Project Title: **Carbon cycling at the landscape scale: the effect of changes in climate and fire frequency on age distribution, stand structure, and net ecosystem production.**

Principal Investigator(s): Michael G. Ryan[1], William H. Romme[2], Monica G. Turner[3], Daniel B. Tinker[4]

Affiliation: [1]USDA Forest Service, Rocky Mountain Research Station, [2]Colorado State University, [3]University of Wisconsin, [4]University of Wyoming

Address: 240 West Prospect RD, Fort Collins, CO, 80526

Telephone/Facsimile Number(s): 970.498.1012/ 970.498.1212

E-mail: [1]mgryan@fs.fed.us, [2]romme@cnr.colostate.edu, [3]mgt@mhub.zoology.wisc.edu, [4]Tinker@uwyo.edu

Duration of Project: 3 years

Annual Funding Requested from the Joint Fire Science Program: $445,373 (year 1), $24,647 (year 2), $25,657 (year 3).

Total Funding Requested from the Joint Fire Science Program: $497, 648

Total Value of In-Kind and Financial Contributions: $ 297,730

Abstract: Our project addresses Task 1 in RFP 2003-1. Climate, fire (frequency and intensity), and forest structure and development are strongly linked, but our knowledge of the interactions of these factors is poor. We lack the ability to make robust predictions about how changes in climate will alter these interactions and change the carbon balance of a landscape. Our objective is to estimate how changes in fire frequency, pattern, and intensity will alter the distribution of forest age and structure across a landscape and how these changes, in turn, will change the landscape carbon balance. We will determine the current carbon balance for the Yellowstone National Park (YNP) landscape and how much carbon was lost in the 1988 fires by (*a*) mapping the current distribution of forest age and tree density for the YNP landscape, (*b*) measuring how annual net carbon storage (NEP) varies with forest age and tree density using replicated chronosequences, (*c*) estimating how much carbon was removed from the landscape by the 1988 fires through direct combustion, and (*d*) extrapolating stocks and fluxes to the landscape using the detailed maps and measurements. We will then determine how NEP will change for the YNP landscape with changes in climate and fire regimes (*a*) by calibrating the Century biogeochemical model to assess how changes in climate will alter NEP across stand development, (*b*) using models developed in past research to simulate fire frequency, fire spread, and the resulting landscape structure (the distribution of stand age and tree density) for alternative climatic conditions, and (*c*) by combining (*a*) and (*b*) to estimate landscape NEP for different climates and the different fire regimes they cause. The lodgepole pine ecosystems of YNP are ideal for this research because the landscape mosaic is complex (high variability in tree density and stand age), the structure within a patch is simple (generally one species with even-aged cohorts of trees), and, because soils and climate are similar across the plateau, information from replicated plot studies can be extrapolated to the landscape. We hypothesize that variation in tree establishment after a fire and the legacy of the prior stand will control the trajectory of NEP through time, and that climate and fire frequency will change the distribution of forest age and structure, and these changes will alter net carbon storage for the landscape. **This research will significantly improve our knowledge of how NEP changes with stand development after a fire, and how climate-induced changes in the disturbance regime will affect landscape age and stand structure and NEP for the landscape. Because we will examine the entire C budget we will also tightly link fuels (litter, CWD, foliage, etc.) with overstory characteristics on a landscape scale.**

Investigator: ______________________________ RMRS Representative:______________________________

Michael G. Ryan, Research Ecologist Janine Powell, Assistant Director

Institutional Contact: Carolyn Lumar, USDA Forest Service RMRS, 240 West Prospect Rd, Fort Collins, CO 80526, Phone: 970.498.1172, Fax: 970.498.1396, clumar@fs.fed.us

INTRODUCTION

Understanding the interactions between climate, fire behavior, and forest characteristics is an important challenge. Despite tremendous advances in understanding ecosystem processes in relatively small study areas, little theory exists for predicting variability in ecosystem processes across broader spatial scales, because the interactions are complicated. For example, forest structure affects fire intensity locally and spread across the landscape—but, fire intensity, prior stand structure, and climate will affect the developmental trajectory and structure of the new forest. Our proposed research would contribute to progress in understanding these areas by focusing on the interactions of climate, fire, and landscape structure and how these interactions affect the carbon balance of the landscape. Our previous work has shown that fires create tremendous spatial heterogeneity within this landscape, especially with respect to tree density and leaf area index (LAI), and that this structural heterogeneity is associated with substantial variability in ecosystem processes such as productivity, carbon allocation, and carbon storage. **We propose to build upon this previous work to determine how initial post-fire structural heterogeneity controls carbon dynamics over the full life cycle of individual forest stands, and how climate-mediated changes in the fire regime could potentially alter the behavior of the entire Yellowstone ecosystem as a net sink or source of carbon in the global carbon cycle**. This proposal addresses Task 1 of RFP 2003-1. We propose using a combination of measurements and modeling to determine how changes in climate and fire frequency will change landscape patterns of stand age and tree density, and how these landscape patterns alter carbon storage for the landscape.

A fire oxidizes biomass almost instantaneously and sends a large pulse of carbon into the atmosphere, but longer-term processes after the fire are equally important in controlling carbon cycling (Auclair and Carter 1993). Immediately after severe fire, primary productivity is reduced or eliminated, formerly live roots become available for decomposition, litter quantity and quality changes, soils and litter become warmer, and soils are wetter for longer periods as transpiration and interception decrease. These changes can lead to increased decomposition and soil respiration (Burke et al. 1997), which release up to three times as much carbon (C) into the atmosphere as the initial fire (Auclair and Carter 1993). Over longer times, however, assimilation of atmospheric carbon by new plant growth may entirely compensate for the C released into the atmosphere by the fire and immediate post-fire processes (Crutzen and Goldhammer 1993). In addition, a significant amount of stable C, in the form of charcoal, is left behind after a fire and may persist for centuries as a long-term C sink (Seiler and Crutzen 1980, Schulze et al. 1999, 2000; Tinker and Knight 2000).

Fires also create a mosaic of different stand ages across a landscape (Anderson and Romme 1991, MG Turner et al. 1997a and b, Foster et al. 1998). Carbon pools (e.g., live biomass) and fluxes (e.g., respiration) may differ substantially among stands of different ages (Kurz and Apps 1999). By summing the components of C pools and fluxes in all of the individual stands that comprise a forested landscape, we can characterize the C budget of the landscape system as a whole. For example, a landscape dominated by recently burned forests probably functions as a net C source, whereas a landscape of mature forests may be a C sink (Kasischke 2000b). Future changes in fire frequency and extent, as forecast by current climate models (e.g., Dale et al. 2001), therefore, could have substantial impacts on global C cycling (Bonan et al. 1990, Moreno and Oechel 1994, Overpeck et al. 1990, Romme and Turner 1991, Crutzen and Goldhammer 1993, Swetnam 1993, Leenhouts 1998). Quantifying the important components of the C cycle during ecosystem recovery from fire is a fundamental need for determining how changes in fire regimes may alter local, regional, and global C budgets and net C storage in biomass (Auclair and Carter 1993, Houghton 1996, Burke et al. 1997, Amiro et al. 2000).

Changes in productivity over the life of a stand are relatively well understood (Ryan et al. 1997), but information about changes in the complete C balance and ecosystem C storage over the same time span is limited (Kurz and Apps 1999). Productivity represents C input, but to understand the complete C balance, we must also understand how decomposition and the change of C stocks in long-term pools (coarse woody debris and soil C) are regulated (DP Turner et al. 1995, Kurz and Apps 1999, Tilman et al. 2000). *Net ecosystem production* (NEP) is the annual net change in C stored in an ecosystem—the difference between net primary productivity (NPP) and heterotrophic respiration. NEP thus follows a different trajectory than NPP over stand development after fire, because NEP represents the net balance of NPP, decomposition, and the slow change in C stored in soil (Slaughter et al. 1998, Kurz and Apps 1999).

