CLIMATE-DISTURBANCE INTERACTIONS
IN THE ALASKAN BOREAL FOREST

A Proposal to Renew
Interaction of Multiple Disturbances with Climate in Alaskan Boreal Forests

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of the
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Project summary

The Bonanza Creek Long-Term Ecological Research program focuses on improving our understanding of the long-term consequences of changing climate and disturbance regimes in the Alaskan boreal forest. Our overall objective is to document the major controls over forest dynamics, biogeochemistry, and disturbance and their interactions in the face of a changing climate. The forest dynamics theme addresses successional changes in population and community processes following disturbance, emphasizing the relative importance of historical legacies, stochastic processes, and species effects in determining successional trajectories and the sensitivity of these trajectories to climate. Changes in the carbon cycle during succession hinge on changes in forest dynamics and other element cycles, but also influence nutrient availability and microenvironment and therefore successional changes in forest dynamics. Regional and landscape controls over disturbance regime focuses on regional and landscape processes that are responsible for the timing, extent, and severity of disturbance. Our research design uses experiments and observations in intensive sites in three successional sequences (floodplains, south-aspect uplands, north-aspect uplands) to document the processes that drive successional change. We establish the regional context for these intensive studies by analysis of ecosystem processes in two large regions, one in a relatively uniform region in interior Alaska and a second along a climate gradient from the warmest to the coldest areas in Alaska. Synthesis of our research addresses three important ecological issues: Species effects on ecosystem and landscape processes explores how species characteristics and diversity influence biogeochemistry and disturbance regime. Spatio-temporal scaling provides the conceptual basis for linking process and pattern. Ecosystem sustainability explores how the positive and negative feedbacks that operate within ecosystems influence the sensitivity of ecosystems to perturbations such as changes in climate and disturbance regime.
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Bonanza Creek LTER site Project Personnel

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Fig. 1.1. The relationship of climate to white spruce productivity at four time scales. A. Mean annual temperature decreased from 1000 years BP until 1900. B. Since 1800, there has been a generally positive relationship between ring width in Alaskan white spruce and North American annual temperature. C. Ring width in Alaskan white spruce is generally greatest in years with cool moist summers. D. During the period of the BNZ LTER research, there has been a positive relationship between ring width and production per tree.
CLIMATE-DISTURBANCE INTERACTIONS IN THE ALASKAN BOREAL FOREST

Section 1 Results of prior support

The Bonanza Creek (BNZ) LTER program was initiated in 1987 to study succession in the Alaskan boreal forest. The successional paradigm that emerged from this research is based on Jenny's (Jenny 1941) state factor approach. The Central Hypothesis of our prior research was that "the pattern of succession is determined primarily by the initial soil physical and chemical environment of the site and by the life history traits of component species. The rate of successional change is determined by vegetation-caused changes in environment and ecosystem function." Our research has largely supported this hypothesis (Van Cleve et al. 1991, Yarie et al. 1998) but showed that successional pattern in the boreal forest is regionally variable (Mann et al. 1995, Mann and Plug 1999), reflecting stochastic variation in disturbance and recruitment.

1.1 Major Findings

Environment

Upland and floodplain forests that we studied in the BNZ LTER develop in fundamentally different geochemical environments. The acidic upland soils are low in nitrogen due to N depletion by repeated fires. In contrast, the floodplain soils, which form from glacial silt, are strongly alkaline, due to surface evaporation (Marion et al. 1993). These soils bind phosphorus and are inherently low in nitrogen, leading to strongly nutrient-limited plant growth in the early stages of succession. Disturbance regimes differ radically between upland and floodplain ecosystems, with upland landscape pattern controlled largely by fire (Kasischke et al. 1995a) and floodplains responding to fluvial processes (Yarie et al. 1998, Adams 1999).

Microclimate in the boreal forest differs dramatically between north- and south-aspect slopes, due to large differences in solar radiation and soil temperature, allowing us to study the impact of climate on ecosystem processes under conditions where other state factors are held relatively constant (Jenny 1941). Permafrost, which is generally present on north-facing slopes and valley bottoms (but absent on south-facing slopes) dramatically reduces rates of biogeochemical cycling, nutrient supply, and forest productivity (Van Cleve et al. 1983, Van Cleve et al. 1991). Permafrost temperatures were relatively stable from the 1950s to the mid-1970s, but have increased in response to the recent warming (Osterkamp and Romanovsky 1999). In ice-rich sites, melting of permafrost has caused widespread thermokarst (slumping of the ground surface) (Osterkamp et al. 1994), causing large changes in soil moisture and temperature.

Following a gradual cooling over the last 1,000 years, the Alaskan climate has warmed since about 1850, and more dramatically since the mid-1970s, due to changes in atmospheric circulation, perhaps superimposed on greenhouse warming. (Hammond and Yarie 1996, Mantha et al. 1997, Overpeck et al. 1997, Serreze et al. In press). Tree-ring analysis shows that this warming is unprecedented in the past 200 years (Juday et al. 1998) (Fig. 1.1). The average annual area burned has doubled in boreal North America in the last ten years, in parallel with the warming trend (Kasischke et al. 1999). Lake cores suggest that the fire return time in the 20th century is only half as long as the average for the last 1000 years. The increase in early successional deciduous vegetation caused by fire increases regional albedo and evapotranspiration and reduces sensible heat transfer to the atmosphere. This acts as a negative feedback to regional warming (Chapin et al. in press).

In summary, changes in the Earth's Climate System have led to pronounced warming in the Alaskan boreal forest, causing melting of permafrost, increased fire frequency, and fire-induced vegetation changes that may cause a negative feedback to regional warming. As
Fig. 1.2. Successional sequence on the floodplain of the Tanana River in BCEF. We recognize a series of twelve seres and six turning points in the floodplain successional sequence (A). Turning points represent critical points in ecosystem development where species exert particularly strong control over system physical properties. Changes in percent cover and soil temperatures associated with these turning points are shown in (B) and (C) respectively. Soil temperatures are expressed as degree-day sums, which represent the sum of degrees above 0°C over the growing season. Note that plant cover and soil temperature show an inverse relationship as both shading and moss cover increase, culminating in the development of a permanently frozen layer (permafrost).
discussed below, forest dynamics and biogeochemical cycling play a critical role in this interaction between the boreal forest and climate.

Forest Dynamics

The differences in environment and disturbance regime between upland and floodplain and between north- and south-facing slopes promote colonization by different plant species, leading to different successional trajectories (Van Cleve et al. 1991). [See detailed vegetation descriptions on the BNZ website.] Following plant colonization in this low-diversity biome, the successional change in dominant forest species results in dramatic threshold changes in the physical and chemical environment (Fig. 1.2). For example, alder invasion in early succession increases nitrogen availability and productivity (Van Cleve et al. 1971, Uliassi et al. In press, Uliassi and Ruess Submitted). The late-successional change from deciduous trees to spruce alters the physical structure of litter, allowing the establishment of mosses. These mosses insulate the soil and greatly reduce soil temperature, decomposition rate, and nitrogen supply (Flanagan and Van Cleve 1983, Van Cleve et al. 1991, Van Cleve et al. 1996). The switch to the moss-conifer-dominated ecosystem, dramatically increases flammability and probability of fire (Starfield and Chapin 1996). These turning points associated with changes in the dominant tree species are some of the most dramatic examples of species effects on ecosystem processes that have been reported and are likely to occur in many low-diversity ecosystems (Chapin et al. 1997).

Succession produces repeatable patterns in species diversity (Rees 1997, Waide et al. 1999), with hot spots of insect and bird diversity in early successional floodplain stands (Johnson unpubl.) and nonvascular diversity increasing in late successional spruce forests (Willsrud 1997). Early successional plants exhibit a broad spectrum of tannins that have species-specific effects on insect herbivores (Ayres et al. 1997). The resulting host specificity contributes to the high insect diversity in early succession. Climate and land use are the global-change drivers that will probably have the greatest impact on boreal diversity over the next century (Rees 1997, Chapin and Danell In press, Sala et al. In press).

Mammalian herbivores strongly influence the rate of successional change. Selective browsing by moose and hares on pioneer willows leads to the competitive release of mid-successional species such as alder and poplar (Kielland and Osborne 1998) and accelerates successional change (Kielland and Bryant 1998). The browsing-induced reduction in canopy density has cascading effects on nutrient cycling through changes in physical environment, litter chemistry, and the proportion of nutrients returned as feces (Kielland et al. 1998, Kielland and Bryant 1998). Moose account for a third of the aboveground nitrogen input to soils in the willow stage (Kielland and Bryant 1998), indicating a key role of herbivory in the biogeochemistry of early succession.

Coarse-resolution analysis of Holocene pollen cores indicates that regional expansion of white spruce ca 8500 yr BP and of black spruce 4500 yr BP coincided with increased effective moisture. This is consistent with LTER dendroecological data indicating strong moisture limitation to white spruce growth (Barber et al. 1998). The black spruce expansion was accompanied by increased charcoal, suggesting a vegetation-induced increase in fire frequency, despite the wetter climate (J. Clark, unpubl.). This surprising result indicates a pronounced effect of vegetation on fire regime.

In summary, topographic differences in physical environment and disturbance regime give rise to strikingly different suites of initial colonizers and successional trajectories between floodplains and north- and south-aspect uplands. The pattern of species change after colonization is controlled by strong species effects on the soil physical environment, biogeochemistry (see below), and disturbance regime and by herbivory. These strong species effects reflect the low functional diversity of trees in boreal forest and their interaction with understory mosses.

Production and Biogeochemistry

Tree ring-climate correlations, carbon isotope analyses, and experimental manipulation of water and nitrogen suggest that the productivity of upland white spruce stands is primarily limited by water and nitrogen, despite the cold climate (Yarie and Van Cleve 1996, Barber et al. 1998, Billings 1998). Allocation, however, is responsive to temperature. Alaskan interior forests
Table 1.1. Spatial data sets available to or developed by the BNZ LTER.

<table>
<thead>
<tr>
<th>Data Set</th>
<th>Grain Size</th>
<th>Areal Extent</th>
<th>Date</th>
</tr>
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<tr>
<td>AVHRR images</td>
<td>1.1 km at nadir</td>
<td>Statewide</td>
<td>Archived at UAF daily since 1994</td>
</tr>
<tr>
<td>Vegetation classification</td>
<td>1-km</td>
<td>Statewide</td>
<td>Derived from multi-temporal 1991 AVHRR data</td>
</tr>
<tr>
<td>Statewide hydrography, transportation, 1990</td>
<td>1:250,000</td>
<td>Statewide</td>
<td>Derived from USGS 1:250k map series</td>
</tr>
<tr>
<td>Population</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Color Infrared Aerial Photography</td>
<td>1:15,840</td>
<td>Statewide</td>
<td>1978-86</td>
</tr>
<tr>
<td>Elevation</td>
<td>25 meter</td>
<td>Statewide</td>
<td>Derived from USGS 1:63 360 contour maps</td>
</tr>
<tr>
<td>Lightning Strikes</td>
<td>+/- 2km</td>
<td>Interior Alaska</td>
<td>Alaska Fire Service Detector Network 1980s - present</td>
</tr>
<tr>
<td>Fire: Scar Polygons</td>
<td>Sketched on 1:63,360 maps</td>
<td>Statewide</td>
<td>Alaska Fire Service 1950s - present</td>
</tr>
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<td>SPOT HRVscene</td>
<td>10.20 meter</td>
<td>BNZ area</td>
<td>July 1990</td>
</tr>
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<td>Vegetation classification</td>
<td>25 meter</td>
<td>BNZ Area</td>
<td>Derived from 1991 Landsat TM data</td>
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<tr>
<td>Color Infrared Aerial Photography</td>
<td>1:15,840</td>
<td>BNZ Area</td>
<td>1994-95</td>
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<td>Color Infrared Aerial Photography</td>
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<td>1999</td>
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<td>Color Infrared Aerial Photography</td>
<td>1:60,000</td>
<td>BNZ Area</td>
<td>1986</td>
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Additionally, the following variables have been derived (or are in the process of being derived) for the state of Alaska at 1 km scale: AVHRR Bands 0,1,2, composite; onset of greenness; peak greenness; duration of greenness; maximum greenness; mean greenness; mean monthly precipitation; mean monthly temperature; monthly range of temperature; elevation; slope; aspect; hydrologic regions; soils; permafrost; ecoregions; physiographic divisions; mean annual precipitation; vegetation; insect kill areas, 1989-1995; burned areas, 1960-1991; geology; land status/ownership; maximum NDVI; NDVI composites by 1/2 months during the growing season.
have the highest allocation to root production of any forest yet reported. This high proportion of total ecosystem C allocated below ground contributes to large soil C stocks. Most soil respiration is derived from root rather than heterotrophic respiration (Ruess et al. 1996, Ruess et al. 1998). Approximately three times more N is cycled through fine roots than through aboveground litterfall. These studies indicate the critical role of the belowground environment in explaining patterns of production.

