DEPARTMENT OF ZOOLOGY

UNIVERSITY OF WISCONSIN – MADISON
Birge Hall, 430 Lincoln Drive
Madison, WI 53706

June 25, 2009

William Robertson IV
The Andrew W. Mellon Foundation
140 East 62nd Street
New York, NY 10021
wr@mellon.org

Dear Bill,

This letter contains the final report for the project, "How do disturbance-generated landscape patterns influence the spatial dynamics of ecosystem processes?" The original award covered the time period January 1, 2001 – December 30, 2005. We were granted a three-yr extension (to December 30, 2008) to continue and complete this research, with an additional three months (to March 2009) added to accommodate university transfer dates on tuition remission. Here, I provide a synopsis of our research accomplishments to date (including highlights, general contributions, and findings organized by question). A listing of publications from this funding is included; to date, this award has directly produced 25 papers that are published or in press and four theses. Another eight manuscripts are in preparation, and analyses for several of these have progressed substantially since we submitted our interim report. I have included greater detail on those results here, and would be happy to send copies to you as they come out. This grant has allowed us to develop a much richer understanding of how the Yellowstone landscape functions in the face of disturbance, and I am deeply grateful for the opportunities provided.

My collaborators and I greatly appreciate having this award from the Andrew W. Mellon Foundation. We have been able to conduct novel studies in Yellowstone and be responsive to new opportunities (e.g., the 2003 fires and the infestation of bark beetles). I would be happy to discuss our accomplishments further, or provide any additional documentation that would be helpful to you. Thank you again for your support.

Best wishes,

Monica G. Turner

Monica G. Turner
Eugene P. Odum Professor of Ecology
Tel: 608-262-2592
Fax: 608-265-6320
Email: turnermg@wisc.edu
Web: http://landscape.zoology.wisc.edu

How do disturbance-generated landscape patterns influence the spatial dynamics of ecosystem processes?

Final Report to the Andrew W. Mellon Foundation

June 25, 2009

With funding from the Andrew W. Mellon Foundation, we have studied interactions between vegetation and ecosystem processes, with particular emphasis on nitrogen (N) cycling, carbon (C) dynamics and the role of post-fire coarse wood, following stand-replacing fire. This study maintained a key focus on areas burned by the 1988 fires, but we also initiated studies in areas burned during 2000 and 2003 and across a chronosequence of stand ages. To understand more fully the natural disturbance regime in the Greater Yellowstone Ecosystem (GYE), we initiated studies of bark beetles on vegetation and ecosystem processes. In addition, to broaden our context, we studied within-stand spatial heterogeneity in soil processes and microbial communities in an Alaskan boreal forest that burned in 2001. Analyses have revealed important interactions between the post-fire vegetation, newly fallen coarse wood, and nutrient cycling. We summarize some key findings below, then present results for each of the questions posed in the initial proposal and a listing of publications.

Research highlights in a nutshell

The Yellowstone ecosystem is remarkably resilient to large, severe, stand-replacing fires. The recovery of forest structure and function after the 1988 fires through natural processes was rapid; the fires were not catastrophes for the plants and animals.

The 1988 fires were a source of significant landscape heterogeneity, and this heterogeneity was associated, in turn, with substantial spatial variability in many ecosystem processes.

- Postfire tree density ranged from 0 to 500,000 stems ha^{-1} and did not change significantly (i.e., no density-dependent mortality) through 2005.
- Non-native invasive plants did not increase in the burned forests.
- Young trees were already producing many cones (up to 4,000,000 cones ha^{-1}) in 2003.
- The variation in tree density produced a mosaic of process rates across the landscape
- Net primary productivity at the stand level increases with increasing tree density.
- Primary productivity of some areas was in the range for mature lodgepole pine forests by 1998, and productivity continued increasing through 2005.
- Litter production increases with increasing tree density.
- Ecosystem N retention may increase with increasing tree density.

After fire, the burned forests seem to retain their remaining nitrogen (rather than losing it, as is seen in eastern deciduous forests).

- Although extractable soil N is elevated soon after fire, soil microbes consume more N than they produce, leading to net immobilization of soil N.

- In years 2-4 following fire, an N fertilization experiment showed no response of lodgepole pine seedlings to added N, although a common grass (*Calamagrostis rubscens*) did respond positively.
- By 15 years after fire, lodgepole pine foliage is a strong sink for nitrogen.
- Total foliar N pools increase with increasing tree density, although foliar N concentrations decline.
- Foliar N concentrations in lodgepole pine do not yet indicate N limitation.
- Soil inorganic N availability declines with increasing tree density.

Many of the trees killed in the 1988 fires have now fallen, but treefall rates vary across the landscape; this influx of coarse wood to the forest floor influences ecosystem processes.

- Decomposition rates were lower under elevated logs compared to other microsites, and in stands with a greater abundance of fallen, elevated logs.
- Litter microarthropods were most abundant under fallen logs that were in contact with the forest floor.
- In situ net N mineralization rates were lower under elevated logs, although laboratory measurements of gross production and consumption of ammonium indicated no differences among microsite positions.
- The fallen coarse wood does not seem to protect aspen seedlings from elk browsing.

The spatial pattern of the fires, especially landscape patterns of stand age and tree density, are likely to structure the Yellowstone landscape for up to 200 years.

- Spatial heterogeneity in forest structure and function declines over time.
- N stocks are recovered within 40 years after stand-replacing fire.
- Self-thinning and infilling both contribute to change in stand density.
- Stands converge by ~200 years in density and growth rates.

