Alaska’s Changing Boreal Forest: Resilience and Vulnerability
2004 Bonanza Creek LTER Renewal Proposal

Project Summary

The cornerstone of the Bonanza Creek (BNZ) LTER research has been the state factor approach, which allows prediction of ecosystem properties based on “independent” controls such as climate, parent material, topography, potential biota, and time and interactive controls, i.e., the processes internal to ecosystems that both affect ecosystem processes and are affected by them. The intellectual merit of the proposed research involves expansion of this theoretical framework to address processes underlying ecosystem resilience and vulnerability. The objective is to identify factors that buffer systems from radical changes in structure and functioning (resilience) vs. factors that might precipitate changes to alternative states (vulnerability). This requires an extension beyond the assumptions of steady state dynamics to ask under what conditions changes in drivers might trigger a fundamental change in the nature of boreal ecosystems. The research address three over-arching questions:
1. What currently controls and constrains the resilience of Alaska’s boreal forest?
2. What recent and projected changes in drivers make this system vulnerable to change?
3. How do factors influencing the balance among alternative states respond to recent and projected changes in climate, disturbance regime, human impacts, and exotic species?

The research design combines long-term observations, long-term experiments, and process studies to identify ecological changes and to document controls over ecosystem processes in two types of successional sequences (floodplain primary succession, and upland post-fire secondary succession). Hypotheses about controls over ecosystem dynamics are tested by manipulating selected interactive controls. These plot-level studies are extended to larger spatial scales (watersheds, regions, and the state of Alaska) in a hierarchical research design, using extensive measurements, remote sensing, and modeling. Temporal scales of the research span hours (weather), years (growth, populations), successional cycles (stand-age reconstructions), and millennia (vegetation and climate reconstructions). The research is organized into three themes. Forest dynamics addresses the structure, diversity, and population dynamics of the boreal forest. Biogeochemistry addresses the underlying biogeochemical mechanisms that link population processes with physical drivers of change. Landscape dynamics integrates community and biogeochemical processes at regional scales. New investigators address patterns and consequences of fungal diversity, landscape modeling, fire effects on N cycling, and 14C estimates of long-term C accumulation and turnover. Involvement in LTER cross-site comparisons enables us to understand boreal processes in a broader context.

The research has broad societal implications. The study of resilience and vulnerability directly addresses the ways in which recent and projected changes in climate, disturbance, human activities, and exotic species are changing the dynamics of ecosystems and the services they provide to society, including climate regulation, subsistence resources for local users, and the potential for recreation and aesthetics. To make this information available and useful to a broader community, we work closely with schools, community outreach programs, the broader scientific community, and resource managers through collaborations, outreach, and web-based data management. Information management emphasizes secure archival of the information we have collected, promotion of its use in synthesis, and development of web-based databases to facilitate its use by the scientific community.
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Section 1 Results of Prior Support

Bonanza Creek (BNZ) LTER research has emphasized successional dynamics in the Alaskan boreal forest. Initially we focused on state factors (independent controls) and interactive controls (factors that influence, and are influenced by, ecosystems) (Jenny 1980, Van Cleve et al. 1991, 1996, Chapin et al. 1996, Yarie et al. 1998). Due to rapid recent changes in climate, fire, and insects (Kasischke and Stocks 2000, Serreze et al. 2000), we expanded our goals in the previous funding cycle to ask “How have changes in climate and disturbance regime altered the functioning of the Alaskan boreal forest?” The following text summarizes the highlights of our second book synthesizing Alaskan boreal research (Van Cleve et al. 1986, Chapin et al. In press-a), with an emphasis on recent accomplishments.

1.1 Forest Dynamics

Alaska warmed rapidly at the end of the last glacial period. The early Holocene (ca 11,000-9000 years ago) was the warmest period. Climate then became wetter and gradually cooler (Lloyd et al. In press). Deciduous woodland and shrubland dominated in the early Holocene (Edwards et al. Submitted); subsequently, white spruce, then black spruce forest developed. The expansion of black spruce coincided with a threshold increase in fire frequency 6,000 years ago, despite cooler, moister climate, suggesting that vegetation rather than climate drove long-term trends in fire regime (Lynch et al. 2003, Lloyd et al. In press) (Fig. 1).

The response of boreal vegetation to 20th century warming has been decreased growth of white spruce, due to warming-induced drought stress (Jacoby et al. 1999, Barber et al. 2000), with projections of zero net annual growth and perhaps the loss of white spruce and birch from uplands before the end of the 21st century (Lloyd and Fastie 2002, Wilmking 2003, Juday et al. In press) (Fig. 2). At the southern limit of the Alaskan boreal forest, spruce bark beetle outbreaks have eliminated extensive areas of forest, because warmer temperatures have reduced tree resistance to bark beetles and shortened the life cycle of the beetle from two years to one, shifting the tree-beetle interaction in favor of the insect (Werner and Holsten 1985, Wallin and Raffa In press, Werner et al. In press). At its altitudinal and latitudinal limits, the boreal forest is expanding into tundra because of high rates of tree recruitment beyond treeline during recent warm decades (Silapaswan et al. 2001, Lloyd and Fastie 2002). At arctic treeline, spruce establishment in tundra depends at least partially on thawing permafrost (Lloyd et al. 2003). In summary, current trends show slow expansion of forest into tundra in the north, retreat of boreal forest in the south, and impending major compositional changes in central portions of Alaska’s boreal forest.

Fire may trigger future changes by altering successional trajectories. Self-replacement, in which the prefire tree species returns to dominance shortly after fire, generally occurs in extreme environments, whereas a successional sequence with multiple stages is more common in intermediate sites (Fig. 3) (Dymess and Grigal 1979, Viereck et al. 1983, Yarie 1983, Viereck et al. 1992, Youngblood 1992, Mann and Plug 1999, Fastie et al. 2002). Late-successional conifers establish during the initial 1-2 decades after fire, but their establishment success is sensitive to the depth of the organic mat remaining after fire (Johnstone et al. In press), understory species composition (Cater and Chapin 2000), and seed availability from on-site serotinous cones (black spruce) or off-site seed sources (white spruce) (Viereck 1973, Zasada et al. 1992, Mann and Plug 1999, Cater and Chapin 2000, Johnstone and Chapin 2003). Insect outbreaks can disrupt or redirect succession by reducing abundance of preferred hosts (McCullough et al. 1998). Mammalian herbivores speed succession by eliminating early successional species and shifting the competitive balance in favor of the less palatable, more slowly growing late successional species (Bryant and Chapin 1986, Kielland and Bryant 1998) (Fig. 4). Changes in any of these processes could alter vegetation composition and successional trajectory.

After initial establishment, competition, facilitation, and herbivory interact to drive successional
change (Walker et al. 1986, Walker and Chapin 1987, Adams 1999). Ecosystem controls change at key turning points (thresholds), where a shift in dominance of plant functional types radically alters the physical and chemical environment that govern ecosystem processes and disturbance probability (Van Cleve et al. 1991) (Fig. 5). In the floodplain, intense herbivory by moose initially constrains canopy development, creating an ecosystem dominated by physical controls over soil water movement, surface evaporation and gypsum accumulation at the soil surface (Dyrness and Van Cleve 1993, Marion et al. 1993, Van Cleve et al. 1993, Kielland and Bryant 1998). Colonization by alder shifts the system from physical to biological control (Van Cleve et al. 1991, Viereck et al. 1993), adds 60-70% of the nitrogen that accumulates during succession (Van Cleve et al. 1971, Van Cleve et al. 1983, Van Cleve et al. 1993, Uliassi et al. 2000, Uliassi and Ruess 2002), and causes herbivory to change from a deterrent to an accelerator of succession by eliminating palatable early successional species (Fig. 4) (Bryant and Chapin 1986, Bryant et al. 1991, Kielland et al. 1997, Kielland and Bryant 1998). Other key turning points include (1) a shift to balsam poplar dominance, where changes in productive potential and litter chemistry enhance NPP and nitrogen cycling rates (Van Cleve et al. 1983, Schimel et al. 1996) and (2) the shift to white spruce dominance, where mosses grow rapidly in the absence of smothering broadleaved litter (Oechel and Van Cleve 1986), reduce nutrient cycling rates by sequestering nutrients in low-quality litter (Yarie 1997), and increase fire probability by producing fuels that dry quickly and support fire spread (Chapin et al. 2003) (Fig. 5).

Species diversity is low in the boreal forest (Waide et al. 1999) and varies dramatically through succession with peaks in early succession (e.g., fire-specialist plants, herbivorous insects, neotropical migrant birds, and mammals) (Rees and Juday 2002, Rexstad and Kielland In press) and late succession (non-vascular plants and saprophagous insects) (Chapin and Danell 2001). Logging reduces plant diversity by 30% by eliminating fire specialists (Rees and Juday 2002). Using bacterial genomics, we are beginning to document patterns of microbial diversity (Microbial Observatory).

Many boreal animals exhibit large population fluctuations. Moose and hare densities appear to be sensitive to food availability and predation (Flora et al. Submitted), whereas Microtus and Clethrionomys densities correlate more strongly with climate (Rexstad and Kielland In press). Two native insects have changed from decadal outbreaks to consistently low populations (large aspen tortrix since 1985; spear-marked blackmoth since 1975), whereas other species that had negligible populations before 1990 have shown large outbreaks (eastern spruce budworm, spruce coneworm, larch sawfly, and aspen leaf miner) (Werner 1994, 1996)(Table 1).

Long-term forest harvest studies permit an assessment of potential future human impacts on Alaska’s boreal forest. Low intensity forest harvest (no scarification) reduces initial seedling establishment but maximizes long-term growth of tree seedlings (Wurtz et al. In press). Overstory retention treatments had no long-term effect on tree recruitment and growth (Wurtz and Zasada 2001). These studies suggest that low-intensity management after clear-cutting, an approach that mimics certain aspects of natural fire cycles, may maximize ecological recovery.

1.2 Biogeochemistry

Aboveground production varies by more than an order of magnitude among major forest types in interior Alaska, primarily due to variation in topography and successional age (Van Cleve et al. 1983, Yarie and Van Cleve In press). It is greatest in midsuccesional stands on floodplains, where soil temperature and moisture are relatively high. On south-facing slopes, production is constrained by moisture and on north-facing slopes by soil temperature. On temperature-limited sites, mosses account for half of aboveground production. A nitrogen productivity model, in which growth is a function of nitrogen supply, confirms these effects (Yarie 1997, Yarie and Van Cleve In press).
Carbon and nutrient cycling rates in fine roots are several orders of magnitude faster than in aboveground tissues because of high belowground allocation (Ruess et al. 1998, Ruess et al. 2003, Vogel et al. Submitted) (Fig. 6). Fine root production is concentrated close to the soil surface, and fine root production increases progressively into deeper soil layers as the soil warms through the season, suggesting that soil temperature strongly influences root depth distributions. Fine root life span and the associated physiological and morphological traits of roots vary across sites in a fashion that parallels that observed for aboveground tissues. The average maximum growth rate of fine roots in floodplain ecosystems is inversely correlated with the mean life span of those roots (Ruess et al. In press). Cross-site studies demonstrate that most woody plants have similar morphological, phenological, and physiological traits of first-order roots and differ primarily in root allocation, size distribution, and lifespan (Burton et al. 2002, Pregitzer et al. 2002).

Ratios of aboveground litterfall to soil respiration in interior Alaskan forests are among the lowest recorded in North American forests (Raich and Nadelhoffer 1989, Ruess et al. 1996), suggesting that a large proportion of boreal soil respiration originates from root-derived C. Using two independent approaches, we estimate that fine root respiration constitutes approximately 60% of total soil respiration in black spruce forests (Ruess et al. 2003, Vogel et al. Submitted). Trenching to eliminate root production caused a 27% loss of total soils C within 2 years (Fig. 7), suggesting that much of the soil carbon is labile and can decline rapidly in the absence of continued inputs. These results are confirmed by laboratory incubations.

N$_2$-fixation inputs by *Alnus crispa* (uplands) and *A. tenuifolia* (floodplain) account for the largest percentage of total N accumulated during succession and appear to be strongly limited by soil P availability (Ulissi and Ruess 2002, Anderson et al. In press). Fixation inputs appear to exceed plant N demand, and significant amounts of fixed N may be lost via leaching or denitrification, particularly in mid-successional stages (Ulissi and Ruess 2002), where nitrification potential is high and soil microbial biomass is more C- than N-limited (Brenner et al. Submitted) (Fig. 8).

Mammalian herbivores play a key role in the biogeochemistry of the boreal forest. In the floodplain willow communities, they consume 40% of aboveground NPP (Kielland and Bryant 1998). When herbivores are experimentally excluded, biogeochemistry changes more quickly from a system dominated by inorganic C cycling and solubility equilibria, to a biologically controlled pattern of cycling dominated by NPP and decomposition (Kielland and Bryant 1998, Ruess et al. 1998).

Despite the large quantities of organic N present accumulated in boreal soils, the vegetation is strongly N-limited (Yarie and Van Cleve 1996, In press). However, much of this organic N is quite dynamic. Amino acids turn over more rapidly than inorganic N (Kielland 2001a, Jones and Kielland 2002) and are a major source of N absorbed by both plants and microbes (McFarland et al. 2002) (Fig. 9). $^{15}$N natural abundance in vegetation suggests that uptake of organic N plays a significant role in the N nutrition of the boreal forest.

A large fire disturbance that occurred synchronously across northern North America in the 1860’s was a legacy that set the stage for the current stand age distribution in Alaska and Canada that controls C dynamics across northern North America (McGuire et al. In press). Differences in fire severity have substantial effects on patterns of vegetation C storage across the circum-boreal north; western and central Siberia are dominated by ground fires that do not tend to kill trees, whereas far eastern Siberia and boreal North America are dominated by crown fires that do tend to kill trees (McGuire et al. 2002). This may partially explain why application of an inversion model suggests that uncertainties concerning net ecosystem production for high latitudes (Chapin et al. 2000) may be less in boreal North America than in Europe and boreal Asia (Dargaville et al. 2002).
1.3 Landscape Processes and Disturbance

Presence or absence of permafrost is probably the most important threshold regulating the structure and functioning of Alaska’s boreal forest. Permafrost is discontinuous in our study sites, being generally present on north-facing slopes and valley bottoms, where it leads to cold water-logged soils, and absent on south-facing slopes, where soils drain freely. Permafrost temperatures are now typically warmer than -2°C, and have warmed about 0.7°C per decade since 1970 (Osterkamp and Romanovsky 1999) in response to regional warming and changes in insulation by snow and vegetation. Continued warming will likely lead to extensive permafrost degradation within 10-25 years (Romanovsky et al. 2001). Currently 38% of our research watershed (CPCRW) has unstable or thawing permafrost (Hinzman et al. In press-a) (Fig. 10). Thus we anticipate a greater loss of permafrost in the coming decades than the 2.1% loss that occurred in the last 90 years.