Successional changes in vegetation dramatically alter carbon and nutrient turnover. In the floodplain, for example, nitrogen fixers add nitrogen and organic matter (Van Cleve et al. 1971, Uliassi et al. In press, Uliassi and Ruess Submitted), which acidifies the soil and increases the availability of both N and P. When poplars dominate, their tannins cause a decline in N fixation, but provide sufficient labile C to enhance N mineralization (Clein and Schimel 1995, Schimel et al. 1996, Schimel et al. 1998) and N supply to vegetation (Yarie and Van Cleve 1996). As spruce replaces poplar, the increase in lignin content, C:N ratio, and lignin:N ratio and the moss-induced decline in soil temperature together reduce decomposition and N mineralization (Flanagan and Van Cleve 1983, Van Cleve et al. 1983, Van Cleve et al. 1996). These are among the best-documented examples of vegetation-driven changes in biogeochemistry.

Vertebrate herbivory also affects soil processes. The warm dry soils of heavily browsed early successional sites have higher rates of soil respiration and higher decomposition potentials than do browser-free exclosures (Kielland et al. 1997). The high decomposition rates in browsed areas reflects increased labile C and N concentrations in litter (Kielland et al. 1997) and increased root turnover (Kielland et al. 1997, Ruess et al. 1998). The combination of reduced fine root biomass (Rossow et al. 1997) and increased root turnover in browsed areas leads to a reduction in soil C content outside the exclosures.

The biogeochemistry of Alaskan boreal forests has important implications for trace-gas feedbacks to the atmosphere. Upland Alaskan forests are a sink for atmospheric methane. N addition inhibits CH₄ consumption at some sites but not others, due to site differences in CH₄ oxidizer populations rather than to differences in N cycling (Gulledge et al. 1997, Gulledge and Schimel 1998b, Gulledge and Schimel 1998a, Gulledge et al. 1998). This work is one of the strongest examples of ecosystem processes being controlled by the structure of the microbial community. Models based on LTER research suggest that interior Alaska is currently a net sink of CO₂ (McGuire and CCMLP Submitted, Yarie and Billings Submitted) but that interannual variation in climate and disturbance strongly affect the direction and magnitude of carbon exchange (McGuire and CCMLP Submitted).

In summary, the major state factors (climate, topography, parent material, biota, and time) (Jenny 1941) each exert strong effects on ecosystem processes in the boreal forest (Van Cleve et al. 1991, Van Cleve et al. 1996), leading to important interactions among microclimate, soil resources, functional types of organisms, and disturbance regime (Chapin et al. 1996c). The vegetation-driven changes in biogeochemistry are critically important in explaining patterns of successional change.

Hydrology and Aquatic Processes

Permafrost is a major "ecological adjective" modifying hydrology, thermal regimes, chemical fluxes from uplands to streams, and biotic processes in streams (Oswood 1997). Stream flow from permafrost-dominated watersheds has more dissolved organic C but less dissolved minerals than in permafrost-free watersheds (MacLean et al. 1997, MacLean et al. In press). Permafrost apparently acts as a partial barrier to percolation of water from organic soil horizons to underlying mineral soils and so generates rapid storm-flows rich in dissolved organic C but relatively impoverished in dissolved minerals (MacLean et al. In press). In-stream decomposition is influenced not only by water temperature and invertebrate community structure but also by the species composition and grazing history of the terrestrial leaf litter input (Irons et al. 1991). Macroinvertebrates account for an increasing proportion of in-stream decomposition (relative to microbes), as one moves northward along a latitudinal gradient (Irons et al. 1994). The recent warming and melting of permafrost has important implications for the coupling of land-water systems at high latitudes.
Fig. 1.3. Comparison between field-based (eddy covariance) estimates of carbon fluxes and simulated carbon fluxes by the high-latitude version of the Terrestrial Ecosystem Model (TEM). Fluxes are (a) gross primary production, (b) total ecosystem respiration, and (c) net ecosystem production at an old black spruce stand in the northern study area of the Boreal Ecosystem Atmosphere Study (BOREAS) (Clein et al. Submitted). TEM was parameterized with information from the Bonanza Creek Experimental Forest.
1.2 Regionalization

We have developed regional data sets of input parameters required for regional modeling. Maps of climate (Hammond and Yarie 1996, Mock et al. 1998, Fleming et al. In press) document the geographic pattern of warming from the 1960s to the 1980s (Table 1.1). Decadal maps of fires since 1950 (Kasischke In press) and of lightning strikes (Dissing and Verbyla in prep) suggest an increase annual area burned in the last decade (Kasischke et al. 1999), presumably due to warmer temperatures and lower fuel moisture. Bark beetles have eliminated spruce forests over broad areas of southern Alaska in association with recent warming but have not yet reached outbreak proportions in interior Alaskan forests (Holsten et al. 1995, McCullough et al. 1998, Malmström and Raffa In press). Our 20-year population record of major insect defoliators indicates high populations of several insect defoliators in BCEF within the past decade. A 200-yr chronology of river height developed from correlations of river height at LTER sites (1989 – present) and USGS gauging stations (1962 – present) and a 200-yr ring-width chronology for the floodplain (Yarie et al. 1998, Adams 1999) indicate large variation in flood frequency but no directional trend.

We have supported many studies to evaluate the utility of airborne and satellite remote sensing data for extrapolating our understanding of ecosystem processes from BNZ to broader spatial and temporal scales. These studies have developed the technology needed for vegetation mapping and biomass estimation (Rignot et al. 1994a, Rignot et al. 1994b, Way et al. 1994, Williams et al. 1994, Harrell et al. 1995), monitoring of effects of temperature change (Kwok et al. 1994, Rignot et al. 1994a), monitoring the effects of fire on soil moisture (French et al. 1996), estimating patterns of C release during fires (Kasischke et al. 1995b), and testing for non-biological artifacts such as switching among satellites and overpass time (Malmström et al. 1997). The results suggest, for example, that the temporal trends in NPP inferred from satellite data (Myneni et al. 1997) are over estimated (Malmström et al. 1997).

1.3 Synthesis and Modeling

Our modeling has used LTER data on ecosystem processes to develop and parameterize models as a basis for extrapolating results to the regional scale. For example, a carbon balance model parameterized from black spruce data in Alaska reproduces the seasonal and interannual variation in net ecosystem carbon exchange in the BOREAS old black spruce sites in Canada (Fig. 1.3) (Amthor et al. Submitted, Clein et al. Submitted, Potter et al. Submitted). We then apply these models at larger scales to estimate the current carbon budget of Alaska (McGuire and CCMLP Submitted, Yarie and Billings Submitted) and future scenarios of carbon storage at the circumpolar scale (McGuire et al. In press-b, Clein et al. Submitted). We have also used these models to explore the role of winter ecosystem processes of high-latitude ecosystems in seasonal aspects of the global carbon cycle (McGuire et al. In press-b). Sensitivity analyses with these models highlight the importance of: (1) root dynamics and labile soil carbon in C-budget models; (2) vegetation structure (specifically trees and moss) in soil thermal models; and (3) C-N interactions in predicting future forest productivity. Changes in vegetation caused by climatic warming could have profound regional effects on landscape processes, including fire spread, seed dispersal and feedbacks to climate. We document these changes through remote sensing and explore their consequences through landscape-scale modeling of fire-climate-vegetation interactions (Starfield and Chapin 1996, Chapin and Starfield 1997, Rupp et al. In press-a, Rupp et al. In press-b).

We have integrated our research into a larger context through participation in many LTER cross-site comparisons (Table 1.2) and through a synthesis of high-latitude ecosystem feedbacks to climate involving comparisons of ARC and BNZ LTER sites and the BOREAS sites in Canada (Chapin et al. In press). Together with HJA, we have contributed to an effort by the US Vice President and Russian Prime Minister to develop ILTER sites in Russia.
Table 1.2. BNZ involvement in cross-site comparisons of LTER sites.

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<td>Fine root dynamics</td>
<td>Pregitzer, Allen, Hendrick, Burton</td>
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<td>Mycorrhizae</td>
<td>Allen</td>
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1.4 Summary

Research at the BNZ LTER site has contributed substantively to understanding the relationship between “independent” state factors (Jenny 1941) and internal ecosystem dynamics (Chapin et al. 1996c) in causing successional change. We have shown that:
1. Species effects are strong in the boreal forest.
2. Successional changes in species composition are not a simple consequence of changes in competitive balance but involve species-driven changes in biogeochemistry and the physical environment.
3. Vertebrate herbivores are a powerful force driving successional change through their effects on plant competitive interactions and biogeochemistry.
4. Succession influences exchanges of CH₄, CO₂, water, and energy in ways that could feed back to climate.

Our research on succession raises important questions about the broader regional context in which succession occurs. Our research for the next phase of LTER addresses the question: How do changes in climate and disturbance regime alter the functioning of the Alaskan boreal forest?

1.5 LTER Publications (1994-1999)

Journal Articles
Beget, J. In press. Continuous late Quaternary paleoclimate proxy records from loess in Beringia. Quaternary Science Reviews.


Werner, R.A. 1995. Toxicity and repellency of 4-allylanisole and monoterpenes from white spruce and tamarack to the spruce beetle and eastern larch beetle (Coleoptera: Scolytidae). Environmental Entomology, 24: 151-158.


Books


Book Chapters and Conference Proceedings


Werner, R.A., and Illman, B.L. 1994. The role of stilbene-like compounds in host tree resistance of Sitka spruce to the spruce beetle, *Dendroctonus rufipennis*. In Behavior. population


Theses and Dissertations


Other Publications


Papers Submitted


1.6 Online Data and Usage

Data sets currently available online are listed in Table 1.3. We track usage primarily through download information, which does not separate out our own investigators from others (Figure 1.3). Total downloads have gone from about 100 in 1995 to approaching 3000 when we made this graph toward the end of 1999. This is due to a combination of both increased data availability and overall increased online usage.

Table 1.3. Data sets available online as of October 31, 1999.

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Figure 1.3. Online data accesses from January 1995 through October 1999. There has been about a 30-fold increase in data accesses over the past 5 year period. This is due to a combination of both increased data availability and overall increased online usage.
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Fig. 2.1. Hypothesized characteristics of boreal forest relative to other biomes. The boreal forest has a low diversity of dominant tree species, making ecosystem processes highly sensitive to changes in tree species composition. There are relatively few highly co-evolved interrelationships in the boreal forest, making species highly responsive to changes in the physical environment. The extremely cold dry environment of the boreal forest makes it highly sensitive to climatic change. The patchy nature of the boreal landscape makes it sensitive to landscape processes. The research theme in which each of these issues is addressed is indicated in each graph.
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Section 2  Proposed research

2.1  Note to Reviewers

There are two issues about this LTER that should be considered when reviewing this proposal. (1) This proposal is for 4 years of funding rather than the standard six. In 1998 we submitted a proposal for 6 years of funding. We were given 2 years of funding and asked to resubmit a better-integrated proposal in 2000. (2) This site receives co-funding from the U.S. Forest Service. This allows us to expand our studies beyond what would be possible with only NSF funds and gives us the latitude to explore relationships between long-term ecology and management that are of particular interest to the USFS. Because we manage these funds as a single project, our operating budget and number of investigators is larger than for many LTER sites.