General contributions

Our work produced several general contributions within terrestrial ecosystem and landscape ecology. We produced a synthesis of the key findings of our studies following the 1988 fires (Turner et al. 2003) and a more recent synthesis that incorporated the ecosystem-level work we accomplished in the past few years (Schoennagel et al. 2008). We prepared a mini-review of nitrogen cycling following natural, stand-replacing fires, which noted the paucity of empirical data and identified key research needs (Smithwick et al. 2005). A conceptual framework for considering ecosystem processes in heterogeneous landscapes was presented at the tenth Cary Conference (Turner and Chapin 2005) and included in an invited presentation at the International Congress of Landscape Ecology in Darwin, Australia (Turner and Cardille 2007). The Mellon-funded studies also contributed to two recent reviews on landscape ecology (Turner 2005a, 2005b) and a guest-edited special issue of PLANT AND SOIL (Smithwick 2006).

Our research has also been informative for resource managers in Yellowstone and the northern Rockies. It featured prominently in an invited keynote address Turner presented in October 2005 at the biennial science meeting sponsored by Yellowstone National Park, and also in a keynote talk at the September 2008 conference on the 20th anniversary of the Yellowstone fires in Jackson, WY (http://www.iawfonline.org/yellowstone/). Romme, Tinker and Turner also jointly led a two-day field trip in conjunction with this meeting that was very well received; we had > 30 people join our first day, and 12 participate in the overnight version. Our Yellowstone research was featured in a full-length article in the June 2008 issue of ON WISCONSIN (http://www.news.wisc.edu/on-wisconsin/rising-from-the-ashes/), the University of Wisconsin-Madison's alumni magazine (which has a circulation >350,000), and we have been responding to media requests about our findings given the two decades that have now passed since the 1988 fires.

Research findings

Question 1. *Do the enormous differences in postfire tree density produce differences in carbon and nitrogen availability across the landscape? Or, is nutrient availability governed largely by broad-scale (i.e., 10's of km) abiotic gradients (e.g., climate, substrate) and/or fine-scale (i.e., < 10 cm) heterogeneity in resources or the microbial community, such that nutrient variability is not sensitive to the spatial variation in plant community structure?*

Our earlier studies had demonstrated an extremely wide range of postfire tree densities ranging from zero to 500,000 trees ha^{-1}. Of 90 stands that we initially sampled in 1999 and measured tree density, aboveground net primary production (ANPP) and leaf area index, 14 stands that spanned the range of tree densities were sampled again in 2003 to explore N dynamics and changes in ANPP (Turner et al. 2009). We addressed two questions: (1) How do foliar nitrogen (N) concentration and total foliar N vary with lodgepole pine density and aboveground net primary production (ANPP)? (2) Is foliar N related to litter production and rates of gross production, consumption and net production of soil NH_4^+ and NO_3^-? A new set of lodgepole pine saplings was harvested so that the allometric relationships we had developed in 1999 could be evaluated for applicability in 2003. The new vegetation measurements showed that ANPP was continuing to increase in most of the stands, although sapling densities had not changed significantly. Foliar N concentration of new lodgepole pine needles averaged 1.38%; only stands at very high density (> 80,000 trees ha^{-1}) were approaching moderate N limitation. Foliar N concentration in composite (all-age) needles averaged 1.08%, varied among stands (0.87–1.39%) and declined with increasing tree density. The foliar N pool averaged 48.3 kg N ha^{-1}, varied among stands (3.6–218.4 kg N ha^{-1}) and increased with ANPP. Total foliar N was not related to laboratory estimates of net production of NH_4^+ or NO_3^- in soils. Lodgepole pine foliage is a strong N sink, and N does not appear to be limiting at this early successional state. This may reflect elevated N availability following fire as well as decreased vegetative demand. However, this study clearly demonstrated that the initial spatial patterns of postfire tree density strongly influence landscape patterns of N storage. The forest canopy in these developing lodgepole pine forests acts as a strong N sink, but our results also indicate that the strength of the N sink varies substantially across the postfire landscape as a function of tree density.

To extend this work, MS student Liz Levitt sampled 25 stands (including the 14 above) in 2005 to measure the quantity and quality of litter on the soil surface as well as in situ inorganic N availability for summer only (June-August 2005) and a full year (June 2005-June 2006). Free resin bags were used as an index of nitrogen availability and distributed randomly in each stand in June 2005. Half the bags were retrieved in September 2005, and the remainder were retrieved in July 2006. Results showed a strong negative relationship between summer N availability and tree density (Levitt 2006). Overall, vegetation explained 58% and litter explained 19% of the variability in summer soil N availability among 25 stands. Of these attributes, graminoid cover (grasses and sedges) explained 51%, while pine sapling density explained 7% of the variation in the model. Litter quantity and quality explained 14% and 5% of the variation, respectively. Pine sapling density was negatively related to N availability ($R^2 = 0.25$; $p = 0.01$). However, this may reflect more complex vegetation dynamics; stands with lower pine density generally had higher herbaceous cover, and stands with more herbaceous cover had more soil organic matter and higher litter quality. We suspect that there are relatively strong feedbacks from the developing vegetation to the soil, but this will require further study. Nonetheless, our studies are demonstrating clearly that initial spatial patterns of postfire tree density strongly influence landscape patterns of C and N transformations and retention.