Permafrost response to climate warming involves multiple ecosystem feedbacks that involve changes in insulation by snow, moss, and the surface organic mat (Osterkamp and Romanovsky 1999, Sazonova and Romanovsky 2003). Insulation declines dramatically following fire, increasing the layer of thawed soil from about 50 cm to 2-4 m. As permafrost recovers during post-fire succession, an unfrozen layer (talik) forms between a seasonally frozen or newly developed upper permafrost layer and the lowered surface of original permafrost (Fig. 11). In sloping terrain, water drains laterally through the talik, drying surface soils. Thawing of ice-rich permafrost may cause subsidence of the ground surface (thermokarst). Depending on the local terrain and hydrologic regime, water may accumulate at the surface forming ponds or waterlogged soil. Thus the impact of climate warming on soil moisture in permafrost terrain depends strongly on factors controlling talik formation and drainage conditions (Yoshikawa et al. 2003).

Low-permafrost watersheds or watersheds with well-developed taliks have greater base flow (80% of discharge) and are less flashy (i.e., less likely to cause floods) than high-permafrost watersheds, in which base flow increases from 50-60% of discharge in early summer to about 80% in late summer when mineral soils have thawed (Ishikawa et al. 2001, Hinzman et al. 2002) (Fig. 12). Areas with abundant groundwater flow also generate aufeis (areas of thick winter ice that forms when groundwater is forced to the surface by freezing soil) that kills most woody vegetation, substantially altering riparian dynamics. Groundwater flow also generates higher concentrations of base cations, inorganic nitrogen, and dissolved CO₂ and less dissolved organic carbon and nitrogen than in permafrost-dominated watersheds, where most water flows through the organic mat (MacLean et al. 1999, Petrone et al. 2000). Thus permafrost and talik distribution strongly influence soil moisture, land-water interactions, and stream discharge and chemistry. In contrast to temperate ecosystems, nitrate losses in streams are 4 to 5-fold greater than deposition inputs, a result that we cannot currently explain in light of the strong nitrogen limitation of watershed vegetation.

Fire is the dominant disturbance agent in interior Alaska but is highly variable in space and time. In the average year, the fire season lasts only three weeks, sandwiched between early summer, when soils are wet from snowmelt, and late summer, when precipitation increases. However, 55% of the total area burned between 1961 and 2000 occurred in just 6 years, when the fire season lasted much longer, giving rise to very large fires (Kasischke et al. 2002, Kasischke et al. In press). Thus the fire regime is dominated by unusual years rather than by average conditions. The 7% increase in area burned in Alaska in the last 40 years (Kasischke et al. In press) is much less than the doubling reported for western Canada (Murphy et al. 2000). Fire return time varies regionally from <50 years to over 100 years (Yarie 1981, Fastie et al. 2002). Annual area burned correlates positively with temperature (r = 0.63) and vegetation cover (r = 0.65) and negatively with precipitation (r = -0.61) (Kasischke et al. 2002). Lightning, which accounts for 90% of the area burned (Kasischke et al. In press), is controlled by both...
synoptic processes related to El Nino and by local factors such as topography and presence of conifer
vegetation (Dissing and Verbyla 2003) (Fig. 13). Human ignitions, which account for 60% of the fires in
Alaska, generally produce small fires because they are lit at times and places where fire does not readily
spread (Kasischke et al. 2002, Chapin et al. 2003). Human activities reduce area burned because
suppression has greater impact than human ignitions (DeWilde 2003).

Recent and projected changes in the boreal forest could feed back to the climate system. The
lower albedo and greater sensible heat flux of spruce compared to deciduous forests or non-forested
wetlands (Chapin et al. 2000, Chambers and Chapin 2003) suggest that northward forest expansion
could be a positive feedback to regional warming, but that loss of forests to the south or net conversion
from conifer to deciduous forests resulting from fire could have a net cooling effect, one of the few
negative feedbacks to high-latitude warming that has been identified (Chapin et al. 2000, McGuire and
Chapin In press) (Fig. 14). Boreal forests contain approximately 27% of the world's vegetation carbon
inventory and 28% of the world's soil carbon inventory (equivalent to 75% of the total atmospheric
carbon) (McGuire et al. 1997), so warming effects on net ecosystem production (NPP – respiration) or
on fire regime could substantially alter the global climate system (Potter et al. 2001, Clein et al. 2002).
Warming appears to enhance carbon release in dry areas, enhance uptake in wet areas, and enhance
methane release in wet areas. The net effect of fire depends on fire severity and on changes in fire
frequency (Kasischke et al. 1995, Zhuang et al. 2002). All of these effects on trace-gas feedbacks hinge
on permafrost and hydrologic changes, which are poorly known (Chapin et al. 2000, Harden et al. In
press, McGuire and Chapin In press) (Fig. 15). The recent shrinkage of lakes and wetlands in interior
Alaska suggests, however, that drying predominates and therefore CO$_2$ efflux may be increasing and
Bonanza Creek LTER Publications (1998-present)

Journal Articles (150)


Books (6)


Book Sections (34)


and B.J. Stocks, editors. Fire, climate change and carbon cycling in the boreal forest. Springer-Verlag, New York, New York, USA.


Dissertations/Theses (19)


Other Publications (10)


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<td>Precipitation (WB Rain Gauges) at BCEF LTER sites: Weekly</td>
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<td>1999</td>
<td>Production and foliage biomass and nitrogen from LTER sites 1989</td>
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<td>1999</td>
<td>Snow Depth at LTER weather stations: Daily</td>
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<tr>
<td>1999</td>
<td>Wind Direction and Velocity for Upper (10 meter) Sensor:Daily</td>
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<td>1998</td>
<td>Artificial communities experiment</td>
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<td>1998</td>
<td>Fine root length and width measurements from digitized minirhizotron images</td>
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<td>1998</td>
<td>Fine root production and mortality - (Minirhizotrons)</td>
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<td>1998</td>
<td>Height of Dominant Woody Plants Inside and Outside Exclosures Located in FP1</td>
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<td>1998</td>
<td>Litterfall and Hare Pellet Summary at Bonanza Creek Experimental Forest Control Plots</td>
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<td>1998</td>
<td>Litterfall Weights From LTER Study Site Treatment Plots; 1990-Present.</td>
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<td>Log Decomposition - Photographs</td>
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<td>1998</td>
<td>Precipitation at LTER weather stations: Daily</td>
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<td>1998</td>
<td>Seasonal patterns of nitrogen fixation by Alnus tenuifolia within successional floodplain forests - 1992</td>
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<td>1998</td>
<td>Solar radiation at BCEF (LTER1 and LTER2) climate stations, Hourly</td>
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<td>1998</td>
<td>Stem height and diameter for Long Term Forest Reserve Plots in CPCRW</td>
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<td>1998</td>
<td>White Spruce Seedling Counts at BCEF Vegetation Plots (4 sq m)</td>
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</table>
Section 2  Proposed Research
Introduction and Conceptual Framework

Perhaps the most urgent challenge facing humanity is to understand the factors determining the limits to resilience of regional systems that are changing directionally in response to altered physical, biological and social drivers (Vitousek et al. 1997, Berkes and Folke 1998). The boreal forest is an ideal region in which to explore the dynamics of change for several reasons. (1) Its cultures and natural ecosystems are relatively intact, making it easier to understand the natural coupling of physical, biological, and social components of regional systems. (2) The biophysical and social drivers of regional processes are changing as rapidly as anywhere on Earth (Serreze et al. 2000, Krupnik and Jolly 2002, Hinzman et al. In press-b). (3) Key variables that regulate regional processes exhibit thresholds within the boreal forest or its margin with other biomes; these include permafrost, the forest-tundra boundary, and outbreak behavior of key forest mammals and insects. (4) The boreal region is the second largest biome on Earth and plays a major role in the functioning of the global climate system. (5) Long-term research by the BNZ LTER program has documented natural patterns of interannual and successional variability against which we can detect threshold changes in system behavior.

The cornerstone of our research has been the state factor approach, which allows prediction of ecosystem properties based on “independent” controls such as climate, parent material, topography, potential biota, and time (Jenny 1980). We have extended this conceptual framework through study of interactive controls, i.e., the processes internal to ecosystems that both affect ecosystem processes and are affected by them (Fig. 16). These include functional groups of organisms, soil resources, microclimate, disturbance regime, and human activities (Van Cleve et al. 1991, Chapin et al. 1996). Through study of these internal dynamics, we have learned that important negative feedbacks (e.g., successional changes in flammability) tend to maintain the system within certain bounds but that the system also exhibits critical thresholds (turning points) where positive feedbacks push the system toward a new state (Van Cleve et al. 1991, Chapin et al. 1996) (Fig. 5). We have also learned that legacies such as past fire history, post-fire recruitment, or persistence of species by vegetative reproduction constrains ecosystem response to environment and disturbance.

We will place the next phase of the BNZ LTER research in the broader theoretical framework of resilience theory (Folke et al. 2002, Gunderson and Holling 2002, Berkes et al. 2003). This framework has emerged to identify factors that buffer systems from radical changes in structure and functioning (resilience) vs. factors that might precipitate changes to alternative states (vulnerability). This requires that we reach beyond the assumptions of steady state dynamics to ask under what conditions changes in drivers might trigger a change in ecosystem state (Holling 1986, Gunderson and Holling 2002, Scheffer and Carpenter 2003) (Fig. 17). This framework builds on our earlier research on external controls (state factors), internal dynamics (interactive controls), positive feedbacks (turning points), and negative feedbacks (repeating successional cycles). In this way our long-term measurement program and experiments become essential tools to address new hypotheses. A weakness in current resilience theory is that it is derived primarily by induction based on frequently observed patterns and does not specify the underlying mechanisms of resilience (Holling and Gunderson 2002). Our goal is to explore the mechanisms that underlie the resilience and vulnerability of Alaska’s changing boreal forest. We address three over-arching questions:

1. What currently controls and constrains the resilience of Alaska’s boreal forest?
2. What recent and projected changes in drivers make this system vulnerable to change?
3. How do factors influencing the balance among alternative states respond to recent and projected changes in drivers?
Fig. 1. Charcoal influx at Dune Lake Alaska over the last 10,000 years. Fire became much more frequent about 6000 yr BP, coinciding with arrival of black spruce on the landscape (Lynch et al. 2003).

Fig. 2. Past and projected future summer temperature and radial growth of white spruce in interior Alaska (Juday et al. In press). Temperatures before 1917 were reconstructed from tree rings. Future temperatures and ring-width are projected from GCM simulations of climate and the observed climate-ringwidth relationship. Projections suggest that white spruce will approach zero annual growth by the end of the 21st century.

Fig. 3. Representative successional trajectories on upland sites in interior Alaska along gradients of soil temperature and soil moisture. Changes in environment, disturbance regime, or post-disturbance seed availability can shift a stand to a new successional trajectory, but in the absence of these changes, succession tends to repeat the same successional trajectory following each disturbance event (Chapin et al. In press-b).
Fig. 4. Ratio of alder and poplar to willow biomass in browsed (control) and unbrowsed (exclosure) plots in the Tanana Floodplain. Browsing speeds succession by removing early successional willows (Kielland and Bryant 1998).

FLOODPLAIN PRIMARY SUCCESSION

Fig. 5. Floodplain primary successional sequence of vegetation and soils, showing the major research sites, their ages, and the major turning points where changes in species composition exert positive feedbacks causing switch to the next successional stage (Van Cleve et al. 1996).

Fig. 6. Contributions of trees (aboveground; 13%), shrubs (11%), bryophytes (20%), and fine roots (56%) to total stand production in floodplain black spruce stands. Also shown are contributions of roots (Rr) and heterotrophs (Rh) to total soil respiration (Ruess et al. 2003).
Fig. 7. Root exclusion (trenching) at 3 black spruce reduces stands total soil carbon after only 2 years, demonstrating that forest floor C depends on substantial annual root inputs to maintain or accumulate carbon (Vogel et al. Submitted).

Fig. 8. Response of microbial C and N in fertilized balsam poplar (BP) and white spruce (WS) stands on the Tanana floodplain. The lack of microbial response to fertilization suggests that microbial biomass is limited more by C than by N (Brenner et al. Submitted).

Fig. 9. Relationship between excess (above ambient) $^{13}$C and $^{15}$N in fine roots derived from $^{13}$C$^{15}$N-glycine injected in situ and followed over a 14-day period. The rapid attenuation in slope over time demonstrates substantial root uptake of naturally occurring organic N. The dotted line shows the 2:1 ratio of injected glycine (McFarland et al. 2002).
Fig. 10. Modeled mean annual surface temperature of CPCRW for 1997-98. Currently 38% of the watershed has unstable or thawing permafrost (Hinzman et al. In press-a).

Fig. 11. As permafrost recovers during post-fire succession, an unfrozen layer (talik) forms but disappears later in succession (top panel). In a warmer climate (bottom panel), fire disturbance could lead to persistence of a talik (Hinzman et al. In press-a).

Fig. 12. Conceptual model of the influence of permafrost on watershed hydrology and biogeochemistry. Permafrost forms an impermeable barrier and restricts subsurface flow to the shallow active layer of soils. The hypothesized consequences for N cycling are shown.
Fig. 13. Both topography and vegetation type influence lightning occurrence (Dissing and Verbyla 2003), which is responsible for 90% of the area burned in Alaska (Kasischke et al. In press).

Fig. 14. Conifer forests tend to warm the atmosphere, whereas deciduous forests tend to cool the atmosphere. Expansion of boreal forests northward could lead to a positive feedback to warming, whereas expansion of deciduous forests in the event of more frequent fires could lead to a negative feedback to warming (Baldocchi et al. 2000, Chapin et al. 2000, McGuire and Chapin In press).

**Losts of Potential NEP to the Atmosphere**

Fig. 15. The response of carbon storage in interior Alaska to climatic change depends on fire severity and frequency, which are influenced by changes in the hydrologic state of the system (Harden et al. 2000).

Table 1. Insect abundances

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
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<tbody>
<tr>
<td>Spruce beetle</td>
<td>20235</td>
<td>210039</td>
<td>286505</td>
<td>744989</td>
<td>595725</td>
<td>1114587</td>
<td>1265364</td>
</tr>
<tr>
<td>Spruce budworm</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>45540</td>
<td>651099</td>
</tr>
<tr>
<td>Larch sawfly</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>45540</td>
<td>651099</td>
</tr>
<tr>
<td>Larch bud moth</td>
<td>202350</td>
<td>4047</td>
<td>238773</td>
<td>0</td>
<td>36018</td>
<td>4087</td>
<td>651099</td>
</tr>
<tr>
<td>Spear-marked black moth</td>
<td>2347260</td>
<td>526110</td>
<td>1092690</td>
<td>159452</td>
<td>32552</td>
<td>4832</td>
<td>0</td>
</tr>
<tr>
<td>Large aspen tortrix</td>
<td>0</td>
<td>2590080</td>
<td>19426</td>
<td>54877</td>
<td>261367</td>
<td>60379</td>
<td>24036</td>
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</table>
Research Design and Research Overview

The BNZ LTER site consists of two intensive study areas: (1) At Bonanza Creek Experimental Forest (BCEF), we maintain permanent plots in primary floodplain succession and secondary post-fire succession (3-5 successional stages x 3 replicate sites/stage; Table 2). (2) At the Caribou-Poker Creek Research Watersheds (CPCRW), we maintain three intensive watersheds, two of which are unmanipulated (low vs. high % permafrost), and a watershed with intermediate % permafrost that was experimentally burned in 1999. We extend observations from intensive studies at BCEF and CPCRW to the surrounding 100 x 100 km area, using remote sensing, modeling, and extensive sampling. Where possible, we maintain databases for all of interior Alaska. This gives us a hierarchical study design from plots/watersheds to interior Alaska as a whole (Fig. 18). We also initiated a climate transect (one of the IGBP high-latitude transects (McGuire et al. 2002)), that links the BNZ and ARC LTER sites with other long-term ecological monitoring programs (Fig. 18).