2.2  Background

The boreal forest is the second most extensive terrestrial biome on earth (Whittaker 1975) and has many characteristics that set it apart from other ecosystems (Fig. 2.1). It has a cold dry climate, making it potentially sensitive to climatic change. It has few dominant tree species, so changes in these tree species have large ecosystem impacts. It is relatively undisturbed by current human activities. Productivity is low relative to other forests (Gower et al. 1997), but boreal forests provide habitat for fish, grazers, and birds, and are used by people for recreation, hunting, fishing, and timber. During the relatively brief (10,000 yr) history of the boreal forest in its current location, it has experienced radical changes in climate, vegetation, and fauna (Brubaker et al. 1983, Guthrie 1990, Muhs et al. In press). Warming during the last 25 years (Chapman and Walsh 1993, Keyser et al. In press, Serreze et al. In press) has been associated with warming and melting of permafrost (Osterkamp and Romanovsky 1999), changes in growth rates of dominant trees (Barber et al. 1998, Juday et al. 1999), increased area burned (Kasischke et al. 1999), insect outbreaks (Reynolds and Holsten 1994, Fleming and Volney 1995), and changes in vertebrate populations (Stephenson et al. In press). We do not yet know all the causal links among these changes, nor their implications for the functioning of the boreal forest and the people who inhabit this region. Research in the Bonanza Creek LTER focuses on documenting these changes, their causes and interactions, and their implications for regional sustainability (Chapin et al. 1996c, Chapin and Whitman 1998).

The structure and functioning of the boreal forest determines and is influenced by its disturbance regime (Stocks 1991, Van Cleve et al. 1991, Apps et al. 1993, Mann et al. 1995, Mann and Plug 1999). Fire, flooding, and insect outbreaks are important natural disturbances (Viereck 1973, Werner and Holsten 1983, Payette 1992, Kasischke et al. 1995a). Millions of hectares of the Alaskan Interior burn each decade. The extent and distribution of these disturbances are changing rapidly as climate warms, and fire control is extended near population centers (Stocks et al. 1996, Kasischke et al. 1999), as timber harvest expands to meet the fiber needs of a growing human population (Meliillo et al. 1996), and as insect outbreaks increase with climatic warming (Fleming and Volney 1995, Malmsröm and Raffa In press). In order to understand the current and future structure, diversity, and functioning of the boreal forest, we must understand the interactions between changes in climate and disturbance regime.

Our research focus is primarily local and regional, but has implications for the global system. The boreal forest contains 40% of the world's reactive soil carbon (McGuire et al. 1995). The current and future role of the boreal forest in the global carbon cycle is uncertain, however. High-latitude carbon storage responds sensitively to temperature and precipitation (Van Cleve et al. 1986, Oechel et al. 1993) so that recent trends (Chapman and Walsh 1993, Keyser et al. In press, Serreze et al. In press) and projected patterns (Kattenberg et al. 1996) of rapid warming at high latitudes could alter high-latitude carbon exchange (Oechel et al. 1993, Zimov et al. 1996, Goulden et al. 1998). Boreal forests could be part of the "missing sink" of CO$_2$, if they are accumulating carbon (Ciais et al. 1995, Myneni et al. 1997, Randerson et al. 1999) or a carbon
Table 2.1. The application of important ecological concepts to BNZ research. This table lists examples of important issues and the types of related questions that are addressed by the BNZ LTER research program.

**Theme 1: Forest dynamics**
1. The role of environmental variability in structuring communities (Chesson 1986): How do equilibrium and stochastic processes interact to control the functioning of the boreal forest in a directionally changing environment?
2. The role of species diversity in ecosystems (Tilman et al. 1996, Chapin et al. 1998): How do the number and identity of species influence the vulnerability of ecosystems to a changing environment?
3. Animal population cycles (Krebs et al. 1995): How do variations in herbivore abundance influence forest recruitment and succession?
4. Environmental thresholds for vegetation change (Davis 1981): How do changes in climate and disturbance influence community structure and dynamics?

**Theme 2: The changing boreal carbon cycle**
2. Interactions of biogeochemical cycles (Rastetter and Shaver 1992): To what extent does the use of organic nitrogen by plants and microbes short-circuit the mineralization process?
3. Role of disturbance in net ecosystem production (Schulze and Heimann 1999): Can we simulate the impacts of disturbance on biogeochemistry adequately to capture interannual variation in the boreal carbon cycle?

**Theme 3: Regional and landscape controls over disturbance regime**
1. Landscape effects on regional processes (Turner et al. 1995): How do landscape structure and grain influence the functioning of ecosystems?
2. Hierarchical scaling of processes (Allen and Starr 1982): How do processes occurring at multiple scales interact to determine the pattern measured at one particular scale?

**Synthesis Areas (See section 2.10)**
1. Species effects on ecosystem and landscape processes
2. Spatio-temporal scaling
3. Ecosystem sustainability
source if recent warming trends enhance fire frequency or decomposition more than they enhance plant production (Kasischke et al. 1995a, Kurz and Apps 1995, Zimov et al. 1999).

The boreal forest also influences climate through regional energy exchange and the hydrologic cycle. The northward movement of the arctic treeline could amplify the expected rapid climatic warming at high latitudes (Thomas and Rowntree 1992, Foley et al. 1994, Bonan et al. 1995). Alternatively, increased deforestation or a shift from predominance of conifer to deciduous forest resulting from logging or fire could cause regional cooling (Chapin et al. In press). The boreal forest accounts for 80% of the watershed area that drains into the Arctic Ocean. The quantity and salinity of water that moves from the Arctic Ocean to the North Atlantic influence deepwater formation and the strength of the thermohaline circulation that drives latitudinal heat transport by the earth's oceans. Changes in this circulation are implicated in past switches between glacial and interglacial periods. Thus, the boreal forest plays a critical but uncertain role in the future climate of the Earth.

2.3 **History of climate-disturbance-vegetation interactions in the boreal forest**

There is evidence for both stability and rapid change in boreal ecosystems at all time scales. At large temporal and spatial scales, the boreal forest has responded sensitively to climate, with changes from birch-shrub tundra to poplar woodland (9,000 to 12,000 yr BP) to white spruce forest (5,000-9,000 yr BP) to a landscape mosaic with abundant black spruce forests (4,000-6,000 yr BP) (Hu et al. 1993, Anderson and Brubaker 1994, Edwards and Barker 1994). At the end of the ice age 12,000 yr BP, the climate ameliorated rapidly and remained relatively warm until 5-9,000 yr BP, when Neoglacial cooling began (Mann and Hamilton 1995, Barber and Finney In press). Fire frequency increased dramatically with the arrival of black spruce, despite the trend toward a cooler wetter climate at that time, indicating strong vegetation effects on fire regime. During the last 1,000 years, the vegetation has remained remarkably stable, despite large changes in climate, including the medieval warm period, the Little Ice Age, and recent warming to temperatures that are the warmest in 400 years (Overpeck et al. 1997). The large waves of species immigration during the Holocene appear to have been driven by threshold climate changes. The apparent stability during the last millennium suggests that no new thresholds existed for new migrations. However, potential migrants, such as lodgepole pine, have already migrated the Alaskan border from the east and been planted in interior Alaska, so imminent future changes in forest dominants are plausible.

At the decade-to-century time scale there are both stochastic processes that generate landscape variability and processes that lead to repeatable cycles of disturbance and succession. Our LTER1 and LTER2 research documented relatively repeatable changes in species composition, environment, and ecosystem processes occurring at key "turning points" associated with change in the dominant tree species (Viereck et al. 1986, Van Cleve et al. 1991). Turning points occur in Alaskan forest succession because there are only 1 or 2 dominant tree species in any one stand, and each of these species exerts strikingly different effects on ecosystem processes (Hobbie 1992, Chapin et al. 1997). Consequently, successional changes in forest dominants translate into strong autogenic control over biogeochemical and population processes. However, many of the processes that generate these repeatable patterns are stochastic and regionally variable. Population and disturbance studies suggest that the boreal forest is constantly rebounding from a series of past "extreme" events. Stand-replacing fires occur every 40-200 yr (Dymess et al. 1986, Kasischke et al. 1995a, Mann and Plug 1999). White spruce recruitment following fire requires seed dispersal onto a mineral seedbed within 5-10 yr after fire. However, good cone crops occur only every 3-10 yr and disperse seed only modest distances. Plant mortality from herbivory (snowshoe hare, spruce budworm, larch sawfly, aspen tortix, birch spear-marked black moth) and snow-breakage events occur in pulses separated by years or decades. Together, these events introduce a stochastic element to vegetation dynamics (Pickett et al. 1987) that contributes to substantial variation in species composition and successional trajectory across the landscape (Drury 1956).
Table 2.2. Summary of intensive field sites and measurements for the Bonanza Creek LTER. "Early", "mid", and "late" refer to successional phases.

<table>
<thead>
<tr>
<th>Stand type</th>
<th>Disturbance type</th>
<th>Year of disturbance</th>
<th>Vegetation Dominance</th>
<th>When measurements initiated</th>
<th>Frequency of sampling Stocks</th>
<th>Frequency of sampling Fluxes¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>South facing uplands</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early Fire</td>
<td>Fire</td>
<td>1983</td>
<td>Herbs and saplings</td>
<td>1989</td>
<td>3 yr</td>
<td>1 yr (n=1)</td>
</tr>
<tr>
<td>Insects</td>
<td>Insects</td>
<td>1999</td>
<td>Moss</td>
<td>1999</td>
<td>1 yr</td>
<td>1 yr (n=3)</td>
</tr>
<tr>
<td>Mid Fire</td>
<td>Fire</td>
<td>1940</td>
<td>Birch or aspen</td>
<td>1989</td>
<td>6 yr</td>
<td>1 yr (n=1)</td>
</tr>
<tr>
<td>Late Fire</td>
<td>Fire</td>
<td>1700</td>
<td>White spruce</td>
<td>1989</td>
<td>6 yr</td>
<td>1 yr (n=1)</td>
</tr>
<tr>
<td>North facing uplands</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early Fire</td>
<td>Fire</td>
<td>1999</td>
<td>Herbs</td>
<td>1998</td>
<td>1 yr</td>
<td>Monthly</td>
</tr>
<tr>
<td>Mid Fire</td>
<td>Fire</td>
<td>1971</td>
<td>Willow</td>
<td>1971</td>
<td>6 yr</td>
<td>1 yr (n=1)</td>
</tr>
<tr>
<td>Late Fire</td>
<td>Fire</td>
<td>1915</td>
<td>Black spruce</td>
<td>1998</td>
<td>6 yr</td>
<td>Monthly</td>
</tr>
<tr>
<td>Floodplain</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sandbar</td>
<td>Flooding</td>
<td></td>
<td>Bare soil</td>
<td>1 yr</td>
<td>1 yr</td>
<td></td>
</tr>
<tr>
<td>Open shrub</td>
<td>Flooding</td>
<td></td>
<td>Willow</td>
<td>1989</td>
<td>3 yr</td>
<td>3 yr</td>
</tr>
<tr>
<td>Closed shrub</td>
<td>Flooding</td>
<td></td>
<td>Alder</td>
<td>1989</td>
<td>3 yr</td>
<td>3 yr</td>
</tr>
<tr>
<td>Poplar</td>
<td>Flooding</td>
<td></td>
<td>Poplar</td>
<td>1989</td>
<td>6 yr</td>
<td>1 yr (n=1)</td>
</tr>
<tr>
<td>White spruce</td>
<td>Flooding</td>
<td></td>
<td>White spruce</td>
<td>1989</td>
<td>6 yr</td>
<td>1 yr (n=1)</td>
</tr>
<tr>
<td>Black spruce</td>
<td>Flooding</td>
<td></td>
<td>Black spruce</td>
<td>1989</td>
<td>6 yr</td>
<td>6 yr</td>
</tr>
</tbody>
</table>

¹ Annual fluxes include only annually integrated measurements (litterfall, tree diameter, litterbags, etc.). Monthly fluxes also include CO₂ exchange.
2.4 Conceptual Framework

Our central question in LTER3 is: How do changes in climate and disturbance regime alter the functioning of the Alaskan boreal forest? Our overall objective is to document the major controls over forest dynamics, biogeochemistry, and disturbance and their interactions in the face of a changing climate (Fig. 2.2). The research is organized around three interactive themes: (1) Forest dynamics; (2) The changing boreal carbon cycle; and (3) Regional and landscape controls over disturbance regime.

The forest dynamics theme addresses successional changes in population and community processes following disturbance. We will examine the relative importance of historical legacies, stochastic processes, and species effects (autogenic processes) in determining successional trajectories and the sensitivity of these trajectories to climate. An improved understanding of forest dynamics and their mechanistic controls is essential to management for forest products, wildlife, and forest health. Changes in the carbon cycle during succession hinge on changes in forest dynamics and other element cycles, but also influence nutrient availability and microenvironment and therefore successional changes in forest dynamics. Climate affects the carbon cycle directly through changes in net primary production and heterotrophic respiration and indirectly through changes in species composition and their effects on biogeochemistry. An improved understanding of the boreal carbon cycle is critical to projections of future changes in global carbon and climate dynamics. Regional and landscape controls over disturbance regime focuses on regional and landscape processes that are responsible for the timing, extent, and severity of disturbance. Disturbance regime is affected by and influences successional trajectories of forest dynamics and biogeochemistry. Understanding controls over disturbance regime is critical to long-term regional planning for sustainable use of natural resources.