Question 2. *Does the disturbance-created mosaic leave a persistent functional legacy? What mechanisms in vegetation development may contribute to convergence (or divergence) in ecosystem structure and function across the landscape as succession proceeds?*

We addressed this question in several ways, using a chronosequence approach and simulation modeling. First, as part of Dan Kashian's doctoral research (Kashian 2002), stands varying in age and stand density were sampled across the forested area that did not burn during the 1988 fires. This work revealed striking changes in stand structure (density) and function (growth rates) across both space and time, with the notable pattern of variance declining through time (Kashian et al. 2005a, 2005b). The persistence time for the "legacy effect" is estimated at 175-200 years; mechanisms that lead to convergence include self-thinning of initially dense stands of lodgepole pine and gradual infilling of stands that were initially sparse. We then sampled a subset of these stands along the chronosequence and measured the rates of net nitrogen mineralization and microbial community composition in the soils. These results showed similar trends in variance reduction through successional time, supporting the notion of long-term convergence in ecological function (Smithwick et al. 2005b).

Chronosequence studies of N stocks and in situ soil N availability during long-term stand development were conducted in collaboration with a grant we received from the US Forest Service's Joint Fire Sciences Program (JFSP) focused on carbon dynamics in Yellowstone. We measured N stocks in a chronosequence of stands (Smithwick et al. 2009) and also developed a model that included both carbon and nitrogen (Smithwick et al. 2008) to understand the integrated behavior of these two cycles and the effects of fire. Among age-classes in the chronosequence, N availability ranged from 0.63 (<25 yrs) to 1.67μN bag^{-1} d^{-1} (170-230 yrs), largely due to increases in nitrate availability, and remained high thereafter (1.10 μN bag^{-1} d^{-1}, >250-yrs). N availability decreased with increasing stand density (0.49 vs. 0.92 μN bag^{-1} d^{-1} in dense and sparse stands, respectively), suggesting a persistent legacy of tree density. The lack of observed decreases in soil N availability in older stands suggests factors in addition to N may limit lodgepole pine productivity. Total ecosystem N was lowest in the < 25 yr age-class but recovered by 40 yrs and did not increase subsequently. The lack of changes in total ecosystem N beyond the 40-70 yr age-class suggests that reasonable changes in fire frequency in sub-alpine Rocky Mountain forests will have a minimal effect on soil N accumulation potential over long timescales.

In the modeling study, we found that both young (early post-fire) and mature stands had elevated forest production and net N mineralization under future climate scenarios relative to current climate (Smithwick et al. 2008). Forest production increased 25% (Hadley (HAD)) to 36% (Canadian Climate Center (CCC)), compared to 2% under current climate, among stands that varied in stand age and post-fire density. Net N mineralization increased under both climate scenarios, e.g., +19 to 37% (HAD) and +11 to 23% (CCC), with greatest increases for young stands with sparse tree regeneration. Simulation results indicated that recovery of total N stocks following fire would be rapid because of the relatively low N storage in aboveground pools and modest N losses. Overall, our results suggest that fire return intervals would need to be dramatically reduced to affect long-term N and C storage in the Yellowstone ecosystem due to low aboveground N losses via combustion, the large soil N pool, and relatively fast recovery of aboveground C pools (Smithwick et al. 2008).

A key agent of change in stand structure and function through successional time is the effect of bark beetles and their interaction with fire. These native beetles can thin forest stands during the interval between fires, and they comprise the other key agent of natural disturbance in the Yellowstone landscape. The mountain pine beetle (*Dendroctonus ponderosae*) has reached epidemic conditions in many parts of the intermountain West, affecting more than 400,000 ha of lodgepole (*Pinus contorta*) and whitebark pine (*P. albicaulis*) stands. Other species of bark beetles, namely spruce beetle [*Dendroctonus rufipennis*], Douglas-fir beetle [*Dendroctonus pseudotsugae*]) are also showing increased populations in many parts of the Greater Yellowstone Ecosystem (GYE). Although infestations primarily occur in mature stands, the complete suite of factors that explain the presence and severity of bark beetle damage are unknown. In 2006, we initiated a study to determine the factors that explained the broad-scale patterns of damage and mortality caused by the three species of bark beetles in the GYE. We used broad-scale field surveys to determine (1) forest attributes (composition, % mortality, serotiny for lodgepole pine); (2) stand structure (density, diameter, and age); (3) presence and damage by bark beetles; (4) soil characteristics; and (5) site conditions (elevation, slope, aspect, site index, surficial deposits, etc.) in lodgepole pine, whitebark pine, Douglas-fir (*Pseudotsuga menziesii*), and Engelmann spruce (*Picea engelmanii*) stands that were either severely damaged or undamaged by the beetles. Logistic regression analysis was used to relate bark beetle damage to the biotic and abiotic explanatory variables. This research is being led by PhD student Martin Simard, and we obtained additional funding for this work from the Joint Fire Sciences Program. The Mellon funding was used for our first year of this work, and continues to support the study by covering tuition remission costs (which are disallowed by JFSP funding). Simard is currently analyzing these data, and his first manuscript should be submitted during fall 2009 (Simard et al., in prep.).

