manitoban Forest Management License Areas (Figure 2) and the northern fire belt.

Since 1920, fire incidence in Canada has increased steadily, though for the first four decades of the record the actual area burned per annum decreased. Since 1960, annual area burned has increased, though fire suppression efforts in some areas have also increased. Recent studies show that wildfires in unprotected areas of the Canadian boreal forest are much larger than fires in intensively protected regions (Stocks et al., 1996). In Manitoba specifically, the areas licensed for eventual timber removal are subject to especially intense fire protection (Natural Resources Canada, 2001). In the future it is likely that areas of fire suppression (and timber harvest) will increase relative to areas where fires are allowed to burn unchecked. Determining how the carbon distribution signature of harvested lands differs from fire-originated stands is important for improving the resolution of the terrestrial carbon budget in this region.

Fire as disturbance

Specific effects of fire on forest ecosystems include: 1) biomass combustion, 2) release/loss of nutrients in smoke and gas, 3) combustion of the soil organic layer, 4) increased soil pH due to cation leaching, 5) increased soil temperature due to increased solar radiation, and 6) stimulation of serotinous and semi-serotinous cones to open (Aber and Melillo, 1991, p. 270). Wildfire essentially restarts the successional clock by creating favorable light conditions and nutrient availability for recolonization. While hardwoods dominate early-successional systems due to their higher growth rates, fire also

prepares the substrate for conifer germination. Black spruce and jack pine both require seedbed such as moist rotten wood, burned peat strata, or mineral soil that is exposed or only thinly covered (Natural Resources Canada, 2001). After a fire, some percentage of black spruce boles are left standing, and the cones are retained until conditions permit their opening and dispersal. As the deciduous stands mature, shade-tolerant conifers such as black spruce, tamarack, and jack pine colonize the understory. Gradually the hardwood saplings are out-competed and the stands become dominated and overtopped by conifers. Time since fire is therefore a key determinant of species composition. Furthermore, species composition also influences the severity or spread of a fire because tree species vary in the flammability of their foliage and bole fuel.

Thus, the rate at which fire returns both affects and is affected by, the species composition of a forest. Fire return intervals vary globally and by ecozone. Estimates vary (Table 3) but a reasonable estimate for boreal forests in Manitoba is an average of 70-100 years. Due to storm patterns as well as the random nature of lightening strikes, however, some areas may burn more or less frequently than others. Examination of firestart incidence across many years shows that a NW-to-SE diagonal belt across northern Manitoba experiences much more frequent fire than the rest of the province (Natural Resources Canada, 2000). It is important to constrain estimates of fire return interval because many large-scale models of carbon flux rely on age class-dependent ecosystem characteristics.

Most of the carbon-cycle-oriented studies to date in the North American boreal forest have examined processes in naturally burned areas, most notably the Boreal Ecosystem Atmosphere Study (BOREAS) Northern Study Area (NSA) and Southern

Study Area (SSA). The NSA is located approximately 40-60 km west of Thompson, Manitoba, Canada, while the SSA is located in the Prince Albert National Park, Nipawin Provincial Forest region in central Saskatchewan, Canada (Gower et al. 1997). I use chronosequences and studies conducted at these two sites as comparisons for much of the data presented in this study because they are so well examined. The climate at the Wabowden study site is intermediate compared with these two areas (Table 4).

Logging as disturbance

Harvesting of trees by definition decreases local aboveground living biomass. Tree biomass is transported offsite for 1) combustion, 2) short-term storage such as paper products, or 3) long-term storage such as home construction. Depending on environmental regulations, slash is either left concentrated in piles at staging areas or at the site of tree harvest. This input of coarse woody debris is eventually integrated into the forest floor and then the soil substrate. Harvest also disturbs soil layers. Even in winter harvests when the ground is frozen, significant disturbance is possible, and in Manitoba virtually all logging takes place in the summer months when the soil is not frozen. Heavy equipment and the dragging of trees mix carbon from the forest floor into the mineral soil. “A study of 13 partially cut hardwood stands in New York found that skid trails covered an average of 38% of the area, with 99% of skid trail area disturbed (Nyland and Gabriel 1971). Three whole-tree harvested sites in New England had 8 to 18% of mineral soil exposed; some type of disturbance affected 71 to 92% of the area (Martin 1988)...Ryan and others (1992) found mineral soil exposed in 25% of a whole-tree harvested watershed at Hubbard Brook. Buried organic horizons were found in 10%

of the area” (Yanai et al, in review). Besides physical mixing, organic and mineral soil carbon stores may be affected by post-harvest soil warming. The absence of a forest canopy increases solar radiation on the forest floor, but the degree to which soil warming occurs, as well as its effects on decomposition rates, is not known.

Species composition during succession, as well as the rate of regeneration, may differ from that of post-fire boreal forests. Commercial harvesting in Manitoba target conifers, so mature trembling aspen, balsam poplar, and paper birch may be left standing after the cut. Trembling aspens primarily reproduce vegetatively, and heavy machinery has been shown to damage their suckers (Peltzer et al. 2000). During harvest, black spruce cones are either transported off-site with the timber or integrated into the forest floor on sites that may or may not be suitable for germination. Because forest managers in Manitoba are primarily interested in regrowing black spruce at harvested sites, they use techniques such as scarification, seeding, herbiciding of hardwoods, and even replanting young black spruce trees to encourage commercially valuable stands.

While much effort has gone into studying the effects of fire and insect outbreaks on boreal forests for economic interests, far less effort has been expended studying the actual effects of commercial harvesting and subsequent site preparation. In the long run, accurately characterizing harvested regions may be easier since there are only certain areas that are profitable to harvest. Due to a number of factors, the state of the forestry industry in Manitoba is much more limited than in the Pacific Northwest and eastern provinces. Manitoba’s forest cover is not significantly less dense than its neighbors (Figure 3) but the forests are much less productive. The volume of coniferous and deciduous wood per hectare in Manitoba is lower than in all other southern provinces

(Figure 4) because of environmental constraints on growth rates. The areas licensed for timber harvest in Manitoba are primary forest, so secondary forest regrowth does not constrain timber removal rates. Nonetheless, in 1997 (most recent data available) 2.1 million cubic meters of wood were harvested in Manitoba, well below the annual allowable harvest of 9.7 million cubic meters (Natural Resources Canada, 2001). Along with the economic climate, access and transportation costs seem to control the rate of harvest. Excluding the northern territories, Manitoba has the most limited road system (Figure 5). Snow routes and winter highways connect much more of the province when there is snow cover, but timber harvesting is primarily conducted in the summer months. Between permafrost and swamplands, road construction is a costly enterprise for timber companies in Manitoba and harvest areas tend to be clustered around provincial highways.

MATERIALS AND METHODS

Site Description

The study site is located off of Route 6, southeast of Wabowden, Manitoba, Canada, at 98°38' N, 54°55' W (Figure 6 and Figure 7). It is several hundred kilometers south of the BOREAS NSA. Elevations in the surrounding area range from 180 to 314 meters above sea level. The soils are characterized as Mesisols and Grey Luvisols (CANSIS 2001). Surficial geology for this region of Manitoba is thick and continuous till overlaid with silt and clay, and occasional organic deposits (bogs, fens, and swamp areas). Occasional sand ridges were underlain with clay in all areas sampled, and rocks are rare in the first half-meter of soil (personal observation). Mean January temperatures range from -22.7°C to -24.7°C , while mean July temperatures range from 15.9°C to 18.5°C . Mean annual rainfall is 315mm, while mean annual snowfall is 147.5cm.

Study Design

The four stands are located along Rt. 373 between the "18" and "38" kilometer markers (Figure 7). The chronosequence consists of stands aged 11, 18, 30, and approximately 65 years (hereby referred to as 1990, 1983, 1971, and 1935). In using a chronosequence we substitute space for time and rely on the assumption that age is the only factor varying between sites. However, because commercial timber harvesting is a relatively recent phenomenon in this area of Manitoba, the oldest harvested sites available were 31 years old, though not actually accessible. Therefore the oldest stand we were able to include in the chronosequence was cut in 1971. All stands were all harvested for softwoods, and they were all harvested after clear-cutting became a

common practice. We therefore see less variability in logging practice than has been experienced in other chronosequence studies (Yanai et al, in review) and are more able to attribute inter-site differences to stand age rather than time of cutting. However, the recent advent of clearcutting in this locale means that there are no mature stands with which to compare the young stands. We therefore included a fire-originated stand aged at approximately 65 years, which is geographically proximate to the other three. This mature stand may be viewed as the state from which the other stands were taken when they were cut, but the mature stand should not be seen as the endpoint towards which the harvested stands are eventually progressing. It is the product of a different disturbance history and as an older stand gives some general measure of how much biomass can accumulate as a stand ages.

The study design consisted of four blocks of two plots each at the four stands (Figure 8). Plots in each stand were assessed individually for vegetation and soil characteristics, and at some future date will be separated into fertilized and control treatments for further study. At each plot in every block, four samples were taken of: understory herbs, forest floor/organic soil, mineral soil at 0-15 cm depth, and mineral soil at 15-30 cm depth. Coarse woody debris was sampled using one chainsaw transects per block. Aboveground woody biomass was sampled using 2-4 variable radius plots within each marked plot.

To convert the stem density measured in individual plots into units of mass per hectare, site-specific allometric equations were developed, relating the biomass of various aboveground components (i.e., stem mass, branch mass, foliage mass, etc.) to stem diameter at 1.37m. Equations were developed for jack pine, black spruce, and trembling

aspen, the most common species at all four sites, as well as for balsam poplar at the youngest stand. Equations for balsam poplar were applied at all stands to the two understory shrubs occasionally present, willow and green alder, because of their similar morphology. Likewise, equations for trembling aspen were applied to paper birch at the 1971 stand (the only stand where that species was present) because their morphology was deemed similar enough not to introduce a large amount of error in biomass calculation, and because we had a limited amount of time and human resources to devote to destructive sampling. The allometric equations were used to convert the variable radius plots into a mass-per-hectare unit. Belowground biomass was not directly addressed in the allometry component of this study due to human resources and the time required to dig up roots. Although roots ≤ 2.5 cm were included in the forest floor samples, coarse roots were not included in any sample category and biomass estimates are therefore low.

All carbon and nutrient analyses were performed by the University of Wisconsin Soil and Plant Analysis Lab, 5711 Mineral Point Rd, Madison, Wisconsin 53705.

Carbon Reservoirs Defined

The reservoirs assessed for carbon content were: aboveground biomass, woody debris, forest floor leaf litter, and soil substrate down to 30 cm.

Aboveground biomass consists of trees, shrubs, and herbs. To sample trees, two to four variable radius plots (VRP's) were set up in each plot at each site, using the prism appropriate for site stem density. Diameter at breast height (DBH, 1.37 meters) and species were recorded for every stem within the VRP's. These data were then applied to site-specific allometric equations of the form:

$$\text{Log}(C) = a + (b * \log \text{DBH})$$

where C is the mass of a given component (i.e. stem mass, branch mass, foliage mass, etc.), and a and b are regression coefficients. Derivation of the allometric equations is described below. Biomass of the various tree components was then converted to mass carbon, with the assumption that woody tissue was 50% carbon by dry weight, and foliage was 45% carbon by dry weight (Gower et al. 1997). Shrubs were not sampled separately, as they tended to have a DBH and were therefore included in the VRPs. Understory herbs were sampled in randomly situated quarter-meter clip plots within the stands, dried immediately at 65°C, and weighed. Understory was assumed to average 50% carbon by dry weight. Four samples were collected from each plot at each site, yielding 32 samples per site.