Research in each theme addresses important issues in ecology (Table 2.1), as described below. We have identified three synthesis areas that cut across all themes as a focus for integration and synthesis: Species effects on ecosystem and landscape processes explores how species identity and diversity influence biogeochemistry and disturbance regime. Spatio-temporal scaling provides the conceptual basis for linking process and pattern. Ecosystem sustainability explores how the positive and negative feedbacks that operate within ecosystems influence the sensitivity of ecosystems to perturbations such as changes in climate and disturbance regime.

Our research themes address the five core research areas mandated by LTER: population processes/trophic structure, primary production, organic accumulation, nutrient cycling, and disturbance regime (Fig. 2.2).

2.5 Linkages to Previous Bonanza Creek LTER Research

Our research in the first two funding cycles of the BNZ LTER program (1987-1998) focused primarily on interactive changes in forest dynamics, environment, and biogeochemistry during succession after fire or flooding (see prior research). In LTER3 we build on the successional paradigms developed in LTER1 and LTER2 by expanding our research to a broader regional scale and by adding new modeling approaches. This broadening allows us to consider both the causes and consequences of disturbance and the ways in which disturbance regime and post-disturbance succession might respond to temporal and spatial variation in climate. We also extend the temporal and spatial scope of the BNZ LTER research (1) by studying regional variation in boreal processes and (2) examining paleoecological records of boreal vegetation and disturbance regime to past variation in climate. We focus in the proposal text on the conceptual basis, general research design, and integration. We provide details of the implementation of the research in the tables and figures and on our website: http://www.lter.alaska.edu/html/publications.html.

2.6 Integrated Research Design

Our research design utilizes a combination of intensive sites, where we focus on observations and experiments to study processes, and extensive sites, where we analyze the
Fig. 2.2. Structural overview of the BNZ LTER research program, showing the relationships among major driving variables (state factors), the BNZ LTER research program (subdivided into three major themes), the Core Research Areas of the National LTER network addressed by each theme, and the societal implications of each theme. The details of research conducted in each theme are shown in Fig 2.7, 2.9, and 2.13, respectively. The integration of research across the three themes is shown in Fig. 2.15.
regional pattern in these processes. There is a strong interaction between pattern and process studies, with pattern representing the consequences of processes operating at multiple spatial scales, and process informing us about the mechanisms underlying these patterns. Paleoecological studies extend our observations in time, and modeling integrates process with pattern across a range of temporal and spatial scales.

**Intensive sites.** Our intensive research sites are at the Bonanza Creek Experimental Forest (BCEF), which is dissected by the glacially fed Tanana River, and the Caribou-Poker Creek Research Watershed (CPCRW), which has several well-defined upland watersheds. Our intensive studies focus on three chronosequences: succession following flooding in the Tanana River floodplain at BCEF, post-fire succession on south-facing uplands at BCEF, and post-fire succession on north-facing uplands at CPCRW. These sites enable us to compare primary and secondary succession and to compare post-fire succession in two dramatically different thermal and disturbance regimes (Table 2.2). The floodplain-upland contrast allows us to compare a moisture-rich system (floodplains) with a moisture-limited upland system. The post-fire successional sequences allow us to compare warm, dry, south-facing slopes without permafrost to north-facing, permafrost-dominated slopes. For each of these sequences we study early, mid, and late successional sites, except in the floodplain, where the more complex successional dynamics require six successional stages. Each of these stages is replicated three times. In many of these intensive sites we have experiments to test the importance of particular processes (Table 2.3). In each successional stage we measure microenvironment continuously, those population and ecosystem variables that respond sensitively to climate annually (e.g., litterfall and tree diameter increment), and slow variables (e.g., species composition and biomass) at 1-6 yr intervals depending on rate of successional change (Table 2.4). For those processes that occur most actively or have greatest impact in particular stages (e.g., establishment of tree seedlings and mammalian herbivory in early succession), we focus intensive effort on these stages and use less intensive observations at other stages.

**Extensive sites.** The intensive study sites were deliberately selected to minimize variation in all state factors except time within each of our three successional sequences, so that we could study the mechanisms underlying long-term successional change. In LTER3 we will initiate study of two regions to determine how the variability in our intensive study sites compare with the total regional variability. The Fairbanks Region is a 100 x 100-km area centered on our two major study areas (BCEF and CPCRW; Fig. 2.3). This area is relatively uniform climatically and will be the focus of landscape and regional studies in the first two years of proposed research. The Alaska Climate Transect extends from the warmest part of the boreal forest to the coldest part of arctic tundra in Alaska and includes both BNZ and the ARC LTER sites. We will work jointly with the ARC LTER site in seeking external funding for intensive study of this transect. In the research proposed here, we will focus on the forested part of this transect (from Fairbanks to the latitudinal treeline in the Brooks Range). The transect will enable us to quantify relationships among vegetation (Theme 1), biogeochemical (Theme 2), and landscape (Theme 3) processes and their dependence on current climate (Fig. 2.2).

**Modeling.** We use five types of models that operate across a range of spatial and temporal scales to integrate our results in time and space and as a mechanism for testing proposed linkages between pattern and process (Fig. 2.4). (1) Stand-level population models include models of small mammal population dynamics and herbivory (Rexstad 1994) and an individual-based model of tree population dynamics [SKOG, Malmstrom and Juday unpub]. (2) Soil thermal and hydrologic models simulate permafrost temperatures and the probability of thermokarst within stands (Hinzman et al. 1997, Romanovsky et al. 1997). (3) A dynamic vegetation model (DVM), which is currently under development by McGuire and Chapin with external funding, will incorporate understanding gained from stand-level population studies and models to simulate the impacts of species changes on forest dynamics, biogeochemistry, and disturbance regime (Fig. 2.5). The DVM is being designed for use at the stand-scale for investigating the role of different processes in species dynamics and at larger scales to explore the response of species shifts to regional changes in climate and disturbance regime. (4) The Alaska Frame Based Ecosystem Code (ALFRESCO) is a landscape model based on the turning
Table 2.3. Long-term experiments maintained by the BNZ LTER. Many experiments were initiated before the start of LTER or with separate funding but all are now maintained by LTER research. Long-term observations are listed in Table 2.3 (except for floodplain succession and insect population monitoring, for which we have particularly long records).

<table>
<thead>
<tr>
<th>BNZ long-term experiments</th>
<th>Responsible scientist</th>
<th>Date initiated</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Theme 1</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mammalian herbivore exclosures</td>
<td>Kielland</td>
<td>1990</td>
</tr>
<tr>
<td>Alder-spruce competition expt</td>
<td>Wurtz</td>
<td>1990</td>
</tr>
<tr>
<td>Observation of floodplain succession</td>
<td>Viereck</td>
<td>1965</td>
</tr>
<tr>
<td>Insect population monitoring</td>
<td>Werner</td>
<td>1976</td>
</tr>
<tr>
<td>Fire effects on soil thaw depth</td>
<td>Viereck</td>
<td>1983</td>
</tr>
<tr>
<td><strong>Theme 2</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annual N addition</td>
<td>Ruess, Valentine, Yarie</td>
<td>1989</td>
</tr>
<tr>
<td>One-time sawdust or sugar addition</td>
<td>Ruess, Valentine, Yarie</td>
<td>1989</td>
</tr>
<tr>
<td>Summer precipitation exclusion</td>
<td>Ruess, Valentine, Yarie</td>
<td>1989</td>
</tr>
<tr>
<td>Root-trenching experiments</td>
<td>Valentine, Boone</td>
<td>1999</td>
</tr>
<tr>
<td>$^{15}$NH$_4$ post-fire retention</td>
<td>Chapin, Valentine, Mack</td>
<td>1999</td>
</tr>
<tr>
<td><strong>Theme 3</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forest harvest experiments</td>
<td>Wurtz, Zasada</td>
<td>1972</td>
</tr>
<tr>
<td>Experimental burn (FROSTFIRE)</td>
<td>Chapin</td>
<td>1999</td>
</tr>
<tr>
<td>Simulated insect outbreak</td>
<td>Werner, Raffa, Illman</td>
<td>1998</td>
</tr>
</tbody>
</table>
point theory of our previous LTER research. It simulates the interactions of climate, fire, and landscape structure in causing shifts in landscape structure and disturbance spread (Starfield and Chapin 1996, Rupp et al. In press-a, Rupp et al. In press-b) (Fig. 2.6). (5) The high-latitude version of the Terrestrial Ecosystem Model (TEM), which simulates the major C and N fluxes and pools sizes of ecosystems (Fig. 2.7), incorporates understanding gained from soil thermal and hydrology models. TEM has been applied at a variety of spatial scales (stand-level to regional) and temporal scales (seasonal to century) to evaluate the carbon dynamics of high latitude ecosystems (Clein et al. In press, McGuire et al. In press-a, McGuire et al. In press-b, Clein et al. Submitted). The coupling and application of these models (Fig. 2.4, 2.8) provides a mechanism to (1) integrate our research on forest dynamics, boreal carbon dynamics, and controls over the disturbance regime and (2) evaluate the impacts of historical and projected changes in climate on the structure and functioning of the boreal forest at regional scales.

Hierarchical GIS and Spatial Analysis. We are developing a set of hierarchical spatial databases for use in landscape analysis, model parameterization, and site management. Key uncertainties in the application of ecosystem models to the regional scale include the resolution and accuracy of the data used as inputs to these models (Pierce and Running 1995, Nungesser et al. 1999, McGuire et al. In press-a). Our goal in developing these data sets is to focus on key parameters needed for stand, landscape, and regional modeling, including vegetation, soils, surface water, permafrost, and topography. Databases of disturbances (fire history, insect outbreaks, and timber harvest) are essential for model parameterization and validation. We will use a hierarchical approach, because different system controls emerge at different spatial scales (Walker and Walker 1991, Allen and Hoekstra 1992). We will assess the scales and quality of existing data sets (Table 1.1) and incorporate them into a set of hierarchical spatial data sets at the following scales: 1:6,000 (photointerpretation to distinguish white from black spruce at BCEF and CPCRW), 1:25,000 (stand-level [30 m] pixels), 1 km resolution, and 0.5°x 0.5° resolution. These hierarchical data sets enable us to model at scales ranging from the population dynamics within stands to the circumboreal zone.

Temporal scaling. To assess past interactions between climate, disturbance, and ecosystem properties, we will focus on three time scales: (1) the last 300 years, during which climate has warmed (tree rings), (2) the last 1,000 years, which includes relatively rapid, low-magnitude climate changes of the LIA as recorded in lake cores, and (3) lower-resolution records from lake cores for the past 12,000 years, which includes the entire history of the boreal forest, including the period ca. 10,000-6000 yr B.P. when conditions were probably warmer and drier than present.

Summary. Our study design provides several independent tests of the impact of climate on ecosystem processes and disturbance: interannual variability, tree ring reconstructions, lake cores, early vs. late succession, north vs. south-facing slopes, and the Alaska Climate Transect. Together these comparisons provide a powerful test of the impact of climate on boreal forest over a range of temporal and spatial scales.

