

Project title: COLLABORATIVE RESEARCH: Disturbance, succession and forest carbon dynamics: a large-scale manipulation at the University of Michigan Biological Station

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ABSTRACT

1. *Broad project objectives:* a) Quantify C exchange processes during and after a successional shift from mature aspen to a young mixed conifer/deciduous forest; b) Investigate the interactive role of disturbance and succession in governing landscape-level variability in C storage; c) Continue measurements of mass and energy exchange over a maturing aspen-dominated hardwood forest, building on more than eight years of continuous forest C cycle studies.
2. *Location of research activities:* The University of Michigan Biological Station Ameriflux site, Pellston, Michigan.
3. *List of hypotheses to be tested:* a) There will be a brief, 3 to 5-yr, reduction in NEP post-treatment due to reduced LAI and increased heterotrophic respiration. This will be followed by the rapid recovery of LAI and eventual stabilization of NEP above control levels. b) Overstory aspen and birch mortality will result in a pulse of increased fine root turnover that will temporarily increase heterotrophic respiration by up to 25 %, and concurrently reduce NPP by up to 42 %. c) Overstory aspen and birch mortality will increase soil and forest floor C storage by substantially increasing detritus inputs to the soil. d) Successional change in canopy composition will result in more variable forest microclimates and a more patchy distribution of nutrients, both of which will be important regulators of landscape-level variability in C storage. e) The reallocation of N during succession will affect rates of regrowth in the developing canopy.
4. *Methods outline:* We will accelerate forest ecological succession by killing all mature aspen and birch (~37 and 5 % canopy LAI, respectively) within a 33 ha treatment stand close to but outside the flux footprint of the existing meteorological tower and control site. A second tower (already funded) will begin operating within the treatment stand in 2006, 2 years prior to girdling. Three additional, 2 ha stands also will be treated to serve as replicate plots for ecological measurements. Ecological and meteorological measurements will be conducted in the footprint of the treatment and control stands before and after the girdling treatment to quantify effects of climate and succession on C pools and fluxes.
5. *Expected accomplishments/deliverables:* Our objectives support focus 3 of the NICCR RFP-01, strengthening our empirical understanding of spatial and temporal variability in CO₂ sources and sinks for a regionally important ecosystem. We expect this research will allow us to continue the current pace of 3 to 4 peer-reviewed publications per year (29 total/8 years) and more than a dozen presentations annually.

I. BACKGROUND

This proposal forms the fourth stage of the long-term UMBS Forest Carbon Cycle Research Program (UMBS~Flux). Our aim is to enhance the theoretical and empirical understanding of soil-vegetation-atmosphere exchanges of carbon dioxide (CO₂), water (H₂O), and energy balance components based on measurements at this AmeriFlux site in northern lower Michigan. The UMBS~Flux tower facility was designed, constructed, and made operational during the first stage of the project (1997-2000). During the second stage (2000-2003) we established protocols for the collection and analysis of a broad suite of meteorological and ecological data and made substantive progress towards many of our core research objectives. In the third stage (2003-2006), we provided important ecological and meteorological assessments of carbon (C) fluxes and storage (e.g., Schmid et al., 2003; Curtis et al., 2005; Gough et al., 2006).

The purpose this proposal is to request funding to initiate C cycling studies in a novel, ecosystem-scale experimental manipulation designed to accelerate the successional transition from an even-aged aspen-dominated forest to an uneven-aged mixed deciduous-conifer forest and to continue the operation of the existing UMBS~flux AmeriFlux site. Our objectives support focus 3 of the NICCR RFP-01, strengthening our empirical understanding of spatial and temporal variability in CO₂ sources and sinks for a regionally important ecosystem. Our core objectives are to:

- 1. Quantify C exchange processes during and after ecological succession from a mature aspen to a young mixed conifer/deciduous forest.**
- 2. Investigate the interactive role of disturbance and succession in governing landscape-level variability in C storage.**
- 3. Continue measurements of mass and energy exchange over a maturing aspen-dominated hardwood forest, building on more than eight years of continuous forest C cycle studies.**

IA. PATTERNS OF DISTURBANCE AND SUCCESSION IN THE UPPER MIDWEST

A rich history of forest ecological research in the upper Midwest has established the linkage between human and natural disturbances and the trajectory of forest succession in the region. A majority of forests in the upper Midwest were subjected to logging and/or wildfire by the early 20th century (Karamanski, 1989; Frelich, 1995; Friedman and Reich, 2005). These catastrophic stand-replacing disturbances resulted in the establishment of a widespread cohort of aspen (*Populus spp.*). Many aspen-dominated forests in the region are now approaching or are past maturity and beginning to decline (Peterson and Squires, 1995; Stearns and Likens, 2002; Wolter and White, 2002; Hill et al., 2005). Forest inventory data suggest that 70 % of aspen-dominated forests in the region are at least 50 yrs-old and beyond peak production (Cooper, 1981; USDA, 2001). Conversely, red maple (*Acer rubrum*), northern red oak (*Quercus rubra*), and white pine (*Pinus strobus*) representation is increasing in forests of the upper Midwest (Peterson and Squires, 1995; Kneeshaw and Bergeron, 1998; Stearns and Likens, 2002; Wolter and White, 2002). Consequently, current and future forest composition and structure are integrally linked to formative disturbance events of the past.

The disturbance regimes these forests currently experience are considerably different from those of a century ago (Frelich, 1995). Maturing forests in the upper Midwest now are less prone to stand-replacing fire and clear-cut harvesting because of fire suppression and the migration of intensive forestry operations to the western and southeastern U.S. (Frelich and Reich, 1995; Houghton et al., 1999). As a result, the distribution of young, even-aged forests will continue to diminish, giving way to uneven-aged forests with multi-layer canopies and many canopy gaps (Palik and Pregitzer, 1993; Frelich and Reich, 1995; Kneeshaw and Bergeron, 1998; Stearns and Likens, 2002; Hill et al., 2005).

While harvesting and fires a century ago depleted C stored in forests of the upper Midwest region, estimates of annual C storage, or net ecosystem production (NEP), suggest that these ecosystems are now C sinks (Birdsey and Heath, 1995; Birdsey et al., 2000). Reforestation has resulted in C storage at modest rates and recent C inventories indicate that northern U.S. forests, despite a short growing season, are harvested less than forests in other regions, making them an important terrestrial C sink (Birdsey et al., 2000). However, the current trajectory of succession suggests a widespread change in forest structure, composition, and C cycling dynamics in the coming decades.

IB. DISTURBANCE, SUCCESSION, AND C CYCLING: PRIOR RESEARCH

Although the successional dynamics likely to occur in these forests are well-understood, the C cycling processes in the emerging ecosystem are not. Successional events shape forest structure and composition, both of which are integrally linked to NEP and C cycling processes (e.g., Law et al., 2001, Law et al., 2003; Humphreys et al., 2005). Most studies that have investigated C cycling through a successional shift did so in forests following a stand-replacing disturbance. While this severe disturbance is common in fire prone and intensively managed ecosystems, many maturing forests of the upper Midwest and Eastern U.S. are likely to undergo a less severe and subtler successional transition that includes the emergence of a more diverse and complex forest, but does not involve complete canopy replacement (Frelich and Reich, 1995; Stearns and Likens, 2002).

There are only a few examples of ecosystem-scale studies conducted within the AmeriFlux network that have used meteorological methods to examine NEP or net ecosystem exchange (NEE) at different forest developmental stages. Law et al. (2001) investigated changes in NEP with forest age in a ponderosa pine (*Pinus ponderosa*) forest chronosequence. Chen et al. (2002) compared net ecosystem exchange (NEE) in young and old-growth Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) forests. Both studies found lower rates of forest C storage in old-growth forests. In the Midwest, Desai et al. (2005) compared NEP in a mature hardwood forest with that of an old-growth hemlock-hardwood forest, reporting a smaller C sink for the old-growth forest. In a synthesis of Midwestern AmeriFlux sites, including UMBS, Desai et al. (2006) showed that stand age, canopy height, and vegetation type were important factors for explaining spatial variability of carbon fluxes across the region. These studies provide an important assessment of changes in forest C storage through succession by making use of existing stand developmental gradients. This approach of substituting space for time to investigate changes in C storage through succession assumes that stand-level variability due to differences in climate, soils, and land-use histories is negligible. None of these studies used an experimental manipulation, as we propose here, to examine ecosystem-scale C storage through successional change.

Within the traditional forestry and forest products community, the relationship between canopy structure and C cycling processes also has not been fully characterized. Although benefits of selective thinning or partial harvest on wood production are well documented for some managed forests, most studies have been conducted in stands lacking the diverse composition and multi-layer canopy with many gaps that we expect to observe following a 42 % canopy reduction at UMBS (e.g., Gilmore, 2003; Juodvalkis et al., 2005). A decline of aspen will result in a patchy canopy structure that is both vertically and horizontally heterogeneous (Peterson and Squires, 1995; Hill et al., 2005). This is in contrast to managed thinning operations in which selective partial harvesting results in a relatively uniform canopy distribution to maximize accessibility of water, nutrients, and light resources (Mitchell et al., 1996).