Questions of convergence and divergence apply not only to measures of stand structure, but also to community composition. The abundance and composition of plants that comprise the understory of forested ecosystems are important for many ecological processes, including maintenance of biodiversity, net primary productivity, and litter inputs to forest floor. As part of our ongoing studies of how the vegetation community varies in space and time after disturbance, we have two additional papers near completion (Tinker et al. in preparation, Romme et al in preparation). In the first of these (Tinker et al., in preparation), we aimed to evaluate the relative influences of three deterministic factors (elevation, annual precipitation, and geologic substrate), and two stochastic variables (herbaceous leaf area index (LAI) and post-fire lodgepole pine sapling density) on understory species diversity and plant community composition within 90 sites that were widely distributed throughout the area burned in Yellowstone National Park (YNP) during 1988. We addressed two main questions: (1) How do understory species richness and community composition vary in the young postfire lodgepole pine stands in YNP, and what is the relative contribution of measured deterministic and stochastic factors in explaining this variation? (2) Do selected herbaceous plant species respond individualistically to spatial variation along gradients of deterministic and stochastic factors, or are patterns of occurrence and abundance similar among these species?

Much of the variation in plant species richness (72%) was explained by a combination of deterministic (substrate, precipitation) and stochastic (lodgepole pine sapling density) factors (Tinker et al., in preparation). In addition, plant species richness was highly correlated with understory productivity and leaf area index. Ordination analyses indicated that mean annual precipitation, lodgepole pine sapling density, and herbaceous net primary productivity best explained differences in plant community composition among our study sites, although the relationships were much less robust. Our findings suggest that while both deterministic and stochastic factors influence plant species richness in post-fire understory plant communities, none of our measured variables were strong predictors of either presence or abundance of particular plant species, suggesting that pre-fire community structure is likely the most important influence on post-fire plant community composition (Tinker et al., in preparation).

We have developed a reasonable understanding of vegetation dynamics following the 1988 fires from our prior studies, yet we do not know whether the patterns and trajectories we have documented permit us to predict community patterns after other fires in this landscape. During summer 2001, we initiated studies in two stand-replacing fires (the Glade and Moran fires) that burned during summer 2000 (Romme et al., in preparation). We again evaluated the relative contribution of deterministic (e.g., the abiotic template and prefire stand conditions) and stochastic factors (e.g., variable fire severity and postfire climatic conditions) in explaining the variation in early postfire vegetation. Our *deterministic* predictions of greater biotic cover in unburned stands located on fertile than on infertile substrates; of greater species compositional similarity within a site than between sites; of greater post-fire density of lodgepole pine seedlings where local propagule availability (i.e., serotinous cones) was greater; and of divergence between sites over time in cover, richness, and compositional similarity within burned areas -- were all supported by the data collected after the 2000 fires. Also supported were our *stochastic* predictions of greater biotic cover and first-year species richness in moderate-severity than in high-severity burned stands at Glade; of greater compositional similarity between unburned vs. moderate-severity burned stands than between unburned vs. high-severity burned stands at both Glade and Moran; of convergence over time between burned and unburned stands with respect to biotic cover, richness, and compositional similarity at both Glade and Moran; and of differences in first-year biotic cover and lodgepole pine seedling density between the 1988 and 2000 fires.

The most surprising results in our study are those that we suggest are the result of interactions between deterministic and stochastic processes. We had not expected to find no difference between the less fertile Glade site and the more fertile Moran site in biotic cover and species richness the first year after the fires. We suggest that these unexpected results may have been additional consequences of the unusually dry and warm conditions in 2001 (a stochastic influence). In addition, the unanticipated lack of convergence in biotic cover and species richness from 2001-2004, between stands burned at moderate and high severity at both Glade and Moran, may be another consequence of unusually low rates of initial establishment of plants, with establishment and survival possibly even lower in the exposed environment of the high-severity burned stands (Romme et al., in preparation).

Question 3. *How does the spatial pattern of coarse woody debris vary across the post-1988 landscape, and what is the importance of this variation for ecosystem function? Are patterns of coarse woody debris abundance related to both prefire stand structure and postfire sapling density?*

This question has been answered well by our field studies. Heather Lyons, a MS student who worked with Bill Romme at Colorado State University (but unfortunately did not complete the final thesis), sampled widely in 2002 and 2003 across the areas burned in 1988 to quantify and explain treefall rates. These data showed that, on average, 80% of the trees killed by the 1988 fires had now fallen to the ground, but among stands, that percentage varied from 0 to 100%. Thus, the abundance of fallen trees is a conspicuous feature of the forests that burned in 1988, and many of the fallen trees are resting on top of each other and not yet in contact with the ground (Romme and Lyons, in prep.).

We conducted intensive studies of the influence of fallen trees, pine saplings and bare soil on ecosystem processes in three 0.25-ha stands within the 1988 burn. MS student Alysa Remsburg found that litter decomposition was significantly slower under the elevated logs in comparison to other microsites (Remsburg and Turner 2006). The soils under the elevated logs were relatively dry, and the logs seem to intercept precipitation then direct it down the bole, thereby acting as an “umbrella” over the soil underneath. The effect of elevated logs scaled up to the landscape, with decomposition rates decreasing significantly with the percent area of a stand that was covered by elevated logs (Remsburg and Turner 2006). Intensive studies of net nitrogen mineralization also showed that *in situ* annual rates of net nitrification were significantly lower under elevated logs compared to other microsites (Metzger et al. 2008). We were surprised to observe the highest rates of net nitrification and net N mineralization in exposed bare soil. Furthermore, gross production and consumption of ammonium and microbial community composition did not differ in soils under new or legacy coarse wood, pine saplings, or in bare soil (Metzger et al. 2008).

Remsburg also used litterbags incubated at six different post-fire microsite treatments to investigate the role of coarse wood and vegetation in structuring leaf litter microarthropod communities. Using modified Tullgren funnels, we extracted microarthropods from 360 litterbags of 1.5 mm mesh screening. Leaf litter beneath logs contacting the ground had highest abundance and species richness of microarthropods. These data will be also be analyzed further and written up for publication (Remsburg and Turner, in prep.).