2.7 Theme 1. Forest dynamics

Conceptual model

Our goal in the forest dynamics theme is to understand the processes governing the patterns and changes in community composition over a range of temporal and spatial scales (Fig. 2.9). We include here studies of climate, dominant tree populations, vegetation cover, and key vertebrate and invertebrate populations. We hypothesize that initial tree establishment is strongly influenced by landscape-scale factors that have a strong historical legacy and substantial interannual variability (i.e., both spatial and temporal stochasticity) (Chesson 1986). These include (1) the type, severity, and size of disturbance (Turner et al. In press), (2) the local seed availability of potential colonizers (Walker et al. 1986), and (3) populations of resprouting species from the pre-disturbance communities (Mann and Plug 1999). Once seedlings have established, a series of biotic filters governs the early survival and growth of tree seedlings at a site (Lambers et al. 1998). These include their competitive ability relative to herbaceous
Table 2.4. Parameters measured in BNZ intensive sites.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Location</th>
<th>Dates</th>
<th>Responsible PI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Climate</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Air temperature</td>
<td>LTER, BCEF, CPCRW</td>
<td>1984-</td>
<td>Hinzman, Viereck</td>
</tr>
<tr>
<td>Soil temp at 6 depths</td>
<td>LTER, BCEF, CPCRW</td>
<td>1984-</td>
<td>Hinzman, Viereck</td>
</tr>
<tr>
<td>Relative humidity</td>
<td>LTER, BCEF, CPCRW</td>
<td>1984-</td>
<td>Hinzman, Viereck</td>
</tr>
<tr>
<td>Precipitation</td>
<td>LTER, CPCRW</td>
<td>1984-</td>
<td>Hinzman, Viereck</td>
</tr>
<tr>
<td>Evaporation</td>
<td>LTER, CPCRW</td>
<td>1984-</td>
<td>Hinzman, Viereck</td>
</tr>
<tr>
<td>Wind speed, direction</td>
<td>LTER, CPCRW</td>
<td>1984-</td>
<td>Hinzman, Viereck</td>
</tr>
<tr>
<td>Solar radiation (global)</td>
<td>LTER</td>
<td>1984-</td>
<td>Hinzman, Viereck</td>
</tr>
<tr>
<td>UV</td>
<td>LTER</td>
<td>1984-</td>
<td>Hinzman, Viereck</td>
</tr>
<tr>
<td>PAR</td>
<td>LTER</td>
<td>1984-</td>
<td>Hinzman, Viereck</td>
</tr>
<tr>
<td>Shortwave in/out</td>
<td>CPCRW</td>
<td>1988-</td>
<td>Hinzman, Viereck</td>
</tr>
<tr>
<td>Longwave in/out</td>
<td>CPCRW</td>
<td>1988-</td>
<td>Hinzman, Viereck</td>
</tr>
<tr>
<td>Sun photometer</td>
<td>LTER</td>
<td>1994-</td>
<td>Viereck</td>
</tr>
<tr>
<td>Snow depth</td>
<td>LTER</td>
<td>1968-</td>
<td>Hinzman, Viereck</td>
</tr>
<tr>
<td>Soil moisture</td>
<td>LTER</td>
<td>1992-</td>
<td>Hinzman, Viereck</td>
</tr>
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<td>Thaw depth</td>
<td>LTER</td>
<td>1983-</td>
<td>Hinzman, Viereck</td>
</tr>
<tr>
<td>River height</td>
<td>LTER</td>
<td>1985-</td>
<td>Hinzman, Viereck</td>
</tr>
<tr>
<td>Theme 1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree density, biomass</td>
<td>BCEF</td>
<td>1989-</td>
<td>Walker, Juday</td>
</tr>
<tr>
<td>Tree seedling density</td>
<td>BCEF</td>
<td>1989-</td>
<td>Walker, Juday</td>
</tr>
<tr>
<td>Understory cover, biomass</td>
<td>BCEF</td>
<td>1989-</td>
<td>Walker, Juday</td>
</tr>
<tr>
<td>Root biomass</td>
<td>BCEF</td>
<td>1989-</td>
<td>Russ</td>
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<td>Seed rain</td>
<td>BCEF</td>
<td>1955-</td>
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<td>Insect defoliators (index)</td>
<td>BCEF</td>
<td>1976-</td>
<td>Werner</td>
</tr>
<tr>
<td>Microtine density</td>
<td>BCEF</td>
<td>1999-</td>
<td>Rexstad</td>
</tr>
<tr>
<td>Snowshoe hare density</td>
<td>BCEF</td>
<td>1999-</td>
<td>Rexstad</td>
</tr>
<tr>
<td>Theme 2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carbon and nutrient stocks</td>
<td>BCEF</td>
<td>1989-</td>
<td>Ruess, Viereck</td>
</tr>
<tr>
<td>Trees</td>
<td>BCEF</td>
<td>1989-</td>
<td>Ruess, Viereck</td>
</tr>
<tr>
<td>Understory</td>
<td>BCEF</td>
<td>1989-</td>
<td>Valentine, Viereck</td>
</tr>
<tr>
<td>Soils</td>
<td>BCEF</td>
<td>1989-</td>
<td>Ruess, Viereck, Boone</td>
</tr>
<tr>
<td>Litterfall</td>
<td>BCEF</td>
<td>1975-</td>
<td>Ruess</td>
</tr>
<tr>
<td>Diameter increment</td>
<td>BCEF</td>
<td>1989-</td>
<td>Ruess, Viereck</td>
</tr>
<tr>
<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-</td>
<td>Kielland</td>
</tr>
<tr>
<td>Soil respiration</td>
<td>BCEF, CPCRW</td>
<td>1998-</td>
<td>Ruess, Valentine, Boone</td>
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<td>N mineralization</td>
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<td>Nitrogen deposition (NADP)</td>
<td>CPCRW</td>
<td>1993-</td>
<td>Hinzman</td>
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<td>Net C, H2O, energy exchange</td>
<td>BCEF, CPCRW</td>
<td>1998-</td>
<td>Chapin</td>
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<tr>
<td>Stream chemistry</td>
<td>CPCRW</td>
<td>1978-</td>
<td>Hinzman</td>
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*LTER = LTER1 and LTER level 1 climate stations at BCEF; BCEF = intensive-site measurements at BCEF; CPCRW = measurements made at CPCRW

Many of these measurements were made by earlier BNZ investigators, particularly Keith Van Cleve, John Yarie, John Bryant, and Chuck Slaughter. These are the PIs currently responsible.

Intermittent
colonizers (Goldberg and Barton 1992, Gurevitch et al. 1992), their palatability to herbivores (Bryant and Kuropat 1980, Pastor and Naiman 1992), and tolerance to herbivory (Rosenthal and Kotanen 1994), all of which vary with environmental stress (Grime 1979) and therefore have a stochastic component that is sensitive to climate. Tree establishment is rare after the first decade of post-disturbance recruitment (Timoney et al. 1997), and we hypothesize that further changes in community composition and ecosystem processes are relatively synchronous within a stand and are strongly influenced by the biology of the dominant species (Hobbie 1992). This results in relatively rapid changes in vegetation and soil structure and function ("turning points") that are triggered by successional changes in species dominance (Van Cleve et al. 1991). The major turning points that we have identified following the establishment phase are (1) alder dominance, (2) canopy closure of deciduous forest or shrub species, and (3) the shift from deciduous to conifer/moss dominance. Each of these turning points causes large changes in biodiversity, ecosystem processes, and disturbance probability. Our major hypotheses regarding forest dynamics are:

H1.1. Climate influences the probability of stochastic events that govern initial floristic composition (e.g. seed rain, disturbance, and herbivory) more strongly than it influences the rate or pattern of species replacement through succession.

H1.2. Population densities of small mammals (which strongly affect plant recruitment) and insects (which strongly affect mortality and survivorship) are governed primarily by climate, whereas population densities of large mammals (which strongly affect competitive interactions among shrubs and trees) are governed primarily by predation.

H1.3. There is a change through succession from dominance by a boreal to an arctic flora due to the development of permafrost and consequently more "arctic" soil conditions. Regional reductions in permafrost extent may reduce the influence of the arctic flora.

H1.4. Disturbance severity has greater effect than disturbance type on the trajectory of post-disturbance succession.

H1.5. Over the past 10,000 years, the characteristic pattern of regional changes in tree species dominance has been triggered by rapid threshold changes in available moisture.

Approach

Research on forest dynamics uses a combination of approaches including long-term observations, experiments, paleo-records, mapping and remote sensing, and modeling. We use long-term observations on permanent plots to document initial species composition and the changes in environment, species composition, and biogeochemistry through time. Many of our plots that were originally established in mid-successional "turning point" sites appear to have "turned", allowing us to test hypotheses related to successional trajectories (H1.1, H1.3). Monitoring interannual variation in sensitive population and ecosystem parameters also enables us to study interactions between climate and other ecological controls (H1.1, H1.2). Mammal transects, agency data, and insect plots give us information on animal population turnover rates and controls (H1.2). Exclusion experiments give us explicit data on how mammal populations control successional trajectories and rates (H1.2). Regional studies and modeling allow us to test and explore the generality of the conceptual models that we develop from long-term observation and experiments, and provide us with explicit data on the interplay between deterministic and stochastic controls on overall landscape pattern (H1.1). Dynamic vegetation models provide a basis to project future landscape patterns of forest composition in response to scenarios of climatic change and interactions of disturbance, climate, and vegetation pattern (H1.1, H1.4, H1.5). Finally, we test for the effects of climate on forest dynamics by examining interannual variability in processes, spatial variability in processes along a climate gradient, and paleo-reconstruction of processes over time periods during which climate has changed (H1.1, H1.5).
Fig. 2.3. Location of major study areas and transects. The Fairbanks Region (100 x 100 km section shown expanded) includes the Bonanza Creek Experimental Forest (BCEF) and the Caribou-Poker Creek Research Watershed (CPCRW).
Observations of Stand-Level Pattern and Process

Climate. (Hinzman and Romanovsky) We maintain 5 complete meteorological stations (2 in BCEF and 3 in CPCRW) to document temporal and spatial variation in climate (Table 2.4). The BCEF weather stations are level-1 LTER weather stations that enable us to compare climate between Alaskan uplands, floodplains and other LTER sites. The CPCRW weather stations are situated in and above a forest canopy, allowing us to document the climate experienced by vegetation. Comparison between the standard installations and the forest installations documents the impacts of vegetation on energy balance and microclimate. We have produced a 1 km-resolution data set of monthly averages of the climate of Alaska (Table 1.1) and are working with the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP-Members 1995, Kittel et al. 1997) to produce a spatially distributed climate data set for Alaska from 1900 to 2100. The long-term climate measurements and regional climate data sets provide the basis for testing effects of temporal and spatial variability in climate on ecological processes.

We continue to monitor microclimate in major successional stages following flooding in the floodplains and after fire in the uplands (Table 2.4). These measurements enable us to understand how key environmental variables such as radiation beneath the canopy, soil temperature, soil moisture, and thaw depth relate to successional changes in vegetation structure and composition (H1.1, H1.3). We will adapt soil thermal and hydrologic models developed in arctic Alaska (Hinzman et al. 1996, Romanovsky et al. 1997, Hinzman et al. 1998) to the boreal forest, based on these environmental measurements. Coupling these climatic measurements in the various successional stages with spatially distributed models of environmental processes will allow us to extrapolate our knowledge of the soil thermal and hydrologic regimes over space (Fairbanks Region) and time (the last 100 years).

Vegetation composition in permanent plots. (Walker, Viereck, and Juday) We will continue monitoring community composition and rates of plant establishment and mortality on permanent post-fire and post-flooding successional plots in BCEF and will add new permanent plots to the black spruce successional sequence that we are initiating in the uplands in this proposal (Table 2.2). We monitor plots annually for the first five years after disturbance, on a 3-yr cycle through age 15, then on a 6-year cycle. In these plots we permanently mark all trees and tall shrubs, and measure stem diameter, height, and mortality. Seed traps and seedling counts on subplots document annual seed rain and recruitment. For non-woody species (e.g., mosses and grass), we document presence and percentage cover, height, and/or density, which are converted to biomass values using allometric equations. These measurements allow documentation of population parameters for woody species and species composition, diversity, and biomass of the entire flora. These measurements have annual resolution in early succession and 3-6 yr resolution in later stages. The data provide input parameters and validation data for population dynamics and dynamic vegetation models. In collaboration with the University of Alaska Herbarium, we are developing a reference collection of voucher specimens, and tissue samples for future genetic analysis of vascular and non-vascular plants for our main study areas (BCEF and CPCRW) and for the Fairbanks Region and Alaska Climate Transect. The vegetation sampling allows a test of our hypotheses about controls over establishment and successional trajectory and the resulting patterns of biomass and diversity (H1.1, H1.3, H1.4).

Insect population dynamics. (Werner) We conduct an annual survey of insect abundance at permanent plots in BCEF, focusing on species typified by large population fluctuations (e.g., spruce bark beetle, spruce bud worm, aspen tortrix) and their natural predators and parasites (Niemeijer 1997). The long-term (23-yr) record of population dynamics of these forest “pests” and their predators will be compared with LTER observations of climate and productivity (H1.2) (Mattson and Haack 1987) and with patterns of tree growth and mortality to determine the role of defoliating insects in forest dynamics (H1.1, H1.2).