For a number of reasons, the successional transition to a more diverse, multi-layer canopy is likely to alter biotic and abiotic factors that control C and water cycling processes. First, diversification of canopy composition and structure will alter microclimatic variables of importance to C cycling and storage, and to ecosystem water relations. For example, soil temperature and moisture changed following structural

modifications in northern hardwood forests (Cater and Chapin, 2000; Wang and Kemball, 2005). Canopy light interception, air temperature, and vapor pressure deficit are also affected by canopy structure (Tappeiner and Cernusca, 1996; Lewis et al., 2000; Mariscal et al., 2004). Baldocchi et al. (2004) found that canopy structure and albedo were important determinants of ecosystem water and energy fluxes in an oak woodland and grassland canopy, affecting the net radiation balance and partitioning of latent and sensible heat. Second, changes in leaf phenology and canopy structure affect radiation use efficiency (RUE) and C storage capacity. In some cases, structurally diverse canopies have higher RUEs than uniform canopies, resulting in higher NPP (Tappeiner and Cernusca, 1996; Ahl et al., 2004). The recovery of leaf area following disturbance is positively correlated with NEP (Humphreys et al., 2005) and the time required for a forest to transition from a C source to sink. Third, tree mortality and subsequent decomposition may affect N availability, an important driver of NPP (Reich et al., 1997; Cater and Chapin, 2000; Curtis et al., 2002). Because of interspecific differences in N requirements and internal cycling, species composition is an integral determinant of N availability (Compton et al., 1998; Ste.-Marie and Pare, 1999). Nitrogen availability limits production at the plant and ecosystem scales (Curtis et al., 2002; Gough et al., 2004), and N reallocation to the developing canopy following aspen mortality may be an important determinant of landscape-level variability in C storage.

IC. CARBON STORAGE AND FOREST DEVELOPMENT: THEORETICAL BACKGROUND

Odum (1969) predicted that NEP follows a sinusoidal pattern with stand age, with an initial post-disturbance reduction in C storage due to higher respiration rates and an eventual climax corresponding with maximum canopy assimilation. This climax, he hypothesized, is followed by a drop in C storage that stabilizes upon forest maturation. This trend has been documented in a few ecosystems using forest chronosequences established from clearcuts (Law et al., 2001; Campbell et al., 2004). However, the compositional and structural transition occurring in maturing aspen-dominated forests of the upper Midwest is fundamentally different from those following stand-replacing disturbance. This subtler transition to a heterogeneous secondary forest is likely to be much more common across the region because fire suppression and less aggressive forest harvesting have greatly reduced catastrophic stand replacement (Birdsey et al., 2000; Caspersen et al., 2000).

We hypothesize that NEP in our experimental sites will be constrained by both successional stage and climate, and that the influence of these two factors over C cycling processes will change with time (Figure 1). In the existing even-aged forest, climate provides the primary constraint over NEP (Gough et al., 2006). Net ecosystem production at UMBS varied between 0.80 - 1.98 Mg C ha⁻¹ yr⁻¹ from 1999 to 2003

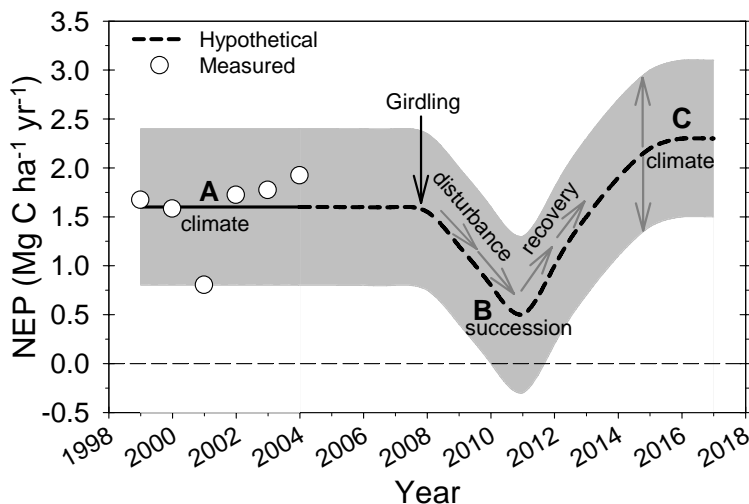


Figure 1. Measured and hypothetical NEP at UMBS before and following aspen and birch decline. (A) Current NEP varies interannually due to climate. (B) A period constrained by disturbance and recovery is hypothesized immediately following aspen and birch mortality girdling. (C) Over the longer-term, diversification of canopy structure and composition is expected to increase average annual NEP.

in response to annual variation in photosynthetic photon flux density (PPFD) and soil temperatures, which were correlated with NPP and annual heterotrophic soil respiration, respectively (Figure 2). During succession, we expect that mortality in the overstory will result in an initial decline in NEP, and that during this entire period the effects of disturbance and the dynamics of the subsequent recovery are the forces that primarily limit NEP. We expect that the transition to a younger, uneven-aged forest will eventually result in NEP that is higher than that of the pre-treatment and control forests. At this point, climate will once again become the primary factor constraining NEP.

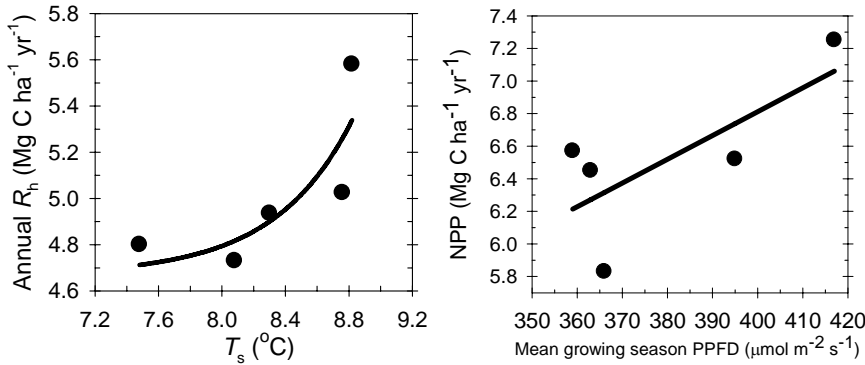


Figure 2. The relationship between annual heterotrophic respiration (R_h) and mean annual soil temperature (T_s), and net primary production (NPP) and mean growing season PPFD (Gough et al., 2006).

IV. LANDSCAPE-LEVEL SPATIAL VARIABILITY IN CARBON STORAGE

In maturing forests of the upper Midwest, patchy disturbances prompted by wind, insects, and disease are important to stand development and successional change (Frelich and Reich, 1995). This pattern of disturbance is giving rise to late successional forests with multi-layered canopies and many gaps of 50 – 200 m (Peterson and Squires, 1995; Hill et al., 2005). At UMBS, we found that a 5-fold range in NEP

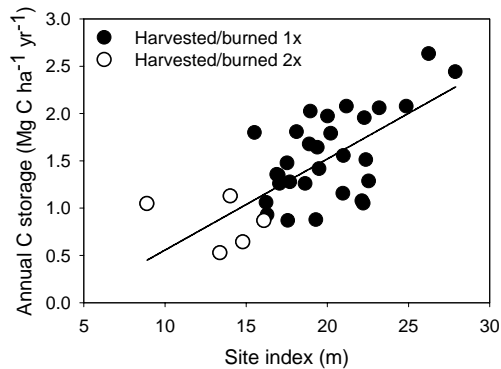


Figure 3. Spatial variability in annual C storage is correlated with site index at UMBS.

across the landscape was well-correlated with site index and disturbance frequency (Figure 3). While site index is a useful, integrated indicator of site quality, this metric does not resolve the specific mechanisms responsible for the high spatial variability in C storage. We expect that our experimental acceleration of ecological succession will further increase the range in annual C storage observed across the landscape by creating a mosaic of microenvironments, soil nutrition, disturbance intensity, and canopy age. We will take advantage of this ecosystem-scale experiment and our knowledge of variation in C storage at UMBS to identify mechanisms driving spatial variation in NEP at the landscape-level.

II. OBJECTIVES AND HYPOTHESES

OBJECTIVE 1: QUANTIFY C EXCHANGE PROCESSES THROUGHOUT A SUCCESSIONAL SHIFT FROM A MATURE ASPEN TO A YOUNG MIXED CONFER/DECIDUOUS FOREST.

Hypothesis 1: There will be a brief, 3 to 5-yr, reduction in NEP post-treatment due to reduced LAI and increased heterotrophic respiration. This will be followed by the rapid recovery of LAI and eventual stabilization of NEP above control levels.

We hypothesize that a transient reduction in NPP and concurrent increase in heterotrophic respiration (see hypothesis 2) will briefly reduce NEP to near zero. This decline in NPP will be followed by a period of recovery that is positively correlated with LAI, as has been seen in other ecosystems (Humphreys et al., 2005). A 6-yr-old forest at UMBS reached 93 % of its maximum NPP after clear-cutting, largely because understory leaf area production compensated for overstory leaf area losses (Gough et al., AGU Fall Meeting 2005).

Over the long-term (5 to 8 yrs), we predict an increase in NEP exceeding that of mature aspen at this site. Modeling results show that higher radiation use efficiency (RUE) in multi-layered canopies may result in higher NPP (Ahl et al., 2004), although this has not been experimentally tested. In a managed southern pine forest, Martin and Jokela (2004) observed a reduction in RUE upon canopy closure, which suggests that deeper light penetration to the understory may enhance RUE in uneven-aged stands.

Hypothesis 2: Overstory aspen and birch mortality will result in a pulse of increased fine root turnover that will temporarily increase heterotrophic respiration by up to 25 %, and concurrently reduce NPP by up to 42 %.

Fine roots are the largest component of NPP in the UMBS forest, comprising 41 % ($2.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) of annual NPP (Gough et al., 2006). We hypothesize that aspen and birch mortality will increase annual heterotrophic respiration by up to 25 %, equivalent in magnitude to fine root detritus production prompted by canopy tree mortality. Fine root decomposition is a significant contributor to soil respiration in other ecosystems (Dioumaeva et al., 2002; Ruess et al., 2003). We predict that a 42 % reduction in canopy LAI will reduce NPP by an equivalent amount, but this will be short-lived due to rapid recovery in LAI.

Hypothesis 3: Overstory aspen and birch mortality will increase soil and forest floor C storage by substantially increasing detritus inputs to the soil.