Finally, using the Romme and Lyons data on downed wood and in concert with a separate NSF grant, PhD student James Forester explored the potential influence of fallen trees to protect aspen seedlings from browsing by naturally excluding elk. However, the data indicated that the elk were still utilizing the forests with abundant downed wood (Forester et al. 2007), and the fallen trees were unlikely to offer much protection to the aspen.

<u>Question 4</u>. *Does the spatial heterogeneity of processes such as ANPP, nitrogen mineralization, and decomposition change with time since fire? How quickly do spatial patterns in processes develop following a large fire?*

With the occurrence of stand-replacing fires in Greater Yellowstone in both 2000 and 2003, we initiated new studies to examine post-fire N cycling and how spatial relationships may develop between vegetation and soil processes in burned stands. In summer 2001, we established 10 study plots (0.25 ha each) in areas that burned during summer 2000. Five plots were in the Glade Fire, and five were in the Moran Fire. Vegetation development, aboveground productivity and inorganic N availability were studied through summer 2004. In our initial analyses, we focused on the differences among (rather than within) the plots. Annual net mineralization rates were largely negative from 2001-2004, indicating substantial immobilization of ammonium (Turner et al. 2007a). Although net nitrification rates were positive, annual net nitrogen mineralization (net ammonification + net nitrification) remained low. Aboveground net primary production (ANPP) increased from 0.25 to 1.6 Mg ha^{-1} yr^{-1} from 2001 to 2004, but variation in ANPP among stands was not related to net nitrogen mineralization rates. In areas burned during 2003, we established a study of net N mineralization very soon after the fires were over. Our results indicated that immobilization of ammonium was very pronounced during the first post-fire year (Turner et al. 2007a). Our results suggest a microbial nitrogen sink for several years after severe, stand-replacing fire, confirming earlier hypotheses about post-disturbance succession and nutrient cycling in cold, fire-dominated coniferous forests. Post-fire forests in Yellowstone appear to be highly conservative for nitrogen, and microbial immobilization of ammonium plays a key role during early succession.

Understanding how fine-scale patchiness of vegetation changes during early succession and whether these patterns influence ecosystem function would add new insights about post-disturbance ecosystem development. Soil nutrient pools and transformations are notoriously heterogeneous in terrestrial ecosystems, and the scale(s) of variability in such patterns are not well known. Thus, we also conducted intensive studies to explore fine-scale (within plot) spatial variation in vegetation and soil processes. In particular, we were interested in determining the extent to which vegetation and soil microbial communities and N cycling were either coupled or de-coupled during the years the follow severe, stand-replacing fire. These studies were performed in four of the 10 study plots, two in the Glade Fire and two in the Moran Fire. We are near completion of two major papers from this work (Smithwick et al., in prep. and Turner et al., in prep.). Response variables include in situ N mineralization and vegetation cover for four years, and microbial community data and potential N mineralization (measure through ^{15}N isotopic methods). The lack of general understanding of the effects of stand-replacing fire also led us to initiate a small comparative study of postfire N cycling in a spruce forest in Alaska, implementing the same intensive sampling design in Alaska as we used in the areas of Yellowstone burned in 2000 (Smithwick et al., 2005c).

The study we initiated in 2001 to examine the spatio-temporal patterns of vegetation and N cycling in the Glade and Moran fires addressed three main questions: (1) How do within-stand variability and spatial structure of aboveground cover change during the first four years following stand-replacing fire, and how do these differ from comparable but unburned forests? (2) How do within-stand variability and spatial structure of soil inorganic N pools, nitrification and net nitrogen mineralization change during the first four years following stand-replacing fire? (3) Are within-stand patterns and scales of variability of soil inorganic N pools and N transformations related to within-stand patterns of aboveground cover? In each of the four study plots, we established a cyclic sampling grid (n = 81 points/plot) with a minimum separation distance of 2 m between sampling points. This design is efficient when geostatistics are planned, as it gives similar statistical power over a range of lag distances. The grid covered an 18 m x 40 m area positioned in the center of the plot and including nine parallel rows, each separated by 2 m. Vegetation and soils were sampled from 2001 to 2004 at each sampling point (n = 324). In 2004, we established four additional plots following the same sampling design in comparable forests that were not burned during summer 2000. We recorded vegetative cover for comparison with the burned plots; because of logistical constraints and cost, no soil nutrient measurements were made in the unburned forest plots.

Results of this study have proven to be complex and somewhat challenging to interpret. During the first four years of postfire succession, aboveground vegetative cover increased (as expected), and graminoid cover was especially patchy. By 2004, variability in aboveground cover measurements was comparable to that observed in comparable unburned forest. Soil ammonium concentrations decreased by about half from 2001 to 2003. Soil nitrate concentrations were much lower than soil ammonium concentrations, but nitrate pools increased four- to five-fold from 2001 to 2003. Within-plot variability was greater for soil nitrate pools than for soil ammonium pools, but we observed more spatial structure (i.e., patchiness) in soil ammonium pools than in soil nitrate pools. For annual net N mineralization rates, despite the observation that most variance occurred among cores (rather than between sites or burn severities), there was relatively little spatial dependence in N transformations at the scales we measured. When spatial dependence was observed, it was generally at scales < 5 m, although the severe-surface burns had estimated ranges exceeding the plot size for some N transformations. In sum, we have detected a considerable among of spatial structure in soil N pools, but little spatial structure in soil N transformations and little coherence among scales of patchiness for different variables.