Vertebrate population dynamics. (Kielland, Rexstad, and Doak) We document the abundance of major vertebrate herbivores because of their impact on forest dynamics (Starfield and Chapin 1996) and biogeochemistry (Fig. 2.9) (Bryant and Chapin 1986, Pastor et al. 1988, Kielland and Bryant 1998, Ruess et al. 1998) and their importance to humans. We use mark-
Fig. 2.4. The transfer of understanding among major modeling activities in LTER3. These modeling activities include efforts focused on stand population models, soil thermal and hydrology models, a dynamic vegetation model (DVM), a landscape model of vegetation shifts and fire spread (ALFRESCO), and a biogeochemical model (TEM). The research themes that provide data and understanding for each model are indicated. The models are described in general in the text and in detail in Figures 2.5, 2.6, and 2.7.

Fig. 2.5. Structure of the dynamic vegetation model. The DVM more intimately integrates vegetation dynamics, biogeochemistry, and controls over the disturbance regime. Whereas the coupling between ALFRESCO and TEM focuses on modeling transitions among extant vegetation types without information from the biogeochemical model, the structure of the DVM will provide the capability to describe more subtle shifts in species composition of communities based on competitive interactions among plant functional types that are governed by changes in climate and biogeochemical cycling. The ability to describe shifts in species composition is important because climatic change has the potential to create new community types that do not currently exist. By comparing the regional applications of the DVM with the ALFRESCO-TEM coupling, we can evaluate the implications of more sophisticated interactions among ecosystem structure, ecosystem function, and the disturbance regime on the structure and function of boreal forest at regional scales.
recapture studies to estimate population abundance and survival of snowshoe hares (Boulanger and Krebs 1996) and microtines (Paradis 1995) in early successional habitats where these animals are common (H1.2). From these measures, we can test the relationship between climate and population density and turnover (predation or emigration) (Hik 1994, Krebs et al. 1995, Stenseth 1995). We use transects of browsed stems (moose and hares), and pellet counts in litter trays in each intensive study site each year to rapidly assess the relative use of different sites by hares and moose. We collaborate with state and federal agencies to obtain long-term records of population densities, movement patterns, and mortality of moose in the Tanana Valley. We compare plant growth, mortality, and species composition inside and outside of exclosures to relate animal population densities to vegetation dynamics. We relate these vegetation changes to specific herbivores by documenting diets from evidence of browsing by moose and hares in the vegetation surveys on permanent plots. We compare stable isotope composition of tissues from small mammals and hunter-killed moose with an established “library” of isotopic signatures of potential forage species to determine whether the diet composition in our study plots is regionally representative (Fig. 2.10). These measurements are important for linking models of animal population dynamics (Rexstad 1994), forest succession, and biogeochemical cycling (Pastor et al. 1988, Pastor et al. 1993, McGuire et al. 1995, Kielland and Bryant 1998).

Experimental Tests of Controls over Processes

Herbivore exclosure experiments. (Kielland) We will continue monitoring moose/hare exclosures that were established in 1990 in early successional floodplain and upland sites and which have shown a dramatic reduction in rate of successional change (H1.2), relative to plots exposed to herbivores (Table 2.3). We will compare the response of the vegetative community outside the exclosures with the findings of Dale and Zbigniewcz (1997) who report some species of shrubs respond rapidly to the reduction of herbivory following a hare decline.

Experimental disturbances

Insects. (Raffa, Illman, and Werner) To determine how bark beetle populations and their microbial associates respond to disturbances that provide susceptible hosts, an experiment was initiated in 1998 that provided host trees with three different degrees of tree susceptibility (felled, girdled, and control). These trees are baited annually with pheromones, and tree colonization by bark beetles and their fungal associates is documented. Emphasis is placed on the population responses of several competing bark beetle species, the response of live trees (growth and resin production), understory plant species, and pathogenic fungi. This long-term population and community approach complements the long-term LTER survey of insect densities (see above) and the more intensive experimental studies in a natural outbreak of spruce bark beetle in southern Alaska (Raffa, Illman, and Werner externally funded project; Table 2.5). The experiment tests the controls over a major tree-mortality agent (H1.1), and the relationship of that mortality agent to insect and microbial diversity (H1.3). We hypothesize that plant physiological controls over resin production (Loomis 1932, Bryant et al. 1983, Coley et al. 1985, Waring and Pitman 1985, Herms and Mattson 1992) and competition among competing species of insects and insect-borne fungi buffer the system from frequent outbreaks.

Fire. (Valentine, Chapin) In 1999 there was an externally funded experimental burn of a watershed in CPCRW. Funding for this FROSTFIRE project ends in September 2000. The LTER will continue to follow the ecological consequences of this fire. To test the hypothesis that post-disturbance seed availability and competitive environment determine successional trajectory (H1.1), we will sow seeds and plant seedlings of all the major upland forest species (plus lodgepole pine—a potential future colonizer) in a recently burned black spruce forest (the FROSTFIRE site; Table 2.3). By following these plots and those that regenerate from natural seed rain, we can determine the limitations on establishment by seed rain, disturbance type and severity, and competitive environment. Similar experiments have already been done in floodplains (Walker and Chapin 1986, Walker et al. 1986), south-aspect post-fire sites (Cater and Chapin In press), post-glacial landscapes (Chapin et al. 1994), and will be initiated in logged sites in the next phase of LTER (2004). A comparison of these experiments allows a test of the
Fig. 2.6. Vegetation transitions simulated by the model ALFRESCO. This spatially explicit model simulates landscape-level responses of vegetation and fire to transient changes in climate (Rupp et al. In press-a, Rupp et al. In press-b). The model consists of 5 submodels (frames; the boxes in the figure): tundra, deciduous forest, white spruce forest, black spruce forest, and dry grassland. The switches between frames (the arrows in the figure) are governed by climate (summer temperature and precipitation) and disturbance (fire or insect outbreaks). The disturbance may occur within a grid cell or spread from adjacent grid cells. The model explicitly simulates the spatial processes of fire spread and seed dispersal, providing a mechanism to simulate the effects of landscape structure on forest dynamics and disturbance regime. Model inputs are maps of temperature and precipitation, topography, and vegetation. Model outputs are maps of vegetation type, fire, and biomass.

Fig. 2.7. The Terrestrial Ecosystem Model (TEM). The state variables are: carbon in the vegetation ($C_v$); structural N in the vegetation ($N_{vl}$); labile N in the vegetation ($N_{vs}$); organic carbon in soils and detritus ($C_s$); organic N in soils and detritus ($N_s$); and available soil inorganic N ($N_{av}$). Arrows show C and N fluxes: GPP, gross primary production; $R_A$, autotrophic respiration; $R_H$, heterotrophic respiration; $L_C$, litterfall carbon; $L_N$, litterfall N; NUPTAKE$_L$, N uptake into the structural N pool of the vegetation; NUPTAKE$_S$, N uptake into the labile N pool of the vegetation; NRESORB, N resorption from dying tissue into the labile N pool of the vegetation; NMOBIL, N mobilized between the structural and labile N pools of the vegetation; NETNMIN, net N mineralization of soil organic N; NINPUT, N inputs from outside the ecosystem; and NLOST, N losses from the ecosystem.

**Forest harvest**. (Wurz) The LTER will continue efforts begun this year (through a separate USFS grant) to evaluate the two longest-running silvicultural experiments in interior Alaska. We are seeking outside funds to implement a large-scale biomass removal/forest harvesting experiment, with implementation projected for the year 2004. We will use LTER funds to organize and host a symposium to develop the design of long-term forest harvesting experiments in northern systems.

**Spatial Scaling** (Walker, Lloyd, Fastie, Hinzman, Chapin)

Research in our extensive sites (Fig. 2.3) will focus on the climatically uniform (relatively speaking) Fairbanks Region in the first two years and the Alaska Climate Transect in the second two years of our proposed research. During this period, we will study the black-spruce chronosequence on north-facing slopes and bottomlands because this is the most widespread forest type and the type most prone to disturbance by fire and thermokarst. In subsequent phases of LTER, we will expand our regional studies to include south-facing slopes, floodplains, and wetlands. Data on biomass and productivity, as assessed by remotely sensed NDVI and successional stage (recent burn, deciduous phase, black spruce phase), will stratify road-accessible black-spruce-dominated sites. At least 50 stands will be randomly selected from the stratified design for documentation of stand structure and diversity. In the Fairbanks Region we will include the few black spruce stands that have received previous intensive study (e.g., Washington Creek) (Van Cleve et al. 1983, Van Cleve et al. 1986). Along the Alaska Climate Transect, sites will include Kasischke’s chronosequence (Kasischke et al. 1995a) and sites adjacent to a transect of lakes that have already been calibrated for modern lake characteristics (Edwards et al. In press, Gregory-Eaves et al. In press). These lakes will be used for temporal scaling (see below).

Most sites will be visited only once to document the relationship between remote-sensing signature (e.g., NDVI and other spectral combinations) and stand structure and diversity. The information will be used to develop a hierarchical, floristically based classification of black spruce stands. We will also obtain simple measures of environment, community structure, and ecosystem processes, which can be measured rapidly in a large number of sites (Table 2.6). Trees will be cored and the largest trees will be examined for fire scars to determine the age distribution of trees and the time of the last stand replacing disturbance (Mann and Plug 1999). We will use an ordination of species distributions combined with site physical and soil chemical parameters to determine the strongest environmental correlates of vegetation and other ecosystem characteristics (Walker et al. 1994). These analyses will tell us the regional variation in successional trajectory (Hl.1) and the climatic influences on herbivore abundance (Hl.2) and plant diversity (Hl.3).

**Temporal Scaling**

The last 300 years: Tree Ring Studies. (Juday) We have used tree-ring climate analyses in collaboration with the Lamont-Doherty Earth Observatory to document recent changes in growth rates of white spruce (Fig. 1.1). In the current funding cycle we will expand this data set to black spruce and to a longer-term record of white spruce, so that we can identify how late successional species have responded to climate in the Fairbanks Region and along the Alaska Climate Transect. We will extend these studies to other species (birch, aspen) to determine how the major tree species of the Interior differ in their climatic response.

The last millennium. (Edwards and Finney) We will document the fine-scale (1 to 100 yr) changes in charcoal, pollen, and climate proxies in two annually varved lakes in the Fairbanks region to determine patterns and rates of change in vegetation (H1.5). We will focus on the last 1000 years, when there have been dramatic climate changes without obvious vegetation change and the period prior to 4000-5000 years ago (only in the older of the two lakes), when there was a gradual climate cooling, coinciding with increases in black spruce and fire. We will determine whether the change in climate/fire regime caused large-scale species turnover or individualistic change in community composition (Davis 1981). The longer-term history of the boreal forest
**Fig. 2.8.** We integrate our research on forest dynamics, boreal carbon dynamics, and controls over the disturbance regime through use of two models: (1) ALFRESCO is a frame-based spatially explicit model that prescribes vegetation types and focuses on the roles of climate and fire in causing shifts in community types (Starfield and Chapin 1996, Rupp et al. in press-b). (2) TEM is a model that can be used at any spatial or temporal scale to simulates the major C and N fluxes and pools sizes of ecosystems (Clein et al. in press, McGuire et al. in press-a, McGuire et al. in press-b, Clein et al. Submitted). We will modify and test these two models based on research from each of the themes.

**Fig. 2.9.** Hypothesized relationship among processes governing forest dynamics (theme 1). We hypothesize that initial stand composition following disturbance depends on climate, the type and severity of disturbance, and landscape controls over propagule availability (links to themes 2 and 3). These stands support dense herbivore populations, whose selective browsing determines the rate and pattern of change in forest composition. When dominance shifts from deciduous trees to conifers, there is no longer a “smothering” litter layer, allowing the development of a thick layer of mosses and lichens, which insulate the soil. The combination of cold soils and poor litter quality alters biogeochemistry (link to theme 2). Successional changes in diversity reflect the changes in plant, animal, and microbial species composition associated with changes in vegetation and soil environment. Changes in diversity (especially the types and abundance of mosses and lichens determine flammability and therefore disturbance regime.)
will be addressed by an NSF-PALE funded study of climate and vegetation change in northern and interior Alaska, and at sites along our Alaska Climate Transect.