We maintain four primary weather stations to measure macroclimate (uplands and floodplain at BCEF; valley bottom and Caribou Peak at CPCRW) (Table 3). These stations document climate variation in our two intensive study sites, relative to the long-term climate record at Fairbanks (since 1918) and a 200-year record reconstructed from tree rings. In permanent plots in each successional stage we monitor microclimate, plant and microbial diversity, population dynamics of selected species, major ecosystem pools and fluxes, and disturbance (Table 3). In selected sites we manipulate those interactive controls that we hypothesize to regulate the internal dynamics of boreal ecosystems (Table 4). These include (1) soil resources (nitrogen [N] addition and reduction [via sawdust addition to double soil C:N ratio], rain exclusion, snow removal), (2) key species (selected plant functional types, moose+hares), (3) microclimate (winter thermal insulation), (4) disturbance (experimental burn of a watershed), and (5) human activities (forest harvest). The methods for these measurements and experiments are described briefly in the following sections and in detail on our web site [http://www.lter.uaf.edu/bcef/exp_design.cfm]. In summary, this experimental design enables us to monitor change and to conduct detailed process-level studies in two types of successional sequences (floodplain primary succession, and upland post-fire secondary succession [both north- and south-facing slopes]). We test hypotheses about controls over ecosystem dynamics by manipulating selected interactive controls. We extend these plot-level studies to larger spatial scales (watersheds, regions, and the state of Alaska), using extensive measurements, remote sensing, and modeling. We address temporal scales spanning hours (weather), years (growth, populations), successional cycles (stand-age reconstructions), and millennia (vegetation and climate reconstructions).

The next three sections describe the details of our research program and its relationship to our conceptual framework of resilience and vulnerability. Forest dynamics addresses the structure, diversity, and population dynamics of the boreal forest. Biogeochemistry addresses the underlying biogeochemical mechanisms that link population processes with physical drivers of change. Landscape dynamics integrates community and biogeochemical processes at regional scales. Within each section we address hypotheses relating to our three over-arching questions: (Question 1) resilience of current dynamics, (Question 2) vulnerability to change, and (Question 3) alternative future states (Fig. 19).
Fig. 16. The relationship between state factors (outside the circle), interactive controls (inside the circle), and ecosystem processes (inside the box). The circle represents the boundary of the current ecosystem, whose structure and functioning respond to and affect interactive controls, which are ultimately governed by state factors. Ecosystem properties are also determined by legacies related to long-term ecosystem development (e.g., past migrations) and short-term succession change. Disturbance and other factors can push the system toward some new state or initiate a new cycle of succession (Chapin et al. In press-c).

Fig. 17. Key vulnerabilities in the Alaskan boreal forest. Changes in climate, human activities, and exotic species drive nonlinear changes in ecosystem dynamics, particularly those related to disturbance (fire, thermokarst) which initiate changes in forest dynamics (animal dynamics and successional trajectory, biogeochemistry, and landscape dynamics (e.g., wetland drainage). These changes in ecosystem dynamics alter the ecosystem services that are important to society.
Fig. 18. Hierarchical experimental design of the BNZ LTER, with intensive study sites and watersheds nested within experimental areas (BCEF and CPCRW), which is nested within the Fairbanks Region and the state of Alaska. Also shown is the climate transect.

Table 2. Successional stages in which vegetation and climate plots are located.

<table>
<thead>
<tr>
<th>Type</th>
<th>Disturbance</th>
<th>Year of disturbance</th>
<th>Dominant Vegetation</th>
<th>Initial measurement</th>
<th>Remeasurement frequency</th>
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<tbody>
<tr>
<td>South facing uplands</td>
<td>Early</td>
<td>Fire 1983</td>
<td>Herbs and saplings</td>
<td>1989</td>
<td>1983-84, Every 3 years</td>
</tr>
<tr>
<td></td>
<td>Mid</td>
<td>Fire 1940</td>
<td>Birch or Aspen</td>
<td>1989</td>
<td>Every 6 years</td>
</tr>
<tr>
<td></td>
<td>Late</td>
<td>Fire 1783</td>
<td>White spruce</td>
<td>1989</td>
<td>Every 6 years</td>
</tr>
<tr>
<td>North facing uplands</td>
<td>Early</td>
<td>Fire 1999</td>
<td>Herbs</td>
<td>1999</td>
<td>Annually</td>
</tr>
<tr>
<td></td>
<td>Mid</td>
<td>Fire 1971</td>
<td>Willow</td>
<td>1971</td>
<td>1971-75, 2002; Every 6 years</td>
</tr>
<tr>
<td></td>
<td>Late</td>
<td>Fire 1915</td>
<td>Black spruce</td>
<td>No site selected yet</td>
<td>Every 6 years</td>
</tr>
<tr>
<td>Floodplain</td>
<td>Early</td>
<td>Fire 2000</td>
<td>Charred ground</td>
<td>2000</td>
<td>Annually</td>
</tr>
<tr>
<td></td>
<td>Sandbar</td>
<td>Flooding 1990</td>
<td>Bare soil</td>
<td>1989</td>
<td>Annually</td>
</tr>
<tr>
<td></td>
<td>Open shrub</td>
<td>Flooding 1980</td>
<td>Willow</td>
<td>1989</td>
<td>Every 3 years</td>
</tr>
<tr>
<td></td>
<td>Closed shrub</td>
<td>Flooding 1960</td>
<td>Alder</td>
<td>1989</td>
<td>Every 3 years</td>
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<tr>
<td></td>
<td>Poplar</td>
<td>Flooding 1900</td>
<td>Poplar</td>
<td>1989</td>
<td>Every 6 years</td>
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<tr>
<td></td>
<td>White spruce</td>
<td>Flooding 1800</td>
<td>White spruce</td>
<td>1989</td>
<td>Every 6 years</td>
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<tr>
<td></td>
<td>Black spruce</td>
<td>Flooding Pre 1500</td>
<td>Black spruce</td>
<td>1989</td>
<td>Every 6 years</td>
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Table 3. Parameters measured at LTER intensive sites.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Location</th>
<th>Dates</th>
<th>Responsible PI</th>
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<tr>
<td>Climate*</td>
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<tr>
<td>Air temperature</td>
<td>BCEF, CPCRW</td>
<td>1984-</td>
<td>Hinzman*</td>
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<td>Soil temp at 6 depths</td>
<td>BCEF, CPCRW</td>
<td>1984-</td>
<td>Hinzman</td>
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<td>Relative humidity</td>
<td>BCEF, CPCRW</td>
<td>1984-</td>
<td>Hinzman</td>
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<td>Precipitation</td>
<td>BCEF, CPCRW</td>
<td>1984-</td>
<td>Hinzman</td>
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<td>Evaporation</td>
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<td>1984-</td>
<td>Hinzman</td>
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<td>Wind speed, direction</td>
<td>BCEF, CPCRW</td>
<td>1984-</td>
<td>Hinzman</td>
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<td>Solar radiation (global)</td>
<td>BCEF, CPCRW</td>
<td>1984-</td>
<td>Hinzman</td>
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<tr>
<td>UV</td>
<td>BCEF, CPCRW</td>
<td>1984-</td>
<td>Hinzman</td>
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<tr>
<td>PAR</td>
<td>BCEF, CPCRW</td>
<td>1984-</td>
<td>Hinzman</td>
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<td>Shortwave in/out</td>
<td>CPCRW</td>
<td>1988-</td>
<td>Hinzman</td>
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<td>Longwave in/out</td>
<td>CPCRW</td>
<td>1988-</td>
<td>Hinzman</td>
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<td>Sun photometer</td>
<td>BCEF, CPCRW</td>
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<td>Hinzman</td>
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<td>Snow depth</td>
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<td>Hinzman</td>
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<td>Thaw depth</td>
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<td>1992-</td>
<td>Hinzman</td>
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<td>Snow moisture</td>
<td>BCEF, CPCRW</td>
<td>1983-</td>
<td>Hinzman</td>
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<tr>
<td>River height</td>
<td>BCEF, CPCRW</td>
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<td>Tree density, biomass</td>
<td>BCEF</td>
<td>1989-</td>
<td>Walker, Juday</td>
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<td>Tree seedling density</td>
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<td>Walker, Juday</td>
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<td>1989-</td>
<td>Walker, Juday</td>
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<td>Root biomass</td>
<td>BCEF</td>
<td>1989-</td>
<td>Ruess</td>
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<td>BCEF</td>
<td>1955-(c)</td>
<td>Walker</td>
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<td>BCEF</td>
<td>1976-</td>
<td>Werner</td>
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<td>1999-</td>
<td>Rexstad</td>
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<td>Snowshoe hare density</td>
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<td>1999-</td>
<td>Rexstad</td>
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<td>Carbon and nutrient stocks</td>
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<td>Trees</td>
<td>BCEF</td>
<td>1989-</td>
<td>Yarie, Ruess</td>
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<td>Understory</td>
<td>BCEF</td>
<td>1989-</td>
<td>Yarie, Ruess</td>
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<td>BCEF</td>
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<td>Valentine</td>
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<td>BCEF</td>
<td>1975-</td>
<td>Yarie, Ruess</td>
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<td>Diameter increment</td>
<td>BCEF</td>
<td>1989-</td>
<td>Yarie, Ruess</td>
</tr>
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<td>Fine root production</td>
<td>BCEF</td>
<td>1992-</td>
<td>Ruess</td>
</tr>
<tr>
<td>Browse consumption</td>
<td>BCEF</td>
<td>1990-(c)</td>
<td>Kielland</td>
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<td>Soil respiration</td>
<td>BCEF, CPCRW</td>
<td>1998-</td>
<td>Ruess, Valentine</td>
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<td>N mineralization</td>
<td>BCEF, CPCRW</td>
<td>1999-</td>
<td>Kielland</td>
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<td>Nitrogen deposition (NADP)</td>
<td>CPCRW</td>
<td>1993-</td>
<td>Hinzman</td>
</tr>
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<td>Hinzman</td>
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<td>CPCRW</td>
<td>1978-</td>
<td>Jones</td>
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*Hollingsworth (site manager) is responsible for climate measurements at BCEF
Table 4. Long-term experiments in the BNZ LTER site

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<th>BNZ long-term experiments</th>
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<td>Mammalian herbivore exclosures</td>
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<td>Wertz</td>
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<td>Insect population monitoring</td>
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<td>Small mammal population monitoring</td>
<td>Rexstad, Kielland</td>
<td>1999</td>
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<td>Herbivore effects on white spruce</td>
<td>Kielland, Wurtz</td>
<td>2002</td>
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<tr>
<td>Fire effects on soil thaw depth</td>
<td>Viereck</td>
<td>1983</td>
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<td><strong>Theme 2</strong></td>
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<tr>
<td>Annual N addition</td>
<td>Yarie</td>
<td>1989</td>
</tr>
<tr>
<td>One-time sawdust or sugar addition</td>
<td>Yarie</td>
<td>1989</td>
</tr>
<tr>
<td>Summer precipitation exclusion</td>
<td>Yarie</td>
<td>1989</td>
</tr>
<tr>
<td>Snow removal</td>
<td>Yarie</td>
<td>2004</td>
</tr>
<tr>
<td>Added insulation</td>
<td>Ruess</td>
<td>2004</td>
</tr>
<tr>
<td>Root-trenching experiment</td>
<td>Valentine</td>
<td>1999</td>
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<td>$^{15}$NH$_4$ post fire retention</td>
<td>Mack</td>
<td>1999</td>
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<tr>
<td>Monitoring floodplain biogeochemistry</td>
<td>Kielland, Jones</td>
<td>2002</td>
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<td><strong>Theme 3</strong></td>
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<tr>
<td>Forest harvest experiments</td>
<td>Wurtz</td>
<td>1972</td>
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<td>Experimental burn (FROSTFIRE)</td>
<td>Chapin</td>
<td>1999</td>
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<tr>
<td>Monitoring watershed hydrology</td>
<td>Hinzman</td>
<td>1970</td>
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<tr>
<td>Artificial alder communities</td>
<td>Chapin</td>
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Fig. 19. Overview of research on forest dynamics. The linkages between external drivers, internal dynamics and the other themes (biogeochemistry and landscape dynamics) are shown together with the hypotheses that will examine these linkages.
Theme 1: Forest dynamics

Hypothesis 1: Physical environment exerts primary control over spatial patterns of ecosystem structure and species composition, whereas ecosystem feedbacks govern temporal change; legacies modify these expected patterns most strongly after disturbance and in late succession. We explore this hypothesis by studying spatial patterns (FD1-1) and temporal patterns within (FD1-2, FD1-3, FD1-4) and among successional trajectories (FD1-5).

FD1-1 (i.e., Forest Dynamics Hypothesis 1-1): Landscape distribution of vegetation is largely predictable from state factors, with the residual variation caused by measurement error and legacies of past events.

Vegetation patterns provide insight into the relative importance of current processes (physical controls and internal feedbacks) and historical legacies in governing ecosystem properties and distribution. By legacies, we mean those past events that are not predictable from state factors but which significantly affect the current structure and functioning of ecosystems. These include fire, land clearing, tree harvest, flooding, insect outbreaks, and snow-breakage events. We will modify and improve existing vegetation maps of our two intensive research areas (BCEF and CPCRW) based on high-resolution aerial photography. We also have a 1 km-resolution vegetation map of Alaska based on AVHRR (Calef et al. Submitted). The new databases will be developed hierarchically with the greatest detail in vegetation composition at the finest scales. We will ground truth the maps using data from existing LTER monitoring plots and randomly located new plots near the road network. For each vegetation polygon, we will estimate state factors (slope, aspect, equivalent latitude, January and July temperature, and summer and winter precipitation, and parent material). Maps of recent fires (1950-present), a key boreal legacy, are available (Kasischke et al. 2002)(Fig. 20), allowing us to test for interactions between state factors and this legacy. We use stand-age reconstructions to develop a longer-term history of fire legacies in selected locations (Yarie 1981, Mann and Plug 1999, Fastie et al. 2002) (See LD1-1). The hypothesis will be tested at each scale by determining the degree of relationship between vegetation type and state factors. Although we cannot quantify legacies with certainty, we will examine sites that appear to be outliers to the relationship between state factors and vegetation type for clues as to the controls over their composition. Products of this research will be maps of our intensive study areas and of Alaska with GIS layers for vegetation, climate, soil type, topography, and human population density. Derived variables will include permafrost distribution and fire probability. These are essential tools for regional modeling and geographic extrapolation of our site-based research. We can also compare the new vegetation map of BCEF with maps developed 20 years previously of BCEF (Yarie and Viereck unpubl.) and the floodplain of the entire Tanana River (Ott et al. 2001). [Walker]

FD1-2: Resilience declines through succession because strong species interactions and feedbacks regulate species composition in mid-succession, whereas legacies are more likely to alter species composition in late successional communities.