With respect to potential relationships between soil N and aboveground cover, non-parametric analyses revealed significant correlations at the level of the individual soil core. Soil ammonium and nitrate pools both were negatively correlated with aboveground measurements related to inputs of organic matter. Notably, soil ammonium was positively correlated with the percent cover of bare mineral soil. For soil nitrate, there were no significant correlations with aboveground cover one year following fire, a time period when soil nitrate concentrations were also very low. Correlations between soil nitrate and aboveground cover increased in 2002 and 2003, with a strong negative relationship observed with unburned litter (or total percent organic matter inputs) and a positive relationship with bare mineral soil. For annual net N mineralization, there were very few significant relationships detected with aboveground cover. From the suite of analyses completed thus far, the absence of clear correspondence in scales of variation (patchiness, as measured by semivariograms) suggests a lack of strong coupling of the spatial patterns among response variables at the scales measured here (Turner et al., in preparation). This lack of coupling during what is sometimes considered the re-organization phase is still informative, however. We suspect that the anticipate plant-litter-soil feedbacks will become more pronounced through time, but they may be more obvious at broader stands, e.g., among stands that vary in structure (as in Question 1, above).

In the Glade and Moran fires, we also measured (in 2002 only) the spatial structure of microbial community composition (lipid analysis) and gross NH_4^+ and NO_3^- production and consumption (laboratory isotopic pool dilution) and developed statistical models to predict nitrogen transformations that include information on microbes, vegetation and soil characteristics (Smithwick et al., in preparation). The ability to readily and rapidly characterize soil microbial communities and the fundamental ecosystem processes they mediate has been an elusive goal in ecosystem ecology. The study was conducted in two years following stand-replacing fire in the Glade Fire, dominated by lodgepole pine, and the Moran Fire, dominated by Engelmann spruce/subalpine fir forests. The pine forest had lower rates of laboratory gross ammonification and nitrification, lower microbial lipid abundance (90 nmol core^{-1} vs. 148 nmol core^{-1}, $p < 0.0001$), lower pH (4.9 vs. 5.4, $p < 0.0001$), and a higher fungal to bacteria ratio (0.84 vs. 0.40, $p < 0.0001$). Semi-variogram analysis on individual lipids indicated that nugget (variance below the scale of sampling) ranged from 3 to 100% of total variance. For those semi-variograms in which nugget was low, individual microbial lipids varied at multiple spatial scales (ranges varied from < 1 m to 11 m). Microbial community composition differed significantly between forest types (non-metric scaling ordination; MRPP, $p < 0.00001$). Rates of laboratory ammonification and nitrification were best predicted by information on microbial, post-fire vegetative cover, and soil pH. We conclude that the spatial structure, abundance and composition of microbial lipids differed between burned spruce-fir and pine sites two years following fire. Moreover, soil nitrogen transformations in burned pine and spruce-fir forests partially reflected differences in vegetation, soil chemistry and microbial communities (Smithwick et al., in preparation). Within the broader context of understanding divergence and convergence in forest structure and function across the landscape, and the role of deterministic and stochastic factors (see Question 2 above), these results suggest a strong influence of the prefire forest community on soil microbial communities.

We are continuing to push further into the analyses of the within-stand variability in vegetation and soils because the results differed considerably from our initial expectations, causing us to re-evaluate our assumptions. This has been challenging, but we have made steady progress, and both papers (Turner et al., in preparation, Smithwick et al., in preparation) are approaching completion.

Additional studies conducted in and near the fires of 2000 provided opportunities for studying how foliar N changes in response to fire and determining whether N was limiting plant growth during early succession. Studies of foliar N concentrations conducted in 2002 in the Glade and Moran fires of 2000 revealed a five-fold difference in foliar N among 14 species, from 0.77 % in the native grass *Calamagrostis rubescens*, to 3.4 % in the native N-fixer *Lupinus argenteus* and the non-native forb *Lactuca serriola* (Metzger et al. 2006). We also observed higher foliar N in the burned stands for four of six species that occurred in both burned and unburned areas.

However, total biomass and foliar N showed no relationships with site, fire severity, or net N mineralization (Metzger et al. 2006).

To test directly for evidence of inorganic N limitation 3-5 years after the stand-replacing fires of 2000, we experimentally manipulated N availability for 4 common native plant species (Romme et al. 2009). Granular reagent grade ammonium nitrate was added around individual plants at a rate equal to the natural background rate of net N mineralization and at 10x this rate. The grass *C. rubescens* exhibited clear evidence of inorganic N limitation: above-ground biomass and shoot:root ratio increased with the high-fertilizer treatment. Nitrogen:phosphorus (N:P) ratio in unfertilized *C. rubescens* plants was <14, also consistent with N-limitation, but N:P ratio shifted to >16 in the high-fertilizer treatment, suggesting the onset of P limitation. The upland sedge *Carex rossii* and seedlings of lodgepole pine were not limited by inorganic N: neither species showed any growth response to N fertilization; N:P ratios were only slightly <14; and foliar N concentrations were greater than critical values reported for mature lodgepole pine. The N-fixing forb *Lupinus argenteus* was not limited by N, for it showed no growth response to fertilization; rather its N:P ratio of 21 indicated P limitation. In this study, to our knowledge the first experimental evaluation of N limitation in subalpine coniferous forests following wildfire, N limitation was seen in only one of four species tested (Romme et al. 2009).