A major research effort is under way to quantify the major pools and fluxes in the global C cycle and to project likely changes in C cycling during the next century (e.g., DP Turner et al. 1995, Schulze et al. 2000, Harmon 2001, Murray et al. 2001). Much of the work to date has focused on mature, stable ecosystems, and has not adequately incorporated the effects of fire and other disturbances (French et al. 2000, Kasischke 2000a,b). In the work proposed here, we will develop a detailed analysis of all the key ecosystem processes involved in C cycling and determine the overall C budget within a large Rocky Mountain coniferous forest landscape. We also will test specific hypotheses about effects of variability in fire frequency and post-fire stand development on C cycling in this system.

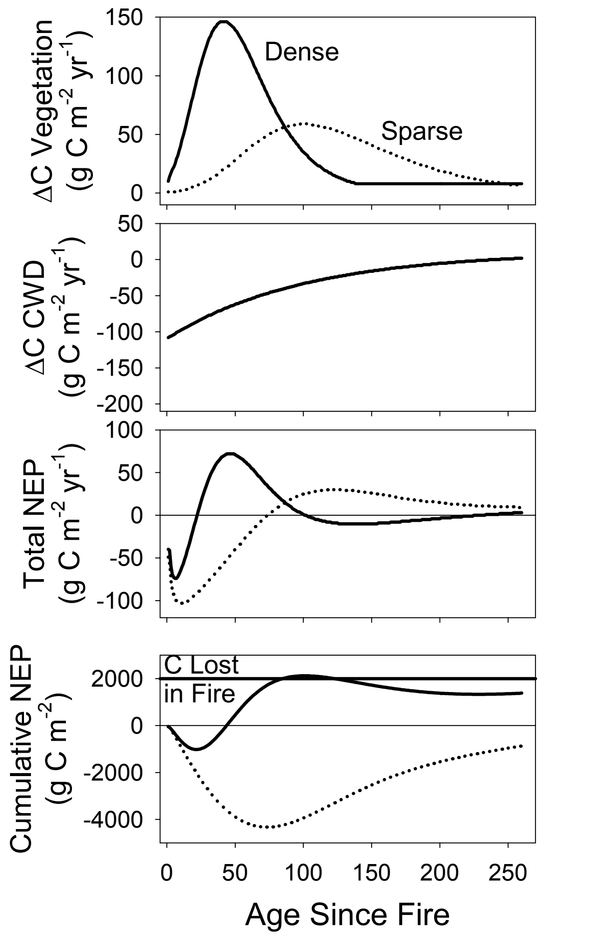
Much current work in C cycling is focused on high frequency measurements of net carbon exchange with the atmosphere using eddy covariance methods (Baldocchi et al. 1988, Mahli et al. 1999, Law et al. 1999). These measurements contribute greatly to our understanding of the environmental controls over net carbon exchange (Goulden et al. 1996, 1998; Valentini et al. 2000), but—because of the expense and micrometeorological constraints on sample location—this technique is impractical for examining C flux where the landscape consists of a complex mosaic of stand ages and tree densities, and the average size of a stand is too small to be measured cleanly. ***Understanding how NEP varies with landscape variability in structure and forest development requires a different approach***. Therefore, we propose to use a C balance approach to measure the components of NEP within 75 or more stands distributed across the large, heterogeneous Yellowstone landscape. The C balance approach estimates NEP from annual changes in C stocks: live biomass, dead wood, forest floor, and soil. For components that change rapidly (e.g., aboveground biomass), we can measure the changes directly. For other components that change slowly (e.g., soil C), we will use a replicated chronosequence combined with on-site measurements to estimate annual changes. This combined approach will allow us to estimate NEP for a wide diversity of stand structures and stand ages and will enable us to account for landscape heterogeneity when extrapolating to the YNP landscape.

The lodgepole pine (*Pinus contorta* var. *latifolia*) forests that cover the subalpine plateaus of YNP are ideal for this kind of research. Because of the gentle topography, spatial variation in soils and microclimate is minimal compared with many other Rocky Mountain landscapes. Also, the forests are dominated by a single overstory species. However, disturbance has created a complex mosaic of stand structure and ecosystem processes within this uniform background. Structural characteristics (stand age, tree density, the amount and size of dead wood) vary in response to fire size, fire severity, fire return interval, and characteristics of the prior stand (cone serotiny, tree age and stem density, and dead wood). The mosaic of lodgepole pine stands in YNP, created by the large fires of 1988 as well as earlier fires that occurred up to 400 years ago, provides a wide range of stand structures within similar topographic and climatic conditions. This relative uniformity in background environmental conditions allows us to use a replicated chronosequence approach effectively, and we already have considerable information about these forests from previous studies.

PRELIMINARY RESULTS

The carbon cycling research that we propose builds directly upon our previous and current research on interactions among spatial pattern, disturbance, and ecosystem function in YNP. Our current NSF-funded research focuses on causes and consequences of spatial variation in lodgepole pine sapling density throughout the areas burned in the 1988 Yellowstone fires. We have mapped the distribution of

Fig. 1. Hypothesized changes in C stocks in biomass and CWD, and NEP and cumulative NEP for two stands with high and low tree density. Cumulative NEP > 2000 g C m^{-2} will replace C lost in the fire.



stands representing various density classes (ranging from <100 to >100,000 stems/ha) from high-resolution aerial photographs (Tinker et al. *Submitted*), and have correlated local sapling density with pre-fire serotiny, fire severity, and fire size (Tinker et al. 1994, Turner et al. *Submitted*). Highest sapling densities are in areas of high serotiny and moderate fire severity, whereas lowest densities are in large patches of crown fire where serotiny is low. The spatial pattern of post-fire sapling density is relatively fine-grained, with most patches being 1-5 ha in size.

We also sampled two key indicators of ecosystem function—ANPP and LAI—across a wide range of variation in sapling density, elevation, and soil type and found that both were positively correlated with sapling density (Reed et al. 1999, Turner et al. *Submitted*). Thus, ANPP and LAI during the first decade after fire appear to be controlled primarily by the density of lodgepole pine saplings that become established soon after the fire. In 12-yr-old stands of the highest density class that we measured, ANPP was ~200 g C m^{-2} yr^{-1}, equal to the peak production measured for a lodgepole pine chronosequence by Smith and Resh (1999). This high post-fire ANPP suggests that rapid canopy closure and high production can occur in young lodgepole pine stands developing after fire. However, many stands with low sapling density have not yet formed a closed canopy, and they have substantially lower ANPP and LAI than the very dense stands.

Fig. 1 presents two scenarios of long-term tends in NEP and its components, derived from our previous work on ANPP in post-fire stands, literature on C stocks in a lodgepole pine chronosequence (Smith and Resh 1999) and our unpublished data on dead wood (CWD, including standing dead trees). These scenarios show that: (1) return to positive NEP after fire can vary strongly with the density of the new forest, (2) recovery of ecosystem C lost in the fire can take > 100 years, and (3) that the interplay between establishment of the new forest, wood left by the burned stand, and length of the fire cycle will be factors important in determining NEP for individual stands and the landscape. Critical uncertainties in constructing these NEP estimates are: (1) the amount and decomposition of standing and down dead wood, (2) the addition of new dead wood in older stands, (3) biomass accumulation or decline in old stands, and (4) the role of soil C. Our major objective is to obtain the empirical values needed to correct and complete the trends depicted in Fig. 1 so we can make accurate landscape extrapolations.