Experimentally induced tree mortality will significantly increase root, leaf, and woody detritus production over a short period of time. This pulse of legacy C may increase both soil and forest floor C storage, and provide an important, yet unresolved, mechanistic explanation for belowground C accretion in developing forests (Latty et al., 2004). In a meta analysis, Johnson and Curtis (2001) showed that increasing detritus inputs to the soil generally resulted in higher soil C storage. Similarly, partial canopy removal augmented long-term mineral soil C by increasing root detritus production (Selig and Seiler, 2006). We hypothesize that recalcitrant legacy C will increase long-term C storage in the O-horizon and mineral soil. This is in contrast to catastrophic events that disturb the soil and may reduce soil C storage by stimulating mineralization (Edwards and Ross-Todd, 1983; Lee et al., 2002; Mallik and Hu, 1997; Gough et al., 2005).

Soil C storage at UMBS is currently lower than that reported for other forests, suggesting that these soils may be capable of storing more C. For example, mineral soil and O-layer C were 32.4 and $6.5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, respectively, in harvested and burned stands, compared with mineral soil and O-layer C of 68.4 and $62.9 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, respectively, in a nearby old-growth stand on the same Rubicon Sand soil series. The lower range of soil C storage at UMBS is considerably lower than that of other northern forests on predominantly sandy soils, including Harvard Forest and Hubbard Brook (Gaudinski et al., 2000; Fahey et al., 2005).

OBJECTIVE 2: INVESTIGATE THE INTERACTIVE ROLE OF DISTURBANCE AND SUCCESSION IN GOVERNING LANDSCAPE-LEVEL VARIABILITY IN C STORAGE.

Hypothesis 4: Successional change in canopy composition will result in more variable forest microclimates and a more patchy distribution of nutrients, both of which will be important regulators of landscape-level variability in C storage.

Our experimental approach will promote a forest mosaic that is comprised of numerous developmental stages, species, and canopy structures (Kneeshaw and Bergeron, 1998). This diversification of canopy structure and composition will prompt greater heterogeneity in the spatial distribution of light, water, and nutrient resources, all of which drive variation in production across forested landscapes (Reich et al., 1997; Wang et al., 2003; Ollinger and Smith, 2005; Kang et al., 2006). We hypothesize that successional change will result in a more diverse forest mosaic that will increase the already high level of variation in landscape-level C storage observed at UMBS (Figure 3), and that this landscape-level variability will be correlated with differences in microclimate, soil nutrition, disturbance intensity, and stand age.

Hypothesis 5: The reallocation of N during succession will affect rates of regrowth in the developing canopy.

White et al., 2004 showed that nitrogen (N) availability differed substantially across forest developmental stages at UMBS. Available N also varies depending on disturbance history and intensity (Lapointe et al. 2005). We hypothesize that aspen and birch mortality and subsequent successional change will result in a high degree of variability in available N across the landscape, and this will in turn be correlated with spatial variation in NPP. Gross et al. (1995) showed that the spatial distribution of available N varied with forest development. For example, spatial variation in N availability may increase following aspen and birch mortality due to the patchy mineralization of N formerly sequestered in overstory plant mass (Cater and Chapin, 2000). Ecological succession and subsequent diversification of the canopy also may change N availability across the landscape because of differences in species-specific N requirements (Compton et al., 1998).

OBJECTIVE 3: CONTINUE MEASUREMENTS OF MASS AND ENERGY EXCHANGE OVER A MATURING ASPEN-DOMINATED HARDWOOD FOREST, BUILDING ON MORE THAN EIGHT YEARS OF CONTINUOUS FOREST CARBON CYCLE STUDIES.

The 46 m control tower and surrounding forest will continue to function as an AmeriFlux 'supersite', providing a research platform for analysis of key micro-meteorological problems (e.g., flux footprints and advection processes), the comparative analysis of biometric vs meteorological estimations of NEP and GPP, ecophysiological studies of photosynthesis, respiration and other flux components, and a variety of other in-depth studies related to goals of the AmeriFlux program. Our group has been a key contributor to numerous cross-site synthesis activities (see annotated bibliography) and requests for collaboration and data sharing have increased in recent months. Examples include collaboration or input requests for the projects; *Model infrastructure to assess the impacts of soil freeze/thaw dynamics on the North American carbon cycle* (Kevin Shaefer, U. Colorado), *Extreme weather and climate anomalies effects on across-site spatial and temporal patterns in surface-atmosphere exchanges of carbon and water* (Chris Williams, Colorado State U.), *Evaluation and comparison of soil carbon pools at AmeriFlux sites* (Julie Jastrow, Argonne National Lab), *Interior continental US AmeriFlux synthesis* (Lianhong Gu, Oak Ridge National Lab), *¹⁸O fluxes of water and CO₂ in eastern forests* (Xuhui Lee, Yale U.). Continuation of our core C cycle studies will allow us to maintain our collaborative role within AmeriFlux and the North American Carbon Program and to further explore climatic effects on C cycling in northern forests. Of great interest, for example, will be the consequences of climate anomalies such as el nino events that occur on a greater than 5 yr time interval. Our high-quality, long-term data set provides an excellent basis from which to study these important elements of climate change.

III. EXPERIMENTAL APPROACH

We propose an ecosystem-scale experiment to examine disturbance, age, and diversity effects on forest-atmosphere exchanges of mass and energy and on responses to climatic variability. This work directly addresses **Focus 3** of NICCR RFP-01, specifically the analysis of biological processes that contribute to spatial and temporal variation in CO₂ sources and sinks, and an improved quantitative understanding of regionally important terrestrial sources and sinks of CO₂ and how these sources and sinks will change in the next 50-100 years. We take advantage of proven, robust meteorological and ecological methods, together with the collective experience and productivity of our well-established collaborative team.

We are aware that to meet our objectives this study must extend beyond the current 3-yr NICCR funding cycle. UMBS-Flux project leaders are committed to seeking and maintaining support for meteorological and ecological measurements at our site extending at least 6 years after treatment. We are confident in our ability to maintain program support for a period sufficient to address our objectives and test our hypotheses.

III.A. SITE DESCRIPTION

Our study site is located at the University of Michigan Biological Station in northern lower Michigan (45°35.5'N, 84°43'W), in the transition zone between the northern hardwood and boreal forests. The area is a gently sloping outwash plain at an elevation of ~320 m with well-drained spodosols (92% sand, 7% silt, 1% clay, pH 4.8). The mean annual (1942-2003) temperature is 5.5 °C and the mean annual precipitation is 817 mm.

The existing study forest (hereafter referred to as the control site) surrounds a meteorological tower from which we have measured net ecosystem CO₂ exchange between forest and atmosphere continuously since 1998. Most of this secondary successional forest is comprised of bigtooth aspen (*Populus grandidentata*), northern red oak, red maple (*Acer rubrum*), paper birch (*Betula papyrifera*), and eastern white pine. The understory is dominated by bracken fern (*Pteridium aquilinum*). The forest was heavily logged in the late 1800s and disturbed by fire until 1923 (Kilburn 1957, 1960). Since then the area has been relatively free of major disturbances. Average overstory tree age is 85 years, but individual stands range in age from 30 to 90 yrs. Net ecosystem production (NEP) varied from 0.80 - 1.98 Mg C ha⁻¹ yr⁻¹ from 1999 to 2003, averaging 1.52 Mg C ha⁻¹ yr⁻¹ (Gough et al., 2006).

The UMBS forest is similar in species composition and age to other aspen-dominated forests in the upper Midwest. The current composition of aspen, red maple, and northern red oak is typical of nearly half of the forested area in the upper Great Lakes region (USDA, 2001). Average age of the UMBS forest is somewhat greater than that of most other aspen-dominated forests in the region (Figure 4), providing an ideal setting to study an emerging ecosystem ahead of widespread aspen mortality in the coming decades. Site indices (base age 50 yrs) at UMBS generally span those of other forests in the region, indicating

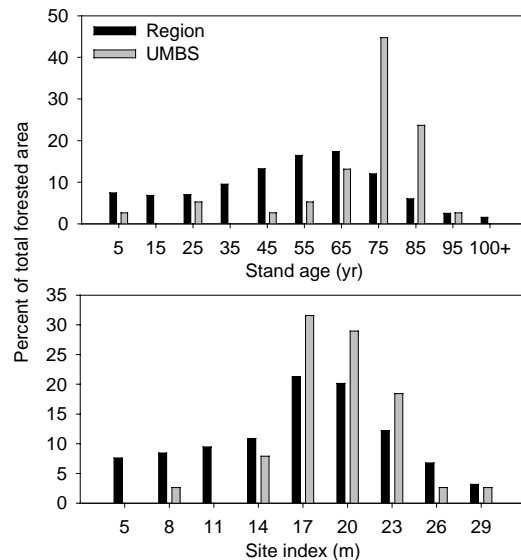


Figure 4. Stand and site index (base age 50 yrs) for aspen-dominated forests in the region and at UMBS. Regional stand age and site index (black bars) were determined from USDA Forest Inventory and Analysis data for Minnesota, Wisconsin, and Michigan.

that climate and soil fertility at UMBS is comparable in range to that found across the region.

IIIB. EXPERIMENTAL TREATMENT: ACCELERATED SUCCESSION

We will accelerate forest ecological succession by killing all mature aspen and birch (~37 and 5 % canopy LAI, respectively) within a 33 ha treatment stand close to but outside the flux footprint of the existing meteorological tower and control site (Figure 5). Tree death will be caused by girdling individual trunks. This treatment will expedite late-succession aspen and birch mortality, which is commonly prompted by insect outbreak, wind, or disease (Frelich and Reich, 1995). A second tower (already funded) will begin operating within the treatment stand in 2006, 2 years prior to girdling. Three additional, 2 ha stands also will be treated to serve as replicate plots for ecological measurements (Figure 5). These replicate stands overlap with existing biometric plots in the control stand, providing 8 years of valuable ecological reference data. However, these treated plots will have minimal impact on fluxes measured at the control tower (See footprint analysis, section IIIC).