Forest floor and the soil organic layer were sampled using PVC collars that were placed inside the understory clip plots and excavated down to mineral soil. Woody debris and roots less than 2.5 cm in diameter were included in the forest floor inventory, as were mosses, leaves, and humus. Four samples were collected from each plot at each site, for a total of 32 samples per site. The samples were collected between June 21, 2001 and June 27, 2001. They were stored in a cool basement and taken to Madison, WI one month later, where they were dried at 65° C, weighed, ground, and analyzed for carbon and nitrogen content. Carbon and nitrogen were calculated as a percent of total dry sample weight, therefore eliminating the need to dry-ash every sample to correct for mineral soil contamination.

Mineral soil samples were taken using a double-cylinder, hammer-driven corer. The outer cylinder absorbs most of the hammer impact to prevent the sample in the inner

cylinder from becoming compacted. The core cylinder was 15 cm in length, and 4.65 cm in diameter. Samples were taken at depths of 0-15 cm and 15-30 cm in the mineral soil. Four soil samples from each depth were taken from each plot (at the forest floor removal spots), between June 21, 2001 and July 7, 2001. The samples were stored for approximately one month, then dried at 65° C, weighed, ground, and analyzed for pH, organic matter, and nutrient content.

Coarse woody debris consists of fallen logs, branches and sticks greater than 2.5 cm in diameter measured in the middle of their length, as well as snags less than 1.37 m off the ground. Methods for CWD evaluation were derived from Harmon and Sexton, 1996. Snags over breast height were sampled at the same time as trees, their DBH measured and their height either measured or estimated. Snags less than breast height (leaning, not resting on the ground) were included in the coarse woody debris survey.

One-meter wide transects were cut out with chainsaws along the outside of one randomly chosen border of one plot for each block, for a total of four cut transects per site. All CWD was collected and sorted into three size classes and three decay classes. The size classes were as follows: small = 2.5-5 cm diameter, medium = 5-10 cm diameter, large = 10+ cm diameter. The decay classes were numbered 1,2, and 3 and defined as follows: 1 = chaining pin would stick in <1/8th inch; 2 = chaining pin would stick in a few inches but not go all the way through; and 3 = chaining pin would stick easily all the way through a piece of wood. Objectivity was maintained by the same field crew of three collectively assessing CWD at each site. Therefore there are nine different categories, though proportioning between categories was not of primary interest. The size and decay classes were utilized primarily to fine-tune the water content estimates, so a sample from

each size and decay class was taken at each block to dry. Dry/wet ratios for the samples were applied to the field weights, which yielded a measure of CWD dry mass per hectare. Dry mass was assumed to be 50% carbon. The cut transects may underestimate actual CWD because of the difficulty in completely removing wood that was in an advanced state of decay. Furthermore, it proved extremely difficult to completely extract stumps by cutting them out; measuring their dimensions might have given a more accurate portrayal.

Site-specific allometry

Site-specific allometric equations were developed for the three most common species at all four sites: trembling aspen, black spruce, and jack pine, as well as balsam poplar at the 1990 stand. Tree harvest was conducted between July 11, 2001 and July 19, 2001. Based on the variable radius plot data, each species was divided into three DBH classes at each site. Two trees from each size class were harvested, and four of those were processed as follows ($n = 20$ for aspen, $n = 18$ for black spruce and jack pine, $n=6$ for balsam poplar).

DBH was recorded before felling. Immediately upon felling we recorded: tree height, height to base of live crown, and length of live crown. The live canopy was divided into thirds, and the lengths of two representative branches from each canopy third were recorded. The tree was then limbed and the branches were weighed in bundles according to their canopy position. Dead branches were removed from the canopy bundles and weighed all together. The tree stem was then cut into 2-meter sections and weighed. All field weights were taken on 50-kg and 100-kg hanging scales. Since water

content is not constant throughout a stem, stem disks, or “cookies” were cut from the bottom end of each 2-m section in the field. Less than eight hours later, the stem disks were weighed on an electronic balance to ± 0.01 g. They were stored in a cool basement until they could be taken to the lab in Wisconsin, where they were subsequently dried at 65°C and reweighed. These moisture contents were then applied to the respective stem sections to calculate dry masses.

Field branch weights were also corrected for water content, and analyzed for old wood:new wood and old foliage:new foliage ratios. One sample branch was selected from each canopy third on each tree. In the case of the aspen samples, all foliage was new foliage, so all new growth was clipped off and separated into branch and foliage. Old branch, new branch, and new foliage were all weighed before drying. For the conifers, all of the new growth was clipped off and depending on the amount, either all of it or a subsample was separated into branch and foliage. These were dried to give dry new foliage to new woody tissue ratios. The tissue from previous years was first dried and then separated into foliage and wood, since it is possible to simply shake the needles off of larger twigs once they are dry. Based on the dry weights, average ratios of new foliage to new wood to old foliage to old wood were derived. Relating these dry ratios to the branch weight measurements taken in the field proved difficult, however.

Correction Branches

The complication arose that we were unable to separate all the branches into components immediately in Canada, and additionally that immediate drying would have been impossible at any rate. All the branch samples were stored in a cold room until they

could be transported (unrefrigerated) to the University of Wisconsin lab in Madison. They were stored for approximately two weeks, until August 1, 2001, at which point they made the two-day journey to the 0° C cold room in Madison. They were processed over the next week and a half but it was visibly evident that many of the branches, aspen and conifer alike, had lost a significant amount of moisture by that point. Additionally, many of the aspen samples were clearly in various stages of molding and decay. Therefore the decision was made to dry the aspen and balsam poplar branches immediately and the conifer branches as soon as the new growth was clipped off.

To achieve estimates of branch and foliage water content, another set of branch samples was collected on August 11, 2001. We used two DBH size classes for each species at each site, and collected samples from one tree in each size class. For the trees in sites other than the 1990 stand, canopy thirds were estimated from the ground, as branches were removed by shooting them down with a shotgun rather than felling entire trees. DBH's for these trees were also recorded. These "correction" branches were transported to Madison, Wisconsin immediately, stored in the 0° cold room, and processed within five days of their arrival. Aspen and balsam poplar branches were processed first since they were the most susceptible to desiccation. New growth and old tissue were separated, then foliage and woody tissue were separated. The components were weighed to ± 0.01 g, dried to constant mass and then reweighed. Moisture contents for each branch component turned out to be fairly consistent by site (Table 5). These average moisture contents were then applied to the dry weight proportions of the original sample branches to achieve simulated wet weight proportions. The wet weight proportions were then applied to the field branch bundle weights. The issue must be

addressed that the “correction” branches were collected after almost three more weeks of dry summer weather had passed. In situ tree tissue moisture content may have changed between the time of the initial allometry harvest and the collection of the correction branches. The reported allometric equations may therefore be biased due to inaccuracies in the estimated moisture contents of the branch tissues. We felt, however, that the error so introduced would be less than if the extremely low moisture contents of the original sample branches at the time of processing were used.

Statistical Analysis

All carbon pools were subjected to a one-way analysis of variance, with data grouped by block. In our CWD survey we took only one sample per block, but for the rest of the carbon pools, at least eight samples were averaged to achieve a block average. The four block averages were then compared to calculated standard deviations at each site. This is an extremely conservative method because for each carbon pool there is essentially a sample size of four at each site. However we did not think it justified to treat each plot within a block as a separate sample because they were not independent; in every case there was only a 5-meter buffer between plots. We used a regression analysis for tree biomass components to derive allometric coefficients. Because the data were log-log transformed, a correction factor was applied as per Sprugel (1984).

RESULTS

COMPONENT POOLS OF CARBON

Carbon in aboveground tree biomass increased steadily with time since disturbance ($F < .0001$) with all stands significantly differentiated from each other except the 1983 and 1971 stands (Figure 9). Relative size of the aboveground biomass pool also increased with stand age from 9% of total ecosystem carbon (TEC) in the 1990 stand to 39% of TEC in the 1935 stand (Table 6).

Soil organic carbon stores to a depth of 30 cm were similar in each stand both in magnitude and percent of TEC. Stores ranged from 46.2 to 53.0 t C ha⁻¹, and 37-44% of TEC. The 1935 stand had the most SOC, equal in magnitude to the living aboveground biomass pool for that stand. The chronosequence of harvested stands shows a non-significant trend for SOC, which decreases slightly with time since harvest. None of the stands were significantly different from one another ($F = 0.2491$), primarily because of the large standard deviations at the 1990 and 1971 stands. Because the mineral soil was only sampled to a depth of 30 cm, all values reported are underestimates of actual carbon stores in the soil. The 1935 and 1990 stands both exhibit significantly more SOC at the 0-15 cm depth than at the 15-30 cm depth ($F = 0.0011$ and 0.0006 , respectively) (Figure 10). The 1983 and 1971 stands show the two different strata to be indistinguishable in terms of organic carbon, though the 1971 stand is slightly more partitioned. Although the shallow soil in the 1971 stand does not contain increased organic carbon relative to the 1983 stand, the deeper soil has decreased organic carbon.

Carbon in the forest floor carbon is highest in the youngest stand and lower in the other three stands, but the large standard deviation for the youngest stand makes the

difference statistically insignificant ($F = 0.113$). None of the stands differ significantly from one another in the net amount of carbon in their forest floors, but the relative amounts decrease from 36% of TEC in the 1990 stand to 17% of TEC in the 1935 stand. The 1971 and 1983 stands both had approximately 30% less organic carbon than the 1990 stand. That the smallest amount of forest floor carbon is found in the mature, uncut stand is an unexpected result, and is examined further in the Discussion. These values include carbon from fine roots, which technically belong in the tree and/or understory biomass carbon pool, and are therefore overestimates. The amount of forest floor carbon attributable to fine roots likely increases with aboveground biomass and therefore stand age, but the actual magnitude of this “crossover” pool is not known.

Stand age had a significant effect on the coarse woody debris carbon pool ($F = 0.0112$), primarily because the 1990 cut had such massive amounts of debris. CWD exhibits bimodality, declining sharply from 15.6 t C ha⁻¹ in the 1990 stand to 3.0 t C ha⁻¹ in the 1971 stand as would be expected of slash decay, and then increasing in the 1935 stand, as might be expected for stands of this age (Table 6). Commercial harvesting sends a pulse of slash into the CWD pool, but initial amounts for these stands are not known. However, after eleven years of decomposition, the 1990 stand had 6.5 t C ha⁻¹ more in CWD than did the 1935 stand.

For all four stands, carbon in understory biomass represented < 1% of total ecosystem carbon stores. Stand age did not have a significant effect on understory mass per hectare ($F = 0.3069$). This variability was expected due to canopy patchiness. The understory is the most insignificant ecosystem carbon pool.

Total Ecosystem Carbon

The uncut stand had the greatest amount of total ecosystem carbon, followed by the 1990, 1971, and 1983 stands (Table 6, Figure 11). The higher TEC value of 143.32 t ha⁻¹ in the 1935 stand was not significantly higher than the 122.47 t ha⁻¹ in the youngest stand, but is significantly higher than the values from the two middle-aged stands. The higher value in the 1935 stand results from its high values of aboveground biomass, while in the 1990 stand forest floor carbon accounts for a comparable percent of TEC. In each of the harvest-originated stands, the largest carbon store was the mineral soil, and in the 1935 stand soil organic carbon was approximately equal to aboveground biomass carbon. In each of the three younger stands, the second-largest carbon store was the forest floor; in the 1935 stand the forest floor was the third-largest store.

Stand Composition

Tree stem diameter at 1.37 m was generally a good predictor of component biomass, though fits were not as good for foliage as for the other components (Table 7). Aspen decreased in relative importance from 80% of total biomass in the 1990 stand, to 55% of total biomass in the mature stand, while black spruce ranged from 2% of total biomass in the 1990 stand to 36% in the mature stand (Figure 12). Each of the harvested stands had one other species accounting for 12-15% of total biomass; balsam poplar in the 1990 stand, jack pine in the 1983 stand, and paper birch in the 1971 stand. The mature stand had approximately 6% of its biomass in jack pine but was 91% aspen and black spruce.