QUESTIONS AND HYPOTHESES

Our proposed research has three components. First (question 1 below), we will quantify the key components of NEP as functions of stand age and density for the life cycle of any individual forest stand

(Fig. 1). This work will emphasize field measurements in 75 or more stands. Second (question 2), we will use our stand-level data and our maps of stand age and structure to extrapolate to the entire Yellowstone landscape to determine whether the landscape is a source or sink of C before and after the 1988 fires. Third, (question 2) using a modeling approach, we will examine how the C budget of the Yellowstone landscape would function under projected future fire regimes, to determine the conditions under which the extensive coniferous forests of YNP would function as a net carbon sink or source within the global C cycle.

1. Spatial and Temporal Variability: How does NEP vary across space and with stand development?

H1: Tree density, tree age, and the amount of dead wood remaining from the prior stand and produced in the developing stand will control NEP.

Rationale: NEP is largely controlled by the balance between the accumulation of live biomass and the loss of dead woody biomass through decomposition, which vary with stand age and tree density. Tree density will determine LAI and live biomass accumulation, at least until canopy closure (Turner et al. *Submitted*), and biomass accumulation will decline with stand age after canopy closure (Ryan et al. 1997; Smith and Resh 1999). The amount of dead wood will vary with stand age as the wood remaining after the fire decomposes, and as mortality later in a stand's life produces additional dead wood. The amount, size distribution, and decomposition of dead wood may also be related to stand density (see H3 below).

H2: The trajectory of NEP varies with tree density. Specifically, stands having initially high sapling densities shift from negative to positive NEP at an earlier point in long-term stand development than stands having initially low sapling densities.

High initial sapling density promotes rapid canopy closure, which is associated with high leaf area and high ANPP, whereas stands with initially low tree stocking densities take longer to reach canopy closure (Fig. 1), and may have low LAI and ANPP throughout the open-canopy period (Reed et al. 1999, Turner et al. *Submitted*).

H3: C stocks in dead wood after a fire and decomposition rates for dead wood will co-vary with stand density.

Rationale: Our previous work has shown that stand density may perpetuate itself, and impact the diameter of dead wood. For example, dense stands occur where the prior stand had large numbers of serotinous cones (cones that open only after heating), which tend to be stands with high density and small stems. Similarly, regeneration after a fire in a sparse stand will yield a future sparse stand with large stems. Decomposition of dead wood will decrease as stem diameter decreases, so we expect that both the amount and decomposition of dead wood will vary with stand density.

2. Interactions: How do disturbance interval, disturbance size, and post-disturbance stand development patterns (e.g., high vs. low initial sapling densities) interact to control overall NEP across the entire landscape, i.e., to determine whether the Yellowstone subalpine landscape is a net sink or source of carbon?

H4: Despite recovery of ANPP in many stands since the extensive fires in 1988, the Yellowstone subalpine landscape as a whole still functions as a net carbon source.

Rationale: Despite the recovery of ANPP in many of the postfire stands, NEP likely remains negative in all postfire stands because loss of C from dead wood remains high. The majority of the remaining forest is older than 100 years and its slightly positive NEP cannot yet offset losses from the postfire stands.

H5: Under the disturbance regime of the last 300 years, the Yellowstone landscape generally functioned as a net carbon sink, i.e., more stands had positive than negative NEP.

Rationale: Yellowstone's subalpine fire regime during the last 300 years has been characterized by infrequent but sometimes large and severe fires. Except for periods immediately after extensive fires in the early 1700s and the recent fires of 1988, the landscape was dominated by mature forests (Romme 1982, Romme and Despain 1989, Tinker et al. submitted). Based on the relationship between stand age and NEP, we expect an overall positive C budget when NEP of all individual stands is summed across the landscape (Kasischke 2000b).

H6: Under the disturbance regime anticipated for the next century, the Yellowstone landscape will shift from being a net carbon sink to a net carbon source, i.e., more stands will have negative than positive NEP because of more frequent fires.

Rationale: Climate simulations project increasing frequency and extent of fires in the next century (Stocks et al. 2000, Dale et al. 2001). Although it is likely that the Yellowstone landscape functioned mostly as a net C sink in the recent past (H5 above), we do not know how sensitive this area's C budget may be to alterations in the fire regime. More frequent fires may simply reduce the magnitude of annual net C storage in the system without causing a qualitative shift from sink to source, i.e., more individual stands may have negative NEP at any given time but stands with positive NEP still predominate. Alternatively, if the system already is close to the break-point between an overall positive vs. negative C budget, then even a small increase in fire frequency or extent could shift the Yellowstone landscape from functioning as a net C sink to a net C source (Kasischke 2000b). A drier climate that will accompany increased fire frequency may also lower NEP for each stand if ANPP is more sensitive to the lack of summer moisture than decomposition.

METHODS

Answers to question 1 (above), dealing with stand-level variation of NEP in space and time, will come from field measurements in 75 or more stands ~2 ha in size. We will estimate NEP as the sum of the annual change in C stored in aboveground live biomass (C_W), belowground live biomass (C_R), dead aboveground wood, standing and down (C_{DW}), dead coarse roots (C_{CR}), forest floor (C_L) and soil (C_S):

$$\mathrm{NEP} = \Delta[C_W + C_R + C_{DW} + C_{CR} + C_L + C_S] / \Delta t \quad [1]$$

Answers to question 2 (above), dealing with C budgets for the entire Yellowstone landscape, will come from (1) extrapolations of current conditions using a GIS approach, (2) modeling experiments that integrate the field measurements of NEP with a biogeochemical model (Century), and (3) linking our previous work on fire history, fire behavior, and the fire/climate interactions with (1) and (2) to estimate landscape NEP under future climates and fire return intervals.

Methods for Stand-Level Sampling

We will sample all of the components of NEP in 75 stands, stratified by age and density of lodgepole pine. Our intent is to develop three replicated chronosequences, each with a different tree density. Our sampling matrix will have five age classes (< 25, 40-70, 80-130, 170-230, and >250 yr old) and three density classes (low, medium, and high). The actual number of stems in each class will vary with stand age, so that the size classes reflect the trajectory of stem density that would be found with an initial density of $< 10^3$, $10^3 – 10^4$, and $> 10^4$ stems/ha. We will sample five replicate stands in each age/density class. Stand density and dead wood (CWD, standing and down) from the prior stand may not vary in concert (although we hypothesize that it will). If variability in CWD within a given age/density class is too large, we will establish a separate classification for CWD with stand age and, if necessary, sample additional stands for CWD. Because the YNP landscape is large, minor differences in soils and variation in microclimate along an elevational gradient may add additional variation to our chronosequences. However, in prior work, these variables contributed very little to explaining ANPP and LAI in stands developing after the 1988 fires. Consequently, we will include these variables in our analysis, but we do not expect them to be important.

In each stand, we will directly measure all C stocks in Eq. 1, using five 50 m transects in each stand as subsamples (transect width will vary with stem density). We will estimate the annual change in C stocks using several approaches for each component. Primarily, we will directly measure annual changes in rapidly changing C stocks: aboveground live vegetation (foliage and wood of trees, shrubs, and herbs), live roots (coarse and fine), and litter, and will use our chronosequence to develop simple models of annual changes through time of the slowly-changing components of the C cycle—soil C, dead coarse woody roots, and CWD. C stocks will be calculated from the biomass estimates after determining the C content of each component. Additionally, we will measure ANPP and N availability to assist with calibration of the Century model.

Annual changes in C stocks in live vegetation: stands <25 yr old: We will sample aboveground biomass in living tree saplings by measuring basal diameter and height of all saplings in the transects in each stand, and then apply allometric equations that relate foliage, branch, stem, and coarse root biomass to basal diameter and height. These equations were developed under our current NSF funding (Tinker et al. *Submitted*, Litton et al. *In Press*). Fine-root biomass will be estimated from 15 cores (6 cm diameter) per stand (3 per transect) to 30 cm. Additional cores will be taken if variance is very high. The cores will be washed within 48 hours of sampling, live roots will be separated from dead roots by visual examination, the live roots will be dried and weighed, and a subsample will be ashed. We will estimate biomass of shrubs and herbs from visual estimates of percent cover in subplots of each transect using relationships developed under current NSF funding. Subsamples of each component will be analyzed for C and N content.