Future directions

The work that we have conducted under the Mellon Foundation funding has laid the groundwork for several initiatives that are either underway or proposed. Complementing our work on postfire N cycling are studies currently underway in forests that have been affected recently by bark beetles. PhD student Jake Griffin is leading these, with supplemental funding from the US Forest Service. We have also received three grants from the Joint Fire Science Program (JFSP), which is supported by multiple federal agencies, for which our Mellon Foundation has laid important groundwork. One of these awards, which has supported Martin Simard's doctoral studies and contributed to Griffin's, examines how vegetation and fuels change in chronosequences that followed bark beetle infestation. Ultimately, we will be able to compare ecosystem structure and function following both fire and bark beetle infestation. Two new JFSP grants were recently awarded. One will include field studies in areas of recent (2007) fires that burned in forests both with and without prior recent beetle infestation and will allow us to determine whether these disturbances interact synergistically. The second will focus on development of new downscaled climate and fire regime projections for the Yellowstone region and simulations of future forest and C accumulation pathways. Finally, we have two proposals pending that build upon the Mellon research. One is submitted to USDA and focuses on ecosystem services in managed forest landscapes following fire, beetle infestation, and post-disturbance management. The other will be submitted shortly to NSF, and it seeks to determine what factors limit primary production across the landscape in the widely variable post-1988 lodgepole pine stands. We suggest that spatial legacies of disturbance interact with the abiotic template to determine ecosystem processes, creating a functional landscape mosaic that will shift over time with disturbance, succession and climate change. We hypothesize that different factors may also act alone or in concert to limit NPP at different locations on the landscape, even within the same stand age. Thus, we hope to continue to build upon the foundation of research accomplished thus far.

Concluding comments

The award from the Mellon Foundation was instrumental in permitting novel questions to be addressed on the role of natural disturbances in one of our nation's premier wilderness areas, Yellowstone National Park. We have documented the patterns and ecological importance of post-fire heterogeneity across an extensive landscape, addressing variability at fine and broad scales and linking mechanistic studies with carefully planned field observations. This work has generated new insights into ecosystem function in heterogeneous landscapes. On behalf of the students, postdocs and collaborators involved in this study, we sincerely thank the Andrew W. Mellon Foundation for this invaluable support.

Publications

Peer-reviewed articles

Forester, J. D., D. P. Anderson and M. G. Turner. 2007. Do high-density patches of coarse wood and regenerating saplings create browsing refugia for aspen (*Populus tremuloides*) in Yellowstone National Park (USA)? Forest Ecology & Management 253:211-219.

Kashian, D. M., M.G.Turner, and W.H. Romme. 2005a. Changes in leaf area and stemwood increment with stand development in Yellowstone National Park: Relationships between forest stand structure and function. Ecosystems 8:48-61.

Kashian, D. M., M. G. Turner, W. H. Romme and C. J. Lorimer. 2005b. Variability and convergence in stand structure with forest development on a fire-dominated landscape. Ecology 86:643-654.

Metzger, K. L., W. H. Romme and M. G. Turner. 2006. Foliar nitrogen in early postfire vegetation in the Greater Yellowstone Ecosystem (Wyoming, USA). Forest Ecology and Management 227:22-30.

Metzger, K.L., E. A. H. Smithwick, D. B. Tinker, W. H. Romme, T. C. Balser and M. G. Turner. 2008. Influence of pine saplings and coarse wood on nitrogen mineralization and microbial communities in young post-fire *Pinus contorta*. Forest Ecology and Management 256:59-67.

Remsburg, A. J. and M. G. Turner. 2006. Amount, position and age of coarse wood influence litter decomposition within and among young post-fire *Pinus contorta* stands. Canadian Journal of Forest Research 36:2112-2123.

Romme W. H., and M. G. Turner. 2004. Ten years after the 1988 Yellowstone fires: is restoration needed? Pages 318-361 In: L. L. Wallace, editor. After the fires: the ecology of change in Yellowstone National Park. Yale University Press, New Haven, Connecticut.

Romme, W. H., M. G. Turner, D. B. Tinker and D. H. Knight. 2004. Emulating natural forest disturbances in the wildland-urban interface of the Greater Yellowstone Ecosystem. Pages 243-250 In: A. H. Perera, L. J. Buse and M. G. Weber, editors. Emulating natural forest landscape disturbances. Columbia University Press, New York.

Romme, W. H., D. B. Tinker, G. H. Stakes, and M. G. Turner. 2009. Does inorganic nitrogen availability limit plant growth 3-5 years after fire in a Wyoming lodgepole pine forest? Forest Ecology & Management 257:829-835.

Schoennagel, T., M.G. Turner, A. Fall and D. M. Kashian. 2006. Influence of fire regimes on lodgepole pine stand age and density across the Yellowstone National Park (USA) landscape. Landscape Ecology 21:1281-1296.

Schoennagel, T., E. A. H. Smithwick and M. G. Turner. 2008. Landscape heterogeneity following large fires: insights from Yellowstone National Park, USA. International Journal of Wildland Fire 17:742-753.

Smithwick, E. A. H. 2006. Editorial: Role of microbial communities in mediating ecosystem response to disturbance. Special Issue in Plant and Soil 289:1-3

Smithwick, E. A. H., D. M. Kashian, M. G. Ryan and M. G. Turner. 2009. Long-term ecosystem nitrogen storage and soil nitrogen availability in post-fire lodgepole pine ecosystems. Ecosystems (In press).