*Modeling the Linkage of Pattern and Process* (McGuire, Chapin, Juday, Rexstad)

We use vegetation modeling to link our observations of patterns and our understanding of processes across the various temporal and spatial scales of measurement. SKOG will be used to simulate successional trajectories following changes in factors governing recruitment (meters to kilometers; H1.1, H1.2). The animal population models will explicitly link small mammal population dynamics with stand-level herbivory. The DVM, which simulates changes in species composition through succession, will link our studies of species dynamics, herbivory, microenvironment (H1.1, H1.2, H1.5), biogeochemistry (theme 2), and disturbance regime (theme 3). The DVM will be parameterized to capture the dynamics of recruitment (SKOG) and herbivory and will be driven by inputs available in our regional database. We will evaluate the consequences of different hypotheses of stand-level controls over successional patterns on historical (including the paleorecord) and projected vegetation and biogeochemical dynamics across climatic gradients at the regional scale. ALFRESCO is complementary to the DVM in that it uses information on landscape pattern to simulate the spread of fire and seeds to simulate long-term changes in vegetation and fire regime in response to variation in climate, disturbance, and landscape pattern (H1.5). The dynamics of the vegetation transitions in ALFRESCO will incorporate understanding gained from our field studies, SKOG modeling of seed spread, and DVM modeling of vegetation changes.

### 2.8 Theme 2. The Changing Boreal Carbon Cycle

#### Conceptual Model

The objective of the research in this theme is to improve our understanding of the functional response of C balance to interactions between the physical environment, vegetation dynamics, soil processes, and disturbance and to integrate these effects at the regional scale (Fig. 2.11). Understanding mechanisms responsible for variations among ecosystem types in these interactions is essential for regional scaling of boreal forest C cycling. By incorporating this understanding into process-based models that are initialized and driven by geographically referenced data on the physical environment, vegetation structure, and soil types, we will improve our ability to estimate interannual C balance of forest stands in interior Alaska. At the regional scale, the annual C balance of the boreal forest is the integral of emissions associated with fire and the C balance of individual stands (Schulze and Heimann 1999).

Changes in C cycling cannot be understood without considering interactions with other element cycles (Rastetter and Shaver 1992). Nitrogen availability is high in early post-fire succession and following alder invasion in floodplains. Successional changes in the physical environment and species-specific litter chemistry (Hobbie 1992) reduce mineral N availability in late succession and, we hypothesize, drive shifts towards more organic-based N cycling and plant dependence on mycorrhizal N uptake (Read 1991, Nasholm et al. 1998). Following disturbance, stand-level C balance is the difference between net primary production (NPP) and heterotrophic respiration (RH). Our conceptual model of stand C balance has three phases (Fig. 2.12): (1) a phase of negative C balance immediately after a disturbance, (2) which is followed by a phase of positive C balance, and (3) finally a phase where NPP and RH are sufficiently similar that C balance is determined primarily by interannual variation in climate. This is only a general trajectory but is supported by work in Manitoba (Harden et al. 1997, Rapalee et al. 1998) and Alaska (K. O'Neill pers. comm.). The duration of each phase and magnitude of NPP and RH during each phase probably depend on the severity of disturbance (theme 3), the vegetation trajectory subsequent to disturbance (theme 1), and the underlying patterns of and mechanisms controlling C fluxes (theme 2). We do not yet know the length of each phase, the mechanisms controlling the magnitude of C changes that occur, or how the C balance of each phase responds to interannual variation in hydrological and meteorological processes. For example, if NPP and RH change slowly after disturbance, they may be a function of several past disturbance events and never show a simple equilibrium response to climate.
The population turnover of small mammals is generally less than a year, due to high rates of mortality during spring and autumn. Increasing the duration of these sensitive periods may have potentially deleterious impacts on small mammals. The turnover of large-bodied ungulates is increasingly influenced by predation, up to 90% of the annual calf crop, and up to 25% of the adult population (ADF&G data). 15N natural abundance in primary producers, primary consumers, and secondary consumers will be used to monitor trophic relationships (panel D), and examine how population fluctuations and climate affects these ecological processes. Isotopic enrichment within the range of inter-trophic variation is similar to other values reported in the literature (e.g., DeNiro and Epstein 1978, Minagawa and Wada 1984.). Isotopic analyses of plant tissues were carried out as described in Kieland et al. (1998) and Kieland and Bryant (1998). Isotopic signatures of primary and secondary consumers were determined on muscle tissues provided by the Alaska Department of Fish & Game (large mammals) and animals collected by local residents in the Bonanza Creek Experimental Forest (small mammals). Estimated abundance (and 95% confidence intervals) of snowshoe hares on an early successional floodplain stands along the Tanana River exhibit large inter- and intra-annual variation due to high recruitment during the summer and high rates of mortality during early spring and autumn (Panel E). Estimates were derived from 4-day live trapping sessions using Tomahawk traps in a rectangular pattern spaced at 50m intervals. Total trapping area was approximately 9ha. Animals were weighed, sexed, and marked with 2 ear tags. Abundance estimates were produced from closed population models (Rexstad 1994).
Our research will examine how climate (H2.1) and herbivory (H2.3) influence patterns of plant C allocation and stand production, how these patterns affect and are affected by the cycling and storage of carbon (H2.3), and how at the regional scale, landscape structure and disturbance influence C balance by controlling the spatial distribution of stand types (H2.4). The specific hypotheses that we will examine during this phase of the research are:

H2.1. The sensitivity of NPP to climate increases through succession because (1) root production is both a large component of total NPP and increases at the expense of aboveground growth under drought conditions, and (2) mosses, which are drought-sensitive, become an increasing proportion of NPP in late succession.

H2.2. Labile organic matter becomes a progressively greater fraction of total soil organic matter inputs later in succession because roots, which are readily decomposed, become an increasing fraction of total NPP. Low temperature induced by the thickening moss layer slows its decomposition and the decomposition of root-derived organic matter, promoting accretion of a large pool of labile soil carbon. This pool enhances the overall climate sensitivity of heterotrophic soil respiration (Fig. 2.13).

H2.3. Increases in vertebrate herbivory following disturbance speed carbon and nitrogen turnover by (1) reducing carbon and nutrient accumulation in vegetation, (2) short-circuiting decomposition of plant litter, and (3) increasing the quality and turnover of aboveground and belowground litter.

H2.4. Climate warming has greater impact on regional carbon balance through its effect on fire regime and stand age distribution than through its direct effects on the carbon balance of undisturbed stands.

Approach
Our investigations use the same general study design described in theme 1. We will study C balance and C-N interactions using ¹⁴C studies of soil organic matter turnover and C exchange measurements at intensive study sites in three successional sequences. We will relate this to regional patterns, by studying black spruce sites in the Fairbanks Region and the Alaska Climate Transect. After incorporating our understanding of controls into process-based models, we will validate the interannual dynamics of the models with measurements of C balance and N mineralization over several years and over a broader geographic region. This testing strategy will provide confidence of our understanding of controls over the temporal C dynamics at the intensively studied stands, which span the major topographic and environmental variation in interior Alaska. For the regional testing of our understanding, we will implement an extensive measurement program in the Fairbanks region and along the Alaska climate transect.

Observations of Stand-Level Pattern and Process

Biomass, NPP, and Element Pools. (Ruess, Sveinbjornsson, Valentine) Our long-term vegetation measurements are designed to examine the extent to which increasing leaf area and the proportional allocation to leaves (leaf area ratio) constrain NPP from early to mid-succession (Field 1991, Potter et al. 1993). We also study whether decreasing nutrient availability and species changes in late succession cause a decline in production efficiency (production per unit foliage) and aboveground NPP (Ryan et al. In press) due to a shift in NPP allocation from foliage to wood, roots, and mosses. At the beginning of the BNZ LTER study we documented the stocks of C and other elements in trees and soils of all intensive sites on the floodplain and on south-facing uplands (Van Cleve et al. 1983). We repeat measurements of tree biomass every 3-6 yr (see theme 1). In the next two years we will repeat the inventories of soil and large woody debris to document changes in these stocks. Our current estimates of aboveground NPP neglect understory vegetation. Over the next four years we will improve these estimates by documenting production of mosses and understory shrubs and confirming band dendrometer estimates of wood production with tree-ring counts. These estimates will be combined with minirhizotron measurements of root production, mortality and decomposition, annual measurements of litterfall, and 3-6 yr estimates of tree mortality to estimate long-term patterns of aboveground
Table 2.5. Other sponsored research projects by BNZ PIs that contribute to LTER research. These projects build on and directly contribute to LTER-funded research.

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<td>Forest Harvest Experiment</td>
<td>Viereck</td>
<td>DOE</td>
<td>1994-</td>
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<td>Sveinbjornsson</td>
<td>NSF</td>
<td>2000-</td>
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<td><strong>Theme 2</strong></td>
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<td>USFS/NADP</td>
<td>1993-</td>
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<td>Secondary chem effects on soils processes</td>
<td>Schimel</td>
<td>NSF</td>
<td>1995-</td>
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<td>Ecosystem roles of organic N</td>
<td>Kielland, Ruess, Boone</td>
<td>USDA</td>
<td>1999-</td>
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<td>Regional Carbon Budgets</td>
<td>McGuire</td>
<td>NASA</td>
<td>1997-</td>
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<td>Land-Cover Change</td>
<td>McGuire, Verbyla</td>
<td>NASA</td>
<td>1997-</td>
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<td>Alaskan fire remote-sensing program</td>
<td>Kasischke</td>
<td>NASA</td>
<td>1991-</td>
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<td>Kasischke</td>
<td>DOD</td>
<td>1998-</td>
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<td>Climate feedbacks from fire (FROSTFIRE)</td>
<td>Chapin, Hinzman</td>
<td>NSF</td>
<td>1997-</td>
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<td>Hydrology of the Yukon Basin</td>
<td>Hinzman</td>
<td>JAMSTEC</td>
<td>1997-</td>
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<td>Human (Soc. Sci.) feedbacks to fire regime</td>
<td>Chapin, McGuire</td>
<td>NASA</td>
<td>Proposed</td>
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<td>Boreal-Arctic Transitions (ATLAS)</td>
<td>Chapin, McGuire, Lloyd, Romanovsky</td>
<td>NSF</td>
<td>1998-</td>
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<tr>
<td>Treeline population dynamics</td>
<td>Lloyd, Fastie</td>
<td>NSF</td>
<td>1998-</td>
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and belowground NPP and tissue turnover (H2.1). We will also make initial measurements of vegetation and soils stocks and initiate measurements in our new intensive sites on north-facing uplands (Table 2.2). These and the associated environmental data from these stands provide data for the development, parameterization, and testing of a stand-level biogeochemical model for all the major forest types in interior Alaska.

Comprehensive carbon budget of a black spruce stand (Chapin, Ruess, Sveinbjornsson, Boone, Valentine, McGuire) In a mature black spruce stand, we will begin in year 3 an intensive study of all major C pools and fluxes, including the components of production (roots, mosses, and vascular aboveground) and decomposition (root, moss, and leaf litter, soil organic matter). The purpose of this study is to test the sensitivity of the components of stand C budget to interannual variation in climate (H2.1, H2.4). Comparison of eddy covariance measurements of net ecosystem exchange with chamber measurements of soil respiration (soil + roots) and of ground layer (moss + shrubs + soil + roots) gas exchange and in situ soil incubations (soil) enable us to estimate all the major components of net ecosystem production (NEP), as well as whole-system water and energy exchange. Many black spruce stands in interior Alaska show signs of incipient thermokarst as a result of warming over the past 20 yr. We expect that long-term study of C balance in this old-growth black spruce stand will enable us to document the changes in C flux that accompany permafrost degradation and thermokarst.