This hypothesis of decreasing resilience through succession is a key assumption of resilience theory (Holling 1986, Holling and Gunderson 2002). From landscape patterns alone (FD1-1) we cannot distinguish the relative importance of direct physical controls over vegetation type that are related to slope, aspect, and climate from feedbacks that govern internal dynamics. We can use data from continued monitoring of the LTER permanent plots and long-term experiments to study species interactions and feedbacks because topographic position and parent material of these plots are constant through time. From our 15 years of data on species composition in permanent plots (see Research Design; Table 2), we will compare the timing and magnitude of change in species composition to the
timing of potential legacies (ice-breakage event, snowshoe hare peak). We hypothesize that these events have greatest impact on species composition in late succession. [Walker, Chapin] We will also measure species composition in experiments that manipulate interactive controls (low-level nitrogen- and carbon-addition plots, rain-out shelters, and moose/hare exclosures: FD2-2, BG2-3; Table 4). We expect these experimental manipulations to have stronger effects in mid- than in late succession. Tests of these hypotheses will give insights into controls over both successional dynamics and system resilience.

FD1-3: The resilience of the landscape mosaic is controlled by disturbance regime and seed availability.

There is a spectrum of post-fire successional trajectories in interior Alaska that occur along gradients in soil temperature and moisture (Fig. 3) and which vary along latitudinal gradients, with black spruce becoming less frequent close to treeline (Lloyd, unpub.). This landscape mosaic would be resilient to climate warming, if warming-induced changes in fire regime or seed availability have negligible effects on post-fire successional trajectory (Fig. 21). Alternatively, if fire size, severity, or frequency, or the availability of off-site seed sources alters post-fire succession, we expect that climatically induced changes in these factors would change the upland vegetation mosaic. We currently do not know the frequency with which the development of each post-fire stand repeats the successional trajectory of the stand that preceded it, although field observations suggest that this is common (Mann and Plug 1999) but not universal (Johnstone et al. 2003). Most tree establishment in interior Alaska and adjacent Canada occurs within 1-2 decades after fire (except for black spruce, in which some individuals continue to establish but are less likely to reach the canopy) (Johnson 1992, Fastie et al. 2002, Johnstone and chapin 2003, Yarie and Van Cleve In press).

We will use three complementary approaches to examine the resilience of post-fire successional trajectories. (1) We will document tree recruitment and mortality in the LTER permanent plots and in plots established in earlier post-fire stands by Viereck and Foote (Foote 1983, Johnstone et al. In press). [Walker, Chapin] (2) We will establish permanent plots in several road-accessible burns (aged 10-50 years) in interior Alaska to compare pre-fire tree composition (based on densities of fire-killed trees) and post-fire tree composition (seedlings, saplings, and resprouts) (Johnstone and Chapin 2003). If a successional trajectory is resilient, we expect that the same tree species will be present both before (as adults) and after fire (as seedlings and resprouts) (Fig. 21). Failure of a species to regenerate or arrival of a new tree species that was absent before the fire suggests a shift to a new successional trajectory. We will permanently mark the positions of these plots, so they can be revisited in the future (perhaps decadally) to document subsequent vegetation change. We will document potential controlling factors (slope, aspect, parent material, organic-matter depth, thaw depth, and soil moisture). We will select these plots to span a wide range of environments, fire severities, and distance to seed source [Chapin, Lloyd]. (3) We will use stand demographic data to parameterize a series of matrix population models describing black and white spruce population dynamics along a transect from the interior to arctic treeline. The transect will include the permanent plots described previously as well as plots established north of Coldfoot, Alaska, by Lloyd (unpub.). New plots will be established in the area between the Yukon River and Coldfoot in order to complete the transect. Models will be based on data from tree cores and direct demographic observations. The resilience of populations to varying disturbance regimes can be tested with matrix models by parameterizing ‘non-fire’ matrices (which describe population dynamics in the absence of disturbance) and ‘fire’ matrices (which describe population dynamics in the years following a fire (Wilson, unpublished thesis). The models allow estimation of population stability under different
disturbance regimes: resilient populations should be viable in a wide variety of disturbance regimes. [Lloyd]

These studies will collectively allow us to test two hypotheses about variation in the resilience of the landscape mosaic. First, within interior Alaska we hypothesize that the resilience of post-fire recruitment will be limited by the following factors: (1) fire return interval shorter than the age of first reproduction of black spruce (the only species that regenerates primarily from seeds produced within the burned area), (2) extremes of fire severity (either bare mineral soil or thick post-fire organic mat), and (3) stands distant from seed sources. Second, we hypothesize that resilience will change along latitudinal gradients in two ways. First, we expect that in the interior, succession to white spruce will be the most vulnerable to altered successional trajectory because of its dependence on seed inputs from living trees outside the burn. Seedling transplants will provide an experimental test of this hypothesis (FD3-1). Second, we expect that resilience of black spruce forests will decline with increasing latitude because of climatically determined limits on reproductive success (Black and Bliss 1980) (Wilson unpublished thesis). Results from these observations, when extrapolated regionally based on remote sensing (LD1-2), provide input to a landscape model of succession that projects changes in regional vegetation, based on scenarios of future climate, fire regime, and human activities (LD1-1). [Juday, Chapin]

FD1-4: Fluvial characteristics of the Tanana River control the resilience of the floodplain vegetation mosaic through effects on plant establishment and elimination of stands by erosion.

We will also examine resilience of successional trajectory in floodplains, where erosion is the disturbance that eliminates late successional stages and silt-bar formation provides opportunities for establishment of new stands. A recent satellite-derived map documents the stand types that were removed by erosion and the area of new silt bars formed for the Tanana River drainage (1980-2000) (Ott et al. 2001). We will continue measurements of seedling establishment and vegetation change in permanent LTER floodplain plots (FD1-2). We will assess the stability of the landscape mosaic, using a state-and-transition model of landscape change (LD1-4; Fig. 22) based on data for silt-bar formation, stand establishment, vegetation change, and stand loss by erosion. To explore the underlying mechanisms, we relate river flow regime (documented since 1920) to seedbed conditions for germination and establishment, survivorship in subsequent floods, and nutrient supply for growth through flooding and hyporheic flux. To document the latter effects, we measure nutrient inputs from flooding, litterfall, and hyporheic (i.e., subsurface groundwater) flow, using mass balance and stable-isotope tracers. [Kielland, Jones, Ruess]

FD1-5: The population size of small mammals responds primarily to physical fluctuations in environment, whereas the population size of large animals responds primarily to species interactions (the interaction of food availability and predation). In other words, mammalian species differ predictably in their vulnerability to climatic and biotic change.

The relative importance of biotic and abiotic regulation of microtine population dynamics has been the subject of substantial research and controversy (Batzli 1992, Schweiger and Boutin 1995). At high northern latitudes in Europe, Fennoscandians conclude that biotic forces of predation regulate timing and amplitude of population cycles (Korpimäki et al. 2002). However, they argue that in North America, where microtine communities are dominated by species of Clethrionomys, there will be greater resilience and smaller fluctuations, and consequently abiotic factors may have the opportunity to exert influence. Because we cannot directly manipulate environmental fluctuations at large scales, we will use quasi-experimental designs (Cook and Campbell 1979) in which we will concurrently measure climatic factors (Rexstad and Kielland In press) at LTER instrumented sites along with density of small
mammals. This will be conducted in replicated floodplain and upland sites. Based on our past records, we expect differences between upland and lowland sites in temperature (particularly in winter) and snow depth. Differences in these environmental features among years and among sites will be used to assess our predicted linkage between environmental factors and small mammal population performance.

A population peak in snowshoe hares, an intermediate-sized herbivore, is projected to occur in 2008. Radiotelemetry will be used to track fates of snowshoe hares and measure predation rates. Concurrently, offtake rates will be merged with a rudimentary bioenergetics model to assess possible magnitude of nutritional stress on hares. Demonstrating the interactions of top-down vs. bottom-up regulation in snowshoe hare population dynamics is challenging (Stenseth et al. 1997, Sinclair et al. 2000). However, we intend to determine whether biotic factors (incorporating both top-down and bottom-up processes) are important relative to abiotic influences in affecting the resilience of herbivores in boreal ecosystems. Resource agency data (e.g., Alaska Dept. of Fish and Game: ADF&G) will afford the opportunity to evaluate the response of moose dynamics to historical changes in food availability and levels of predation as altered by predator-control regimes instituted at various times in Alaska (NRC 1997) in a retrospective analysis. [Rexstad, Kielland]

**Hypothesis 2: Changes in interactive controls trigger changes in ecosystem structure and function.**

We test this hypothesis by examining the response of forest dynamics to naturally occurring and manipulated changes in interactive controls: functional types of organisms (FD2-1, FD3-1, BG3-3) and climate/soil resources (FD2-2 and LD2-3) (Fig. 16).

*FD2-1: Early successional vegetation types are vulnerable to invasion by exotic species because (1) there is less biotic control over establishment in early succession, and (2), once establishment occurs, early successional stands are strongly driven by feedbacks that can be modified by invaders, so invaders have a potentially strong effect on ecosystem function.*

This research tests the hypothesis that ecosystem resilience is minimal immediately following disturbance (Holling and Gunderson 2002). Alaskan ecosystems have, until recently, been remarkably resistant to species invasions (Billings 1973). Recently, however, two invasive genera (*Taraxacum* and *Rhinanthus*) have been found in the BNZ LTER site, and larger-scale invasions by an N-fixing species (*Melilotus*) have occurred in the floodplains of southcentral and southeast Alaska (Shephard pers. comm.). *Melilotus* was intentionally sown along roadsides in Alaska by the Dept. of Transportation and has begun colonizing river floodplains where roads cross rivers. About 20 exotic species appear to be expanding their ranges in human disturbances in interior Alaska, but there has been no careful study of their potential establishment in natural ecosystems. This hypothesis is difficult to test, because establishment of exotics is still a rare event in interior Alaska. We visualize two approaches to the problem: (1) In our permanent plots, which represent all successional stages, we will document any establishment of exotics that occurs. (2) We will survey those locations in interior Alaska where we expect exotics to be most likely to colonize non-anthropogenic sites. These include places where roads or other human disturbances are adjacent to natural disturbances and places where exotic species are growing adjacent to natural stands of vegetation (e.g., roadsides or fields). We will collaborate with the State of Alaska in its effort to develop a spatial database of the movement of invasive species in Alaska. This combination of approaches enables us to study the process of species invasion when the process is just beginning. Once we know the geographic pattern and ecological controls over establishment of exotics, we can use our GIS database of vegetation and ecological factors to develop simple models of the spread of exotics, based on alternative projections of future climate, human disturbance regime, and control strategies. [Wurtz] [See also FD3-1 and BG2-2 for other tests of species effects.]
FD2-2: **Intensification of drought stress associated with warming reduces the resilience of south-facing uplands to climatic warming.**

Growth of white spruce correlates negatively with summer temperature because of its sensitivity to drought stress (Barber et al. 2000) (Fig. 2). Over the next phase of LTER research we will document the climate sensitivity of all other major tree species (black spruce, birch, aspen, larch) and determine how landscape position influences this sensitivity (upland vs. lowland black and white spruce; slope and aspect effects on all trees). Using these climate-growth relationships and the GIS database on vegetation distribution pattern and microclimate (FD1-1), we can describe regional patterns of climate sensitivity of forest growth and develop projections of regional vulnerability of each tree species and of the landscape mosaic to scenarios of future climate. [Juday]

We will test this hypothesis experimentally with our long-term rainout shelters, which eliminate summer rainfall, combined with snow-removal treatments (to be initiated in 2004) to eliminate inputs from snowmelt (Table 4) The rainout experiments have shown surprisingly little growth response of white spruce to elimination of summer rainfall (Yarie and Van Cleve 1996), and soil moisture measurements suggest that snowmelt may satisfy tree water requirements. Samples of plant water will be analyzed for $^{18}$O to determine whether the water comes primarily from winter or summer precipitation. We also alter soil N supply (both increases through low-level N fertilizer additions and reductions through sawdust addition; Table 4) to assess the relative importance of water and nutrients as limiting resources (FD1-2). [Yarie]

**Hypothesis 3: Changes in key plant and animal taxa govern the relative frequency of alternative states.** We test this by manipulating tree taxa that colonize after disturbance (FD3-1, BG2-2) and documenting food web structure and effects of predator control programs (FD3-2).

FD3-1: **Changes in post-disturbance tree recruitment alter successional trajectories of species composition and ecosystem processes.**

Research described above (FD1-4) will determine whether successional trajectories are changing in interior Alaska. Here we will test the consequences of these changes by altering experimentally the species composition of tree seedlings that establish after disturbance. In each of two recent burns (one wet, one dry), we will establish plots planted with seedlings of each major native tree species (black and white spruce, alder, aspen, birch, poplar, larch) and two exotic species that have been used extensively in forestry trials (lodgepole pine and Siberian Larch). Seedlings of each species will be grown in the greenhouse for 6 months, then planted out at 1 m spacing in 10 x 10 m plots (3 replicate plots per tree species per site). Seedling success, survival, and growth will be monitored annually for 6 years, then less frequently. Organic matter depth and soil moisture will be used as covariates to explain patterns of seedling success. Seedlings that colonize naturally will be weeded from all except the control (unplanted) plots. We intend to maintain these plots indefinitely, so we can follow the ecosystem consequences of alternative successional trajectories in terms of species composition, herbivory, and biogeochemistry. In addition, we will continue monitoring floodplain plots in which alder and white spruce were planted and maintained (or excluded) for 15 years [Chapin].

FD3-2: **Changes in predation pressure associated with natural population fluctuations or predator control cascade down food webs.**

In previous LTER research, we demonstrated substantial species and geographic variation in stable isotope signatures of soils, water, vegetation, and animals (small mammals, ungulates, and fur bearers) (Kielland et al. 1998, Kielland and Bryant 1998). In the research described here we will collaborate with ADF&G to examine predator-prey relationships across
Fig. 20. Map of large fires that have occurred in interior Alaska since 1950.

Fig. 21. Triggers for change in successional trajectory (Johnstone 2003). Each successional trajectory tends to repeat itself but unusual events can trigger a shift in successional trajectory.

Fig. 22. State and transition model of successional dynamics driven by interactions of herbivory with geomorphic processes (accretion and erosion) and vegetation processes (colonization and succession).
interior Alaska [Kielland]. We will use $^{13}$C and $^{15}$N to document geographic and temporal variation in species-specific isotopic signatures, as we have done previously for moose (Kielland and Finstad 1998, Kielland 2001b). This will be used in combination with earlier diet studies to construct food web relationships (Peterson and Fry 1987) and to document temporal and geographic variation in these food webs. Initial data will come from archived samples of fur bearers over the past 10+ years. Samples will also be analyzed from populations of microtines and snowshoe hares that are currently being monitored by the LTER (FD1-4) and by ADF&G and from populations where wolf populations have been substantially reduced in predator controls programs.

**Theme 2: Biogeochemistry**

Our research in this theme explores the biogeochemical mechanisms and consequences of Alaska’s changing boreal forest (Fig. 23).

**Hypothesis 1: Changes to factors influencing carbon and nutrient cycling determine the rate of transition between successional states.** With this hypothesis, we examine successional changes in microbial (BG1-1), plant (BG1-2, BG1-3), and animal (BG1-4) controls over biogeochemical processes.