Stem girdling is an effective means of killing aspen while minimizing clonal root suckering, and is routinely employed by forest and prairie managers (e.g., Burns and Honkala, 1990). Girdling eliminates transport of photosynthate to roots via the phloem, but allows water transport up the xylem. Unlike trunk removal, root suckering is minimal following girdling because auxins synthesized in the roots do not accumulate, and therefore do not stimulate root sprouting (Schier, 1978; Schier and Smith, 1979). Aspen generally die 1 to 3 years following girdling (Schier and Smith, 1979; Simard et al., 2005). Girdling killed 74 % of all aspen after one year in a mixed broadleaf-conifer forest in British Columbia (Simard et al., 2005), and 94 % of regenerating root suckers were dead 4 years after girdling a pure stand of mature aspen in Utah (Schier and Smith, 1979). In contrast, clearcutting stimulated root suckering and promoted regeneration at both sites (Schier and Smith, 1979; Simard et al., 2005).

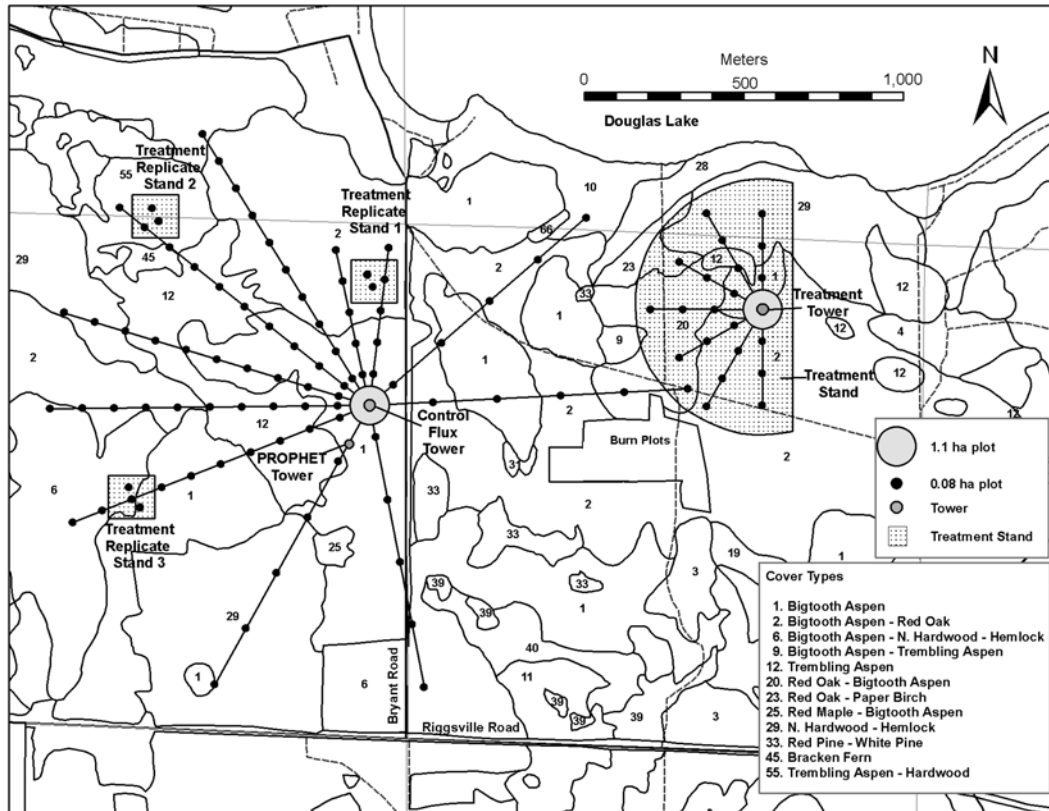


Figure 5. Location of the control and treatment stands and towers at UMBS. Grey-shaded areas illustrate treatment stands in which all aspen and birch will be girdled to accelerate succession.

The girdling treatment will be applied immediately following leaf-out in the Spring of 2008 (average day of aspen leaf out = 160). We will strip away a 2 cm wide swath of the bark, phloem, and cambium around the entire bole of all aspen and birch >5 cm in the 33 ha plot and three, 2 ha plots using a tree girdler (Forestry Suppliers, Jackson, MI, USA). Smaller trees (2 - 5 cm) will be girdled using a beveled knife. Herbicide (glyphosate) will be used as necessary. This will kill ~400 trees ha⁻¹, resulting in a ~42 % reduction in current LAI.

Aspen decline following girdling should promote an emerging canopy that closely approximates projected regional changes in forest composition and structure (Peterson and Squires, 1995; Wolter and White, 2002). Seedlings and saplings now in the understory indicate that eastern white pine will become an important component of the treatment site overstory upon release (Figure 6). Additionally, the prevalence of red maple in the understory indicates that it may replace aspen as the primary overstory species. Both red maple and white pine are beginning to supplant aspen as the dominant canopy species in several maturing aspen-dominated forests in the region (Peterson and Squires, 1995; Stearns and Liken, 2002).

III.C. TREATMENT SITE LOCATION AND FLUX FOOTPRINT ANALYSIS

The treatment site is located 1 km northeast of the control tower (Figure 5). This site was chosen because of proximity to the control site, mild topography, and favorable forest structure and composition. Both sites are located on sandy glacial outwash plain and aspen is the dominant species. This site is easily accessible by roads maintained by UMBS running east-west and north-south. Elevation varies by <5 m, thereby alleviating meteorological challenges associated with complex terrain (Su et al., 2004). The meteorological tower in the treatment site will be placed 100 m

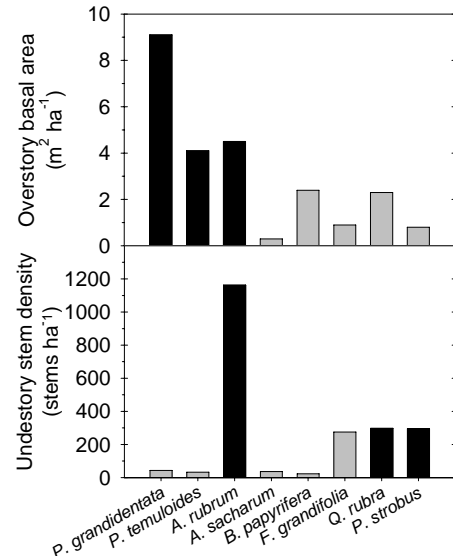
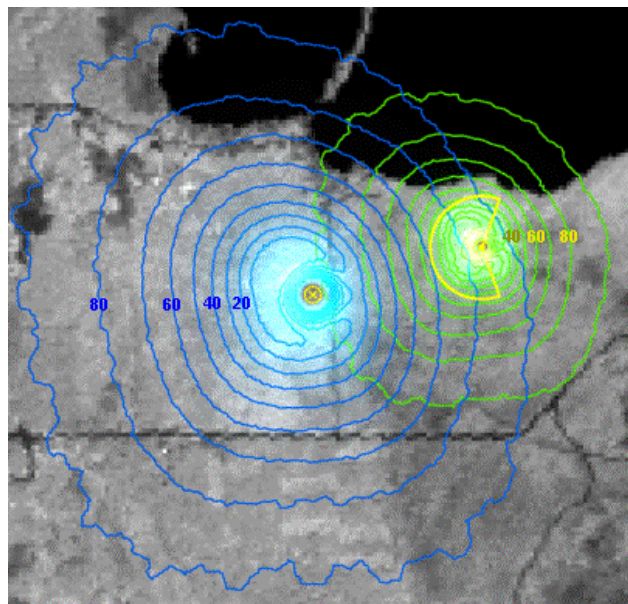


Figure 6. Overstory basal area and sapling stem density at the UMBS control site. The most abundant 3 species are indicated by black bars.

Figure 7. Annual total footprint climatologies for the UMBS control tower and the proposed treatment tower, using 2003 meteorological conditions from the control tower, and the model of Schmid (1997). The background map is Landsat-derived EVI (enhanced vegetation index) at 30 m resolution. Footprint value is intensity of blue for the control tower, intensity of green for the treatment tower; high footprint values saturate as white. Contour lines indicate percentage of the total footprint contained within a given contour. Each footprint climatology is scaled to an integral of unity. The proposed treatment area is indicated by a bold yellow line. It is estimated to contain at least 31% of the total annual flux footprint for the girdling tower. Overlap between the two footprints is negligible.



from the eastern border of the 33 ha semi-circular area and 400 m from the perimeter arc of the area running from 15° west and south to 165° (Figure 5).

Simple footprint analyses (using FSAM from Schmid, 1997) suggest that the treatment stand will cover over 30 % of the annual footprint of the treatment tower (Figure 7). For daytime conditions during the vegetative season, coverage increases to over 36%, and during sunny, high-flux conditions the footprint is contained almost completely in the treatment area. We will use the backward Lagrangian footprint model of Kljun et al. (2002), with turbulence data from the treatment tower to assess the extent to which hourly fluxes are influenced by the treatment area. Once the geometry of the treatment stand changes after girdling, the footprint modeling will need to be modified to take the change in stand height and roughness into account. We will assess effects of accelerated succession on CO₂ fluxes by using footprint analyses to isolate fluxes originating from the treatment stand and comparing them with fluxes measured simultaneously on the control tower.