Total basal area increased as well, from approximately 5 m²/ha in the 1990 stand, to 25 m²/ha in the mature stand (Table 2). Deciduous species decreased from 97% of relative basal area (RBA) in the 1990 stand to 56% of RBA in the mature stand. Aspen was the dominant species in every stand, occupying from 84% of RBA in the 1990 stand to 56% of RBA in the mature stand (Figure 13). Black spruce gradually increased in the harvested stands from <1% of RBA in the 1990 stand, to approximately 5% in the 1971 stand. In the mature, uncut stand however, black spruce accounted for 35% of RBA. Jack pine accounted for 3-9% of RBA in the 1990, 1971, and mature stands, but basal area in the 1983 stand was 21% jack pine. Balsam poplar occupied 12% of RBA in the 1990 stand and 3% of RBA in the mature stand, but was not present at the other two. In the 1971 stand paper birch accounted for 1.5% of RBA, and alder 1%.

DISCUSSION

The changes in carbon storage as ecosystems age after harvesting bear on several issues of forest management and global carbon cycling. Below, I discuss changes in total ecosystem carbon and how they compare to those found in the literature. I compare the aboveground biomass data to other boreal chronosequences and mature stands in various locations. I address the forest floor decrease seen in this study in the context of Covington's (1981) controversial response curve. I discuss the mineral soil stability and CWD carbon stores. I address how changes in species relative abundance, especially the increase in black spruce through time, are relevant to forest management. Finally, I discuss the implications of this study for logging in the boreal forest and its importance relative to the global carbon cycle. Sources of error are identified, and areas of future research suggested.

Total Ecosystem Carbon

I have found no comparable boreal harvested chronosequences with which to contrast this dataset. Turner et al. (1995) present generalized estimates of total ecosystem carbon for large regions of the United States. The North Central and North East regions are listed as containing approximately 190 t C ha⁻¹ and 220 t C ha⁻¹, respectively. In contrast, TEC in the harvested stands in Wabowden ranged from 112.5 t C ha⁻¹ to 143.3 t C ha⁻¹ (Table 6). Mature aspen-dominated stands that originated from fire at the BOREAS NSA and SSA had TEC values of 176.4 t C ha⁻¹ and 158.4 t C ha⁻¹, respectively (Gower et al. 1997). In the NSA, mineral soil accounted for 55% of TEC and living vegetation 32% (Gower et al. 1997), whereas in the Wabowden mature stand,

the two carbon pools were nearly equal in importance at 37% and 39% of TEC, respectively. This difference may be due to the fact that mineral soils at the NSA were sampled to a depth of 70 cm, whereas in the Wabowden stands mineral soils were sampled to 30 cm and their carbon content was therefore underestimated. Sampling the mineral soil to a greater depth would not only increase its relative importance but would also increase TEC for all of the Wabowden stands. To simulate doubling the sampling depth, we may double the SOC values observed in the 1935 stand, giving a TEC value of 196.4 t C ha⁻¹. This value is almost certainly an overestimate for the Wabowden sites because SOC decreases with depth in undisturbed sites (Figure 10), but it provides an upper limit to soil carbon stores and therefore TEC. Another approach is to adjust the TEC by changing the observed aboveground biomass carbon value of 53.03 t ha⁻¹ from 39% of TEC to 32% of TEC. The resulting TEC value is 173.6, which is similar to that of the mature NSA sites. The SOC for this scenario would then be 83.3 t ha⁻¹.

The three younger harvested stands are not significantly different from one another in terms of TEC, but the carbon distribution changes with stand age. Individual carbon stores are discussed below.

Aboveground biomass

The growth potential for the younger stands in Manitoba provides a context for understanding the current aboveground biomass found in these stands. The 1935 stand is more similar in its aboveground biomass to northern hardwood sites than to other boreal sites of comparable age. Biomass values for the 1935 stand are higher than those reported for fire-originated boreal sites, and somewhat lower than those found in northern

hardwood forests. The 65-year old Wabowden stand had approximately 111 t ha^{-1} biomass (roughly double the carbon amounts), while a 71-year old black spruce stand at the BOREAS NSA had 96 t ha^{-1} aboveground biomass. At the BOREAS SSA in Saskatchewan, a jack pine stand aged 65 years had 62 t ha^{-1} aboveground biomass. Some of this biomass discrepancy may be a function of species composition, as hardwoods generally grow faster than conifers. A 63-year old stand in Wisconsin dominated by trembling aspen had approximately 128 t ha^{-1} biomass (Pare and Bergeron 1995). Pare and Bergeron (1995) also report that in a birch-fir-aspen forest in Quebec, aboveground biomass increased to a maximum of 173 t ha^{-1} at 75 years and then declined progressively. For that particular study the authors acknowledge that the biomass value(s) are high, given that the climate of the study area is typical of the boreal zone. However, younger coniferous forests south of the continental boreal zone show trends similar to the Wisconsin site. Sprugel (1984) reports that a 55-year old balsam fir forest in New York averaged 118 t ha^{-1} biomass, while a 40-year old balsam fir forest in New Brunswick ranged from 103 to 154 t ha^{-1} in aboveground biomass (Baskerville 1965).

Following harvest, the aspen stands in Wabowden also accumulate aboveground biomass faster than fire-originated black spruce and jack pine stands at the NSA and SSA (Figure 14). For instance, a 12-year old jack pine stand at the SSA had 5.2 t ha^{-1} aboveground biomass (Howard, personal communication) compared to 21.3 t ha^{-1} in the Wabowden 1990 stand. A 20-year old black spruce stand at the NSA had 6.4 t ha^{-1} aboveground biomass (Bond-Lamberty, personal comm.), whereas a 25-year old jack pine stand at the SSA had 33.6 t ha^{-1} aboveground biomass (Howard, personal comm.). Both of these values are low relative to the 47.0 t ha^{-1} biomass in the Wabowden 1983

stand (Table 6). For both of these comparison sites, the slower growth rates of conifers than hardwoods probably explain most of the biomass disparity. The key question, then, is the extent of the influence of disturbance history on succession and species relative importance.

Peltzer et al. (2000) provide a useful comparison of disturbance types and subsequent effects on plant diversity and tree responses. Their study was conducted at the SSA, and disturbance treatments included wildfire, natural regeneration after harvest, and several methods of silvicultural site preparation as well as control stands. The authors found that 10-12 years after treatment, aspen density was significantly lower in two of the silvicultural treatments than in the burned or naturally regenerated stands. White spruce grew fastest in one of the intense silvicultural treatments, but volunteer seedlings were most dense for the burned treatment. The highest density of aspen was found at the burned sites as well, but the same sites showed the slowest growth for aspen, indicating that perhaps increased competition was limiting their growth (Peltzer et al. 2000). Taken together, these results suggest that as harvesting disturbance increases, growing conditions favor aspen over white spruce. More generally, timber harvest decreases conifer establishment rate, though subsequent site preparation may be beneficial to the seedlings that do grow or are planted. This study helps to explain why the aboveground biomass values are so much higher for the Wabowden stands than for conifer-dominated sites of similar ages. I predict that when the harvested stands reach 65 years, they will have more aboveground biomass than the 1935 stand does at the moment because aspen will continue to be more abundant than black spruce. Trends in species composition are discussed in more detail below.

Forest floor

The nature of the forest floor response to disturbance varies with disturbance type. Nalder and Wein (1999) found that following fire in western Canada, forest floor carbon was positively related to stand age in jack pine and trembling aspen sites, though also affected by species and climatic zone. In contrast, the fire-originated jack pine chronosequence at the BOREAS SSA shows a decrease in forest floor mass, from 26.9 t C ha⁻¹ in a 1-year old stand to 8.6 in a 65-year old stand (Figure 15). Brais et al (1995) found that 5 to 12 years after harvest, four stands in northwestern Quebec had about half as much forest floor mass as the paired four uncut stands (reported in Yanai et al., in review). Covington (1981) describes a northern hardwood forest floor response to harvesting (the “Covington curve”) in which cut stands lose 50% of their forest floor mass within 20 years, then slowly recover, with old stands having the most massive forest floors. This model, and the studies it instigated, have recently been re-examined and criticized (Yanai et al., in review).

Covington originally posited accelerated decomposition and changes in litter inputs as explanations for the drastic post-harvest loss in forest floor mass. As other researchers attempted to reproduce Covington’s results with varying degrees of success, an alternative explanation emerged. Yanai et al. (in review) propose that logging practices employed at the time of harvesting are more important than stand age in determining forest floor dynamics after harvest. During commercial harvesting activity, some degree of physical mixing occurs between the forest floor and the mineral soil. The degree of mixing changed over the timescale represented in Covington’s chronosequence as logging equipment evolved from horse teams to tracked vehicles such as crawlers, and

then to wheeled vehicles such as skidders. In the context of the Covington curve, two important results from this study are highlighted. The first is the decline in forest floor carbon following harvest; the second is the relatively small amount of forest floor carbon in the oldest stand.

The decrease in forest floor carbon with stand age after harvest, though not statistically significant (Table 6), is important because the logging practices were relatively uniform between these three stands. All of the stands in the harvested chronosequence were cut after the popularization of mechanical clear-cutting and the introduction of wheeled skidders. Furthermore, they were all harvested in the summer months when the ground was not frozen, though specific weather conditions and soil moisture levels are not known. (Dry soils are less prone to rutting.)

There is evidence, however, that the 1971 and 1983 stands may have been subjected to more disturbance than the 1990 stand, which may explain the greater amount of forest floor carbon in the youngest stand. In the 1935 and 1990 stands, soil carbon levels are well partitioned between the two arbitrary sample depths, with the more shallow strata having significantly more organic carbon (Figure 10). In the 1983 and 1971 stands, however, the mineral soil strata are uniform in their carbon storage, suggesting that more mixing may have taken place there. These two stands also have similar amounts of forest floor carbon, which are less than that in the 1990 stand. Assuming that the forest floor carbon decrease is caused by forest floor and mineral soil mixing, one might then expect to see elevated levels of total soil organic carbon where forest floor carbon declines following logging. This hypothesis is not supported by the data (Figures 10 and 11). If the physical disturbance due to harvesting was actually

similar at each of the Wabowden stands, then it is important to identify the mechanism by which the amount of carbon in the forest floor declines.

If the 1935 and 1990 stands are examined as before logging/after logging snapshots, we see an increase of almost 100% in forest floor carbon following harvest (43.8 t C ha⁻¹ in the 1990 stand vs. 24.8 t C ha⁻¹ in the 1935 stand). In Covington's study, the recently harvested stands showed a marginal *decrease* in forest floor organic matter compared with an uncut stand. I would attribute the increase in forest floor carbon following harvest to input from the biomass pool via woody debris and root death. Johnson et al (1985) also report an increase in forest floor mass immediately following harvesting in an oak forest in Virginia. Within two years however, forest floor mass had declined to pre-harvest levels, which is not the case for the 1990 stand in Manitoba.

The long-term history of the Virginian stand is not known, but the stands cut in Covington's study were secondary forest, while those in Manitoba were primary. The low forest floor carbon in the 1935 stand may therefore be a function of its fire-origination. Fire has the potential not only to burn much of the woody debris that might eventually end up in the forest floor carbon pool, but also to burn the organic material that is already there. Fires in black spruce-lichen forests burn as much as 70-90% of ground layer biomass (reported in AuClair 1983). In Alaskan black spruce forests, 40-60% of ground layer biomass is lost during fire (Dyrness and Norum, 1983). Thus, the immediate effect of fire is to reduce forest floor carbon, while the immediate effect of harvesting is to increase it. The 1935 stand, then, may have started out with less carbon in its forest floor after the fire than the harvested stands did after cutting.

Net amounts of forest floor carbon at the SSA jack pine fire chronosequence were less than for the Wabowden chronosequence, and decreased continually from the 1-year old stand through the 65-year old stand (Figure 15). The lingering elevated forest floor mass seen in the Wabowden chronosequence may therefore be a function of logging disturbance coupled with the slow decomposition rates characteristic of the region.