*BG1-1 (i.e. Biogeochemistry hypothesis 1-1): Increased specialization of fungi through succession impacts the rate and pathways of N and P uptake by host plants through increased diversity of exoenzymes synthesized.*

In collaboration with a recently funded fungal genomics project, we will document successional changes in fungal composition and their ecological consequences, using molecular fingerprinting techniques. This will enable us to test several predictions that have biogeochemical implications: (1) Fungi with significant proteolytic capabilities (“protein fungi”) will comprise a larger proportion of the fungal community than in temperate sites. (2) Ectomycorrhizal fungi will always dominate fungal biomass, but the ECM/saprophyte biomass ratio will decline in late succession. (3) Fungal diversity enhances enzymatic diversity, so both fungal diversity and substrate specialization will increase through succession. (4) Increased substrate specialization will be reflected by increased activity of fungal protease and acid phosphatase through succession. (5) Successional changes in fungal composition and diversity influence the growth, lifespan and decomposition of fine roots. If these hypothesized trends are confirmed, they would show increased connectedness through succession, as hypothesized by resilience theory (Holling and Gunderson 2002).

We will extract community DNAs from soil using the MoBio UltraClean Soil kit, then amplify the ribosomal ITS region, which is diagnostic of fungi at the species-level, using fungal-specific primers (Gardes and Bruns 1993). The diverse ITS amplicons will be separated using the new T-RFLP method (Dickie et al. 2002). Band sizes on the T-RFLP gels can be predicted from the sequences in our massive soil clone library and herbarium databases, derived from the funded genomics project. Hence, the majority of taxa will be identified and can be categorized as saprophytic, parasitic or mycorrhizal. Primers for RT-PCR will be designed based on conserved motifs in the extracellular alkaline proteases and acid phosphatases from the genome sequences of known arbuscular mycorrhizal, ectomycorrhizal, and saprophytic fungi. These studies will be among the first to characterize the relative abundances and gene expression of saprophytic and ectomycorrhizal fungi and to relate them to biogeochemical processes. [Taylor, Ruess, Kielland].

*BG1-2: Proportional allocation to fine root production declines with increasing total NPP both within and among forest types.*
Although we have considerable understanding of the controls over aboveground NPP (ANPP) (Yarie 1997, Yarie and Van Cleve In press), belowground NPP (BNPP) (Ruess et al. 1996, 2003, In press), and non-vascular NPP (NVNPP) (Ruess et al. 2003) (Fig. 6), we have never integrated these studies into a common conceptual framework, as we propose to do here. Annual low-level additions of nitrogen (doubling annual N cycling through vegetation) clearly demonstrate that aboveground tree production is N-limited and can be modeled based on a nitrogen-productivity relationship (Yarie and Van Cleve 1996, Yarie 1997). However, if root allocation increases with increasing nitrogen limitation, as expected from allocation theory (Garnier 1991), the relationship for total NPP may be quite different than for ANPP. We will focus initially on black spruce, which exhibits a near order-of-magnitude variation in ANPP in interior Alaska. We will expand our black spruce minirhizotron studies (measuring root production, longevity and decomposition) currently focusing on low-productivity floodplain stands to include 3 additional upland sites at mid to upper levels of ANPP. Aboveground N productivity equations (Yarie 1997) will be developed from site-specific allometric equations to evaluate the utility of foliar N as a surrogate for ANPP. In addition N-productivity relationships will be developed that include the belowground component and total NPP (trees, shrubs and moss) across this production gradient. Verification of the N-productivity relationships will entail establishing low-level N addition (100 kg N ha\(^{-1}\) yr\(^{-1}\)) experiments in black spruce. [Yarie, Mack, Ruess]

We have documented % cover of all species in our permanent plots. We will develop regression relationships between %cover and ANPP for major understory species to extend our previous work (Yarie and Mead 1988). [Yarie, Chapin]. We will extend ongoing work on the productivity of mosses and lichens to incorporate nonvascular plants into our ecosystem-scale estimates of NPP [Sveinbjornsson, Mack].

**BG1-3: Root respiration and root-derived heterotrophic respiration account for an increasing proportion of soil respiration as NPP declines because of increased root allocation and more rapid tissue turnover and decomposition of below- than aboveground tissues in unproductive stands.**

Estimates of root respiratory contributions to total soil CO\(_2\) efflux agree well between soil trenching methods and more direct estimates (minirhizotrons combined with root and soil respiration measures) (Ruess et al. 2003, Vogel et al. Submitted). However, these estimates are greater than those derived from \(^{14}\)CO\(_2\) (Schuur, unpublished), and all methods have not been compared at the same sites. Across the expanded set of black spruce sites (BG1-2), we will estimate total belowground C allocation using litterfall and soil respiration (C balance method), minirhizotrons (intensive sites only), soil trenching experiments (Vogel et al. Submitted), and \(^{14}\)CO\(_2\) studies. Finally, we will initiate a pilot study using whole-tree trace labeling with \(^{14}\)CO\(_2\) (followed by sampling, fractionation and AMS analysis) to determine the fate of dead fine root C. Together these experiments and measurements will enable us to document ratios of aboveground to belowground NPP, tissue turnover above and belowground, and heterotrophic respiration, as a basis for regionalization and extrapolation. [Ruess, Mack, Schuur, Yarie]

In addition to intensive studies in black spruce, we will continue annual measurements of aboveground litterfall in upland and floodplain successional stages (continuing our 15-year record in permanent LTER plots) and in mature forest types in the Fairbanks region (continuing a 35-year record maintained by the Forest Soils Lab). Soil carbon and nitrogen stocks were estimated at the beginning of these studies. We will resample these plots to assess long-term changes in carbon storage. This provides us with information on the controls by climate, vegetation type, and successional stage on litter inputs and their relationship to carbon storage. We will be able to combine this information with the 10-year
litterbag study that was recently completed across all the LTER sites and the log decomposition study that will start its tenth year in 2004. [Valentine, Yarie]

**BG1-4: Vertebrate herbivory has strong effects on biogeochemical processes throughout succession.**

Early in succession, herbivores control biogeochemistry through their direct effects of nutrient return and indirect effects on alder dominance (Kielland and Bryant 1998). During mid-succession, herbivore effects on biogeochemistry are mediated through control over vegetation composition and structure – both of which have short-term (soil water and nutrient balance) and long-term impacts on stand development and response to disturbance (Fig. 4). Late in succession (white to black spruce), herbivore effects are indirect, and primarily on the physical (thermal) environment through changes in canopy shading. We will expand our long-term vertebrate exclosure study by adding a permanent exclosure (15 X 15 m) to each mid- and late-successional site (n=3) in both the floodplain and upland forests within BCEF. These plots will be incorporated into our long-term sampling of soil climate, vegetation growth and litterfall. [Kielland, Ruess]

**Hypothesis 2: Critical biogeochemical processes influential in ecosystem function are vulnerable to the interaction between disturbance and climatic change.** We test this hypothesis by examining both direct (BG2-1, BG2-3) and vegetation-mediated effects (BG2-2).

**BG2-1: The carbon balance of boreal forest soils is highly sensitive to disturbance and climate fluctuations because a large proportion of the soil carbon is above the mineral soil (the surface organic mat), much of the soil organic matter is “thermally protected” rather than recalcitrant, and mineral soil C is not highly stabilized by soil minerals.**

We have collected samples to estimate the quantity of organic matter removed by recent fires in black spruce forests in wet and dry sites. We will assess the quality of these post-fire samples and unburned controls using long-term laboratory incubations under a factorial combination of cold (3°C) vs. warm (10°C) and wet vs. dry (120 and 50% of field capacity, respectively) conditions. Based on these measurements we can determine the relative proportions of labile and recalcitrant carbon before and after fire and whether this carbon is environmentally protected by cold and/or wet conditions. We can also determine whether the carbon in organic and mineral horizons differ in recalcitrance. [Valentine, Schuur]

We will continue ongoing measurements post-fire field measurements of soil respiration and its isotopic composition in the dry (FROSTFIRE) site and extend these to wetter sites in the Survey Line burn. Recent data from dry sites suggests that there is sometimes (but not always) an increase in heterotrophic respiration after fire (O’Neill et al. 2002, 2003), but there is not a large contribution from old (pre-1950) carbon to post fire respiration fluxes. This suggests that direct combustion of soil C by fire may play the largest role in determining the loss of old soil C stored over multiple fire cycles. By extending these measurements to the Survey Line site, we can determine whether these same conclusions apply to wet sites, which typically have the greatest soil carbon storage. [Valentine, Schuur]

**BG2-2: Because key species and functional groups play a dominant role in biogeochemical processes and ecosystem response to disturbance, boreal forest C and N balances are vulnerable to changes in their growth characteristics and abundance.**

Successional trends in biogeochemistry exhibit threshold changes at turning points that coincide with changes in dominant plant functional types (Fig. 5; FD1-2). We hypothesize that environmental changes that alter the abundance or activity of species responsible for successional turning points will
dramatically alter biogeochemistry. Here we focus on alder and mosses, which precipitate key turning points in both upland and floodplain succession, and on lodgepole pine, a conifer that could become important in the future.

With alder, we focus on the interaction among alder, *Frankia* (its nitrogen fixing symbiont), and its ectomycorrhizal associates. N\textsubscript{2}-fixation inputs appear to (a) decline through succession due to changes in the abundance of alder, nodulation rates and nitrogenase activity, (b) be greater in forests with *A. tenuifolia* compared with *A. crispa*, and (c) be strongly influenced by plant P status. It also appears that the genetic structure of the *Frankia* community differs between the 2 hosts and likely is influenced by ectomycorrhizal associations uniquely suited for P solubilization. What is less clear is how the *Frankia*/ectomycorrhizal associations respond following fire (where alder genets rapidly resprout), or as alder invades new environments. What is also poorly understood is the fate of fixed N, or the influence of fixed N in either accelerating or suppressing soil organic matter decomposition. We will expand work on the ecophysiology and genetics of the *Alnus, Frankia, ectomycorrhizae* triangle across successional stages and disturbance sites and set up experiments to study the effects of N inputs on SOM decomposition, i.e., a key mechanism linking nitrogen fixation to carbon cycling. [Ruess, Mack]

In the absence of N inputs from symbiotic fixation by alder, mosses regulate the rate at which N inputs become available to plants and soils because (1) atmospheric N is deposited on the moss canopy, (2) relatively high (1-2 kg ha\textsuperscript{-1} yr\textsuperscript{-1}) amounts of asymbiotic fixation occur in the moss canopy, and (3) mosses accumulate N in recalcitrant tissues that have a long turnover time. We will test the role of mosses as regulators of N cycling using a combination of observations and experiments. In the LTER permanent plots, we will use estimates of moss biomass and production (FD1-2) and nitrogen content to estimate the stock and annual flux of nitrogen through mosses in each successional stage and the sensitivity of moss composition to fire. We will use the long-term low-level N-fertilization plots to estimate the sensitivity of moss biomass, production, and N sequestration to N inputs in the major boreal forest types. In white spruce forests, nitrogen, water, and hardwood-litter addition experiments provide additional opportunities to explore the controls over moss production and N sequestration, and in black-spruce forests \textsuperscript{15}N addition experiments allow estimates of N turnover time in mosses and the long-term fate of moss-sequestered N. Finally existing moss-removal experiments (*Sphagnum* and *Hylocomium*) provide an opportunity to document impacts of mosses on microenvironment, N supply, and soil C stocks. [Mack, Sveinbjornsson]

Lodgepole pine has been rapidly migrating northwestward. It reached Whitehorse, Yukon Territories within the last 300 years, and is actively expanding its range by colonizing natural wildfires (Johnstone and Chapin 2003) and through cultivation as plantations in Alaska. Plantations near Fairbanks are now over 20 years old, consist of well-established needle carpets that contrast starkly with the forest floors under aspen and birch canopies of similar ages. We will compare soil C and N stocks, N mineralization, soil respiration, soil properties (e.g., pH, CEC), and fungal community composition between lodgepole pine plantations and similarly aged postfire hardwood stands. Based on these initial surveys, we will develop more explicit hypotheses about the mechanisms by which lodgepole pine alters biogeochemistry and develop an appropriate measurement program. We will also reconstruct interannual variation in tree growth from the tree ring record in this stand and compare it with published records of the climate sensitivity of lodgepole ringwidth in naturally established stands. [Valentine, Taylor, Juday]

BG2-3: *Climate warming will cause shoulder seasons to exert primary controls over C and N mineralization in boreal forests.*
Growing season shoulders (i.e., the snow-covered periods with biologically active soils in fall and spring) are critical periods for biogeochemical processes because (1) their combined length exceeds growing season length, and (2) production and decomposition are uncoupled during a period favorable to soil microorganisms. Climate change will most likely extend the length of these shoulder seasons and invoke strong effects on C and N cycling during these periods. We find that microbial activity is substantial down to –3°C and is sensitive to freeze-thaw events (Schimel and Clein 1996). Consequently, half of the annual N mineralization occurs between September and January (Fig. 24), but we know almost nothing about the controls over mineralization process during the non-growing season.

We will use ongoing LTER monitoring of soil temperature profiles to document the annual pattern of soil temperature and soil moisture (including the unfrozen water content in winter) in our major LTER sites. With soil thermal models (LD2-1) we can estimate long-term trends in the length of the growing and shoulder seasons in interior Alaska and can estimate the volume and depth distribution of unfrozen water content, which we expect to be a critical control over winter microbial activity. We have already established that a large proportion of fine roots die and completely disappear sometime between September and June (Fig. 25). To characterize when this occurs, we will monitor fine root growth, survival and decomposition through the winter using minirhizotrons in black spruce stands. In addition, we will initiate a new long-term experiment examining the effects of snow cover on ecosystem function. Treatments mimicking early snow cover (early October using blue foam insulation covering the moss surface) and no snow cover (using plywood shelters to exclude snow; removing shelters and replacing snow in April) will be implemented in replicated black spruce stands (with 10 X 10 m plots) readily assessable during winter. The long-term constancy of these treatments will be juxtaposed to natural snowfall plots, the timing and depth of which is quite variable among years. Net N turnover (net DIN and amino acid production), C cycling (soil respiration, microbial biomass, filter paper + tongue depressor decay), and live fine root biomass will be measured throughout the fall, winter and spring. Fungal and bacterial communities and exoenzymes in soil will be sampled in summer, fall, winter and spring and characterized by T-RFLP, as described in BG1-1.

**Hypothesis 3: Biogeochemical cycles will respond most dramatically to climate warming following disturbance. The magnitude of the response will scale to the level of the disturbance, and the trajectory of recovery will depend upon the site physiographic factors controlling surface energy balance and the life history traits of organisms.**

**BG3-1: Climate warming and disturbance that initiate thermokarst lead to (1) release of soil organic matter and N from frozen soils, (2) significant landscape evolution, and (3) inputs of sediments, old soil carbon, and nutrients into aquatic ecosystems, causing a net loss of these materials from watersheds.**

Thermokarst topography forms as ice-rich permafrost thaws and the ground surface subsides, leading to high soil moisture in poorly drained areas and surface drying on slopes. Massive ice near the surface is the primary prerequisite for thermokarst. Almost any disturbance that disrupts the insulation by the organic mat can initiate thermokarst. Models of net radiation and permafrost distribution based on slope, aspect, and elevation provide an estimate of CPCRW locations where permafrost is no longer in equilibrium with climate (Fig. 10). Geophysical surveys (ground-penetrating radar) that document subsurface structure and material properties will provide information to validate and refine this model and to document the current status of permafrost distribution and depth within the watershed. These surveys will be repeated at least every 5 years. We have conducted high-resolution terrain survey transects in areas with high potential for thermokarst formation and ground surface subsidence. These transects will be repeated and long-term monitoring will be initiated at sites displaying permafrost degradation. We will initiate sedimentation studies and maintain existing streamwater chemistry and
discharge monitoring to document current and future transfers of materials from land to streams. These studies will yield critical information on the impacts of climate warming in areas dominated by permafrost. [Hinzman, Jones, Romanovsky]

Fig. 23. Overview of research on biogeochemistry. The linkages between external drivers, internal dynamics and the other themes (forest and landscape dynamics) are shown together with the hypotheses that will examine these linkages.