IIID. CONTROL AND TREATMENT SITE CALIBRATION AND UNCERTAINTY ANALYSES

Precision and Uncertainty: Instrument biases will be quantified and corrected by running the two eddy-covariance systems for the control and treatment towers on the same tower for at least a week and comparing flux measurements. Instrumentation from the two towers will be calibrated using regression equations that quantify bias between the two systems. A roving eddy-covariance system (using existing components) will be used for periodical comparisons and calibrations with the control- and the treatment-tower systems during the treatment experiment. These calibration periods, with two systems on the same tower, also allow for detailed uncertainty estimation, using a Monte-Carlo approach similar to Richardson and Hollinger (2005).

Site calibration: After quantifying instrument precision, we will conduct paired eddy-covariance measurements of carbon dioxide (F_C), and water vapor (or latent heat, Q_E), sensible heat (Q_H), and momentum (see section IIIIE) over the treatment and control stands for at least two full growing seasons before treatment (starting in summer 2006, before the start of the project period). These will be augmented by a suite of radiation and other meteorological and soil measurements at both sites (see section IIIIE). We also will conduct parallel measurements of forest C pools and fluxes (see section IIIIF) in the control and treatment stands for ~2 years prior to accelerated succession. Paired C flux measurements in control and treatments stands will be compared quantitatively using regression, prior to treatment. During this time, atmospheric variability is the major influence on C fluxes in both stands, given their similarity in stand composition and soils and their proximity. Thus, pre-treatment equations that quantify the relationship between C fluxes in control and treatment stands will allow us to separate effects of climate from those of succession once accelerated succession is initiated in treatment stands.

Accuracy: See section IIIIH

IIIE. METEOROLOGICAL METHODS

A broad range of meteorological and ecological measurements will be conducted in both control and treatment stands throughout the study. The full suite of measurements in the control stand will continue from a 46 m fixed tower (see Schmid et al. 2003), in a similar fashion to other studies in the FLUXNET community (see e.g. Goulden *et al.* 1996; Baldocchi et al., 2001). The principal micrometeorological approach is to directly measure concentrations and fluxes of carbon dioxide (F_C), and water vapor (or latent heat, Q_E), sensible heat (Q_H) and momentum using eddy covariance equipment. These observations are complemented by measurements of net radiation, incoming short-wave radiation and photosynthetically active radiation (PAR), soil heat flux, soil temperature and moisture, and by standard meteorological measurements. Profiles of air temperature, humidity, and CO₂ concentration are obtained

at multiple levels. Currently, the full suite of eddy covariance and radiation measurements are carried out continuously on the control tower at two levels above the canopy (48 m and 34 m), corresponding to 1.5 and 2.1 times the canopy height. Continual operation of these measurements started in October 1998.

In July 2006, a 33 m tall meteorological tower will begin operating in the 33 ha experimental stand, nearly 2 years prior to the experimental treatment. Instrumentation for the tower has been purchased with existing funds and consists of a Campbell CSAT3 3-D sonic anemometer, LI-COR LI-7500 open-path infrared gas analyzer, Kipp & Zonen CNR1 4-component net radiometer and Campbell CR5000 micrologger. The instruments will be powered by battery, charged by 256 W solar panels.

To avoid systematic bias, identical methods will be used in the quality control and calculations of eddy-covariance fluxes and gap filling for the eddy-covariance measurements of all years (see Schmid et al. 2003), except for differences in data analysis required by using a closed-path system (LI-COR LI-7000) on the control tower and the open path system (LI-7500) on the treatment tower. Measured densities of CO₂ and H₂O from both systems will be converted to mixing ratios with respect to dry air, to account for the WPL correction (Webb et al. 1980). Further details of quality control procedures related to long-term eddy-covariance measurements, and gap-filling strategies are described in Schmid et al. (2003) and Su et al. (2004).

III.F. ECOLOGICAL METHODS: STAND-LEVEL CARBON BUDGETS

Physiological and biometric measurements will continue in 81 existing permanent plots surrounding the control tower. These plots allow for periodic sampling within the tower source footprint area (*sensu* Schmid, 1997). Environmental and ecological measurements in the control plots have proven useful in the validation of meteorologically-based C flux estimates (Curtis et al, 2005; Gough et al., 2006). A similar sampling design will be employed in the treatment stand, within the treatment tower source footprint area (Figure 5). In the summer of 2006, a permanent 1.1 ha plot will be established that surrounds the treatment tower. In addition, 21, 0.1 ha permanent plots will be established in the treatment stand and 3, 0.1 ha plots in each of the three replicate treatment stands. The 2 ha and 33 ha treatment stands span the range in forest composition and site quality present at UMBS. The 2 ha treatment stands will overlap with existing 0.1 ha biometric plots associated with the control site that are outside the primary tower footprint, thus having a minimal effect on the footprint of the control stand (Figure 7).

Forest carbon dynamics will be quantified in these permanent plots with a combination of repeated tree growth and gas exchange measurements as described in detail by Gough et al. (2006). Above- and belowground live mass measurements will continue in control plots and similar measurements will be initiated in treatment plots. We currently measure the growth of >1100 trees (DBH \geq 8 cm) in the control plots using empirical equations that relate DBH to stem mass (Cooper, 1981; Crow and Erdman, 1983; Hocker and Early, 1983; Ker, 1980; Koerper, 1977; Perala and Alban, 1994; Schmitt and Grigal, 1981; Ter-Michaelian and Korzukhin, 1997; Wiant et al, 1977; Young et al, 1980). Complete stem diameter surveys have been conducted twice in the control stand, in 1998 and 2001. We will census all trees in the treatment plots to estimate woody mass changes prior to and after girdling. Litter traps will be placed in each treatment plot to monitor leaf and fine debris production.

Coarse woody debris (CWD, dia. \geq 10 cm), primarily aspen and birch, is currently a small component of total ecosystem C pool (< 1%) and respiratory C flux (< 4%) at UMBS. However, CWD respiration is significant when compared to annual NEP and will become more so as aspen and birch die in increasing numbers over the next several decades as part of normal ecological succession and over the next 3 years in our treatment stands. Following treatment, we expect CWD mass will increase substantially. Therefore, we will measure the volume of standing and fallen boles as well as smaller branches and twigs before and

after the girdling treatment. Temperature, moisture content, and CO₂ efflux will be measured on a subset of CWD samples. Similar efforts will continue in control plots.

Fine root production will be estimated using a combination of methods including soil coring to a depth of 1 m, minirhizotron observations (Hendrick and Pregitzer, 1993; Johnson et al, 2001), N availability approach (Aber et al, 1985) and mass balance (Raich and Nadlehoffer, 1989). Coarse root mass will be estimated using equations that relate aboveground wood mass with coarse root mass (Cairns et al, 1997). In the summer of 2007, we will install 15, 1.8 m long minirhizotron tubes in the 1.1 ha treatment plot and 5 tubes per plot in 6 of the 0.1 ha plots and the 2 ha plots, spanning the range of aspen and birch densities.

Soil CO₂ efflux is a major component of the net C exchange at UMBS and can be reliably modeled using soil temperature and water content (Curtis et al, 2005). Soil CO₂ flux will be measured frequently in control and treatment plots using a LI-COR LI-6400 (LI-COR, Inc., Lincoln, NE, USA) and a 6400-09 soil respiration chamber and in the control plots using an automated system that sequentially samples 8 sites every hour continuously during the snow-free period. Heterotrophic soil respiration will be determined using the component integration methods (Hanson et al., 2000). Soil moisture will be monitored on a frequent, periodic basis using TDR probes set in permanent arrays within the forest, and by 'spot checks' during broader surveys of all permanent plots. We also have several continuously logging Campbell CS615-L Water Content Reflectometers. Continuous measurement of soil temperature and water content will continue near the control tower and will be implemented during the summer of 2007 in the treatment site.

To determine changes in soil C storage, we will sample soils before and on a yearly basis after the treatment. The O-layer will be sampled separately and mineral soil will be cored to a depth of 1 m in 0.2 m increments across the treatment area and measured for C concentration with a Costech 4010 Elemental Analyzer (Costech Analytical Technologies, Inc., Valencia, CA, USA). Soils from around the control tower will be similarly sampled and analyzed.

III.G. LANDSCAPE LEVEL VARIABILITY IN CARBON STORAGE, CLIMATE, AND NITROGEN AVAILABILITY

The control forest is a mosaic of stands characterized by variability in species composition, site quality, and NEP. The treatment site is similarly diverse, with areas dominated by red oak and fewer mature aspen or birch, and others that are almost entirely composed of aspen and birch. In the treatment site, we will install vertical profiles of quantum sensors and thermocouples through the canopy on 25 m aluminum towers located in 4, 0.1 plots that span the range of aspen and birch density. Soil water content and soil temperature profiles will also be continuously measured near each of the canopy profile towers. Leaf area index of the treatment area will be measured along transects weekly during leaf out and leaf off and every 3 weeks during the summer using an LI-2000 Plant Canopy Analyzer (LI-COR, Inc., Lincoln, NE, USA).

Nitrogen mineralization and nitrification in the top 25 cm of the soil profile will be determined in each 0.1 ha plot located in the treatment sites using an *in situ* core-ion exchange resin technique modified from Brye et al. (2002). Incubation periods will range from 30-45 d. Nitrogen mineralization and nitrification measurements will span the range in site quality (assessed as site index) present in the treatment site. Leaf, bole, and root samples of dominant tree species will be collected during the growing season and specific leaf area and N concentration measured. Biometric estimates of individual C pools combined with N budget data will be used to make stoichiometric assessments of the coupling of these two elements, and to determine the effect of N availability on landscape-level variability in NEP.