Mineral soil

The mineral soil carbon values from this study (Table 6) are higher than those found by Vogel and Gower (1998) in the BOREAS NSA and SSA. Vogel and Gower (1998) sampled to a depth of 1 m and measured 53 t C ha⁻¹ in mature jack pine stands with green alder in the understory, compared to 53.03 t C ha⁻¹ in the first 30 cm of mineral soil at the Wabowden 1935 stand. At the NSA, jack pine stands with no green alder had significantly less SOC (34.7 t C ha⁻¹), while mature jack pine stands at the SSA with and without green alder had 27.6 t C ha⁻¹ and 18.2 t C ha⁻¹, respectively. A 5-year old jack pine stand at the BOREAS SSA had 22.0 t C ha⁻¹ while a 10-year old and a 27-year old site had 27.9 and 27.8 t C ha⁻¹, respectively (Howard, personal comm.). The decline in mineral soil carbon seen in the Wabowden stands, though statistically insignificant, is interesting in light of this contrasting increase.

It is unlikely that decreases in inputs of carbon from leaf litter and fine wood litter are responsible for the decrease in SOC. Litter inputs to the forest floor recover fairly quickly after harvesting (Covington and Aber 1980), though it is possible that this recovery is prolonged at higher latitudes. Elevated soil temperatures, a documented consequence of wildfire, may explain some of the carbon loss in this harvest scenario.

Kasischke et al (1995) conclude that, for boreal forests in general, increased soil temperatures cause 20% of the ground layer carbon to be decomposed during the 25 years after fire. Van Cleve et al (1983) found that Alaskan black spruce sites lost >20% of the ground layer carbon when heated by an average 9°C over three years. In Fairbanks, Alaska, 7 years following forest fire, the depth of the active layer had increased from 40 to 140 cm and was still increasing, due to reduction or elimination of the forest floor layer (Dyrness et al 1986). Harvested areas are also subject to increased solar radiation on the forest floor, and mineral soil is even exposed in local areas of high disturbance, such as skid trails. One important difference is that for much of the rest of the boreal forest, permafrost extends up into the dead peat layers, signifying a huge potential pool of carbon that could be released. In the case of the sites in this study, deep peat layers were not present. However, increased decomposition due to increased soil temperatures may help to explain the decreasing soil carbon levels in the young harvested stands.

Coarse Woody Debris

Carbon in CWD is higher in the youngest and oldest stands than in the two stands of intermediate age (Table 6), though the 1990 stand had the most CWD carbon of all. Because of the different stand histories, the 1935 stand may not be a prediction of future CWD levels for the other stands. The 1935 stand may not be at the age of maximum debris production yet, and it may take harvested forests more or less time than burned forests to reach the state of natural tree senescence. Carbon in CWD at the SSA jack pine chronosequence ranges from 5.4 to 2.0 t C ha⁻¹, and decreases with stand age (Howard, personal comm.). However, at the NSA black spruce chronosequence, CWD

total mass (not mass carbon) ranges from 4.1 to 177.5 t ha⁻¹ and does not correlate with stand age at all (Bond-Lamberty, personal comm.) (Figure 16). This stochasticity indicates the importance of fire intensity in determining post-fire ecosystem carbon characteristics. It also illustrates the relative predictability of CWD in harvested forests because the target market generally determines the amount of slash left behind.

Species Composition

Trends in species relative abundances were in agreement with the findings of Peltzer et al. (2000), which are discussed above. From the 1990 to the 1971 stand, deciduous trees decreased from 96.5% to 86.5% of relative basal area, and from 93.9% to 88.4% of aboveground biomass for trees (Figures 12 and 13). After 30 years of post-harvest succession, the biomass was still almost 90% deciduous. In the 1935 stand the picture was quite different; deciduous trees represented only 58.5% of tree aboveground biomass and 56.4% of relative basal area. Here it is necessary to separate the effects of disturbance type from the effects of stand age. Black spruce increases in relative importance with stand age after harvest, but in the mature, fire-originated stand its relative importance is an order of magnitude greater. Aspen relative biomass decreases by 4% over the 21 years represented by the 1990 and 1971 stands. The difference between aspen relative biomass in the 1971 and 1935 stands, however, represents a decrease of 20%. Therefore the relationship of species composition to stand age changes with disturbance type in the boreal forest.

Conclusions

The harvested chronosequence in Wabowden differs from fire-originated stands at the NSA and SSA primarily in its storage of aboveground carbon. In general, the aboveground biomass production rate is greater for the Wabowden sequence. Over the course of the chronosequence, the CWD and forest floor carbon pools decrease, but the increase in aboveground biomass more than compensates for this decrease. Still, CWD and forest floor carbon pools are greater than those in fire-originated stands, and contribute to overall elevated TEC values. It would seem, then, that harvesting increases ecosystem carbon storage outside of the living biomass pool. However, one issue that has not yet been discussed yet is the formation of charcoal by boreal forest fires. Charcoal is an inert form of carbon that may be integrated into the mineral soil but is not released to the atmosphere. The carbon in the CWD and forest floor of the Wabowden stands will either be mineralized or integrated into the mineral soil, but in either case its release to the atmospheric carbon pool is only a matter of turnover time.

A major finding of this study is that even un-harvested stands in this area of Manitoba have different carbon distributions than stands in other areas of the boreal forest. Furthermore, harvested stands behave differently still, and the amount of harvested land relative to land affected solely by wildfire is only going to increase. There are two main uses for the data contained in this study. The first is to constrain existing and future models of carbon cycling on a landscape level. Once the carbon distribution pattern of a given category of land has been determined (for instance, harvested stands 10-15 years in age in the boreal forest) the areal extent of that land type can be calculated and the data can be scaled-up. Secondly, if certain site preparation or harvesting

techniques are found to cause minimal soil and forest floor disturbance, land managers may be encouraged to employ those techniques in the interest of carbon sequestration.

Sources of Potential Error

I have already discussed the problems encountered in calculating the branch portion of the tree allometric equations. While the relative initial moisture contents of the original branch samples vs. the “correction” branches is not known, branch mass constituted on the order of 10% of total woody biomass for aspen and 24% of total woody biomass for black spruce. Using balsam poplar allometric equations for willow and alder introduced a minimal amount of error because these two shrub species together never accounted for more than 1.5 % of total basal area. Paper birch accounted for approximately 11% of total basal area in the 1971 stand, so using aspen allometric equations may have biased the biomass estimate for that stand, but the direction of potential bias is not known. CWD amounts may be underestimates because of our inability to completely remove stumps and extremely decayed wood for weighing. As mentioned above, soil carbon is certainly underestimated because of sampling depth.

Future Research

Many avenues for further research are illuminated by this study. Probably one of the most useful additions to this study would be a stand slated to be logged in the near future. Pre- and post-harvest carbon levels could be measured and compared, and it would give the existing chronosequence a starting point. Specifically, if initial CWD levels were known, decay rates could be calculated fairly easily. It would also be helpful

to restrict the sampling of forest floor into two mutually exclusive categories. These would be 1) areas physically disturbed by logging activity and 2) areas not visibly disturbed by logging activity. Assessing these areas separately would give some indication of how much of the variability seen in this study is due to the random sampling technique. The area of skid trails and disturbed areas could then be quantified, and these areas assessed separately for forest floor and mineral soil carbon. Finally, resampling these stands some years in the future will show whether species composition and aboveground biomass approach the values of the unlogged forest.

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TABLES AND FIGURES

Table 1. Changes in terrestrial carbon stores over the period 1850 to 1980. (adapted from Houghton, 1996)

	Change in Area (Mha)	Changes 1850-1980 (Pg C)		Changes, Pg C Mha ⁻¹	
		Vegetation	Soil	Vegetation	Soil
Tropical evergreen forest	-69	-15	-8	0.22	0.12
Tropical seasonal forest	-302	-36	-25	0.12	0.08
Tropical open forest/woodland	-138	-8	-9	0.06	0.07
Temperate evergreen forest	6	-12	-6	-2.00	-1.00
Temperate deciduous forest	-63	-14	-9	0.22	0.14
Temperate woodland	-34	-1	-2	0.03	0.06
Boreal forest	-4	-6	-3	1.50	0.75
Desert scrub	-271	-1	-15	0.00	0.06
Tropical fallows	30	1	2	0.03	0.07
Tropical grassland and pasture	86	1	8	0.01	0.09
Temperate grassland and pasture	-140	-8	-41	0.06	0.29
Cultivated, temperate zone	501	2	56	0.00	0.11
Cultivated, tropical zone	389	4	22	0.01	0.06
Other ¹	8	0	0	0.00	0.00

¹includes tundra, alpine meadow, marsh, rock, ice, and sand

Table 2. Select stand structural characteristics.

Stand Structural Characteristics.					
Stand	Vegetation Type	Stems ha ⁻¹	Mean Basal Area, m ² ha ⁻¹ (relative basal area in parentheses)	Tree Diameter, cm	
				Mean	Range
1990	Alder	2906	3.0 x 10 ⁻⁴ (< 1%)	0.8	0.6 – 0.9
	Aspen	5299	4.10 (80.3 %)	7.8	1.1 – 53.0
	Balsam Poplar	2331	0.72 (14.1 %)	3.3	1.6 – 5.6
	Black Spruce	1419	4.0 x 10 ⁻³ (< 1%)	0.9	0.8 – 1.0
	Jack Pine	1006	0.26 (5.1 %)	2.6	1.7 – 3.6
	Paper Birch	253	0.02 (< 1 %)	2.2	1.8 – 2.6
	Willow	-	-	-	-
	Sum all species	13214	5.36		
1983	Alder	-	-	-	-
	Aspen	8332	14.9 (83.7 %)	5.5	1.5 – 30.8
	Balsam Poplar	-	-	-	-
	Black Spruce	642	0.33 (1.8 %)	3.9	2.3 – 4.8
	Jack Pine	1428	2.54 (14.2 %)	5.8	2.7 – 8.9
	Paper Birch	166	0.03 (< 1 %)	3.1	3.1 – 3.1
	Willow	354	0.01 (< 1 %)	2.1	2.1 – 2.1
	Sum all species	10923	17.86		
1971	Alder	1206	0.13 (1.1 %)	4.0	1.3 – 1.3
	Aspen	3738	9.02 (78.6 %)	9.1	3.2 – 38.6
	Balsam Poplar	-	-	-	-
	Black Spruce	491	0.67 (5.8 %)	9.5	2.4 – 28.6
	Jack Pine	298	0.36 (3.1 %)	9.2	2.4 – 16.5
	Paper Birch	496	1.31 (< 1 %)	7.1	3.0 – 13.0
	Willow	-	-	-	-
	Sum all species	6228	10.66		
1935	Alder	853	1.9 x 10 ⁻³ (< 1%)	2.0	1.8 – 2.1
	Aspen	1627	14.0 (55.8 %)	16.0	1.9 – 31.7
	Balsam Poplar	95	0.59 (2.4 %)	13.8	9.7 – 18.0
	Black Spruce	575	9.04 (36.1 %)	16.7	6.9 – 27.2
	Jack Pine	26	1.45 (5.8 %)	25.8	21.3 – 33.2
	Paper Birch	-	-	-	-
	Willow	-	-	-	-
	Sum all species	3175	25.07	-	-

Table 3. Fire return intervals for regions of the North American boreal forest.

Region specified	Fire return interval, years	Source
Boreal forest	70-100	Aber and Melillo, 1991, p.260
SE Labrador black spruce	500	Foster, 1983 ¹
Southern Quebec	130	Cogbill 1985 ¹
Central Quebec	<100	Gerardin 1980 ¹
Alberta	34	Larsen and MacDonald, 1998

¹From Table 5.1 in Payette in Shugart's Systems Analysis (p. 151)

Table 4. Select characteristics for the BOREAS SSA and NSA and Wabowden study site.