The annual change in live tree biomass in the young stands will be estimated by measuring the height and diameter of each stem for the current and prior year, applying the allometric equations, and subtracting biomass in year 1 from that in year 2. Height for the prior year will be measured for each tree. Diameter for the prior year will be estimated by harvesting 30 trees per stand, measuring diameter increment on the harvested trees, and using double sampling techniques (Cochran 1977) to estimate diameter growth for all sampled trees. Annual change in shrub, herb, and fine root biomass will be derived from the difference in biomass between samples in years 1 and 2.

Annual changes in C stocks in live vegetation: stands >40 yr old: We have evaluated several allometric models for aboveground tree biomass and found that none currently fit all components well. Therefore, we will develop YNP allometrics for aboveground wood, foliage, and roots > 2 mm, using 30-50 trees. To estimate tree biomass, we will measure the diameter of every tree in the transects, and use the allometric equations. The annual change in live tree biomass will be estimated from the 5-year mean radial increment measured on 30 trees that span the size range in the stand and applied to the population using double sampling (Cochran 1977). Fine root, herb, and shrub biomass and annual increment will be estimated with the same techniques described above for stands < 25 yr old.

Annual changes in C stocks in CWD: In each stand (young or mature), CWD will be estimated separately for standing-dead trees, downed trees not yet touching the ground, and downed wood in contact with the ground, with diameter measured for all samples. Nearly all standing-dead trees are in decay class I, or sound wood (Maser et al. 1979), but downed wood may range from decay class I to V (highly decayed, elliptical logs incorporated into the forest floor). The mass of CWD in standing-dead trees and in fallen trees not yet touching the ground will be estimated by measuring the diameter at 1.4 m and applying Pearson et al.'s (1984) allometric equations, which we tested for YNP in a previous study (Tinker and

Knight 2000). Biomass of CWD in fallen trees in contact with the ground will be estimated by decay class using the planar intercept method (Brown 1974). Annual changes in CWD C will be estimated by two methods. First, we will develop site-specific decay coefficients for different sizes and classes of CWD, using techniques similar to those in Fahey (1983), and apply these to the standing crop of downed CWD in each decay class. Second, we will measure CWD biomass in each decay class throughout our chronosequence and estimate the annual rate of change from change in biomass over time.

Annual change in C stocks in litter: In each transect of each stand, we will measure the mass of each component of the litter layer (fine litter, charcoal, and woody material <7.5 cm) by removing all material down to mineral soil within three randomly located 50 x 50 cm plots (15 plots/stand). The three samples will be composited, and then a subsample of the composite will be separated into litter components, weighed, and dried. A subsample of fine litter will be measured for ash content to correct for any contamination by mineral soil. The annual change in C stocks in litter will be estimated by measuring litter mass for our three replicated chronosequences along our chronosequence of stands, and estimating the annual rate of change from change in biomass over time.

Annual change in C stocks in soil: The challenge in assessing soil C, and especially the rate of change in soil C, is the large point-to-point variability in both C concentration and bulk density. However, a precise estimate can be obtained with a large sample. We will use compositing to gain the benefits of large samples without the analytical costs. Changes in soil C over time, if any, are concentrated in the upper soil (e.g., Richter et al. 1999). Therefore, we will partition our soil samples to enhance detection of changes in the upper layer. We will sample mineral soil from 0-10 cm and 10-50 cm depth at 5 locations per transect in each stand, giving 25 sample locations per stand. Cores from a stand will be composited, sieved to pass 2 mm screen, mixed, and three subsamples dried, weighed, and analyzed for C. Bulk density will be estimated as soil dry weight (root and rock free)/volume. Because changes in soil C are slow relative to the size of stocks and difficult to estimate over short time periods, we will estimate annual changes in soil C by measuring soil C along our chronosequence, and estimate the annual rate of change from change in soil C over time. A preliminary study of changes in soil C using 12 stands burned in 1988 (sampled in 2000) paired with adjacent unburned stands yielded annual soil change of 5 g C m^{-2} yr^{-1} with a 95% CI of $\pm$ 25 g C m^{-2} yr^{-1}.

Annual change in C stocks in dead coarse roots: Dead coarse tree roots are a large pool of C in recently burned forests – a pool that decreases relatively rapidly through time. We will estimate the mass of dead coarse tree roots produced by the 1988 fires by measuring dbh of all trees that were alive in 1988 (still easily recognizable) in each transect, correcting for loss of bark, and then estimating the biomass of coarse roots (root crowns, lateral roots > 10 mm, and lateral roots 2-10 mm) using allometric equations developed with this proposal. We will estimate how much of this root biomass has decomposed since 1988, as well as the annual decomposition for the fire-created dead roots, by developing site-specific root decay coefficients using methods described in Yavitt and Fahey (1982) and applying these coefficients to 1988 biomass for each stand.

C loss in fire: To complete the C balance for our chronosequences, we will estimate the C lost from the ecosystem in the 1988 fires for each of the stands in the youngest age class. Biomass is lost through combustion from five compartments within lodgepole pine stands: live trees, standing-dead trees, down wood, fine woody debris (twigs and branches <7.5 cm diameter plus forest floor litter), and herbaceous and shrubby biomass (Tinker and Knight 2000). We will estimate biomass in the trees that were alive in 1988 by measuring dbh for each tree in each transect, correcting for loss of bark, and then estimating the biomass using allometric equations developed with this proposal. Down and standing dead wood that existed prior to 1988 will be identified in sampling. Litter and herb and shrub biomass will be estimated from values in stands in our chronosequences of the same age as the burned stand. Depending on fire intensity, all or a portion of each of these compartments is consumed or converted in a fire. Based on field measurements in stands that burned in 1988, Tinker and Knight (2000) and Tinker (*unpublished data*) developed equations for predicting C loss from each of these sources. We will apply these equations to our biomass estimates in each stand to estimate the C loss associated with the stand-replacing fire.

ANPP and additional data needed for modeling. To facilitate calibration of the Century model, we will collect litterfall (needed to estimate ANPP from biomass increment + litterfall) and N availability for each stand. We will collect litterfall using three 50 x 50 cm litter traps for each of the 5 transects in each plot. N availability will be assessed using resin bags inserted between mineral soil and the O horizon for a year (3/transect). Additionally, we will establish 2 weather stations on the Yellowstone plateau to measure radiation (PAR), temperature, relative humidity, and precipitation.

Measurement uncertainty and error propagation in our stand-level estimates of NEP: We recognize that variability will complicate detection of differences. However, prior studies on these sites have shown that variability *among replicate stands* is considerably less than variability *within* a stand. For example, the coefficient of variation (CV) for C in forest floor is ~100% within a stand, but only ~25% among replicate stands (of the same age and density). CV for C in biomass, dead wood, and soil among replicate stands at our sites (again from prior studies) is 20-30%. Therefore, given our sample size, we will have an 95% probability of detecting a 20% difference in NEP among age classes and 80% probability of detecting a 20% difference in NEP among density classes. We expect the differences in NEP to be substantially greater than ±20% for most age classes (Fig. 1). Additionally, annual rates of changes in C stocks (and associated error) are well constrained because of the many years between age classes. Finally, Giardina and Ryan (2002) have recently shown that the variance estimated from plot-level estimates of the components contains all available information on subsampling error and 'cumulative' error. Using this C balance method of measuring NEP, Ryan et al. (*in preparation*) successfully detected differences in NEP with stand age, tree density, and fertility.

Testing hypotheses related to question 1 (spatial and temporal variability in stand-level NEP): We will test H1 by analysis of variance of NEP and its components with age and density as the independent variables. We will test H2 by fitting a non-linear model to NEP over time and comparing models among density classes, and by comparing cumulative NEP. We will test H3 comparing the wood from the prior stand among tree density classes with analysis of variance.