Fig. 24. The relative contribution of summer and winter to net N mineralization (from buried bags) in major floodplain ecosystems. The high rates in fall and early winter suggest that Nmin is controlled more by the pulse of autumn root and leaf litter inputs than by temperature.
Fig. 25. Short-lived fine roots decompose more rapidly than longer-lived larger roots. Roots that die in autumn largely decompose over winter, whereas roots that survive over winter decompose more slowly.

Fig. 26. N fluxes in CPCRW subcatchments. Inputs calculated from 10 years of data are from an NADP site at CPCRW. Output in stream flow for 3 years of intensive sampling (1986, 2001, and 2002).

Fig. 27. Nitrate and DON concentrations in streamwater along a latitudinal gradient. Concentrations are highest in zones of discontinuous permafrost in interior Alaska. Using total dissolved N (TDN):Cl as an index of N retention, watersheds in discontinuous permafrost appear to be losing N; whereas more northern latitudes are closer to steady state. Toolik data (Peterson et al. 1992) and BNZ data collected along a transect (Jones and Finlay unpubl.) were used to construct this relationship.
One of our most unexpected recent results is that nitrate losses from N-limited watersheds at CPCRW are four to five-fold greater than deposition inputs, a pattern never-before reported for undisturbed watersheds (Fig. 26, 27). A major focus of our proposed research is to explain this imbalance in watershed nitrogen cycles. With the advent of a warming climate, large stores of organic matter frozen in permafrost are beginning to thaw. We will study the impact of permafrost and disturbance (fire) on watershed nitrogen losses. To determine the source of N in stream export, we will continue our monitoring of stream water fluxes to evaluate interannual inter-watershed variations in N budgets. Within watersheds, the sources of N to stream flow will be evaluated by quantifying N fixation by alders and feathermoss, estimating the sources of N in stream flow using $^{15}$N of nitrate (the dominant form of DIN) in stream water relative to $^{15}$N signatures of atmospheric N, organic soil N (under and away from alders), and mineral soil N; soil water $^{15}$N end members will be sampled using lysimeters. Stable isotope approaches will be confirmed using conservative solute tracers (e.g., Ca$^{2+}$, Mg$^{2+}$) in hydrologic end-member mixing models to determine the sources of ground water feeding stream flow. In addition to N inputs, we will also quantify the role of denitrification to evaluation potential losses of N within watersheds. [Jones, Hinzman, Kielland, Ruess]

BG3-2: Contraction of lakes and wetlands accompanied by a declining water table reduces methane emissions and increases CO$_2$ loss, whereas increases in wetlands and lakes have the opposite effect, especially where sedge is introduced. Spatial and long-term significance of changes to ecosystems and their C budgets depends on permafrost and landscape constraints and on vulnerabilities to disturbance.

In this research we will experimentally increase, reduce, and leave untouched the water table depths of a lowland ecosystem to test the effect of changing water table on vegetation composition and CO$_2$ and methane fluxes. In winter we will install water-impermeable dikes and either pump or flood the treatment plots to manipulate water tables. Before and after treatments, we will measure CO$_2$ and CH$_4$ flux and DOC concentration, collect cores to characterize the quantity and quality of organic matter in each plot, and install sensors to monitor water table, net radiation, soil temperature (5, 10, and 20 cm), air temperature, and relative humidity. Vegetation and soils will be sampled annually to monitor changes in NPP, substrate quality, and isotopic shifts in solid, liquid and gaseous C phases. Empirical models for ecosystem CO$_2$ uptake (i.e., gross primary production, GPP), ecosystem CO$_2$ release (ecosystem respiration, ER), and net CH$_4$ exchange (NME) will be developed based on gas exchange and environmental measurements. The results of these studies will be extrapolated regionally based on remote sensing that documents recent changes in wetland area (LD3-1). [McGuire]

Theme 3: Landscape Dynamics

Our research on landscape dynamics integrates the processes described under forest dynamics and biogeochemistry and incorporates additional processes, such as disturbance, that link patches within a landscape in order to scale processes to larger temporal and spatial scales (Fig. 28).

Hypothesis 1: Landscape processes associated with disturbance increase the resilience of Alaska’s boreal forest. We test this hypothesis, using modeling and remote sensing, by examining fire effects on landscape heterogeneity (LD1-1), fire severity (LD1-2), and carbon balance (LD1-3) and effects of mammals on floodplain landscape structure (LD1-4). 

LD1-1 (i.e., landscape dynamics hypothesis 1-1): Fire enhances regional resilience by maintaining a mosaic of flammable and non-flammable vegetation. Climatic or human changes in fire regime will therefore likely alter the landscape mosaic.
Fire is the dominant disturbance agent in interior Alaska and contributes to the complex mosaic that characterizes interior Alaska. Our goal is to explore the consequences of landscape vegetation patterns for fire regime and the resilience of this vegetation mosaic. The Bureau of Land Management, Alaska Fire Service (AFS) maintains records of the perimeter, size, and discovery date of all large fires (Fig. 20) and a tabular database that records ignition source (human vs. lightning), extinguishment date, and suppression costs (where applicable). Other GIS and historical databases provide information on vegetation type (FD1-1) and climate. From these databases we will determine the probability of burning of different vegetation types in high-fire and low-fire years and in continental vs. maritime portions of interior Alaska. Fieldwork funded elsewhere (Rupp and Mann) is testing whether the probability of burning depends only on vegetation type or changes with stand age. Together this information will enable us to characterize the vegetation and age dependence of fire probability in interior Alaska. This information will be used to improve parameterization of a spatially explicit landscape model (ALFRESCO) that simulates fire spread and seed dispersal on the landscape to assess the interactions among vegetation, fire, and climate (Rupp et al. 2000, 2002). The model is driven by stochastic variation around a mean climate state, so multiple runs of the model allow estimation of the frequency distribution of potential outcomes of a given scenario of average climate and initial vegetation composition (Fig. 29). We will use the model to explore the influence of changes in (1) the size distribution and spatial arrangement of vegetation patches, (2) assumptions about age- and vegetation-dependent probabilities of burning, and (3) the type, duration, and number of potential successional trajectories that can occur after fire (FD1-3, FD3-1) on future fire regime. These sensitivity analyses allow tests of factors governing the resilience of the landscape mosaic. [Rupp]

LD1-2: Seasonality of fire combined with legacies from past fire events control fire severity, which in turn regulates the site thermal/moisture regime (LD2-2), soil carbon storage (LD1-3, BG2-1), and post-fire recruitment and succession (FD1-3, FD3-1).

Data collected over the past several years (Kasischke unpubl.) suggest that, in black spruce forests, the depth of the organic mat at the time of the fire combined with the timing and duration of the fire are more important than fire weather in determining fire severity (i.e., the extent of consumption of the soil organic mat; Fig. 30). We hypothesize that, in sites with permafrost, only after soils have thawed into mineral horizons can the surface organic mat dry sufficiently to be largely consumed by fire. This hypothesis suggests that the seasonality of fire and active layer depth strongly influence ecosystem properties that govern permafrost integrity, successional trajectory, and carbon storage, and therefore the resilience of the boreal forest. We will use satellite images to estimate spatial patterns of burn severity on road-accessible burns (Michalek et al. 2000) and test the validity of these satellite-derived estimates by field sampling (Kasischke et al. 2000a, Kasischke et al. 2000b). We will conduct field measures of depth of remaining organic soils in the different burn severity categories, and document the site conditions (mineral soil profile, and slope, aspect and elevation of site), and from fire records, determine the time of the fire during the growing season. Similar measures will be obtained from adjacent unburned stands to serve as controls. These data will be statistically analyzed to determine which factors have the greatest influence on surface fuel consumption. Finally, soil moisture and temperature measurements will be obtained as a function of burn severity and time after fire for use in understanding how fire severity influences talik and permafrost formation (LD2-2). [Kasischke, Verbyla]

LD1-3: The strength of the carbon sink in Alaska’s boreal forest is vulnerable to vegetation- and permafrost-induced changes in fire frequency and severity.
Carbon sequestration or emission from the boreal forest is sensitive to the frequency and severity of fires and the rate of successional changes in NPP and heterotrophic respiration, as these are integrated across the landscape mosaic (McGuire et al. In press) (Fig. 31). The Terrestrial Ecosystem Model (TEM), which incorporates the impact of permafrost and fire on carbon balance (Zhuang et al. 2001, 2002, McGuire et al. In press) currently simulates regional carbon balance of 1 x 1 km pixels for interior Alaska based on maps of historical climate, vegetation, and fire occurrence. Permafrost spatial distribution and its dynamics during the last millennium influence the fire conditions and especially the probability of a particular successional trajectory after the fire. Using permafrost temperature reanalysis (Romanovsky et al. 2002), we will establish the history of permafrost evolution for each major landscape type for the last millennium. These trajectories of permafrost change will take into account the effect of forest fire on permafrost dynamics (LD2-2). Using the same calibrated models for each landscape type and chosen scenarios of future climate change we will project permafrost dynamic in the 21st century. We will also use the information on fire probability (LD1-1), fire severity (LD1-2), post-fire successional trajectory (FD1-3), and successional changes in carbon balance (BG2-1) to project regional carbon storage from 2000-2100 based on assumptions of current climate, and continued climate warming. We will conduct these simulations with a coupled version of TEM and ALFRESCO, which has been used to evaluate retrospective changes in carbon storage of the Alaska region in the NSF-funded Western Arctic Linkage Experiment (WALE). We will test the sensitivity of future carbon balance to integrity of permafrost by comparing the above simulations with permafrost present and permafrost absent. 

LD1-4: Mammalian herbivores contribute to the resilience of the floodplain hardwood-conifer mosaic by accelerating the turnover of early successional stands (where establishment can occur) and increasing the landscape distribution of late-successional white spruce stands (which provide a conifer seed source).

Mammalian herbivores exert a strong influence on forest dynamics in interior Alaska. We will continue monitoring the impact of herbivore (hare and moose) exclosures (established in 1988 and in 2002) on forest dynamics and ecosystem processes (FD1-2, BG1-5; Fig. 4). In the research proposed here, we will use information collected on the relative abundance of early and late successional stands in areas with high vs. low moose density (Fig. 32) as input to a landscape model of riparian succession to explore the effects of moose on landscape dynamics (Butler 2003; Fig. 22). Our model simulates primary floodplain forest succession from initial colonization of bare silt bars to mature climax white spruce forest. The model will be modified to incorporate the primary life history stages of white spruce from seed production to seedling establishment, identifying the processes that control both the reproductive success and rate of transition from newly exposed silt bars to mature commercially valuable stands. We will use the fieldwork to document white spruce recruitment, growth, and seed production (FD1-3) to inform the model and the model to direct the fieldwork, in an iterative, adaptive fashion (Nicolson et al. 2002). The model will compare scenarios of high and low moose abundance, disturbance frequency (flooding, fire, and white-spruce harvest), and climate change to simulate the rate and frequency of development of commercially valuable white spruce stands. This modeling effort will be used to simulate the effects of future scenarios of these variables on the potential for commercial harvest of white spruce in the Tanana River Valley. 

Hypothesis 2: Changes in key landscape disturbances trigger changes in regional landscape structure and functioning. We use modeling and extensive observations to assess the potential impacts of changes in fire, thermokarst, and insect outbreaks.
**LD2-1:** Past changes in climate-vegetation-disturbance interactions triggered changes in landscape processes that caused threshold changes to new stable states.

We will synthesize information on the spatial pattern of Holocene vegetation changes that have occurred in Alaska and western Yukon (see past results) and use this information to parameterize ALFRESCO (LD1-1). We will model climate-vegetation-fire interactions at times of past vegetation transitions, using alternative scenarios of the role of fire in triggering these threshold changes in vegetation-fire interactions. The same permafrost reanalysis technique in LD1-3 will be used for defining Holocene permafrost evolution trajectories for the key landscape types. We propose to use paleorecords of vegetation, charcoal, and climate trends that have already been documented to develop historical model scenarios. This scenario planning approach (Peterson et al. 2003) to data-model comparisons of historical patterns is unique, and this methodology is currently being developed in a NSF sponsored project (Rupp and Brubaker). The key transitions we will focus on will be the white spruce-black spruce transition in the mid-Holocene and the recent white spruce-lodgepole pine transition in the Yukon Territories. [Rupp, Romanovsky]

**LD2-2:** Changes in fire regime are more important than climate warming in causing talik formation and loss of shallow permafrost.

Forest fires alter surface energy and water budget by drastically altering the surface albedo, roughness, infiltration rates, insulation effect of surface vegetation and organic layer, and moisture absorption capacity in organic soils. Although these processes change most radically immediately after fire, the resulting effects become part of a process of long-term (20-50 years) cumulative impacts associated with changes in thaw depth, drainage, and permafrost recovery (see past results). We will use a combination of long-term monitoring and simulation modeling to explore the consequences of changes in climate and disturbance regime for permafrost integrity. The simulation modeling activities will be based on permafrost temperature reanalysis technique (Romanovsky et al. 2002). For each major landscape type we will develop a calibrated model for undisturbed surface conditions. These models will be used then to investigate the effects of fire and post-fire vegetation change on permafrost evolution through their effects on thermal properties of snow, vegetation, and soils. We will continue monitoring surface and permafrost temperature and moisture in several arrays that document the influences of climate and vegetation at different spatial scales. These include (1) a topographic/vegetational gradient from poorly-drained muskeg to well-drained white spruce, (2) an elevational gradient from valley bottom to ridge top (200-900 m elevational range), (3) a latitudinal transect of boreholes from the Arctic Ocean to Gulkana (plus maritime sites on the Bering Sea coast), and (4) a new set of sites to be established in different-aged burns. At these sites we measure air temperature and vertical gradients in soil temperature and moisture from the soil surface into permafrost. At each site we will periodically measure snow depth and thaw depth above permafrost. Lateral profiles of permafrost extent, active layer thickness and total soil moisture content in the active layer will be developed using ground penetrating radar. These will enable us to document the distribution of massive ground ice from which we can predict the pattern of expected post-fire surface deformation. In areas with massive ground ice we will survey the area initially and at 5-year intervals to document the rate and patterns of thermokarst development. These sites will be used to follow the fate of permafrost, microenvironment, and successional changes in vegetation (FD1-2) and biogeochemistry (BG3-1). [Hinzman, Romanovsky]

**LD2-3:** Increases in summer temperature explain spatial and temporal patterns of change in insect outbreaks.
Temperature is a key regulator of insect dynamics in the Alaskan boreal forest. For example, outbreaks of the spear-marked black moth in birch, the large aspen tortrix on aspen, and the larch budmoth on tamarack occurred at 10-12 year intervals from the late 1960’s to 1980 in interior Alaska (Table 1). These outbreaks ceased during the warmer period of the 1980s to present. However, the first recorded outbreaks of the eastern spruce budworm and larch sawfly began in the 1990s, perhaps in response to warmer temperatures. Summer temperature has also been implicated in the recent spruce bark beetle outbreaks in southern Alaska (see past results). We will continue our 30-year record of monitoring of insect herbivores with potential to exhibit population outbreaks. This monitoring is coordinated with a U.S. Forest Service monitoring network that includes aerial surveys of major insect outbreaks such as spruce budworm. By comparing the locations of these infestations with surface temperatures derived from satellite data, we will test the hypothesis that these sites are warm relative to other spruce stands in the region. This analysis will complement analysis under the forest dynamics section comparing long-term population data with site climate data. [Werner, Verbyla]

Hypothesis 3: Changes in hydrology and human activities are causing widespread changes in boreal forest structure, function, and disturbance regime. We test this hypothesis using long-term spatial records of wetland extent and human impacts on fire regime.