	SSA Prince Albert, SK	NSA Thompson, MB	This study, Wabowden, MB
Location	53°54''N, 104°41'' W	55°55''N, 98°37'' W	54°55''N, 98°38'' W
January temperature (°C)	-19.8	-25.0	-22.7 to -24.7
July temperature (°C)	17.6	15.7	15.9 to 18.5
Annual snowfall (cm)	116	201	148
Annual rainfall (mm)	302	352	315
Average annual growing degree days	1455	1038	N/A

Table 5. Moisture Content of Correction Branch Components¹

	Site	NF		NB		OF		OB		R	
		dry/wet mass	SD ²	dry/wet mass	SD	dry/wet mass	SD	dry/wet mass	SD	dry/wet mass	SD
Aspen	1935	0.41	0.01	0.56	0.01	-	-	0.57	0.02	-	-
	1971	0.39	0.03	0.54	0.03	-	-	0.54	0.03	-	-
	1983	0.39	0.01	0.51	0.02	-	-	0.54	0.01	-	-
	1990	0.39	0.01	0.50	0.04	-	-	0.55	0.02	-	-
Balsam Poplar	1990	0.33	0.02	0.50	0.03	-	-	0.55	0.02	-	-
Black Spruce	1935	0.44	0.02	0.58	0.05	0.49	0.05	0.59	0.02	0.75	-
	1971	0.40	0.02	0.52	0.03	0.45	0.01	0.55	0.04	-	-
	1983	0.39	0.03	0.50	0.07	0.44	0.01	0.57	0.04	-	-
	1990	0.40	0.02	0.47	0.07	0.46	0.01	0.54	0.03	-	-
Jack Pine	1935	0.43	0.01	0.55	0.02	0.49	0.02	0.57	0.05	0.78	0.02
	1971	0.40	0.01	0.55	0.04	0.47	0.01	0.52	0.04	0.55	0.17
	1983	0.35	0.05	0.49	0.05	0.45	0.01	0.49	0.03	0.39	-
	1990	0.38	0.03	0.43	0.06	0.46	0.02	0.47	0.02	-	-

¹Branch Components; NF- new foliage, NB- new branch, OF- previous years' foliage, OB- old branch, R- reproductive tissue (cones)

²SD – standard deviation

Table 6. Carbon partitioning among ecosystem pools. SD = standard deviation among the four blocks at each site. % = percent of total ecosystem carbon in each site.

		Stand Age				
		11	18	30	65	
Aboveground Biomass	Tree Biomass	t ha ⁻¹	10.66	23.5	33.01	55.56
		SD	2.73	5.05	4.89	9.11
		%	9	21	28	39
	Understory	t ha ⁻¹	0.88	0.32	0.81	0.75
		SD	0.23	0.21	0.53	0.62
		%	0.7	0.3	0.7	0.5
	CWD	t ha ⁻¹	15.58	8	3	9.09
		SD	6.28	2.5	3.8	3.78
		%	13	7	3	6
	Forest Floor	t ha ⁻¹	43.81	30.99	32.79	24.88
		SD	16.07	10.13	5.93	2.14
		%	36	28	28	17
SOC	t ha ⁻¹	51.54	49.16	46.23	53.03	
	SD	3.62	2.5	8.37	0.95	
	%	42	44	40	37	
TEC	t ha ⁻¹	122.47	111.98	115.85	143.32	
	SD	19.37	12.72	12.6	11.54	

Table 7. Allometric Equation coefficients, R^2 , MSE, CF. Biomass equations are of the form $\log_{10}(\text{DBH}) = a + \log_{10}(b)$, therefore $\text{DBH} = 10^{(a + \log_{10}(b)) \cdot \text{CF}}$.

		a	b	r²	MSE	CF
Aspen N = 20	AF	-1.474	1.439	0.720	0.170	1.569
	TBR	-1.439	1.807	0.791	0.125	1.393
	S	0.455	0.491	0.988	0.011	1.030
	TW	0.561	0.596	0.983	0.014	1.039
	TB	0.666	0.702	0.966	0.028	1.077
Black Spruce N = 18	NF	-1.526	1.133	0.795	0.117	1.364
	OF	-0.859	1.635	0.945	0.040	1.112
	AF	-.774	1.609	0.950	0.035	1.097
	TBR	-1.192	1.956	0.964	0.036	1.100
	R	0.015	0.105	0.829	1.609	1.041
	S	0.497	0.537	0.979	0.026	1.072
	TW	0.616	0.656	0.980	0.023	1.064
	TB	0.736	0.775	0.972	0.028	1.078
Jack Pine N = 18	NF	-1.933	1.579	0.827	0.085	1.253
	OF	-1.452	1.770	0.720	0.057	1.163
	AF	-1.298	1.708	0.897	.054	1.154
	TBR	-1.745	2.232	0.945	0.047	1.133
	R	0.105	0.105	0.940	1.708	1.321
	S	0.454	0.496	0.990	0.010	1.027
	TW	0.579	0.620	0.994	0.006	1.016
	TB	0.703	0.744	0.996	0.004	1.011
Balsam Poplar N = 6	AF	-1.970	2.105	0.934	0.030	1.083
	TBR	-2.060	2.746	0.958	0.031	1.086
	S	0.639	0.683	0.990	0.004	1.011
	AW	0.771	0.815	0.987	0.006	1.016
	TB	0.903	0.948	0.985	0.007	1.019

NF – new foliage, OF – old foliage, AF – all foliage, TBR – total branch (new wood + old wood), R – Reproductive tissue (cones), S – Stem wood, TW – total wood (stem + branch), TB – total biomass.

Figure 1. Range of global boreal forest.



Map at: <http://www.unep-wcmc.org/forest/world.htm>

Figure 2. Forest Management License Areas in Manitoba

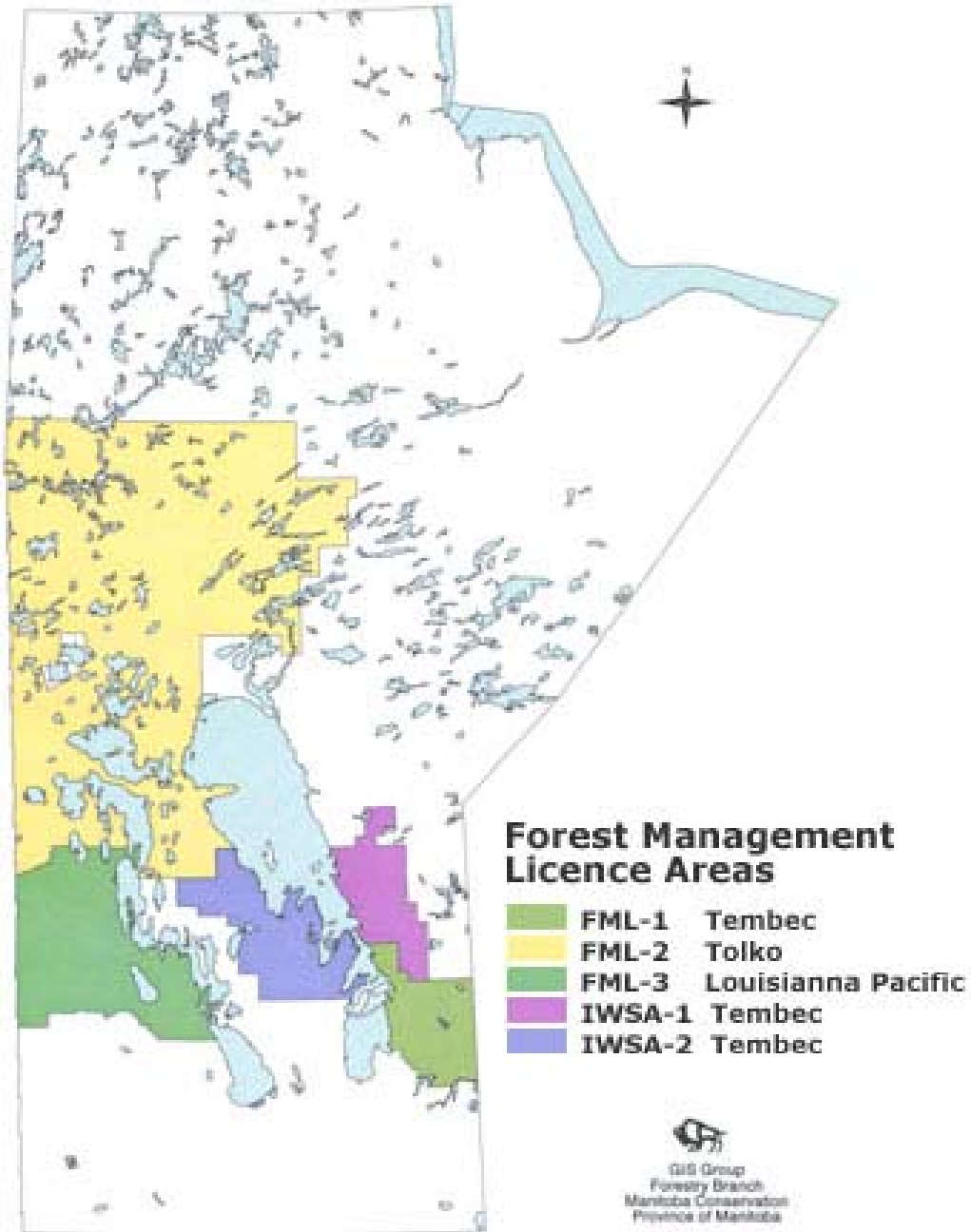


Figure 3. Percent of land cover that is forested.

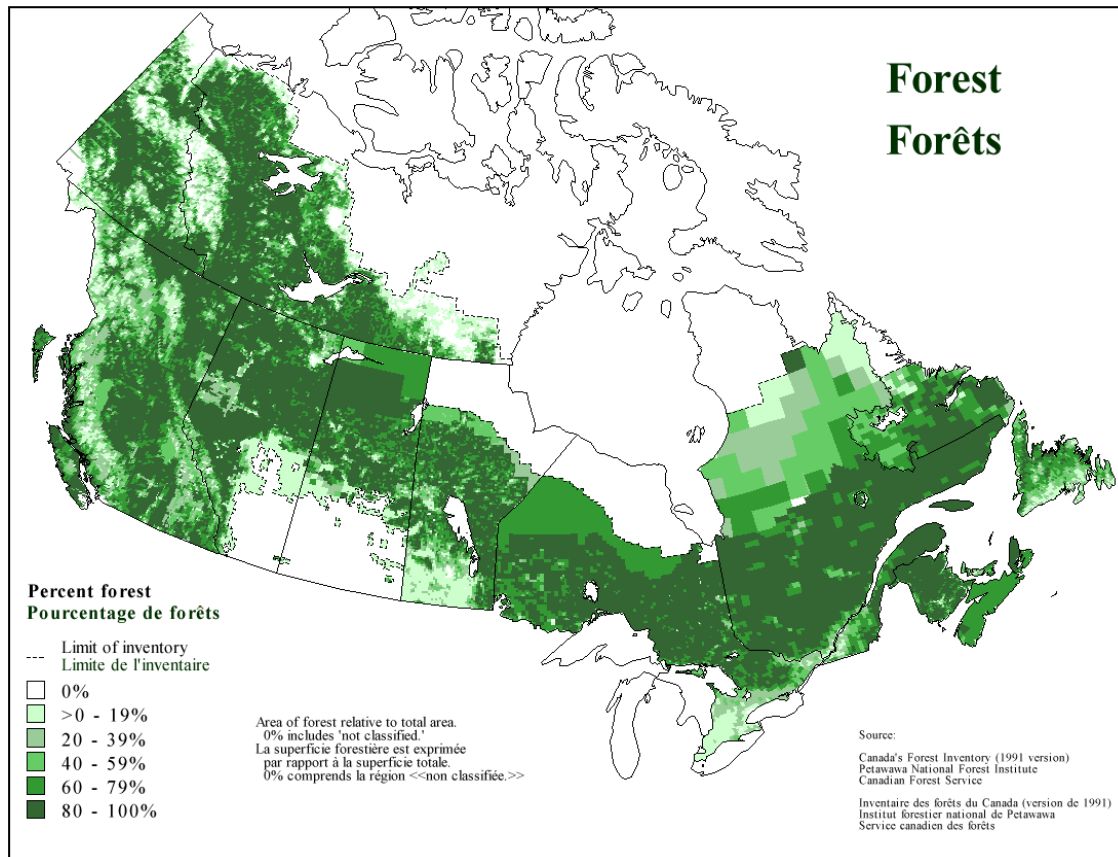


Figure 4. Volume of wood per hectare across Canada.