Methods for Landscape Analyses (Question 2)

Once we have good estimates of NEP and the key components of NEP for individual stands as a function of stand age and density (based on the field work described above for question 1), we will scale up to the entire Yellowstone landscape by depicting the forest mosaic as a grid of individual stands (pixels) within a GIS environment, assigning appropriate NEP values to each pixel, and then summing the values of all individual stands. We will execute this procedure for the actual mosaic of stand ages and densities that characterize the current YNP landscape, and for a wide range of experimental scenarios of landscape structure, i.e., varying relative proportions of stands of different age and density classes. The experimental scenarios will be derived from simulations of fire frequency, fire spread, and postfire succession under alternative climatic conditions, using models developed in our previous NSF-funded research (Gardner et al. 1996, 1999; Hargrove et al. 2000).

This work will have four components. First, we will develop a map of current forest structure (stand age and tree density) for all of the forested portions of the Yellowstone Plateau. We have a fine-scale map of tree density for the areas that burned in 1988, from our previous work, but we do not yet have this information for the areas that did not burn in 1988. Using the 1:30,000 color infrared aerial photos that we used to produce the map of burned areas (flown in 1998), we will interpret stand structure for all of the remaining areas that did not burn in 1988 (details below). Then, we will sum the values of NEP from all individual stands to evaluate the current C budget of the entire Yellowstone subalpine ecosystem (hypothesis H4 above). Third, we will calibrate the Century model to current climate, and use the model to estimate how NEP will change for each stand age and density class under different climate scenarios. Finally, we will evaluate the C budget of the entire Yellowstone ecosystem under alternative climate/disturbance scenarios to test hypotheses H5 and H6. To accomplish this we will predict the proportion of the landscape in each age/density class using our simulations of fire and succession under contrasting climate scenarios (Gardner et al. 1996, 1999, Hargrove et al. 2000), and sum the values of NEP (adjusted for differences in climate using Century) for the different scenarios.

Mapping tree density and stand age of unburned forests on the Yellowstone plateau. We will develop maps of tree density and stand age using the 1:30,000 color infrared aerial photographs that were flown in August 1998 with our previous NSF funding. Mapping procedures will follow those used for mapping post-1988 sapling density (Turner et al. *Submitted*). Each photo in each flight line has been scanned at high resolution (5m) and transformed into a digital orthophoto using the new program OrthoMapper© (Scarpace et al. 2000), and a 30-m digital elevation model of YNP. Multiple orthophotos will be joined using the mosaic function in ERDAS Imagine (ERDAS, Inc. 1991). We will use supervised classification methods to produce the maps of tree density and stand age at a resolution of 50 x 50 m. Digital classification is usually done on satellite imagery, but we have adapted the methods to the aerial photos and found that the method produces the most accurate maps.

An existing set of stand structural data (n = 64 stands, D. R. Kashian, doctoral dissertation research) will be used to develop spectral signature files for stands of age and density. We will supplement these data with sites selected from a detailed stand age map that we developed with previous NSF funding for a 125,000-ha portion of the subalpine plateau (Romme and Despain 1989 and Tinker et al. submitted). Each grid cell in the image is then compared to the values in the signature file and assigned the value to which it is most similar. Accuracy assessment will be completed using independent data from 50 stands sampled in the field during years 1 and 2. Classification error will be assessed by computing the K-hat statistic (Lillesand and Kiefer 1994).

Estimating NEP for the entire Yellowstone landscape: We will use empirically based modeling in a GIS environment to characterize the current state of the Yellowstone landscape for C stocks, loss of C in the 1988 fires, and net annual C uptake. A variety of studies have explored variation in ecosystem processes at regional scales (Zak et al. 1986, 1989, Running et al. 1989, Sala 1988, Groffman et al. 1992, CL Turner et al. 1997), and GIS-based extrapolations have been used successfully to characterize entire landscapes (Burke et al. 1991a, Fan et al. 1998, Hansen et al. 2000). Fits of a non-linear model to NEP over the chronosequence (for each density class) will be used to predict field measurements of C stocks and NEP based on stand age and tree density (question 1) and then be applied to each cell in a GIS (ARC/INFO). The coefficient of variation in predicted C stocks and NEP will also be mapped in the GIS so that the spatial trend in variability in model predictions can be assessed (e.g., Hansen et al. 2000). Predicted values of NEP in each grid cell will be summed for the subalpine plateau to determine whether the current landscape is a source or a sink for C.

Biogeochemical modeling: Changes in climate that alter fire frequency may also change NEP. To adjust our measurements of NEP to reflect the wetter or drier climate that will generate changes in fire frequency, we will use the Century model (Parton et al. 1987, 1988; Burke et al. 1991b; Schimel et al. 1996, 1997). For the model calibration we will use ANPP, C and N stocks in wood, branches, twigs, leaves, coarse roots, fine roots, soil, litter, and dead wood, and N availability. We will also have site-specific information on soil type and depth, and climate data from 2 stations on the Yellowstone plateau. We will calibrate the model using current climate, and use the model to simulate how a drier or wetter climate would change the components of NEP for chronosequences of different density. We will validate the model using data from lodgepole pine chronosequences in drier climates (Ryan and Waring 1992, Smith and Resh 1999).

Assessing alternative disturbance regimes and impacts on overall carbon budgets: Our experimental modeling approach is somewhat similar to that of Kasischke et al. (1995) and Kasischke (2000b), who varied the expected stand age distribution in response to a changing fire return interval, and then summed resulting carbon values from all individual stands in a simulated boreal forest landscape. A *simplified* preliminary example of our modeling approach is as follows: In our previous NSF-supported work (Gardner et al. 1996) we simulated 1000 years of fire and post-fire succession in a 78,389 ha portion of YNP under three climate scenarios: (1) current climate (20^{th} century), (2) a wetter climate, and (3) a drier climate. The average number of pixels in each of four stand age classes during the simulated 1000 years under the wetter scenario is shown in the left two columns of Table 1. The third column contains estimates of NEP for individual stands (pixels) of each age class, derived from the preliminary estimates in Figure 1 and assuming that half the stands are high density and half are low density (hence the numbers in the table are the mean of high and low density stands in the third panel of Figure 1). The fourth column in the table is the product of NEP per pixel times the number of pixels. The sum of all values for all pixels (lower right cell in the table) indicates that this landscape has a net positive NEP. Indeed, these numbers suggest a substantial net carbon *sink* of 341,410 kg C yr^{-1}. A similar analysis for the drier climate scenario (not shown), again using the preliminary values in Figure 1 but assuming that 90% of stands are low density, suggests that more frequent fires, resulting in a greater proportion of very young stands, and less dense postfire stands would cause the landscape to switch to become a net carbon *source* with an annual loss of 25,830 kg C yr^{-1}. The landscape analyses we conduct for this proposed research will incorporate improved values for individual stands, derived from our field work (question 1), plus additional simulations to test the effects of varying stand density and age class distribution. We will conduct an extensive set of simulations of fire regimes in which the return interval and size of fires are varied independently, and we will determine whether the landscape was a net source or sink of carbon during a 1000-yr simulation and also the proportion of simulation years in which the landscape was a carbon source.

Table 1. A *simplified, preliminary* analysis of the carbon budget for the Yellowstone landscape, derived from a simulation of fire and landscape structure under a wet climate scenario (Gardner et al. 1996) plus preliminary estimates of NEP within individual stands (Fig. 1).