LD3-1: Water bodies in Interior Alaska have contracted over the past 40 years as a result of permafrost degradation and subsurface drainage, with minor effects of earlier thaw, annual warming and evapotranspiration that have co-occurred. Although open water and wetlands occupy 10 to 20% of Alaska (Harden et al. In press), we have never included them in our LTER research, which has, until now, focused on forest dynamics. Analysis of aerial images shows that many of interior Alaska’s wetlands are experiencing a reduction of open water (Yoshikawa et al. 2003, Hinzman et al. In press-b) (Table 5). Losses of water bodies in interior Alaska over the past 30 years coincide with an increase in evapotranspiration rates (Oechel et al. 2000) and warming of permafrost (Romanovsky and Osterkamp 1997, Osterkamp and Romanovsky 1999). We will combine regional-scale studies of wetland change detection (this section) and explore their consequences for changes in carbon and methane flux (BG3-2). We will use aerial photography and spectral imagery to quantify the amount of change in the area of closed basin water bodies in several extensive areas of wetlands in interior Alaska. This study will document changes in the area of water bodies over the past 40 years. We will also use remote sensing and wetland classification to determine whether other aspects of wetlands (dominant vegetation, canopy characteristics, total wetland size or morphology) are changing in addition to water body size. We will obtain soil cores of these basins across moisture gradients, and use radiocarbon dating to construct chronosequences of change over the past 40 years. The causal links between permafrost, vegetation, and open water will be related to wetland function through these field efforts. We will use data on C fluxes (BG3-2), aerial measurements of wetland change (this section), and a regional model of carbon and methane dynamics (Zhuang et al. Submitted) to develop a regional understanding of how land-cover changes influence trajectories of regional carbon storage and methane emissions in Alaska. [McGuire, Verbyla]

LD3-2: Human activities reduce the resilience of boreal fire regime by increasing ignition frequency, reducing average fire size and total area burned, and introducing fire-prone species that amplify these effects. The long-term consequence of these effects depends on the edge-to-area ratio of landscape regions dominated by anthropogenic vs. natural fire regime.
Fig. 28. Overview of research on landscape dynamics. The linkages between external drivers, internal dynamics and the other themes (forest dynamics and biogeochemistry) are shown together with the hypotheses that will examine these linkages.

Fig. 29. The sensitivity of fire size distribution in interior Alaska simulated by ALFRESCO in response to potential climate change under a warmer drier scenario and under a warmer wetter scenario. The wetter scenario leads to more large fires because of fuel buildup (Turner et al 2003).
Fig. 30. A comparison of unburned and burned organic matter depths from three different fires near Delta, Alaska. The reduction in organic matter depth is inversely correlated with pre-burn depth (Kasischke unpubl.).

Fig. 31. Cumulative changes in carbon storage of Alaska since 1950 simulated by the Terrestrial Ecosystem Model for assumptions that fire frequency prior to 1950 was more frequent, not different, or less frequent in comparisons with observations since 1950 (McGuire et al. In press).

Fig. 32. Landscape composition of deciduous trees and shrubs along the Tanana River near Fairbanks (high moose density) and Manley (low moose density) (pie chart). Bar chart shows number of stems m\(^{-2}\) (Kielland unpubl.).
Fig. 33. Total number of fires per unit area from 1950-2000 for a heavily populated region (Fairbanks) and two sparsely populated regions (Yukon Basin and Galena) in interior Alaska (DeWilde 2003). Most fires are produced by lightning in sparsely populated regions, but human activities account for most fires and double the length of the fire season in populated areas.

Table 5. Reduction in open water

<table>
<thead>
<tr>
<th>Area</th>
<th>Percent change over 50 years</th>
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<tbody>
<tr>
<td>Innoko Flats</td>
<td>-33</td>
</tr>
<tr>
<td>Copper River Basin</td>
<td>-28</td>
</tr>
<tr>
<td>Minto Flats</td>
<td>-21</td>
</tr>
<tr>
<td>Yukon Flats</td>
<td>-18</td>
</tr>
<tr>
<td>Talkeetna</td>
<td>-19</td>
</tr>
<tr>
<td>Alma Lakes</td>
<td>-15</td>
</tr>
<tr>
<td>Stevens Village</td>
<td>-3</td>
</tr>
<tr>
<td>Forty Mile Flats</td>
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<tr>
<td>North Slope</td>
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Table 6. BNZ involvement in cross-site comparisons among LTER sites

<table>
<thead>
<tr>
<th>Project</th>
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<th>BNZ PI</th>
</tr>
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<tbody>
<tr>
<td>Climate network</td>
<td>Greenland</td>
<td>Hinzman</td>
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<tr>
<td>High-latitude transects</td>
<td>McGuire</td>
<td>McGuire</td>
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<tr>
<td>LIDET (litter decomposition)</td>
<td>Harmon</td>
<td>Yarie, Valentine</td>
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<tr>
<td>Log decomposition</td>
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<td>Yarie</td>
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<td>Productivity-diversity relationships</td>
<td>Waide</td>
<td>Juday</td>
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<td>Fine root dynamics</td>
<td>Pregitzer</td>
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<td>Disturbance dynamics</td>
<td>Turner</td>
<td>Chapin, Yarie</td>
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<td>Hydrologic processes</td>
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<td>Bryophyte production</td>
<td>Sveinbjornsson</td>
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<td>Climate variability and ecosystem response</td>
<td>Greenland</td>
<td>Juday</td>
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<td>Climate/extreme events (XE)</td>
<td>Goodin</td>
<td>Juday</td>
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<td>Controls over moss decomposition</td>
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<td>Sveinbjornsson, Mack</td>
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<td>$^{15}$N Plant-soil tracer experiment</td>
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<td>Paleolimnology of northern lakes</td>
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</table>
The natural fire regime of the boreal forest is highly resilient because any increase in fire regime reduces the proportion of flammable vegetation and reductions in fire increase the proportion of flammable vegetation (Chapin et al. 2003) (LD1-1). Human activities can destabilize this balance if fire suppression leads to fuel buildup (LD1-1), or land-cover change alters the flammability of the landscape for reasons unrelated to fire, for example by increasing the proportion of grasslands that are prone to spring fires or of flammable lodgepole pine plantations. Human ignitions can also dramatically increase fire number for reasons unrelated to vegetation or climate (Fig. 33). Although fire and subsequent fuel buildup should still create a stable negative feedback, it could be stabilized in a quite different ecosystem state, such as aspen parkland (with high fire frequency) or Sphagnum-peatland (with low fire frequency). In the research proposed here, we will document human impacts on fire regime in interior Alaska, comparing these impacts in places with high vs. low population density and in places with high vs. low vegetation flammability, using the fire statistics described in LD1-1. This LTER research will emphasize the role of human activities in modifying the interaction of human and ecological controls over fire regime. Other funded research explores the socioeconomic, cultural, and policy dimensions of human-fire interactions (Chapin, Rupp, McGuire, et al.). This research includes a modeling component (LD1-1) that aims to simulate human influences on landscape dynamics through both direct and indirect effects on the fire regime and vegetation. [Chapin, Rupp, McGuire, Verbyla]

Program Innovation, Integration, and Synthesis

Program Innovation

In this proposal we add several new components to our research program that enable us to address new processes and improve our capacity for temporal and spatial scaling. Through addition of new investigators, we are now able to address patterns and consequences of fungal diversity (Taylor), landscape modeling of human-fire-climate-vegetation interactions (Rupp), fire effects on N cycling (Mack), and $^{14}$C estimates long-term C accumulation and turnover (Schuur). In addition, for the first time we explicitly address human activities, as these affect fire regime, and the role of wetlands in regional processes. Our most important innovation is to move beyond steady-state perspectives on ecosystem dynamics to address ecosystem resilience and vulnerability, in the face of recent and projected environmental and biological change.

Program Integration

Our major programmatic thrust over the last six years has been to increase the level of integration of our LTER research, and we have used this proposal to take that integration to the next level, as described below and in the section on site management. The following features have been key to the integration of our research program:

Use of common sites and experiments by many investigators provides a consistent data set to address multiple questions and facilitates interaction among scientists. Most of the LTER investigators use the intensive sites at BCEF and/or CPCRW in their research.

Hierarchical research design requires that the program address scaling issues in a coherent manner, as we extend our research from plot-level studies to the 100x100 km region around Fairbanks to interior Alaska as a whole. The development of databases at these scales enables LTER investigators and other scientists to access a wide range of data that are essential for data interpretation, regional extrapolation, and projection into the future.

Modeling of key components enables us to incorporate our understanding developed at one scale and explore the logical consequences at other temporal and spatial scales. Our modeling program includes thermal models, biogeochemical models, population models, and landscape models. Although
we rely on certain individuals (McGuire, Rupp, Yarie, Romanovsky, Hinzman, Jones, Rexstad, and Lloyd) to lead these modeling efforts, all investigators have incorporated modeling as an integral component of their research. Over the past six years, modeling has moved from being a peripheral to a core feature of our research program.

**Synthesis**

**Within-site synthesis** has become a major emphasis in our research program (see Information Management section). Over the last two years, our synthesis efforts have focused on the BNZ synthesis volume, which we have just completed and which is summarized in Prior Results. The next phase of our synthesis will involve comparative analysis and modeling, using archived data sets that we are developing at plot, landscape, and regional scales. Each year we will take 2-3 themes and devote focused attention to synthesis. These themes include species diversity and composition, productivity, disturbance regime, climate feedbacks, successional dynamics, nitrogen cycling, watershed budgets, and ecosystem services. We will expect graduate students to take leadership roles in this synthesis as components of their thesis work so they become indoctrinated with the importance of synthesis as an integral part of research.

**Cross-site research and synthesis** will continue to be an important part of our research effort (Table 6). We will lead a synthesis on climate-disturbance interactions and intend to participate in other network syntheses, as they develop.
Section 3 Site Management

Leadership structure

NSF and the USDA Forest Service, through the Pacific Northwest Research Station, jointly fund the BNZ LTER project. The NSF and FS components of the LTER program are thoroughly integrated into a single program, so we describe the management as it actually functions, rather than distinguishing between the NSF and FS components. We have expanded our leadership team from two to four people (Chapin, McGuire, Ruess, Walker) because (1) the increasing complexity of the research program requires additional expertise, and (2) this ensures a continuity of trained leadership in the event of any future change in personnel. Scientific decisions in the BNZ LTER are made at five levels:

1. Chapin serves as the PI of the LTER research program and is ultimately responsible to NSF for the overall design and implementation of the research program.

2. In practice, the four-person leadership team makes decisions jointly about the design and implementation of the research program. Each of us has responsibility for overseeing specific aspects of the program: Chapin, site management; McGuire, data management and modeling; Walker, FS communication; Ruess LTER network synthesis.

3. The LTER executive committee (leadership team plus Verbyla, Hinzman, Yarie, and Valentine) provides feedback about major issues associated with program direction (e.g., conceptual framework and general design of this proposal). In practice, these meetings are open to all LTER personnel, and there is broad participation by the LTER community.

4. Two individuals are responsible for coordination and integration within each research theme: forest dynamics (Walker and Chapin), biogeochemistry (Ruess and Yarie), landscape dynamics (McGuire and Verbyla).

5. Each investigator is allocated a budget and is responsible for designing and implementing her/his portion of the research program (see Budget Justification).

Program integration and communication

All BNZ LTER PIs and graduate students meet annually at our research symposium to present and discuss results and to engage in planning. We broadly advertise to and encourage participation from State and Federal agency personnel throughout interior Alaska. We set a specific goal for each symposium (e.g., LTER interaction with management agencies; project synthesis [to integrate our synthesis volume efforts], research design for the renewal proposal). Presentations or posters by graduate students are a key part of each symposium. In addition, we will meet monthly to address practical issues and to plan and coordinate our within-site synthesis activities. Examples of synthesis themes include (1) temporal and spatial variation in NPP and (2) hierarchical scaling from plots to regions. A final level of communication and integration occurs through joint field work, which is often facilitated by the need to coordinate transportation for travel to field sites.

Budgeting and accountability

Each PI is responsible for her/his own budget and implementation of research. Every two years each investigator must submit a progress report that includes major findings, publications, datasets that are on line or being prepared, and a mini-proposal that describes research plans for the next two years. These reports and mini-proposals serve as a basis for evaluation and budget reallocation by the leadership team. If necessary, more frequent budget reallocations will be made at the time of the annual progress report to NSF, as we have done in the past. Project PIs also obtain separate project funding to complement their LTER work ($7.8/NSF LTER $; see budget justification).

In addition to budgets for each research project, we maintain separate budgets for core research,
data management, and general project costs. Core research includes monitoring of climate, hydrology, vegetation, and other essential long-term site measurements. General project costs include national travel, some infrastructure costs, and a disaster contingency fund (e.g., to replace data loggers after floods, boat motors that die, opportunities for aerial photography, etc.).

**Site security and site management**

The BNZ research program has two intensive research sites: The Bonanza Creek Experimental Forest (BCEF) is within the Tanana State Forest and is managed by the Boreal Ecology Research Unit (i.e., the FS component of the LTER) through a renewable 50-year lease to the FS (expiring in 2018). The Caribou-Poker Creek Research Watersheds (CPCRW) includes lands under the jurisdiction of the University of Alaska and the Alaska Division of Natural Resources. The LTER manages BCEF and CPCRW, with the Interagency Hydrology Committee, which represents agency interests in Alaskan hydrology, acting as an external advisory committee. We have close working relationships with both the Tanana State Forest and the Alaska Division of Natural Resources (see unsolicited letter of support).

The BNZ site manager (Jamie Hollingsworth) is responsible for managing LTER research in the two research sites, including permitting, transportation, and the planning and implementation of the core research program. Significant improvements in site management in the last funding cycle include automation and wireless radio communication with climate and microclimate stations, improved coordination of field work, improved boat communication and safety, and assessment of statistical power and required sample sizes for long-term vegetation measurements. These efforts have substantially improved the quality, continuity, efficiency, and safety of data collection, releasing time to undertake new activities.