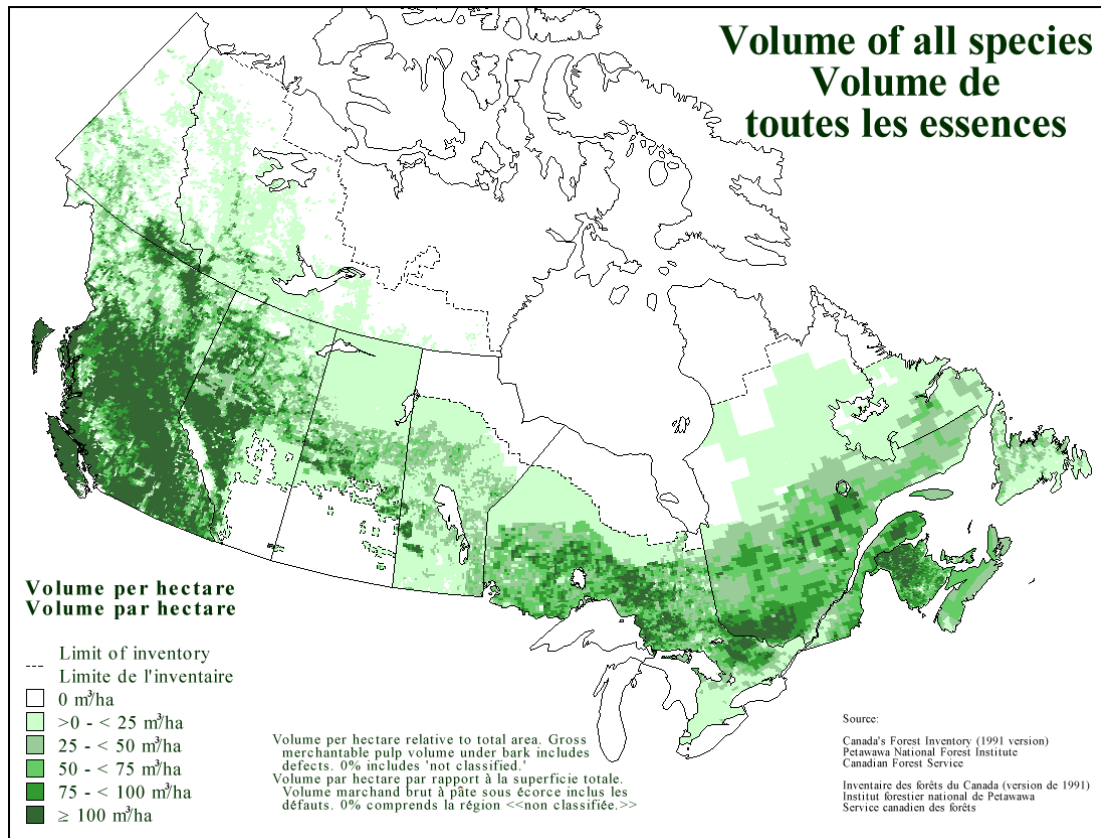
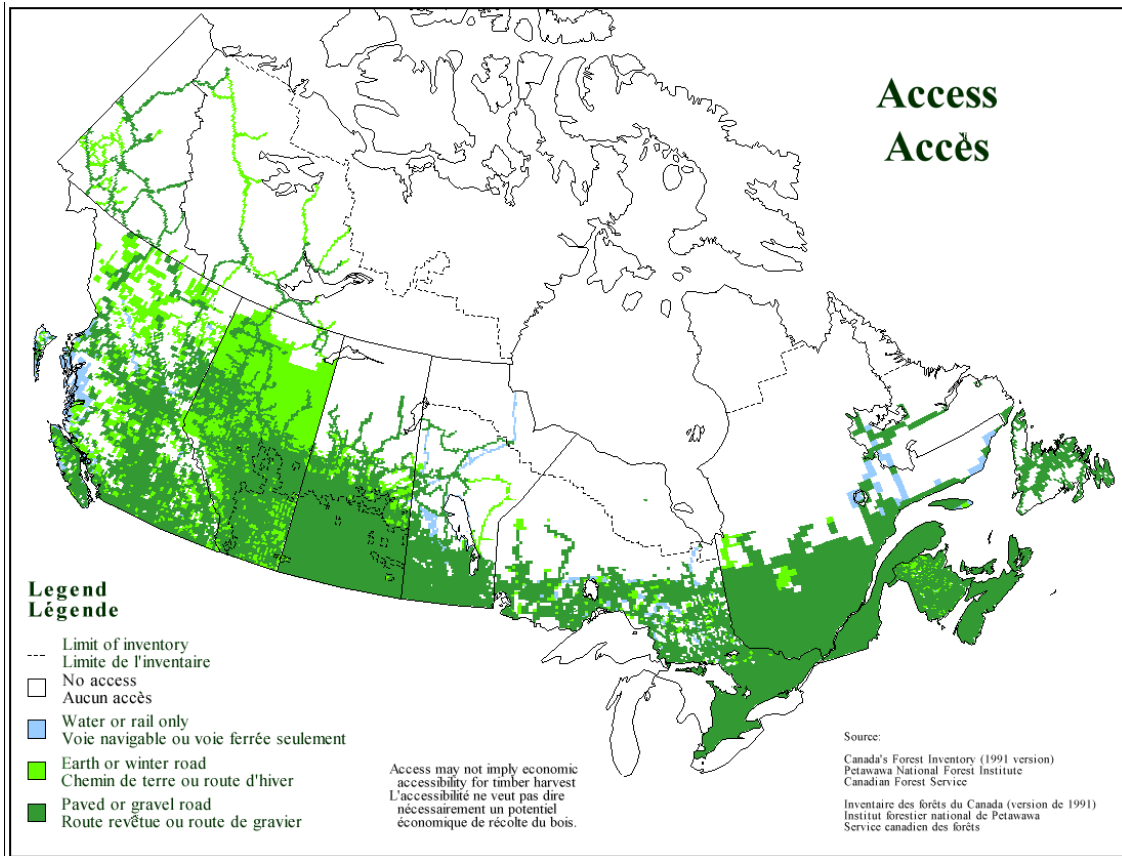


Figure 5. Access to Manitoba's boreal forests is extremely limited relative to the other Provinces.



MAP LEGEND

Trans-Canada Highway		Primary Highway		First Nations Communities		Parks Canada		Railroad	
Yellowhead Highway		Secondary Highway		Unincorporated Urban Centres		Airport		City	
								Town	
								Village	

Figure 7. Close-up map.

Figure 8. Layout of samples taken in each plot, block, and stand.

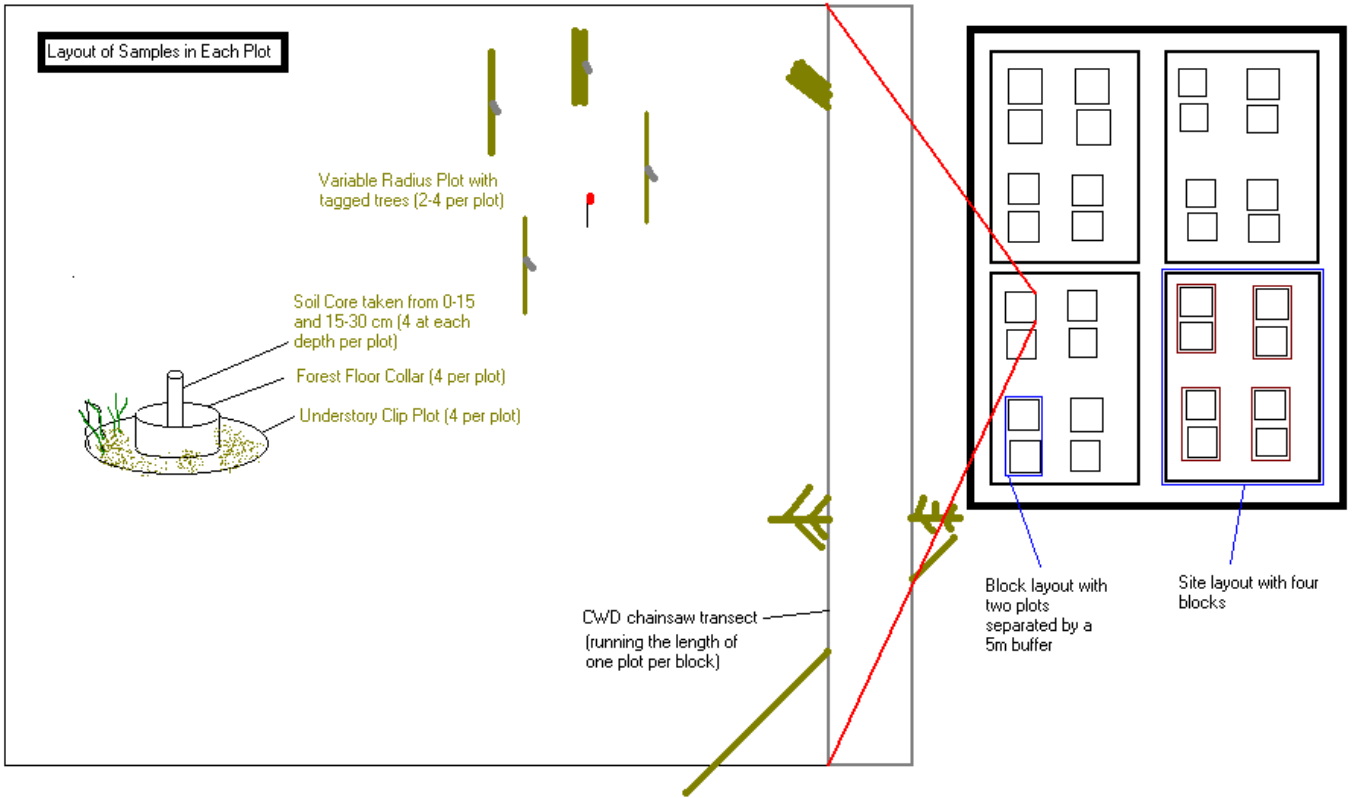


Figure 9. Carbon in tree above ground biomass increases significantly with age.