Stand age	Average number of hectares during a 1000-year	Average NEP per hectare (g C m^{-2} yr^{-1})simulation (assume 50% sparse, 50% dense)	Landscape NEP (kg C yr^{-1})
25	8,738	- 40	- 349,520
75	14,568	+ 20	+ 291,360
150	24,832	+ 10	+ 248,320
250	30,250	+ 5	+ 151,250
Totals	78,389	--	+ 341,410

SIGNIFICANCE

The response of carbon cycling and C storage to different disturbance regimes and the interaction of disturbance, climate, and landscape structure are a critical research issues today, because of concerns about changes in the global C cycle and attendant climatic, ecological, economic, and political implications. The research that we propose will provide a detailed case study of C dynamics from the scale of individual forest stands to a large (ca 500,000 ha) landscape dominated by coniferous forest. We will describe changes in all of the major pools and fluxes of the C cycle at temporal scales ranging from years to centuries, as influenced by periodic fires and successional patterns within a landscape where fire is a key ecological process. Because fire regimes are extremely sensitive to climate, changes in fire frequency will likely accompany changes in global climate, and can potentially alter C cycling dramatically. Indeed, changes in C uptake and release under an altered disturbance regime could be great enough to qualitatively shift the overall landscape from functioning as a C sink to a C source in the global C cycle. By directly and indirectly quantifying all of the stocks and rates of change in the major components of the C cycle in the Yellowstone subalpine landscape, we will contribute to understanding how changes in disturbance regimes may produce qualitatively different patterns of C release and storage in coniferous forests worldwide.

In addition to providing information valuable in assessing global climate change, this research will contribute to answering some of the most interesting, basic questions in ecology – questions related to the interactions of ecological pattern and process within large, heterogeneous ecosystems, and how those interactions are affected by natural disturbance processes. We will build upon and integrate all of our previous work in YNP. From our initial interests in disturbance history (Romme 1982), and recovery of community composition after fire (Tinker et al. 1994, Turner et al. 1997, Romme and Turner *In Press*, Romme et al. *Submitted*), we have increasingly focused our research on the heterogeneity of ecosystem processes in the subalpine landscape. Our recent work has dealt with patterns of aboveground biomass accumulation (Reed et al. 1999, Tinker et al. *Submitted*, Turner et al. *Submitted*) and soil respiration (Litton *Submitted*). We also have just initiated a study of spatial and temporal heterogeneity in nitrogen dynamics, with funding from the Andrew W. Mellon Foundation. With the research proposed here, we will develop a comprehensive understanding of C dynamics in the Yellowstone subalpine landscape, and will eventually be able to link the patterns in C dynamics with long-term patterns in fire regime, plant community recovery, and nitrogen cycling after fire.

PROJECT DURATION, MANAGEMENT, AND SCHEDULE

This is a three-year project. Because this project makes use of much previous and on-going work, we wish to be clear about the tasks to be performed, what data will be derived from currently funded work, and which tasks are to be funded with this proposal.

Task	Source
Δ Live biomass, < 25yr old	**This proposal,** using allometric equations developed in Previous NSF[a] & Litton thesis
Δ Live biomass > 25 year old	
Allometric equation for wood, branches, bark, foliage, and coarse roots	**This proposal**
Sampling diameter change	**This proposal**
Sampling fine roots	**This proposal**
Δ Understory biomass 25 yr old	**This proposal,** using allometric equations developed in Previous NSF[a] & Litton thesis
Δ Dead aboveground biomass (CWD), all ages	**This proposal**
Δ Litter C	**This proposal**
Litterfall	On-going Mellon[d]
Δ Soil C	**This proposal**, plus re-sampling plots from Litton thesis
Δ Dead belowground biomass	**This proposal**
High resolution map of stand density for landscape, < 25 yr old	Previous NSF[a]
High resolution map of stand density & stand age, > 25 yr old	**This proposal** using imagery collected with Previous NSF[c]
Landscape NEP	**This proposal**
Simulations of patterns of stand age distribution with different fire frequencies	**This proposal,** applying models developed in Previous NSF[b]

Calibration/validation of Biogeochemistry models	**This proposal**
Simulations of changed climate on NEP with Biogeochemistry models	**This proposal**
Landscape NEP for different fire frequencies	**This proposal**

Previous NSF[a] = Turner, M.G., W.H. Romme, and D. H. Knight. Causes and consequences of multiple successional pathways following the 1988 Yellowstone fires. National Science Foundation, 7/98-9/02.
Previous NSF[b] = Romme, W.H., M.G. Turner, and R.H. Gardner. Causes and Consequences of Large-Scale Fires in Yellowstone National Park. National Science Foundation, 2/91-12/94.
Previous NSF[c] = Romme, W.H., and D.G. Despain. Fire and landscape dynamics in Yellowstone National Park. National Science Foundation, 8/84-5/88.
On-going Mellon[d] = Turner, M. G., W. H. Romme, and D. B. Tinker. Postfire landscape heterogeneity and ecosystem processes in subalpine forests of Yellowstone National Park. Mellon Foundation, 6/2001 – 9/2006

All four PIs will be involved in every aspect of the research. For purposes of organization and administration, however, individual PIs will take the lead on individual components of the study:

- **Ryan** will have overall leadership of the project. Ryan and a PhD student at CSU directed by Ryan and Romme will take the lead on measuring the ground-based NEP in the field, calibrating the Century model, and assessing the effect of changes in climate on NEP.
- **Romme** will co-direct the PhD student at CSU and take the lead on simulating alternative disturbance regimes.
- **Turner** and a PhD student at UW will take the lead on mapping tree density and biomass in unburned forests from aerial photographs, and scaling up to the landscape.
- **Tinker** will take the lead on measuring CWD and aboveground biomass in the field.

The PIs have all worked together very effectively on previous large-scale research projects. We will confer regularly about field season logistics, scheduling, data sharing, presentations at annual meetings, and manuscript preparation. Most of the fieldwork will be done in the first two years, while landscape extrapolations and manuscript submission will occur in the third year.

TECHNOLOGY TRANSFER

Studies funded under this proposal will lead to (1) a better understanding of how forest age, stand density, and the legacy from the prior stand affect net storage of carbon in the ecosystem, (2) a landscape assessment of how differences in climate and fire regimes will effect the distribution of age classes and stand structure, and (3) how differences in climate and fire regimes will therefore affect carbon storage at the landscape level. We will teach managers and policymakers what we have learned about these processes by holding a workshop in year 3 (either at the University of Wyoming's field camp or Fraser Experimental Forest). The workshop will provide the underlying information and provide a toolkit for managers to assess how different fire and land management strategies alter landscape carbon balance. We will also summarize our work and the workshop in a RMRS GTR.

DELIVERABLES

The project will result in several papers in peer-reviewed journals, a concept/synthesis paper to be sent to Bio Science, a toolkit (spreadsheet programs) for assessing how different current and prior stand conditions alter stand carbon storage over a fire cycle, a workshop explaining our work to land managers, and a RMRS GTR summarizing our work and the workshop. Proposed titles and dates for deliverables are given in the Appendix **.**

APPENDIX

The Appendix contains the following information:
- References
- Budget
- Budget Justification
- Deliverables
- Two-page CVs
- Letters of Collaboration

REFERENCES

Amiro, B. D., J. M. Chen, and J. Liu. 2000. Net primary productivity following forest fire for Canadian ecoregions. Canadian Journal of Forest Research 30:939-947.

Anderson, J.A., and W.H. Romme. 1991. Initial floristics in lodgepole pine (*Pinus contorta*) forests following the 1988 Yellowstone fires. International Journal of Wildland Fire 1:119-124.

Auclair, A.N.D., and T.B. Carter. 1993. Forest wildfires as a recent source of CO_2 at northern latitudes. Canadian Journal of Forest Research 23:1528-1536.

Baldocchi, D. D., B. B. Hicks, and T. P. Meyers. 1988. Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods. Ecology 69:1331-1340.

Bonan, G.B., H.H. Shugart, and D.L. Urban. 1990. The sensitivity of some high-latitude boreal forests to climatic parameters. Climatic Change 16:9-29.