IIII. ROBUSTNESS OF EXPERIMENTAL DESIGN AND METHODS

The robustness of our methods for estimating NEP and the accuracy of our prior results have been assessed using independent meteorological and ecological approaches to evaluate forest C fluxes and storage (Curtis et al. 2005, Gough et al., 2006). For example, the two approaches we used to estimate NEP converged to within 1 % of each other over 5 years, providing an important cross-validation of these independent estimates (Figure 8 and see “Results of related NIGEC research”).

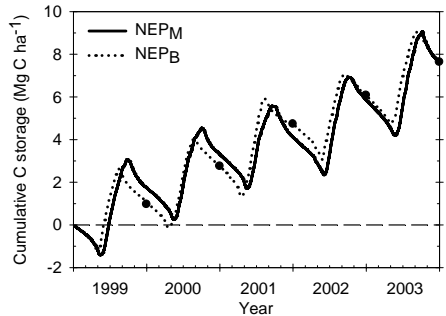


Figure 8. Cumulative C storage based on meteorological and biometric measurements. Meteorological C storage (NEP_M) was based on continuous eddy-covariance measurements. Continuous biometric C storage (NEP_M) was estimated from measured annual C storage (closed circles) and ~weekly growth measurements during the 2001, 2002 growing seasons.

IV. PROJECT PERSONNEL AND TIMELINE

Dr. Peter Curtis will be the primary investigator who will organize and oversee the project. Dr. Christoph Vogel will serve as the on-site director of operations for the UMBS Ameriflux site. He will maintain the meteorological tower and collect essential physiological and ecological data year-round. Dr. Hans Peter Schmid (with the assistance of a graduate student) will process and analyze meteorological data, perform footprint modeling, and coordinate the instrument installations on the treatment tower. Dr. Christopher Gough, currently a postdoctoral scientist in the Curtis lab, will assist in data collection, analyses, and the preparation of manuscripts related to proposed activities. All project team members will participate in field work related to the girdling experiment.

FYR 2006. An already purchased and fully equipped meteorological tower will be erected and begin operating in the treatment site. Biometric plots (0.1 ha) in the treatment sites will be established for baseline data, including species composition and site index. Meteorological and ecological measurements will continue at the control site.

FYR 2007. All ecological and physiological measurements used to estimate C pools and fluxes will be initiated in the 33 ha and 2 ha treatment sites. The same measurements will be conducted in the control plot. Continuous meteorological measurements will continue in both the control and treatment sites.

FYR 2008. Aspen and birch in treatment plots will be girdled in the Spring. Ecological, physiological, and meteorological measurements will continue in the control and treatment plots.

V. SYNERGISTIC ACTIVITIES

The proposed ecosystem-scale experimental acceleration of succession at UMBS will encourage numerous, synergistic activities with other investigators. Collaborators currently are seeking support for concurrent measurements of atmospheric chemistry in the treatment site. This would provide an opportunity to examine how changes in species composition and canopy structure, together with modifications in microclimate, affect atmospheric chemistry as well as C cycling processes.

The UMBS Ameriflux site has provided research and educational training for 20 undergraduates, 14 graduate students, and 5 postdoctoral researchers since its inception in 1998. The UMBS Ameriflux site works closely with the NSF funded Biosphere-Atmosphere Research and Training (BART) and Research

Experience for Undergraduates (REU) programs housed at the biological station, and we expect continued support for graduate and undergraduate research will be provided by both of these programs.

In combination with these efforts to track changes in belowground C pools and fluxes, we are submitting a parallel proposal to Terrestrial Carbon Processes (TCP) Program (DE-FG02-06ER06-11) that would allow us to further explore the fate of legacy root C following aspen and birch mortality. Additional resources from TCP would allow us to capitalize on this unique and novel opportunity to study belowground C storage within this experimental framework. TCP support will greatly improve our capabilities to intensively monitor belowground C fluxes and storage, by providing funding to initiate a ^{13}C labeling study to track the fate of root detritus originating from senescing aspen (i.e., legacy C). This work will enhance our understanding of mechanisms that drive soil C transformations during successional change. **Specific objectives for TCP supported research are to: 1) Quantify the transfer of carbon from senescing roots to soil organic matter, 2) Quantify the contribution of slow and fast soil organic matter pools to soil CO_2 efflux, and to calculate average turnover times of these pools, 3) Identify mechanisms responsible for soil C accretion or loss through a successional shift.**

VI. DELIVERABLES

We expect this research will allow us to continue the current pace of 3 to 4 peer-reviewed publications per year (29 total/8 years) and more than a dozen presentations annually, with many of those delivered at high profile conferences such as the American Geophysical Union Fall Meeting. We will continue to make our research accessible to the public (ex., <http://researchnews.osu.edu/archive/carbstor.htm>). Also, graduate, undergraduate, and post-graduate research training will remain a high priority.

VII. RESULTS OF RELATED NIGEC RESEARCH

Significant progress in the analysis, interpretation, and synthesis of meteorological and biometric data from UMBS~Flux and other AmeriFlux/FLUXNET sites has been achieved by our group. The UMBS~Flux site was initially funded by NIGEC in 1997 and has continued to the present. Multi-year comparisons of meteorological and biometric estimates of net ecosystem production (Gough et al., 2005) and respiration (Curtis et al., 2005), and analyses of eddy covariance data leading to better criteria and techniques for determining and filling gaps (Schmid et al., 2003) and correction of the energy balance and CO_2 and latent heat fluxes (Su et al., 2004) have been reported for the UMBS~Flux site. Over a 5-yr period (1999-2003) we evaluated the meteorological (NEP_M) and biometric (NEP_B) estimates of forest C storage finding that within-year comparisons of the estimates differed from 13 – 148%. However, when compared over the entire 5-yr period these independent estimates of NEP converged to within 1% of each other. Differences in within-year estimates could be partly explained by a 1-yr lag between net canopy photosynthesis and C allocated to tree growth. Weekly assessments of bole radial growth and NEP_M indicated that woody mass growth began prior to positive net canopy photosynthesis in the spring and that > 25% of annual photosynthetic C assimilation occurred after bole radial growth had ceased in late summer.

During the same 5-yr period that NEP_B and NEP_M were investigated, we completed a study of ecosystem respiration (R_e) and C-use efficiency. Carbon losses at the UMBS~ Flux site were important components of the forest C cycle and were sensitive to changing climatic conditions. Carbon losses from soils predominated, accounting for > 70% of the estimated 1425 g C m^{-2} respired from the ecosystem annually. Maximum interannual variation in this loss ($142 \text{ g C m}^{-2} \text{ yr}^{-1}$), while modest compared with total R_e , was of a similar magnitude to overall annual ecosystem C storage. Our estimates of the C-use efficiency of the UMBS forest ranged from 0.40 based on biometric data and consistent with an aging aspen stand, to 0.60 based on meteorological data and consistent with a more productive, multi-aged forest. Meteorologically-based estimates of R_e provided important confirmation that our physiological

measurements and scaling protocols could reproduce much of the hourly and seasonal variation in R_e evidenced in above-canopy nocturnal CO_2 fluxes.

Cumulative NEP_M based on fluxes at two heights above canopy showed marked differences derived from small, but persistent biases that affect CO_2 fluxes more than sensible heat fluxes. Respiratory fluxes measured via eddy covariance under conditions of poorly developed turbulence were systematically underestimated compared to parametric models. This bias, as suggested by other studies, appears to be strongly correlated with friction velocity. At UMBS~Flux a threshold of $u_* > 0.35 \text{ m s}^{-1}$ was found suitable for the acceptance of eddy covariance measurements for both day- and night-time periods. The choice of criteria and strategies of data quality control and gap filling can affect the outcome of annual NEP_M by a factor of 2. However, biophysical arguments and constraints can be used to invest more or less confidence in a given method. Short-term (days – weeks) reductions in respiration and C uptake can be detected during persistent cooler or drier conditions even if the entire year is not classified as dry. During a year of mid-summer drought, the response of respiration and C uptake appear to largely cancel each other. Some indications that reduced respiration in one year may translate into increased respiration the following year, due to a surplus of available soil and litter C, need to be further investigated. During the period 1999 – 2001 the UMBS~Flux forest ecosystem was a consistent C sink ranging from 80 – 170 $\text{g C m}^{-2} \text{ yr}^{-1}$. The variation exhibited by these 3 years underscores the importance of obtaining long-term observations of ecosystem exchange. Both the spectral and co-spectral constants and stability functions for normalizing and collapsing spectra and co-spectra in the inertial subrange were found different from those of Kaimal et al. (1972) based on the Kansas experiment. Such differences also depend on seasonal changes and site differences in canopy morphology. Damping by the long-tube of water vapor fluctuations are much greater than that of CO_2 , and the reduction to water vapor signals also increases with aging or dirtier tubes, in agreement with previous studies. Three methods were used for flux corrections using derived co-spectra formulas and transfer functions during the growing seasons of 1999-2001. On average, such corrections are about 3-4% during the daytime and 6-10% at night for CO_2 . For latent heat flux during the day, the correction range from less than 10% for newer tubes to over 20% for aged tubes.

Our group has participated in a number of synthesis studies that include UMBS~Flux and other AmeriFlux/FLUXNET and CarboEurope sites. In one study the onset of C uptake by forested ecosystems was strongly correlated with the warming of soils in spring to a point where soil temperature equaled the mean annual air temperature (Baldocchi et al, 2005). Analyses of soil respiration across a number of biomes (Hibbard et al., 2005) and the Upper Great Lakes region (Noormets et al., in press) have been completed as well as cross-site comparisons of C storage (Curtis et al., 2002) and belowground C allocation (Davidson et al., 2002).