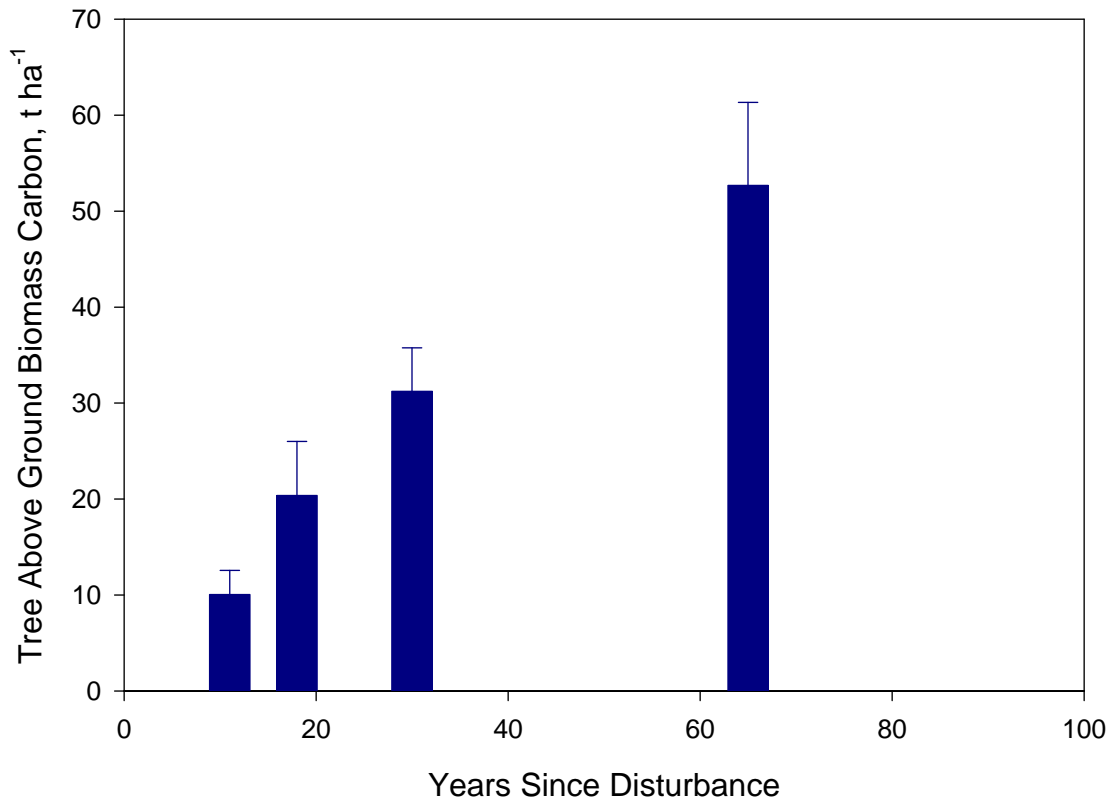


Figure 10. Partitioning of Soil Organic Carbon by Sample Depth

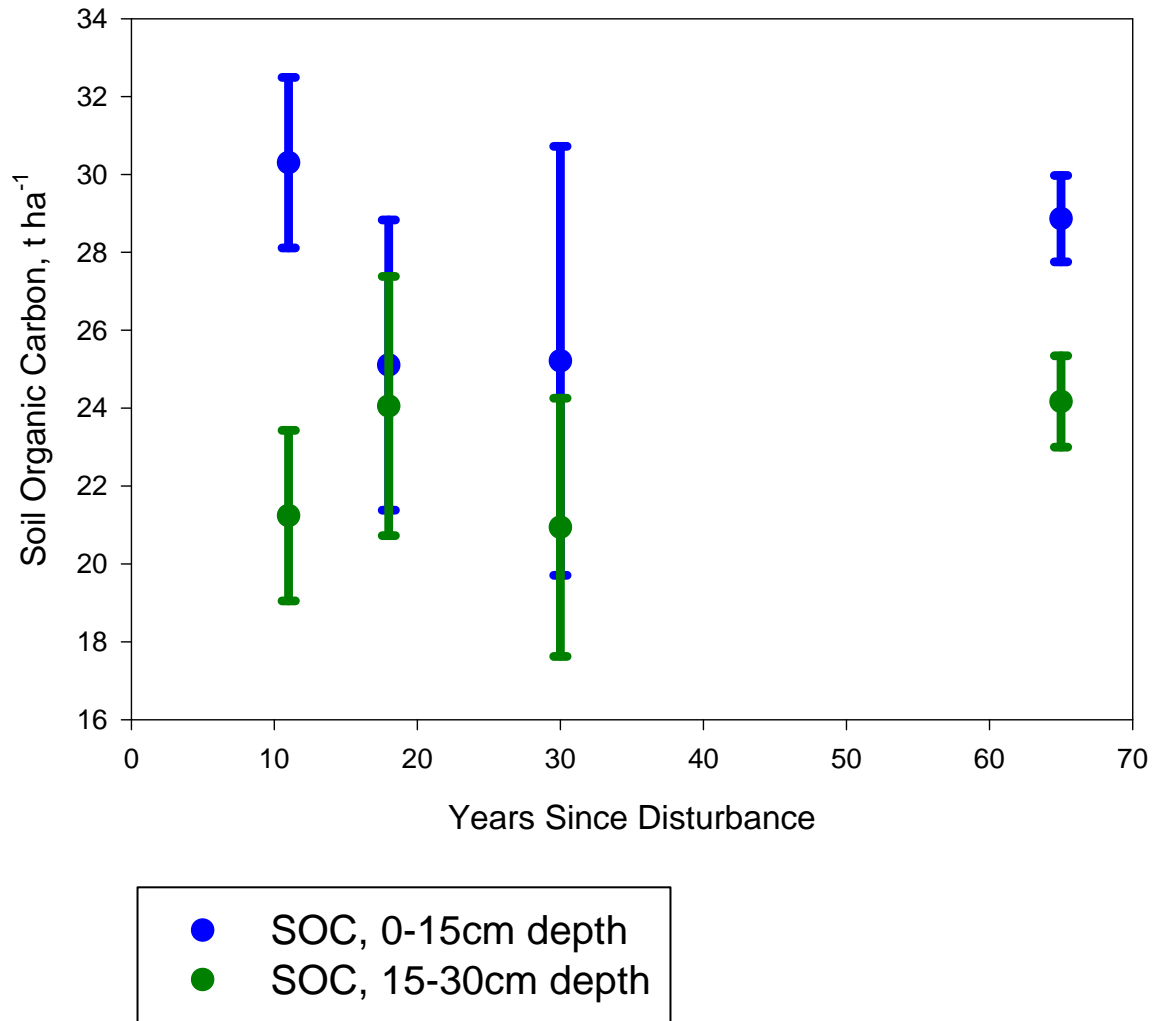


Figure 11. Distribution of Total Ecosystem Carbon

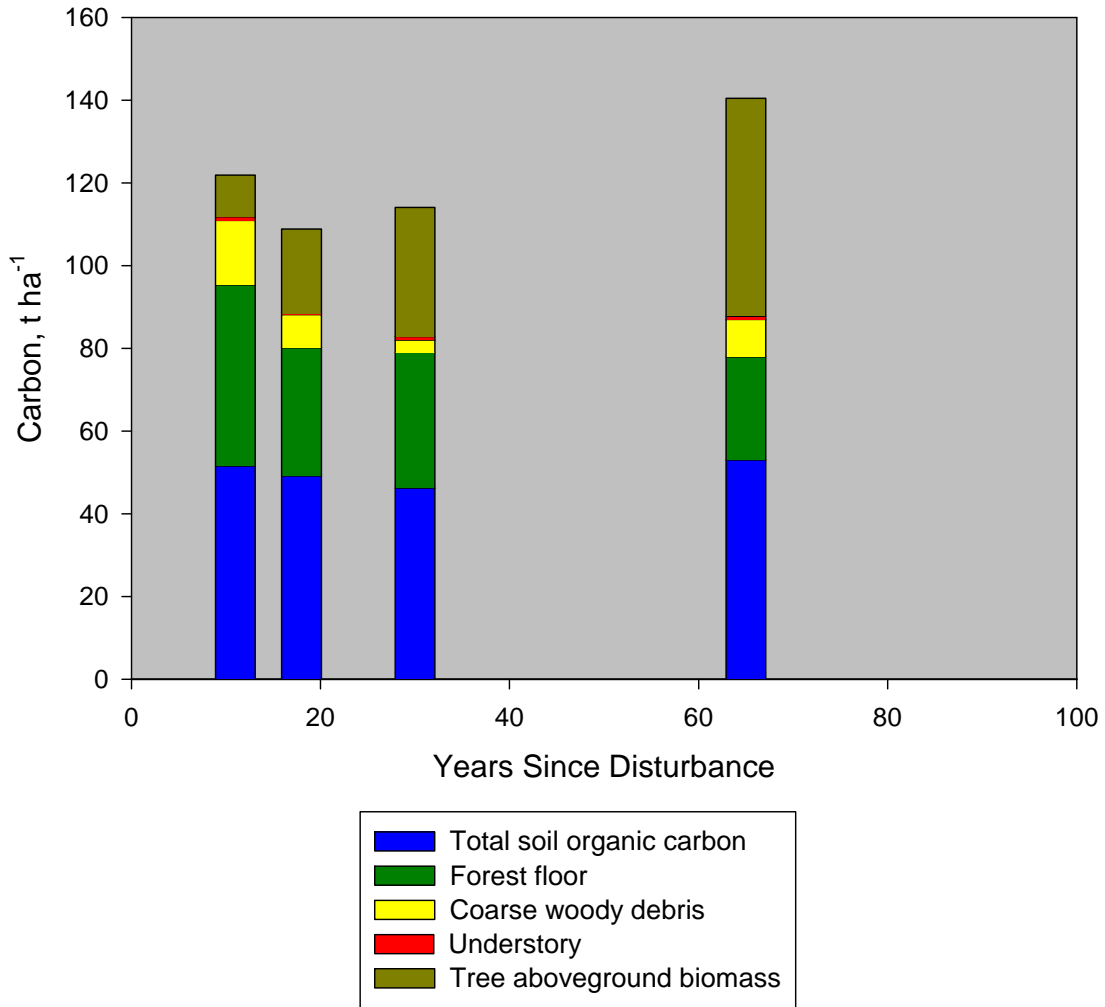


Figure 12. Relative Aboveground Biomass of Tree Species

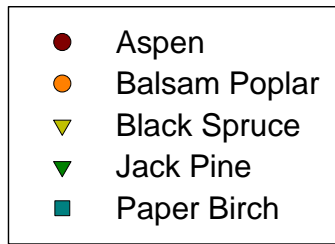
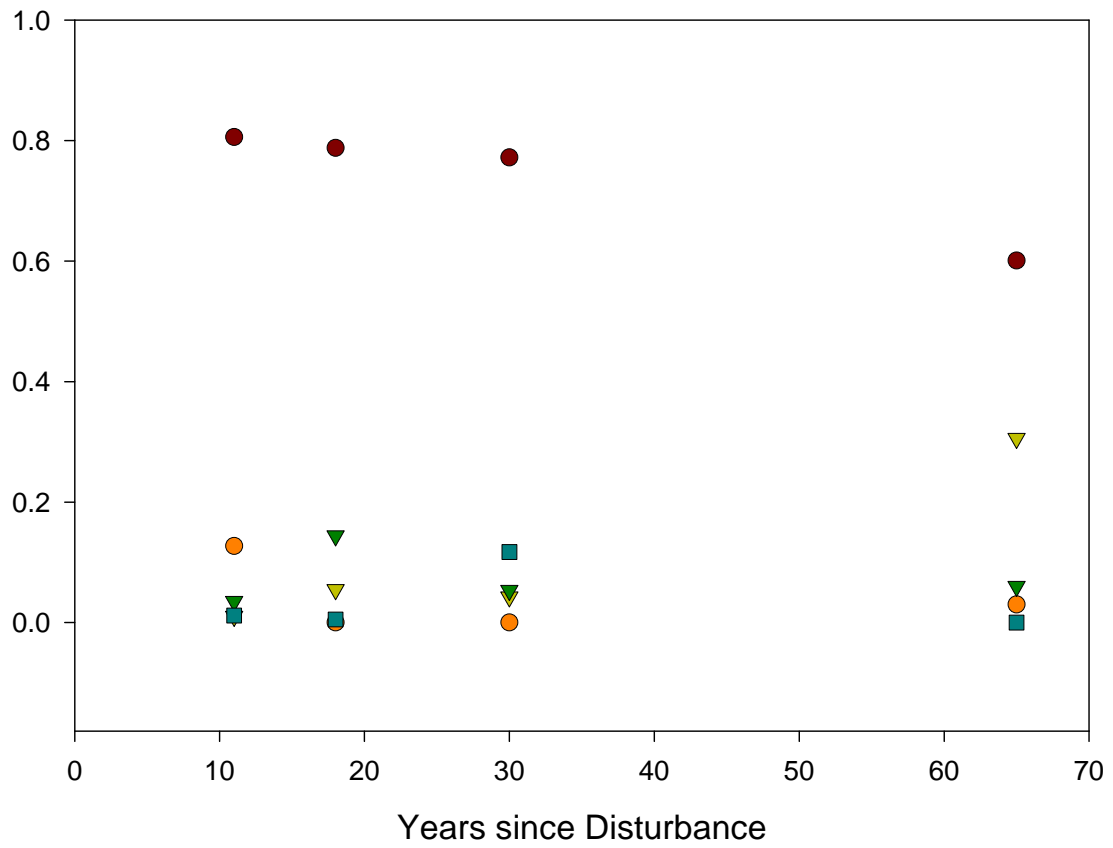


Figure 13. Species Relative Basal Area.