Brown, J.K. 1974. Handbook for inventorying downed woody material. USDA Forest Service General Technical Report INT-16. Intermountain Forest and Range Experimental Station. Ogden, UT.

Burke, I. C., D. S. Schimel, W. J. Parton, C. M. Yonker, L. A. Joyce, and W. K. Lauenroth. 1991a. Regional modeling of grassland biogeochemistry using GIS. Landscape Ecology 4:45-54.

Burke, I. C., T. G. F. Kittel, W. K. Lauenroth, P. Snook, C. M. Yonker, and W. J. Parton. 1991b. Regional analysis of the central Great Plains: Sensitivity to climate variability. BioScience 41:685-692.

Burke, R.A., R.G. Zepp, M.A. Tarr, W.L. Miller, and B.J. Stocks. 1997. Effect of fire on soil-atmosphere exchange of methane and carbon dioxide in Canadian boreal forest sites. Journal of Geophysical Research 102:29,298-29,300.

Carpenter, S.R., and M.G. Turner. 1998. At last: a journal devoted to ecosystem science. Ecosystems 1:1-5.

Cochran, W. G. 1977. Sampling techniques, 3rd edition. John Wiley and Sons, New York, New York, USA.

Crutzen, P.J., and J.G. Goldhammer, editors. 1993. Fire in the environment: the ecological, atmospheric, and climatic importance of vegetation fires. John Wiley & Sons, New York.

Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. J. Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D. Simberloff, F. J. Swanson, B. J. Stocks, and B. M. Wotton. 2001. Climate change and forest disturbances. BioScience 51:723-734.

Fahey, T. J. 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* ssp. *latifolia*) ecosystems, southeastern Wyoming. Ecological Monographs 53:51-72.

Fan, W., J. C. Randolph and J. L. Ehman. 1998. Regional estimation of nitrogen mineralization in forest ecosystems using geographic information systems. Ecological Applications 8:734-747.

Foster, D. R., D. H. Knight, and J. F. Franklin. 1998. Landscape patterns and legacies resulting from large infrequent forest disturbances. Ecosystems 1:497-510.

French, N. H. F., E. S. Kasischke, B. J. Stocks, J. P. Mudd, D. L. Martell, and B. S. Lee.. 2000. Carbon release from fires in the North American boreal forest. Pages 377-388 in: Kasischke, E. S., and B. J. Stocks (editors), Fire, climate change, and carbon cycling in the boreal forest. Springer-Verlag, New York.461 p.

Gardner, R.H., W.W. Hargrove, M.G. Turner, and W.H. Romme. 1996. Climate change, disturbances and landscape dynamics. Pp. 149-172. In: B. Walker and W. Streffen, eds. Global change and terrestrial ecosystems. Cambridge University Press, Cambridge, UK.
Gardner, R.H., W.H. Romme and M.G. Turner. 1999. Predicting forest fire effects at landscape scales. In: D.J. Mladenoff and W.L. Baker, eds. Spatial modeling of forest landscape change. pp. 163-185. Cambridge University Press, Cambridge.
Giardina, CP and MG Ryan. 2002. Total belowground carbon allocation in a fast growing *Eucalyptus* plantation estimated using a carbon balance approach. Ecosystems, *In Press*.
Goulden, M. L., J. W. Munger, S. M. Fan, B. C. Daube, and S. C. Wofsy. 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. Science 271:1576-1578.
Goulden, M. L., S. C. Wofsy, J. W. Harden, S. E. Trumbore, P. M. Crill, S. T. Gower, T. Fries, B. C. Daube, S. M. Fan, D. J. Sutton, A. Bazzaz, and J. W. Munger. 1998. Sensitivity of boreal forest carbon balance to soil thaw. Science 279:214-217.
Groffman, P. M., J. M. Tiedje, D. L. Mokma, and S. Simkins. 1992. Regional scale analysis of denitrification in north temperate forest soils. Landscape Ecology 7:45-53.
Hansen, A. J., J. J. Rotella, M. P. V. Kraska, and D. Brown. 2000. Spatial patterns of primary productivity in the Greater Yellowstone Ecosystem. Landscape Ecology. 15:505-522.
Hargrove, W. W., R. H. Gardner, M. G. Turner, and W. H. Romme. 2000. Simulating fire patterns in heterogeneous landscapes. Ecological Modeling 135:243-263.
Harmon, M. E. 2001. Carbon sequestration in forests: addressing the scale question. Journal of Forestry 99:24-29.
Houghton, R. A. 1996. Terrestrial sources and sinks of carbon inferred from terrestrial data. Tellus 48B:420-432.
Kareiva, P. 1994. Space: the final frontier for ecological theory. Ecology 75:1.
Kasischke, E. S. 2000 a. Boreal ecosystems in the global carbon cycle. Pages 19-30 in: Kasischke, E. S., and B. J. Stocks (editors), Fire, climate change, and carbon cycling in the boreal forest. Springer-Verlag, New York.461 p.
Kasischke, E. S. 2000 b. Effects of climate change and fire on carbon storage in North American boreal forests. Pages 440-452 in: Kasischke, E. S., and B. J. Stocks (editors), Fire, climate change, and carbon cycling in the boreal forest. Springer-Verlag, New York. 461 p.
Kasischke, E. S., N. L. Christensen, Jr., and B. J. Stocks. 1995. Fire, global warming and the mass balance of carbon in boreal forests. Ecological Applications 5:437-451
Kurz, W. A., and M. J. Apps. 1999. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. Ecological Applications 9:526-547.
Law, B. E., M. G. Ryan, and P. M. Anthoni. 1999. Seasonal and annual respiration of a ponderosa pine ecosystem. Global Change Biology 5:169-182.
Leenhouts, W. 1998. Assessment of biomass burning in the conterminous United States. Conservation Ecology 2(1) (electronic journal: http://www.consecol.org).
Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology 73: 1943-1967.
Lillesand, T. M. and R. W. Kiefer. 1994. Remote sensing and image interpretation. 3rd edition. John Wiley and Sons, New York.
Litton C.M., M.G. Ryan, D.B. Tinker, and D.H. Knight. 2003. Below- and aboveground biomass in young post-fire lodgepole pine forests of contrasting tree density. *Canadian Journal of Forest Research*. In Press (6/02).
Litton C.M., M.G. Ryan, D.H. Knight, and P.D. Stahl. *Submitted*. Soil-surface CO_2 efflux and microbial biomass in relation to tree density thirteen years after a stand replacing fire in a lodgepole pine ecosystem. Global Change Biology (7/02).
Litton, C. Above and belowground carbon allocation in developing and mature lodgepole pine stands. *PhD Thesis* University of Wyoming, December 2002.
Malhi, Y., D. D. Baldocchi, and P. G. Jarvis. 1999. The carbon balance of tropical, temperate and boreal forests. Plant, Cell and Environment 22:715-740.