LITERATURE CITED

- Aber JD, JM Melillo, KJ Nadlehoffer, CA McClaugherty, J Pastor. Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of two methods. *Oecologia* 66, 317-321, 1985.
- Ahl DE, Gower ST, Mackay DS, Burrows SN, Norman JM, Diak GR, Heterogeneity of light use efficiency in a northern Wisconsin forest: implications for modeling net primary production with remote sensing, *Remote Sensing of Environment*, 93, 168-178, 2004.
- Baldocchi D, Falge E, Gu LH, Olson R, Hollinger D, Running S, Anthoni P, Bernhofer C, Davis K, Evans R, Fuentes J, Goldstein A, Katul G, Law B, Lee XH, Malhi Y, Meyers T, Munger W, Oechel W, U KTP, Pilegaard K, Schmid HP, Valentini R, Verma S, Vesala T, Wilson K, Wofsy S, FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities, *Bulletin of the American Meteorological Society* 82, 2415-2434, 2001.
- Baldocchi DD, Valentini R, Running S, Oechel W, Dahlman, R, Strategies for measuring and modeling CO₂ and water vapor fluxes over terrestrial ecosystems. *Global Change Biology*, 2, 159-168, 1996.
- Baldocchi DD, Xu LK, Kiang N, How plant functional-type, weather, seasonal drought, and soil physical properties alter water and energy fluxes of an oak-grass savanna and an annual grassland, *Agricultural and Forest Meteorology*, 123, 13-39, 2004.
- Birdsey RA, Heath LS, Carbon changes in U.S. forests. In: Joyce, L.A. (Ed.), *Productivity of America's forests and climate change*. U.S. Department of Agriculture (USDA) Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-GTR-271, Fort Collins, CO, pp 56-77, 1995.
- Birdsey RA, Mickler RA, Hom J, Heath LS. Summary of prospective global change impacts on northern U.S. forest ecosystems. In: Mickler RA, Birdsey RA, Hom J (Eds.), *Responses of northern U.S. forests to environmental change*. Springer, New York, New York, USA, pp 543-568, 2000.
- Brye KR, Norman JM, Nordheim EV, Gower ST, Bundy LG, Refinements to an *in-situ* soil core technique for measuring net nitrogen mineralization in moist, fertilized, *Agricultural Soil Agronomy Journal*, 94, 864-869, 2002.
- Burns RM, Honkala BH, *Silvics of North America, Vol. 2, Hardwoods*. Washington DC: USDA Forest Service Agriculture Handbook 654, 1990.
- Cairns, MA, Brown S, Helmer EH, Baumgardner GA, Root biomass allocation in the world's upland forests. *Oecologia*, 111, 1-11, 1997.
- Campbell JL, Sun OJ, Law BE, Disturbance and net ecosystem production across three climatically distinct forest landscapes, *Global Biogeochemical Cycles*, 18, Art. No. GB4017, 2004.
- Caspersen JP, Pacala SW, Jenkins JC, Hurtt GC, Moorcroft PR, Birdsey RA, Contributions of land-use history to carbon accumulation in US forests, *Science*, 290 (5494), 1148-1151, 2000.
- Cater TC, Chapin FS, Differential effects of competition or microenvironment on boreal tree seedling establishment after fire, *Ecology* 81, 1086-1099, 2000.

- Chen JQ, Falk M, Euskirchen E, U KTP, Suchanek TH, Ustin SL, Bond BJ, Brosofske KD, Phillips N, Bi RC, Biophysical controls of carbon flows in three successional Douglas-fir stands based on eddy-covariance measurements, *Tree Physiology*, 22,169-177, 2002.
- Compton JE, Boone RD, Motzkin G, Foster DR, Soil carbon and nitrogen in a pine-oak sand plain in central Massachusetts: Role of vegetation and land-use history, *Oecologia* 116, 536-542, 1998.
- Cooper AW, Above-ground biomass accumulation and net primary production during the first 70 years of succession in *Populus grandidentata* stands on poor sites in northern lower Michigan. In: West, D.C., HH Shugart, DB Botkin (Eds.), *Forest succession: concepts and application*. Springer-Verlag, New York. 517 p., 1981.
- Crow, TR, Erdmann, GG. Weight and volume equations and tables for red maple in the Lake States. U.S. Forest Service Research Paper. NC-242: 14, 1983.
- Curtis PS, Hanson PJ, Bolstad P, Barford C, Randolph JC, Schmid HP, Wilson KB, Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests, *Agricultural and Forest Meteorology*, 113, 3-19, 2002.
- Curtis PS, Vogel CS, Gough CM, Schmid HP, Su HB, Bovard BD, Respiratory carbon losses and the carbon-use efficiency of a northern hardwood forest, 1999-2003, *New Phytologist*, 167, 437-455, 2005.
- Desai AR, Bolstad PV, Cook BD, Davis KJ, Carey EV, Comparing net ecosystem exchange of carbon dioxide between an old-growth and mature forest in the upper Midwest, USA, *Agricultural and Forest Meteorology*, 128, 33-55, 2005.
- Desai AR, Normeets A, Bolstad PV, Chen J, Cook BD, Curtis PS, Davis KJ, Euskirchen E, Gough C, Martin J, Ricciuto DM, Schmid HP, Tang J, Su H, Vogel C, and Wang W, Influence of vegetation type, stand age and climate on carbon dioxide fluxes across the Upper Midwest, USA: Implications for regional scaling of carbon flux, *Agricultural and Forest Meteorology*, in press, 2006.
- Dioumaeva I, Trumbore S, Schuur EAG, Goulden ML, Litvak M, Hirsch AI, Decomposition of peat from upland boreal forest: Temperature dependence and sources of respired carbon, *Journal of Geophysical Research-Atmospheres* 108, (D3): Art. No. 8222, 2002.
- Edwards NT, Ross-Todd BM, Soil carbon dynamics in a mixed deciduous forest following clear-cutting with and without residue removal, *Soil Science Society of America Journal* 47, 1014-1021, 1983.
- Fahey TJ, Siccama TG, Driscoll CT, Likens GE, Campbell J, Johnson CE, Battles JJ, Aber JD, Cole JJ, Fisk MC, Groffman PM, Hamburg SP, Holmes RT, Schwarz PA, Yanai RD, The biogeochemistry of carbon at Hubbard Brook, *Biogeochemistry*, 75,109-176, 2005.
- Frelich LE, Old Forest in the Lake States Today and Before European Settlement, *Natural Areas Journal*, 15, 157-167, 1995.
- Frelich LE, Reich PB, Spatial Patterns and Succession in a Minnesota Southern-Boreal Forest, *Ecological Monographs*, 65, 325-346, 1995.
- Friedman SK, Reich PB, Regional legacies of logging: Departure from presettlement forest conditions in northern Minnesota, *Ecological Applications*, 15, 726-744, 2005.

- Gaudinski JB, Trumbore SE, Davidson EA, Zheng SH, Soil carbon cycling in a temperate forest: radiocarbon-based estimates of residence times, sequestration rates and partitioning of fluxes, *Biogeochemistry*, 51, 33-69, 2000.
- Gilmore DW, To thin or not to thin: Using the Forest Vegetation Simulator to evaluate thinning of aspen, *Northern Journal of Applied Forestry*, 20,14-18, 2003.
- Gough CM, Seiler JR, Maier CA, Short-term effects of fertilization on loblolly pine (*Pinus taeda* L.) physiology, *Plant, Cell and Environment*, 27 876-886, 2004.
- Gough CM, Seiler JR, Wiseman PE, Maier CM, Soil CO₂ efflux in loblolly pine (*Pinus taeda* L.) plantations on the Virginia Piedmont and South Carolina Coastal Plain over a rotation-length chronosequence, *Biogeochemistry*, 73, 127-147, 2005.
- Gough CM, Vogel CS, Harrold K, George K, Curtis PS, The legacy of forest harvest and burning on ecosystem carbon storage in the northern Midwest, USA. American Geophysical Union, Fall Meeting, San Francisco, CA, 2005.
- Gough CM, Vogel CS, Schmid HP, Su H-B, Curtis PS, Multi-year convergence of biometric and meteorological estimates of forest carbon storage. *Agricultural and Forest Meteorology*, in press, 2006.
- Goulden, ML, Munger JW, Fan SM, Daube BC, Wofsy SC, Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy, *Global Change Biology*, 2, 169-182, 1996.
- Gross KL, Pregitzer KS, Burton AJ, Spatial Variation in Nitrogen Availability in 3 Successional Plant-Communities, *Journal of Ecology*, 83, 357-367, 1995.
- Hanson PJ, Edwards NT, Garten CT, Andrews JA, Separating root and soil microbial contributions to soil respiration: A review of methods and observations, *Biogeochemistry*, 48, 115-146, 2000.
- Hendrick RL, Pregitzer KS, Patterns of fine root mortality in 2 sugar maple forests, *Nature*, 361, 59-61, 1993.
- Hill SB, Mallik AU, Chen HYH, Canopy gap disturbance and succession in trembling aspen dominated boreal forests in northeastern Ontario, *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestiere* 35, 1942-1951, 2005.
- Hocker HW, Jr., Early DJ, Biomass and leaf area equations for northern forest species, New Hampshire Agricultural Experiment Station University of New Hampshire Research Report, 102, 27, 1983.
- Houghton RA, Hackler JL, Lawrence KT, The US carbon budget: Contributions from land-use change, *Science*, 285 (5427), 574-578, 1999.
- Humphreys ER, Andrew Black T, Morgenstern K, Li Z, Nesic Z, Net ecosystem production of a Douglas-fir stand for 3 years following clearcut harvesting, *Global Change Biology* 11, 450-464, 2005.
- Juodvalkis A, Kairiukstis L, Vasiliauskas R, Effects of thinning on growth of six tree species in north-temperate forests of Lithuania, *European Journal of Forest Research* 124, 187-192, 2005.