**Engagement of new investigators and non-LTER scientists**

We added five new investigators (4 of them young faculty members) to our research team in this proposal. We have been modestly successful in increasing diversity at our site, going from one woman and no minorities 6 years ago to one minority and 5 women among the PIs in our current proposal. Our graduate students include two Native Americans and two Asians (11%) and 15 women (43%). Our major effort to enhance diversity is through recruitment of minority graduate students, particularly Alaska Natives. Minority recruitment has been a strong emphasis of the IGERT program in Resilience and Adaptation (see Outreach), and many of these students become involved in BNZ LTER research.

A key way in which we engage additional investigators in our LTER research is through our affiliate LTER investigator program (Table 7). The BNZ LTER affiliates are encouraged to participate in our annual symposium, have the same access to LTER data, field sites, and facilities as do LTER PIs, and are encouraged to archive their data in the LTER database. We attempt to provide transportation costs to the LTER symposium and assist with field logistics whenever possible. Many affiliates have written proposals with LTER investigators as a result of this affiliation and participated actively in the preparation of this proposal.
Table 7. BNZ LTER affiliate scientists and their principal research areas and primary contacts with LTER PIs. BNZ affiliate scientists are encouraged to participate fully in LTER activities (attend symposium, participate in monthly meetings, use and contribute to LTER database) and to receive logistic support to the extent possible, but they do not receive LTER funds to support their research.

<table>
<thead>
<tr>
<th>Research Area</th>
<th>Affiliate scientist</th>
<th>LTER collaboration</th>
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<tbody>
<tr>
<td><strong>Forest Dynamics</strong></td>
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<tr>
<td>Plant pathogens</td>
<td>Christa Mulder</td>
<td>Walker, Chapin</td>
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<tr>
<td>Forest growth and yield</td>
<td>Ed Packee</td>
<td>Valentine</td>
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<tr>
<td>Tree ring studies</td>
<td>Chris Fastie</td>
<td>Lloyd</td>
</tr>
<tr>
<td>Tree ring studies</td>
<td>Val Barber</td>
<td>Juday</td>
</tr>
<tr>
<td>Stand-age reconstructions</td>
<td>Dan Mann</td>
<td>Rupp</td>
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<tr>
<td>Successional trajectories</td>
<td>Jill Johnstone</td>
<td>Chapin, Lloyd</td>
</tr>
<tr>
<td>Plant species effects</td>
<td>Donie Bret-Harte</td>
<td>Mack, Chapin</td>
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<td><strong>Biogeochemistry</strong></td>
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<td>Soil carbon dynamics</td>
<td>Jennifer Harden</td>
<td>McGuire</td>
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<td>Soil carbon turnover</td>
<td>Jason Neff</td>
<td>Schuur, McGuire</td>
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<td>Eddy flux studies</td>
<td>Jim Randerson</td>
<td>Chapin</td>
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<tr>
<td>Stream biogeochemistry</td>
<td>Jacques Finlay</td>
<td>Jones</td>
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<td>Soils</td>
<td>ChienLu-Ping</td>
<td>Valentine</td>
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<td>Microbial ecology</td>
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<td>Chapin</td>
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<td><strong>Landscape Dynamics</strong></td>
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<td>Masami Fukuda</td>
<td>Hinzman, Chapin</td>
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<td>Fire behavior</td>
<td>Sam Sandberg</td>
<td>Chapin, Rupp</td>
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<td>Wetland dynamics</td>
<td>Merritt Turetsky</td>
<td>McGuire</td>
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<td>Climate transect</td>
<td>Ed Berg</td>
<td>McGuire, Chapin</td>
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<tr>
<td>Co-management</td>
<td>Gary Kofinas</td>
<td>Chapin</td>
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<td><strong>Outreach and Agency Interactions</strong></td>
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<td>State Division of Forestry</td>
<td>Chris Maisch</td>
<td>Wurtz</td>
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<td>Tanana Chief’s Conference</td>
<td>Bob Ott</td>
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<td>Randi Jandt</td>
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<td>Jim Kruse</td>
<td>Werner</td>
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<tr>
<td>Alaska Boreal Forest Council</td>
<td>Jan Dawe</td>
<td>Sparrow</td>
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Section 4  Information Management

Goals and objectives

The primary goal of data and information management at the Bonanza Creek LTER is to ensure the long-term archival of the program's datasets. Of primary concern are documentation, quality control, accessibility and security of datasets. Additionally, we wish to employ emerging technologies and data management techniques in order to provide a system that engenders trust, collaboration and efficient information exchange.

Data management system

The current BNZ data management system is housed on two Dell Poweredge 2500 servers. One system runs Windows 2000 Server, houses our main website, and stores data files and project metadata. The second, and newest, system is a Linux/MySQL server that stores our most frequently requested datasets in a client-server database environment. We are gradually transitioning from a system that focuses on text files as the primary means of data dissemination to a more robust client-server relational database system. In the future, our most valuable and frequently accessed datasets, including our core datasets, will be archived in the new relational database system. Most individual datasets, however, will continue to be most efficiently stored and served as text files. By strategically shifting high-volume datasets to a relational database we hope to improve the data quality, accessibility, and usability of the data.

Role of data manager

The primary role of the data manager is to provide the tools and system architecture to accommodate secure long-term archival of LTER datasets. In addition, the data manager provides expertise to investigators in the areas of data management, software selection and use, and keeps aware of new opportunities afforded the program by innovative software and hardware developments or new trends in data management techniques. The data manager also offers advice and expertise in data collection, storage and archival issues where needed as new studies are designed.

Ensuring researcher's participation in data archival

Compliance with our data archival policy is mandatory and supported by our executive committee. Additionally, data archival is an important aspect of our internal review and budget allocation process. Investigators who refuse to archive their data cannot receive continued LTER funding. Nonetheless, many data sets have not been archived, and a major thrust in the coming funding cycle will be to increase to proportion of data archived. In addition, we will link publications with data sets on the web site, so the data that give rise to a given publication can easily be identified and accessed and so use of the data can be properly acknowledged.

Participation in data archival efforts is encouraged by the lead principal investigators and facilitated as much as possible by the LTER data manager. Collaborative relationships evolve on their own when researchers see that data archival as beneficial to them. The reward is knowing their data is secure, accessible, backed up, and well-documented. In addition most researchers are gratified to see their projects and datasets online as the publicity draws attention to their research programs. The data management staff also tries to encourage archival of data by providing useful tools in return that organize and enhance the quality of data for the researchers.
Quality control

Dataset quality control is the responsibility of the submitting principal investigator. Researchers rely on various quality control methods including plotting, visual inspection, and programmatic range checking. The data manager assists in quality control efforts where advanced technical solutions are needed.

Data access

Datasets in the Bonanza Creek LTER databank are made available to other researchers in as timely a manner as possible. The primary means of metadata and data dissemination is the worldwide web. Commonly used datasets, and climate data in particular, are usually made available via our website within a month after its collection, and several of our major weather stations provide web-accessible data in real time. Other core datasets are generally made available as soon as annual field work is terminated and the data entered. The LTER executive committee and support staff encourage investigators to submit new project data within the time mandates required, usually two years. In general, datasets are made publicly available as soon as they are archived, but some datasets may require delayed or restricted access, particularly data from graduate student projects. In such cases the student is preparing for graduation and may not have had a chance to publish their data, but we need to engage them in data archival before they graduate, while their interest is high. Such datasets must be archived but withheld from the public for a period of time to allow the student to fully exploit their data before it is made public. We have not yet had a graduate student request to withhold data from the web.

The worldwide web is an efficient means of serving information about our program. Server logs indicate that our site receives approximately 1500 unique visitors a month with about 30,000 hits a month (Fig. 38). Total annual bandwidth exceeds 4Gb of information annually. The most popular modules include our internet map server, data catalog and personnel information. Much of our meteorological data is available in real time (e.g., http://www.uaf.edu/water/projects/cpcrw/metdata/c4/current.html).

Our intranet website (restricted to LTER personnel) has been used more extensively over the last two years. Approximately 60 people now log into our intranet to update the LTER database, provide news and information to the group as well as archive datasets. This is nearly a tenfold increase from two years ago.

Security

System security is of the utmost importance for a program dedicated to long term archival of information. Our strategy is a balance between informed use of software and hardware defenses to prevent unauthorized intrusion and routine backup of essential data in case the system is compromised.

Data resides on each investigator's computer until it is archived on the main server. Data on the server is backed up weekly to 8mm tape. Additionally, a copy of the entire website, database and data files is burned to compact disk and stored off-site. The server is located in a secure area in a locked room. The servers are protected from unauthorized intrusion by hardware and software firewalls, limited remote accessibility, minimal user accounts, and stringent complex password requirements.

Anticipated system enhancements

We pride ourselves on our data management system at Bonanza Creek LTER and are continually looking for ways to improve our data management system. The following section outlines future system expansions and new services that we are developing.
Expansion of internet map services and GIS capability. We recently expanded our website to employ an emerging technology: internet GIS. In spring of 2003 we launched an internet map server that displays spatial information about our datasets, projects, study sites, administrative boundaries, and ecological characteristics of interior Alaska. The response to this service was positively tremendous. Server access logs indicate that mapping services are the most popular module of our website and we feel that this is one area that distinctly warrants upgrading. At present our map service is an 'out of the box' software solution that provides basic functionality. We know that we are only utilizing the bare minimum of this technology at present and would like to invest more time and energy into developing customized applications that will deliver truly useful mapping benefits to researchers who may not know much about GIS and who may not be able to use the current software because it is overly complex. We are also investigating the possibility of deploying an Oracle geodatabase to power our internet map server. This system expansion would broadly increase our ability to integrate spatial and tabular data as well as expand data accessibility to our personnel.

Database upgrade. The majority of our LTER data is stored in a Microsoft Access personal database with most datasets archived as ascii text files. We have rapidly outgrown the capability of this arrangement and need to build a more robust, accessible system. To this end we have recently deployed a new Linux server running MySQL relational database software. In the next few years we will work on migrating our current database to this server as well as transferring the most frequently accessed datasets from text files to a relational database model.

Ecological Metadata Language. Ecological Metadata Language (EML) has the potential to revolutionize data synthesis and cross-site collaborations. We recognize the potential uses for EML and anticipate incorporating it into our data management system. Major obstacles include a constant pressing need for more immediate services and a distinct lack of training in XML and web services that would be required to truly employ EML in a meaningful way. At present our strategy is to gradually phase into using EML according to the proposed tiered-trajectory system presented at the 2003 All-Scientists Meeting in Seattle.

Fig. 34. Online data access from January 1995 through December 2003. Data from 1995 through 1999 are estimated from data access records from the Bonanza Creek LTER3 proposal. No information is available from 2000-2002. The 2003 data reflects the number of hits on the LTER website that resulted in the display of dataset metadata and/or data files.
Section 5  Outreach

K-12 Education

The Schoolyard LTER program has been one of the most successful components of BNZ outreach. We have teamed up with two similar science education programs, GLOBE (NASA and NSF) and Partners in Science, Global Change Education Using Western Science and Native Observations (NSF), to train science teachers in 38 Alaskan towns and villages. LTER funding enabled 6 Fairbanks elementary and high school teachers to be added to the program. These schools have initiated their own long-term ecological research projects and developed their own web sites. Sparrow, the SYLTER PI, and Verbyla, another BNZ PI, developed a phenology unit that involves K-12 students in ground validation measurements of remotely sensed data, a first such opportunity for many children in rural Alaskan communities. This module has been incorporated into the GLOBE Teacher’s Guide and is now used internationally. In the coming phase of LTER research we will expand efforts to integrate LTER research with programs in rural schools that integrate traditional ecological knowledge into the science curriculum as part of our involvement in the joint SYLTER-GLOBE program.

LTER PIs regularly work with local K-12 teachers, serve as judges in science fairs, and mentor high school students on science-fair projects. Several of these high school students have won top honors in statewide, national, and in the case of one student, an international competition. Two SLTER teachers received the British Petroleum Award for Excellence in Teaching and one SLTER teacher the Presidential Award for Excellence in Math and Science Teaching for secondary teachers.

University Education

University of Alaska faculty regularly use the BNZ research sites for field trips and laboratory exercises because of its proximity to campus. Undergraduates also participate in summer research as REU students or research assistants. An REU symposium at the end of each summer provides opportunities for students to present their results formally and to get feedback from faculty and other students.

At the graduate level, the Bonanza Creek LTER has been an important venue for training University of Alaska graduate students in ecology and more recently for interdisciplinary graduate students in Resilience and Adaptation, an NSF-sponsored IGERT graduate program that links ecological, economic, and cultural aspects of sustainability and resilience. There are currently about 30 graduate students conducting their research through the BNZ LTER program. We expect to maintain active undergraduate and graduate research programs at our LTER site. We also seek to involve more IGERT students in our research program as a way to link our ecological research to societal issues.

Outreach to Communities

We work closely with the Alaska Boreal Forest Council (ABFC), a non-profit group that seeks to develop consensus among scientists, resource managers, legislators, recreationists, commercial interests, and other stakeholders in the sustainable use of the boreal forest. The LTER program provides the scientific expertise for this citizen outreach program and relies on the ABFC for its expertise and energy in public outreach. This collaboration has enabled the LTER program to participate in public information programs, public round-table discussions, surveys of the use of forest products, and other outreach efforts to a much greater extent than if we were to try to organize it independently.

We collaborate with the Alaska Native Science Commission (ANSC) in their program to address the environmental and ecological concerns of Native Alaskans. We participate annually in a community meeting that ANSC organizes, with each year focusing on a different region of Alaska. We provide
information on the long-term ecological changes that we observe and we listen to and discuss with Native leaders their concerns about environmental changes that affect their subsistence and cultural activities.

Outreach to Agencies

We work closely with several state and federal agencies (Alaska Division of Forestry, Alaska Division of Natural Resources, Alaska Fire Service, ADF&G, Tanana Chiefs Conference (a Native resource management agency), National Park Service, etc.) through joint research programs, discussions of management issues, jointly organized seminars, training programs for agency staff, and participation on Citizens’ Advisory Committee for the Tanana Valley State Forest. The active role that these managers have played in our LTER synthesis is indicative of the close working relationship that we have developed with resource managers in Alaska.

Outreach to the General Public

Due to the growing national and international concern about climate warming, we are regularly interviewed by radio and television stations (NBC, CBS, ABC, public television and radio), newspapers (e.g., New York Times, local papers), journals (e.g., Science, Discovery Magazine, National Geographic), and film crews. For example, our experimental burn in 1999 was featured on a NOVA program about fire.

Ties to other Long-Term Research Programs

Our closest ties within the LTER network are with the Arctic LTER site at Toolik Lake. Walker, Chapin, Hinzman, McGuire, and Romanovsky have worked extensively at Toolik and maintain collaborations with ARC LTER researchers. We have worked with the ARC site to design our climate transect, and our research on different aged glacial surfaces near latitudinal treeline (Lloyd) closely parallels research at Toolik (Gough, S. Hobbie).

We have worked closely with the National Park Service to help them design their Long-Term Monitoring (LTEM) program in Alaska and have participated in one another’s research symposia. We also work closely with U.S. Fish and Wildlife Service research programs in the Arctic Wildlife Refuge and the Kenai National Wildlife Refuge, with ecological monitoring programs on military bases in interior Alaska, and with researchers engaged in ecological consulting.
Section 6  Literature Cited
[* indicates BNZ LTER publications]