Maser, C., R.G. Anderson, K. Cromack, Jr., J.T. Williams, and R.E. Martin. 1979. Dead and down woody material. In: . J.W. Thomas (ed.) Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington, pp. 78-85. USDA Forest Service Ag. Handbook No. 553.
Moreno, J.M. and W.C. Oechel, editors. 1994. The role of fire in mediterranean-type ecosystems. Springer-Verlag, New York.
Murray, B. C., S. P. Prixley, R. A. Birdsey, and R. N. Sampson. 2000. Carbon sinks in the Kyoto Protocol: potential relevance for U.S. forests. Journal of Forestry 98:6-11.
Overpeck, J.T., D. Rind, and R. Goldgerg. 1990. Climate-induced changes in forest disturbance and vegetation. Nature 343:51-53.
Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal 51: 1173-1179.
Parton, W. J., J. W. B. Stewart, and C. V. Cole. 1988. Dynamics of C, N, P, and S in grassland soil: A model. Biogeochemistry 5: 109-131.
Pearson, J.A., T.J. Fahey, and D.H. Knight. 1984. Biomass and leaf area in contrasting lodgepole pine forests. Canadian Journal of Forest Research 14:259-265.
Reed, R.A., M.E. Finley, W.H. Romme and M.G. Turner. 1999. Aboveground net primary production and leaf-area index in early postfire vegetation in Yellowstone National Park. Ecosystems 2: 88-94.
Richter, D. D., D. Markewitz, S. E. Trumbore, and C. G. Wells. 1999. Rapid accumulation and turnover of soil carbon in a re-establishing forest. Nature 400:56-58.
Romme, W.H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs 52: 199-221.
Romme, W.H., and D.G. Despain. 1989. Historical-perspective on the Yellowstone fires of 1988. BioScience 39: 695-699.
Romme, W.H., and M.G. Turner. 1991. Implications of global climate change for biodiversity in the Greater Yellowstone Ecosystem. Conservation Biology 5:373-386.
Romme, W. H., and M.G. Turner. *In Press.* Ten years after the Yellowstone fires: is restoration needed? Invited book chapter in: Wallace, L. L., and N. Christensen (editors), After the Fires: The Ecology of Change in Yellowstone National Park. Yale University Press.
Running, S. W., R. R. Nemani, D. L. Peterson, L. E. Band, D. F. Potts, L. L. Pierce, and M. A. Spanner. 1989. Mapping regional forest evapotranspiration and photosynthesis by coupling satellite data with ecosystem simulation. Ecology 70:1090-1101.
Ryan, M.G., and R.H. Waring. 1992. Stem maintenance and stand development in a subalpine lodgepole pine forest. Ecology 73: 2100-2108.
Ryan, M.G., D. Binkley, and J.H. Fownes. 1997. Age-related decline in forest productivity: pattern and process. Advances in Ecological Research 27:213-262.
Ryan, M.G., D. Binkley, J. H. Fownes, C.P. Giardina, and R.S. Senock. An experimental test of test of the causes of growth decline with stand age. *Manuscript in Preparation*.
Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. Ecology 69:40-45.
Scarpace, F. L., P. R. Weiler, and J. Kruepe. 2000. A simplified method of producing orthophotos. Proceedings of the American Society of Photogrammetry and Remote Sensing, Washington DC, May 2000.
Schimel, D.S, B.H. Braswell, R. McKeown, D.S. Ojima, W.J. Parton, and W. Pullium. 1996. Climate and nitrogen controls on the geography and time scales of terrestrial biogeochemical cycling. Global Biogeochemical Cycles 10:677-692.
Schimel, D.S., VEMAP Participants, and B.H. Braswell. 1997. Continental scale variability in ecosystem processes: models, data, and the role of disturbance. Ecological Monographs 67:251-271.
Schulze, E.-D., C. Wirth, and M. Heimann. 2000. Climate change - managing forests after Kyoto. Science 289:2058-2059.
Schulze, E.-D., J. Lloyd, F. M. Kelliher, C. Wirth, C. Rebmann, B. Luhker, M. Mund, K. Knohl, I. M.

Milyukova, W. Schulze, W. Ziegler, A. B. Varlagin, A. F. Sogachev, R. Valentini, S. Dore, S. Grigoriev, O. Kolle, M. I. Panfyorov, N. Tcebakova, and N. N. Vygodskaya. 1999. Productivity of forests in the Euorsiberian boreal region and their potential to act as a carbon sink--a synthesis. Global Change Biology 5:703-722.

Seiler, W. and P.J. Crutzen. 1980. Estimates of gross and net fluxes of carbon between the biosphere and the atmosphere from biomass burning. Climate Change 2:207-247.

Slaughter, K. W., D. F. Grigal, and L. F. Ohmann. 1998. Carbon storage in southern boreal forests following fire. Scandinavian Journal of Forest Research 13:119-127.

Smith, F.W. and S.C. Resh. 1999. Age-related changes in below-ground carbon allocation in Pinus contorta Forests. Forest Science 45: 333-341.

Stocks, B. J., M. A. Fosberg, M. B. Wotton, T. J. Lynham, and K. C. Ryan. 2000. Climate change and forest fire activity in North American boreal forests. Pages 368-376 in: Kasischke, E. S., and B. J. Stocks (editors), Fire, climate change, and carbon cycling in the boreal forest. Springer-Verlag, New York.461 p.

Swetnam, T.W. 1993. Fire history and climate change in giant sequoia groves. Science 262:885-889.

Tilman, D., P.B. Reich, H. Phillips, M. Menton, A. Patel, E. Vos, D. Peterson, and J. Knops. 2000. Fire suppression and ecosystem carbon storage. Ecology 81:2680-2685.

Tinker, D.B, W.H. Romme, W.W. Hargrove , R.H. Gardner, and M.G. Turner. 1994. Landscape-scale heterogeneity in lodgepole pine serotiny. Canadian Journal of Forest Research 24: 897-903.

Tinker, D.B., and D.H. Knight. 2000. Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. Ecosystems 3:472-483.

Tinker, D.B., W.H. Romme, and D.G. Despain. *In Press.* Historic range of variability in landscape structure in subalpine forests of the Greater Yellowstone Area. Landscape Ecology.

Tinker, D.B., M.G. Turner, W.H. Romme, C.M. Litton, and D.H. Knight. *Submitted.* Biomass, aboveground net primary productivity and leaf area in young postfire lodgepole pine stands, Yellowstone National Park, Wyoming. Ecosystems.

Turner, C. L., J. M. Blair, R. J. Schartz, and J. C. Neel. 1997. Soil N and plant responses to fire, topography, and supplemental N in tallgrass prairie. Ecology 78:1832-1843.

Turner, D. P., G. J. Koerper, M. E. Harmon, and J. J. Lee. 1995. A carbon budget for forests of the conterminous United States. Ecological Applications 5:421-436.

Turner, M.G., R.H. Gardner and R.V. O'Neill. 1995. Ecological dynamics at broad scales. BioScience: Supplement S-29 to S-35.

Turner, M.G., V.H. Dale and E.E. Everham, III. 1997a. Crown fires, hurricanes and volcanoes: a comparison among large-scale disturbances. BioScience 47:758-768.

Turner, M.G., W.H. Romme, R.H. Gardner, and W.W. Hargrove. 1997b. Effects of fire size and pattern on early postfire succession in subalpine forests of Yellowstone National Park, Wyoming. Ecological Monographs 67:411-433.

Turner, M.G., W.L. Baker, C. Peterson and R.K. Peet. 1998. Factors influencing succession: Lessons from large, infrequent disturbances. Ecosystems 1: 511-523.

Turner, M. G., W. H. Romme, D. B. Tinker, D. M. Kashian, and D. H. Knight. *Submitted*. Effects of a fire-created landscape mosaic on biomass, leaf area index and aboveground net primary production in Yellowstone National Park, Wyoming. Ecosystems.

Valentini, R., G. Matteucci, A. J. Dolman, E.-D. Schulze, C. Rebmann, E. J. Moors, A. Granier, P. Gross, N. O. Jensen, K. Pilegaard, A. Lindroth, A. Grelle, C. Bernhofer, T. Grunwald, M. Aubinet, R. Ceulemans, A. S. Kowalski, T. Vesala, U. Rannik, P. Berbigier, D. Loustau, J. Guomundsson, H. Thorgeirsson, A. Ibrom, K. Morgenstern, R. Clement, J. Moncrieff, L. Montagnan, S. Minerbi, and P. G. Jarvis. 2000. Respiration as the main determinant of carbon balance in European forests. Nature 404:861-865.

Yavitt, J.B. and T. J. Fahey. 1982. Loss of mass and nutrient changes of decaying woody roots in lodgepole pine forests, southeastern Wyoming. Can. J. For. Res. 12: 745-752.