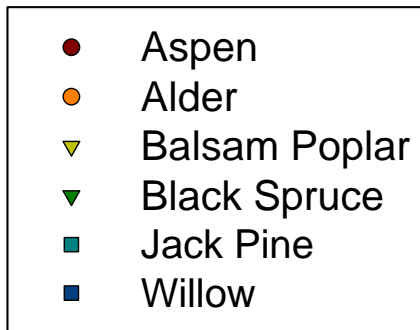
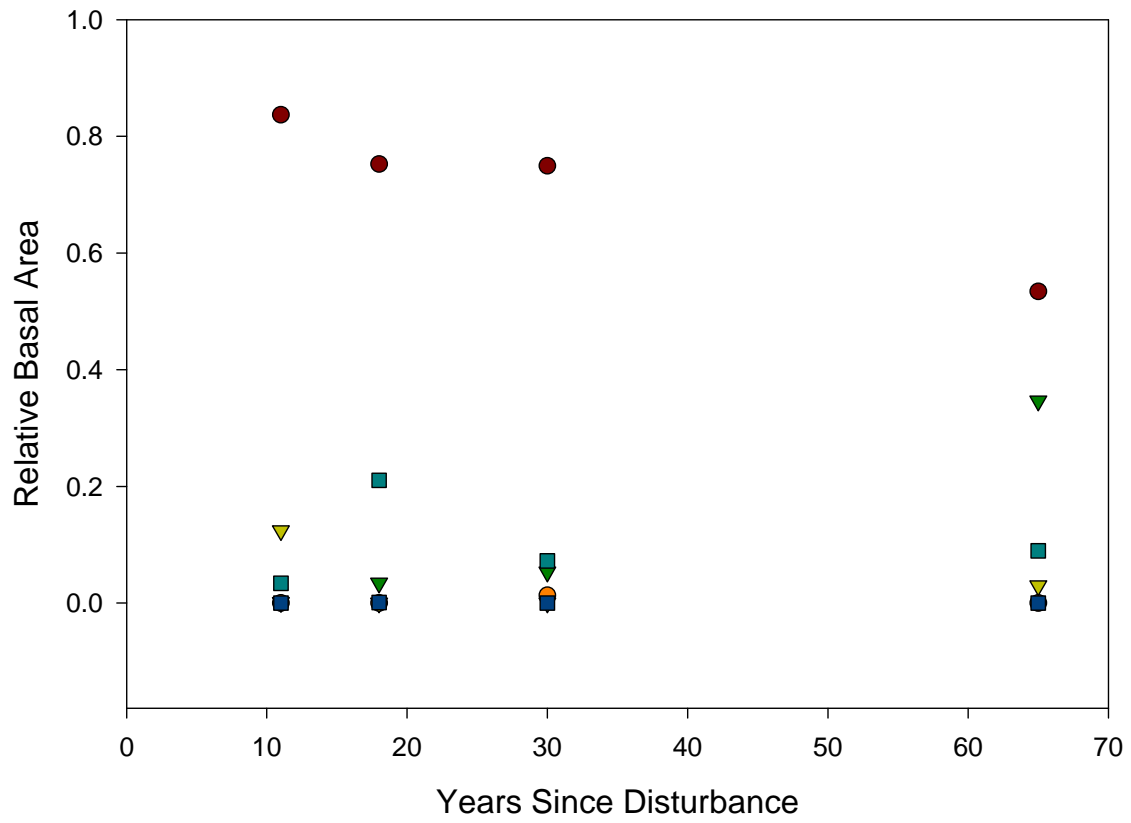


Figure 14. Biomass accumulation at the Wabowden site is greater than at black spruce sites further north (NSA) and jack pine sites to the southwest (SSA).

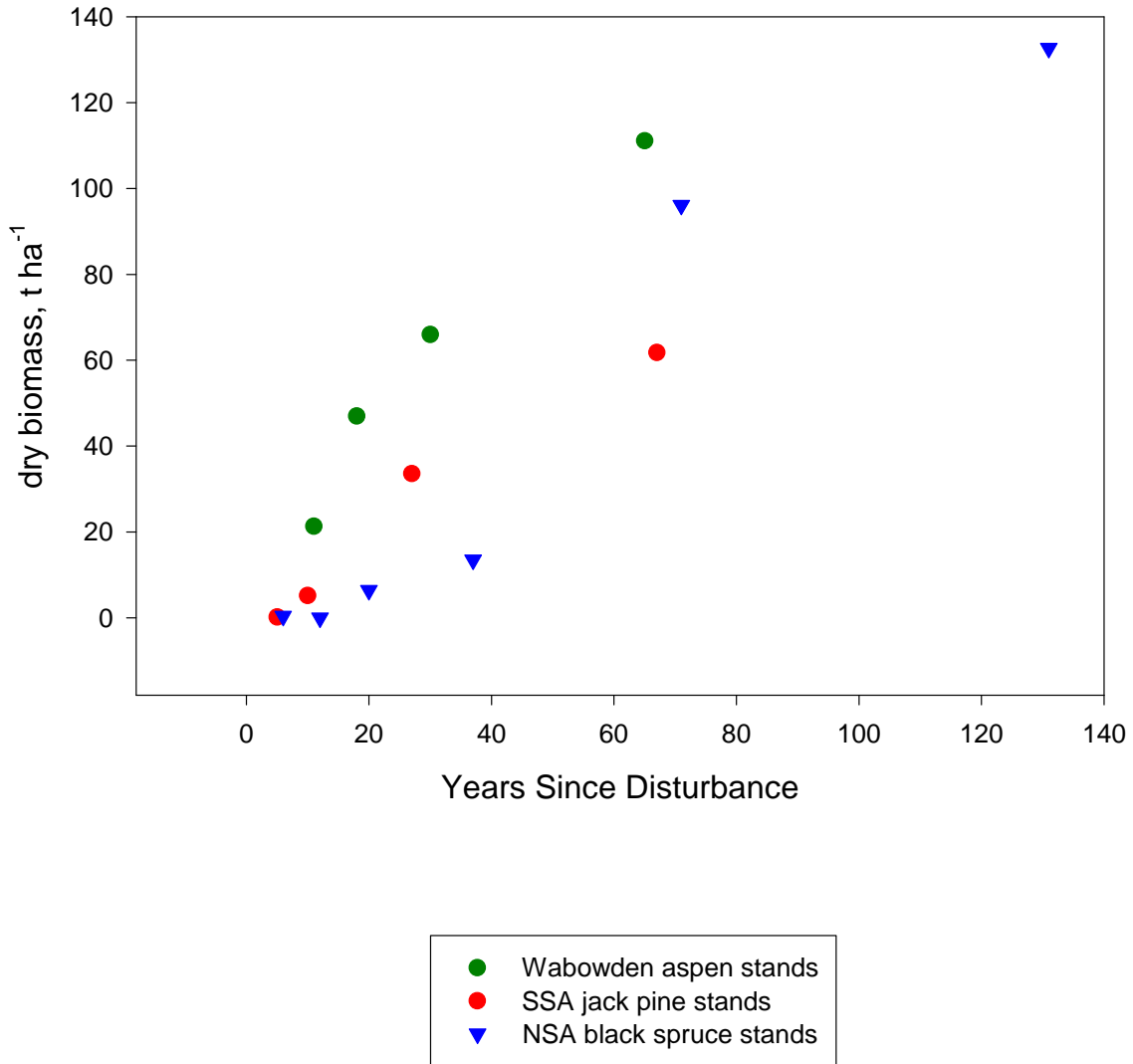


Figure 15. Forest floor carbon is greater in Wabowden aspen stands than in BOREAS SSA jack pine stands.

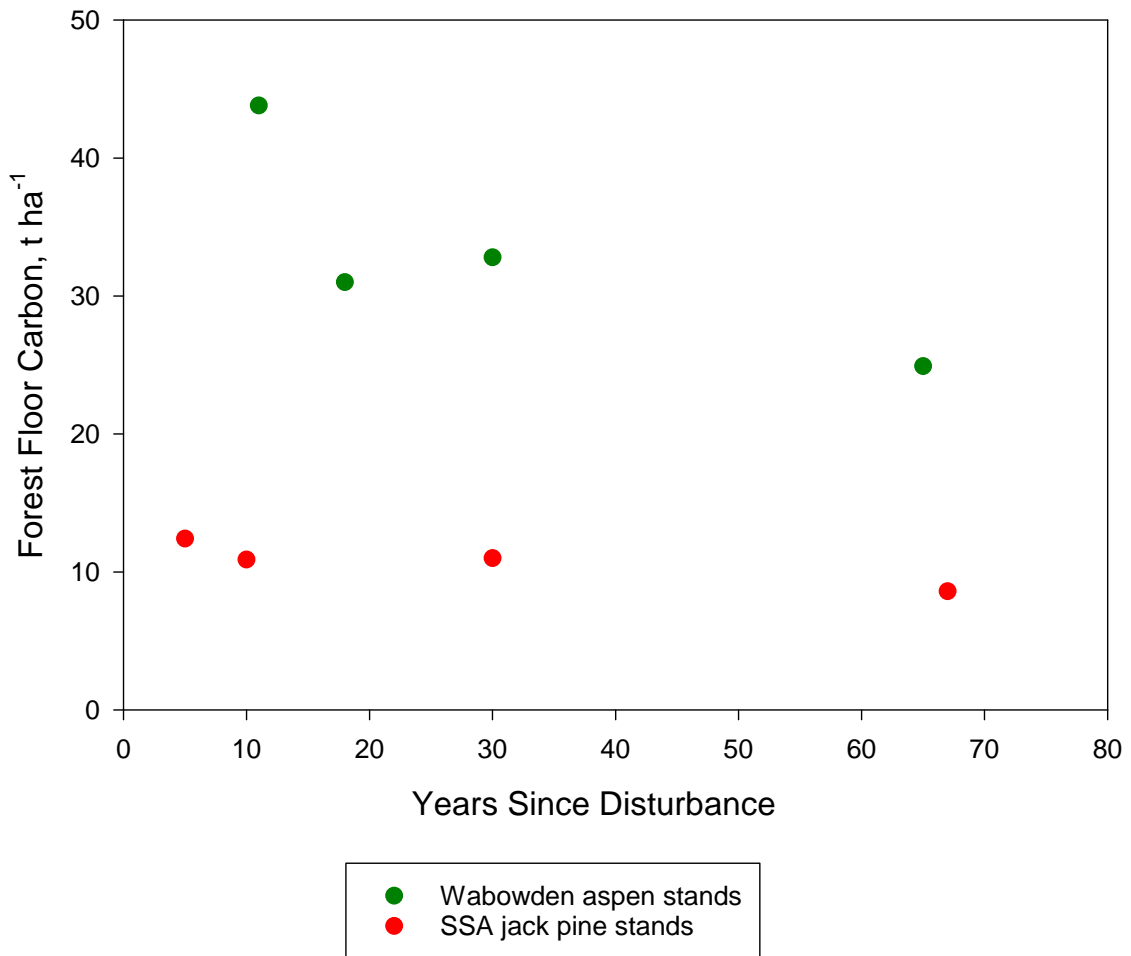


Figure 16. Coarse woody debris carbon.