Smithwick, E. A. H., M. C. Mack, M. G. Turner, F. S. Chapin III, J. Zhu and T. C. Balser. 2005c. Spatial heterogeneity and soil nitrogen dynamics in a burned black spruce forest stand: distinct controls at different scales. Biogeochemistry 76:517-537.

Smithwick, E. A. H., M. G. Ryan, D. M. Kashian, W. H. Romme, D. B. Tinker and M. G. Turner. 2008. Modeling the effects of fire and climate change on carbon and nitrogen storage in lodgepole pine (*Pinus contorta*) stands. Global Change Biology (In press).

Smithwick, E. A. H., M. G. Turner, M. C. Mack, and F. S. Chapin, III. 2005a. Post-fire soil N cycling in northern conifer forests affected by severe, stand-replacing wildfires. Ecosystems 8:163-181.

Smithwick, E. A. H., M. G. Turner, K. L. Metzger, and T. C. Balser. 2005b. Variation in NH_4^+ mineralization and microbial communities with stand age in lodgepole pine (*Pinus contorta*) forests, Yellowstone National Park (USA). Soil Biology and Biogeochemistry 37:1546-1559.

Turner, M. G. 2005. Landscape ecology in North America: past, present and future. Ecology Ecology 86:1967-1974.

Turner, M. G. 2005. Landscape ecology: what is the state of the science? Annual Review of Ecology, Evolution and Systematics 36:319-344.

Turner, M. G. and J. A. Cardille. 2007. Spatial heterogeneity and ecosystem processes. Pages 62-77 in: J. Wu and R. J. Hobbs, editors. Key topics in landscape ecology. Cambridge University Press.

Turner, M. G. and F. S. Chapin, III. 2005. Causes and consequences of spatial heterogeneity in ecosystem function. Pages 9-30 in: G. M. Lovett, C. G. Jones, M. G. Turner, and K. C. Weathers, editors. Ecosystem function in heterogeneous landscapes. Springer-Verlag, New York.

Turner, M. G., W. H. Romme and D. B. Tinker. 2003. Surprises and lessons from the 1988 Yellowstone fires. Frontiers in Ecology and the Environment 1:351-358.

Turner, M. G., E. A. H. Smithwick, K. L. Metzger, D. B. Tinker and W. H. Romme. 2007a. Inorganic nitrogen availability following severe stand-replacing fire in the Greater Yellowstone Ecosystem. Proceedings of the National Academy of Sciences 104:4782-4789.

Turner, M. G., D. M. Turner, W. H. Romme and D. B. Tinker. 2007b. Cone production in young post-fire *Pinus contorta* stands in Greater Yellowstone (USA). Forest Ecology and Management 242:119-206.

Turner, M. G., E. A. H. Smithwick, D. B. Tinker and W. H. Romme. 2009. Variation in foliar nitrogen and aboveground net primary production in young postfire lodgepole pine. Submitted to Canadian Journal of Forest Research (In press).

Theses

Kashian, D. M. 2002. Landscape variability and convergence in forest structure and function following large fires in Yellowstone National Park. PhD Dissertation, University of Wisconsin, Madison.

Remsburg, A. J. 2005. Amount, position and age of coarse wood influence litter decomposition within and among young post-fire *Pinus contorta* stands. MS Thesis, University of Wisconsin, Madison.

Levitt, E. A. 2006. Sources of variation in soil nitrogen availability among post-fire lodgepole pine stands in Yellowstone National Park. MS Thesis, University of Wisconsin, Madison.

Simard, M. (In progress). Reciprocal interactions between bark beetles and wildfire in subalpine forests: landscape patterns and the risk of high-severity fire. PhD Dissertation, University of Wisconsin, Madison.

Manuscripts in preparation (titles are illustrative, not final)

Levitt, E. A., E. A. H. Smithwick and M. G. Turner. Litter quantity, litter quality and nitrogen availability in postfire lodgepole pine stands of varying density.

Remsburg, A.J. and M. G. Turner. Post-fire microsite heterogeneity affects leaf litter microarthropods in young lodgepole pine forests.

Romme, W.H, D.B. Tinker, and M.G. Turner. Spatial and temporal variability in early vegetation development after fire in lodgepole pine forests, northwestern Wyoming, USA.

Romme, W.H., and H. Lyons. Spatial patterns in proportions of standing vs. fallen fire-killed conifer boles 15 years after the 1988 Yellowstone fires.

Simard, M., M. G. Turner, W.H. Romme, D.B. Tinker, K.F. Raffa and E.N. Powell. Explaining broad-scale infestation patterns of three bark beetle species in the Greater Yellowstone Ecosystem.

Smithwick, E. A. H., T. C. Balser, J. Zhu, and M. G. Turner. Spatial distribution of microbial communities and nitrogen mineralization in two forest communities following fire in the Greater Yellowstone Ecosystem

Tinker, D.B., M.G. Turner, and W.H. Romme. Relative importance of deterministic and stochastic factors on understory composition in post-fire forests of Yellowstone National Park. To be submitted to Journal of Vegetation Science.

Turner, M. G., W. H. Romme, E. A. H. Smithwick, D. B. Tinker, and J. Zhu. Within-stand spatial variation in nitrogen availability following stand-replacing fire in the Greater Yellowstone Ecosystem.

Non-technical articles

Turner, M. G. 2009. Ecological effects of the ’88 fires: a story of surprise, constancy and change. Yellowstone Science (In press).

Sakai, J. 2008. Rising from the ashes. On Wisconsin, Summer 2008, pp. 22-27