- Kang S, Lee D, Lee J, Running SW, Topographic and climatic controls on soil environments and net primary production in a rugged temperate hardwood forest in Korea, *Ecological Research*, 21, 64-74, 2006.
- Karamanski, TJ, Deep wood frontier - a history of logging in Northern Michigan. Wayne State University Press. Detroit, 305 p., 1989.
- Ker, MF, Tree biomass equations for seven species in southwestern New Brunswick. Canadian Forest Service Maritime Forest Research Center Information Report, M-X-114, 18, 1980.
- Kilburn PD, Historical development and structure of the aspen, jack pine, and oak vegetation type on sandy soils in northern lower Michigan. Ph.D. Dissertation, U. Mich., Ann Arbor, MI, 267 pp., 1957.
- Kilburn PD, Effects of logging and fire on xerophytic forests in northern Michigan. *Bull. Torrey Bot. Club*, 87, 402-405, 1960.
- Kljun, N., M.W. Rotach, and H.P. Schmid. A 3-D backward Lagrangian footprint model for a wide range of boundary layer stratifications. *Boundary-Layer Meteorol.* 103, 205-226, 2002.
- Kneeshaw DD, Bergeron Y, Canopy gap characteristics and tree replacement in the southeastern boreal forest, *Ecology*, 79, 783-794, 1998.
- Koerper, G. The aboveground biomass and annual net production of bigtooth aspen (*Populus grandidentata* Michx.) on three soil types in northern lower Michigan. University of Michigan Masters Thesis, Ann Arbor, Michigan, 1977.
- Lapointe B, Bradley RL, Shipley B, Mineral nitrogen and microbial dynamics in the forest floor of clearcut or partially harvested successional boreal forest stands, *Plant and Soil*, 271, 27-37, 2005.
- Latty EF, Canham CD, Marks PL, The effects of land-use history on soil properties and nutrient dynamics in northern hardwood forests of the Adirondack Mountains, *Ecosystems*, 7, 193-207, 2004.
- Law BE, Thornton PE, Irvine J, Anthoni PM, Van Tuyl S, Carbon storage and fluxes in ponderosa pine forests at different developmental stages, *Global Change Biology*, 7, 755-777, 2001.
- Law BE, Sun OJ, Campbell J, Van Tuyl S, Thornton PE, Changes in carbon storage and fluxes in a chronosequence of ponderosa pine, *Global Change Biology*, 9, 510-524, 2003.
- Lee XH, Hu XZ, Forest-air fluxes of carbon, water and energy over non-flat terrain, *Boundary-Layer Meteorology*, 103, 277-301, 2002.
- Lewis JD, McKane RB, Tingey DT, Beedlow PA, Vertical gradients in photosynthetic light response within an old-growth Douglas-fir and western hemlock canopy, *Tree Physiology*, 20, 447-456, 2000.
- Mallik AU, Hu D, Soil respiration following site preparation treatments in boreal mixedwood forest, *Forest Ecology and Management*, 97, 265-275, 1997.
- Mariscal MJ, Martens SN, Ustin SL, Chen JQ, Weiss SB, Roberts DA, Light-transmission profiles in an old-growth forest canopy: Simulations of photosynthetically active radiation by using spatially explicit radiative transfer models, *Ecosystems*, 7, 454-467, 2004.

- Martin TA, Jokela EJ, Stand development and production dynamics of loblolly pine under a range of cultural treatments in north-central Florida USA, *Forest Ecology and Management*, 192, 39-58, 2004.
- Mitchell AK, Barclay HJ, Brix H, Pollard DFW, Benton R, deJong R, Biomass and nutrient element dynamics in Douglas-fir: Effects of thinning and nitrogen fertilization over 18 years, *Canadian Journal of Forest Research*, 26, 376-388, 1996.
- Odum EP, The strategy of ecosystem development, *Science*, 164 (3877), 262-270, 1969.
- Ollinger SV, Smith ML, Net primary production and canopy nitrogen in a temperate forest landscape: An analysis using imaging spectroscopy, modeling and field data, *Ecosystems*, 8, 760-778, 2005.
- Palik BJ, Pregitzer KS, The repeatability of stem exclusion during even-aged development of bigtooth aspen dominated forests, *Canadian Journal of Forest Research*, 23, 1156-1168, 1993.
- Perala DA, Alban DH, Allometric biomass estimators for aspen-dominated ecosystems in the Upper Great Lakes. U.S. Forest Service Research Paper, NC-134: 38, 1994.
- Raich JW, Nadlehoffer KJ. Belowground carbon allocation in forest ecosystems: global trends. *Ecology*, 70, 1346-1354, 1989.
- Peterson CJ, Squiers ER, An unexpected change in spatial pattern across 10 years in an aspen white-pine forest, *Journal of Ecology*, 83, 847-855, 1995.
- Reich PB, Grigal DF, Aber JD, Gower ST, Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils, *Ecology*, 78, 335-347, 1997.
- Richardson A.D., Hollinger D.Y. Statistical modeling of ecosystem respiration using eddy covariance data: Maximum likelihood parameter estimation, and Monte Carlo simulation of model and parameter uncertainty, applied to three simple models. *Agricultural and Forest Meteorology* 131, 191-208, 2005
- Ruess RW, Hendrick RL, Burton AJ, Pregitzer KS, Sveinbjornsson B, Allen ME, Maurer GE, Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska, *Ecological Monographs*, 73, 643-662, 2003.
- Schier GA, Root suckering in young aspen, girdled, defoliated, and decapitated at various seasons. In *Proc. 5th North Am. For. Biol. Workshop*. Gainesville, FL., 1978.
- Schier GA, Smith, AD, Sucker regeneration in a Utah aspen clone after clearcutting, partial cutting, scarification, and girdling, *USDA Forest Service Research Note*, INT-253, 1979.
- Schmid HP, Experimental design for flux measurements: matching scales of observations and fluxes, *Agricultural And Forest Meteorology*, 87, 179-200, 1997.
- Schmid HP, Grimmond CSB, Cropley F, Offerele B, Su H-B, Measurements of CO₂ and Energy Fluxes over a Mixed Hardwood Forest in the Midwestern United States, *Agricultural and Forest Meteorology*, 103, 355-373, 2000.
- Schmid HP, Su HB, Vogel CS, Curtis PS, Ecosystem-atmosphere exchange of carbon dioxide over a mixed hardwood forest in northern lower Michigan, *Journal Of Geophysical Research-Atmospheres*, 108 (D14): Art. No. 4417, 2003.

- Schmitt MDC, Grigal DF, Generalized biomass estimation equations for *Betula papyrifera* Marsh., Canadian Journal of Forest Research, 11, 837-840, 1981.
- Selig MF, Seiler JR, Soil CO₂ efflux and soil carbon content as influenced by thinning in loblolly pine plantations on the piedmont of Virginia, Forest Ecology and Management, in press, 2006.
- Simard SW, Hagerman SM, Sachs DL, Heineman JL, Mather WJ, Conifer growth, *Armillaria ostoyae* root disease, and plant diversity responses to broadleaf competition reduction in mixed forests of southern interior British Columbia, Canadian Journal of Forest Research, 35, 843-859, 2005.
- Ste-Marie C, Pare D, Soil, pH and N availability effects on net nitrification in the forest floors of a range of boreal forest stands, Soil Biology and Biochemistry, 31, 1579-1589, 1999.
- Stearns F, Likens GE, One hundred years of recovery of a pine forest in northern Wisconsin, American Midland Naturalist, 148, 2-19, 2002.
- Su HB, Schmid HP, Grimmond CSB, Vogel CS, Oliphant AJ, Spectral characteristics and correction of long-term eddy-covariance measurements over two mixed hardwood forests in non-flat terrain, Boundary-Layer Meteorology, 110, 213-253, 2004.
- Tappeiner U, Cernusca A, Microclimate and fluxes of water vapour, sensible heat and carbon dioxide in structurally differing subalpine plant communities in the Central Caucasus. Plant Cell and Environment, 19, 403-417, 1996.
- Ter-Michaelian MT, Korzukhin MD, Biomass equations for sixty-five North American tree species, Forest Ecology and Management, 97, 1-24, 1997.
- USDA Forest Service, Forest Inventory Analysis (FIA), Washington, DC, 2001.
- Wang GG, Kembell KJ, Balsam fir and white spruce seedling recruitment in response to understory release, seedbed type, and litter exclusion in trembling aspen stands, Canadian Journal of Forest Research, 35, 667-673, 2005.
- Wang HQ, Hall CAS, Scatena FN, Fetcher N, Wu W, Modeling the spatial and temporal variability in climate and primary productivity across the Luquillo Mountains, Puerto Rico, Forest Ecology and Management, 179, 69-94, 2003.
- Webb E.K., Pearman G.I., and Leuning R. Correction of Flux Measurements for Density Effects due to Heat and Water-Vapor Transfer. Quarterly Journal of the Royal Meteorological Society 106, 85-100, 1980.
- White LL, Zak DR, Barnes BV, Biomass accumulation and soil nitrogen availability in an 87-year-old *Populus grandidentata* chronosequence, Forest Ecology and Management, 191, 121-127, 2004.
- Wiant HV, Sheetz CE, Colaninno A, DeMoss JC, and Castaneda F. Tables and procedures for estimating weights of some appalacian hardwoods, West Virginia Agricultural Experiment Station Bulletin, 659(T), 36, 1977.
- Wolter PT, White MA, Recent forest cover type transitions and landscape structural changes in northeast Minnesota, USA, Landscape Ecology, 17, 133-155, 2002.

Young HE, Ribe JH, Wainwright K, Weight tables for tree and shrub species in Maine, Life Sciences and Agriculture Experiment Station, University of Maine at Orono, Miscellaneous Report 230, 84 pp, 1980.