Watershed water, carbon and nitrogen budgets (Hinzman) The hydrologic studies at CPCRW are described below in theme 3. They contribute to theme 2 by documenting watershed budgets of water, carbon and nitrogen. The stream exports of dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) are essential components of any complete carbon budget. Measurements of the stream carbon dynamics also present a more complete picture of the impacts of disturbance and documents linkages between terrestrial processes and aquatic ecology. We will continue to maintain the NADP site, which provides the only data on N deposition for the Alaskan boreal forest, and to document N output in stream water. Currently, N outputs in stream water exceed deposition inputs, even 80 yr after disturbance, indicating the importance of watershed studies for understanding the terrestrial N budgets, which, in turn, regulate the carbon budgets. We are also monitoring the soil and stream chemistry to detect and quantify the effects of the experimental burn on the aquatic system (Theme 3). We will measure $^{15}$O and $^{15}$N of stream-water nitrate to differentiate between physical and biological controls over N loss. For instance, if the $^{15}$N signature of nitrate becomes lighter during storm events in the high-permafrost watershed we can infer that rapid nitrification and/or lower denitrification rates are contributing to increased nitrate fluxes that we observe during storm events. If only the more conservative $^{18}$O nitrate signature changes during the same event, then physical mixing of rain and soil nitrate with consequent leaching is the primary cause. Isotopic analysis of stream-water following snow-melt and rain events provides a measure of the water flow path. Cores of stream aufeis serve as a record of stream chemistry from January through March, when it is often difficult to obtain stream water for analyses due to ice cover. The watershed studies provide crucial information needed to improve modeling of the N constraints on carbon fluxes and of the partitioning of precipitation between runoff and evapotranspiration. These processes are important to aquatic studies and to modeling terrestrial feedbacks to climate.

Stand-level process-based studies (Ruess, Schimel, Valentine, Boone) Our process-based LTER research focuses on mosses and on belowground processes, because these are critical but poorly understood links in the feedback from species change (theme 1) to C and N cycling (theme 2) during succession. We concentrate these studies in floodplain stands of alder, poplar, white spruce, and black spruce, where our information on fine root dynamics and carbon turnover are most complete. We know that fine roots are a large labile input of C and N to the soil but have a poor understanding of the fate of these decaying roots, that is, the controls over and rate at which fine root C is respired, incorporated into microbial biomass, or sequestered into recalcitrant soil organic matter. Our goal is to understand how soil temperature and abiotic condensation reactions interact to regulate labile C turnover and sequestration across succession. We will collaborate with Jennifer Harden to use bomb-derived $^{14}$C-CO$_2$ evolved from long-term soil incubations to infer the lability of historic root inputs to the O horizon of black spruce soils.
Table 2.6. Measurements to be made in the BNZ LTER regional studies. These measurements have been selected because they can be done rapidly and are either important parameters or are indices of important parameters. For example, the number of fine roots produced in July is closely correlated with annual root production in our LTER intensive sites. Index parameters will be calibrated against actual variables of interest (e.g., July root number as an index of fine-root production) in our LTER intensive sites.

<table>
<thead>
<tr>
<th>Microclimate</th>
<th>Air and soil temperatures (hourly) with hobo data loggers; soil moisture and thaw depth measured during sampling visits.</th>
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</thead>
<tbody>
<tr>
<td>Population and community parameters</td>
<td>Plant species composition and diversity; tree density, diameter, and height; understory % cover; biomass (based on allometric relationships); number of twigs browsed by hares and moose; number of moose and hare pellets.</td>
</tr>
<tr>
<td>Ecosystem parameters</td>
<td>Litterfall, tree diameter increment (from tree rings of the past 40 years); number of fine roots produced during July using minirhizotrons; root ingrowth screens; net N mineralization rate (total summer period; total winter period); leaf chemical concentrations of the dominant species (N, 15N, 13C); litterbag decomposition of a common substrate.</td>
</tr>
<tr>
<td>Stand age distribution</td>
<td>Age structures and stand histories from tree cores and fire scars from live and dead trees. This effort is more time-consuming than other activities and will be done at selected sites.</td>
</tr>
<tr>
<td>Lakes</td>
<td>Physical and chemical lake-water parameters (conductivity, surface pH, surface temperature, secchi depth, surface turbidity, salinity, nutrients (P, N, organic C, inorganic C)) and modern sediment parameters (magnetic properties, grain size, major element chemistry, stable isotopes of O, N, and C, pollen and diatoms). Then, based upon the results of the calibrations with watershed species composition and biogeochemistry, a subset of analyses will be carried out down core to establish time series of changes through time. A limnological survey of 50 lakes has been completed. We will seek external funding to conduct the palaeoecological analysis of a subset of these lakes.</td>
</tr>
<tr>
<td>Streams</td>
<td>The ARC LTER site will seek external funding for this research.</td>
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</table>
We will measure pool equilibration (14C-labeled) of labile C proxies into metabolic and acid-insoluble C fractions. These long-term pool equilibration studies will be run both in laboratory microcosms (at various temperatures) and in situ across ecosystem types using simple labeled compounds as surrogates for fine root labile C fraction (H2.2).

Our C flux measurements focus on separating moss photosynthesis/respiration, root/mycorrhizal respiration, and heterotrophic respiration. These studies utilize biweekly CO2 flux measurements in root-trenched and control plots, in situ measurements of fine root respiration (Burton et al. Submitted), and incubations of soil organic matter and roots. This will enable us to determine whether root and rhizosphere respiration are more temperature-sensitive than heterotrophic respiration, as observed in eastern deciduous forests (Boone et al. 1999). We know that belowground root inputs to soil organic matter become larger and more labile relative to aboveground litter inputs late in succession and are focusing on the notion that, as relative allocation of NPP belowground increases, soil respiration will become more responsive to high temperature (H2.1).

Successional changes in the C cycle are intimately linked to N cycling. We have shown that boreal trees absorb amino acids intact in the field. Externally funded research is documenting the successional changes in organic N uptake and its role in vegetation N budgets using natural abundance surveys and 15N/13C amino-acid addition experiments (Table 2.5). The LTER research will link the organic N to C cycling by comparing organic N uptake by plants and microbes (pool dilution experiments and pulse-chase experiments (Davidson et al. 1991, Schimel and Chapin 1996) and estimating the role of labile C in the mineralization of organic N to mineral N.

Gross N inputs to floodplain ecosystems from N2 fixation by alder are much greater than N accumulation estimated by mass balance (Uliassi and Ruess Submitted). This discrepancy increases with succession, suggesting that N losses from leaching (DIN and DON) and/or denitrification increase with succession. The watershed budgets indicate that losses from leaching predominate during late fall and early spring, when there are frequent freeze-thawing events and reduced biological uptake. We have initiated a study to quantify N denitrification and leaching losses in poplar and white spruce forests on the floodplain.

Experimental Tests of Controls over Processes

Manipulation of soil resources. (Valentine and Ruess) Climate and succession are thought to control NPP and C cycling primarily through their effects on the availability of soil resources (Van Cleve et al. 1991). In 1989 we established experiments that altered C:N ratio of soils through chronic additions of N and a one-time addition of sawdust. We also reduced growing-season moisture supply using rain-out shelters (Yarie and Van Cleve 1996). We will continue measuring the components of NPP in these sites. We will measure decomposition rates of leaf litter and standardized substrates to distinguish influences of litter chemistry and soil environment on long-term biogeochemical feedbacks. In other studies we measure effects of N addition on whole-stand C allocation and fine root and mycorrhizal longevity.

Herbivore exclosure experiments. (Kielland) From the estimates of browse consumption in different successional stages (theme 1), and tissue N analysis, we will estimate the C and N inputs by herbivores, relative to direct inputs from plant litter (H2.3). Comparison of aboveground litter inputs and root turnover inside and outside exclosures (Ruess et al. 1998) provides a test of the indirect effects of herbivores on C and N cycling through changes in vegetation and associated changes in litter quality, quantity, and allocation.

Disturbance effects on carbon and nitrogen cycling. (Valentine, Chapin, and Boone) Following the FROSTFIRE experimental burn in summer 1999, we added (15NH4)2SO4 to four replicate burned and unburned stands to follow the long-term fate of N returned to the soil in ash. The plots are large enough (144 m2) and have sufficient label to follow N retention on the site for at least the next 50 yr. As a component of LTER, we will document the mechanisms of N retention (N incorporation into plants, microbial biomass, and physical adsorption) and the rate at which the 15N is diluted by newly fixed N. Using lysimeters we will document N loss to
Disturbance (Theme 3) → Forest dynamics (Theme 1) → CLIMATE

NPP (Plant productivity) → NEP (Net ecosystem productivity) → Root & Soil Resp. (Symbiotic nitrogen fixation, mineralization).

C & N Sequestration (Valuation)

Theme 2
BOREAL CARBON CYCLE

Fig. 2.11. Hypothesized relationship among processes governing the changing boreal carbon cycle (theme 2). We hypothesize that stand productivity is sensitive to climate (including soil environment), disturbance, and stand composition (links to themes 1 and 3). The successional changes in plant litter composition reflect both changes in species composition and allocation. In particular, we hypothesize that the large increase in root production and turnover through succession provide large inputs of labile C and support high rates of root, rhizosphere, and heterotrophic respiration. The balance between NPP and heterotrophic respiration determine net carbon exchange of the stand (NEP), i.e., whether the ecosystem is a net source or sink of atmospheric CO2. The supplies of inorganic and organic N depend on the balance between microbial mineralization and immobilization.

Fig. 2.12. Changes in NPP and heterotrophic respiration (RH) through succession after disturbance as simulated for a boreal forest stand in interior Alaska under a constant climate by TEM. Immediately after disturbance NPP declines dramatically because of loss of leaf area, and increases as the canopy develops through succession. NPP reaches a peak at about 80 years and then declines gradually to pre-disturbance levels as the vegetation loses nitrogen to the soil. The pre-disturbance and post-disturbance "equilibrium" values of NPP depend on the amount of nitrogen in the system. A net loss of nitrogen from the system over the disturbance-recovery cycle will result in a lower "equilibrium" level of NPP, whereas a net gain of nitrogen will result in a high level of NPP. In contrast to NPP, RH increases immediately after the disturbance event because of an increased root mortality associated with the disturbance event. RH gradually declines until approximately year 60 as the amount of organic substrate in the soil declines because losses to decomposition exceed inputs from litterfall production. The system is in positive carbon balance at approximately year 30 when NPP exceeds RH. After year 60, RH increases as increases in litterfall production exceed RH to increase the amount of organic substrate available for decomposition.
groundwater as nitrate, ammonium, and DON. NADP measurements of N deposition, and watershed measurements of N loss at the site provide input-output constraints on the N budget. We seek external funding to support detailed documentation of the mechanisms of N retention, but LTER funding is sufficient to enable us to document the extent of N retention and its partitioning among plants, microbial biomass, and soil-fixed N (Schimel and Chapin 1996).

Spatial and Temporal Scaling

In the floodplain successional sequence we have documented production of trees and roots and are documenting NPP of shrubs and mosses, providing estimates of total NPP. In the next two years we will continue these measurements to document interannual variability in NPP and determine a simplified set of measurements that can be used to estimate annual fluxes at other sites. For example, live root number is a good predictor of biomass on minirhizotron images, allowing fine root production and mortality to be estimated relatively rapidly (Ruess et al. 1998). Based on the relationships that we develop in the first two years of the research, we will establish a simplified sampling protocol to estimate fluxes in north- and south-facing upland stands to test whether the models developed with floodplain data accurately simulate fluxes of C and N in the uplands. These measurements provide a basis for estimating patterns of C and N cycling through succession in each of the major landscape units (floodplain, north- and south-facing uplands).

We will place our biogeochemical studies in a regional context by extensive sampling in the Fairbanks Region and along the Alaska Climate Transect, using the same sites and sampling design described in Theme 1. At these black spruce sites, we will measure critical input variables for biogeochemical modeling (C and N pools in vegetation and soils, soil temperature and moisture, etc.) and simple indices of model outputs of components of NPP and organic matter turnover (ring-width increment, litterfall, root ingrowth screens, net N mineralization, litterbag decomposition of a common substrate). These rapid measures will be calibrated against more intensive measurements at our LTER intensive sites. We will seek separate funding to document soil organic matter turnover, using 14C profiles (Trumbore and Harden 1997).

Using a 30-yr record of ring-width, litterfall, and stand density, we are developing relationships between ring-width and NPP, to extrapolate our estimates of NPP over the 300 yr ring-width record. The 30-yr direct record of NPP provides a useful validation data set for model simulations of NPP. We are in the exploratory phase of extrapolating biogeochemical indicators back through the sediment record. For the last 1000 yr and for the period prior to 4000-5000 yr ago, for which we will have climate and vegetation records (see theme 1), we will analyze sediment samples for chemical and isotopic indices of watershed biogeochemistry. For example, we expect Fe and Mn concentrations to be sensitive to lake pH and therefore organic accumulation in the watershed. If these efforts prove successful, we will apply the same approach to lakes along the Alaska Climate Transect.

Modeling the Linkage of Pattern and Process

We will use the biogeochemical model TEM (parameterized with floodplain data) to provide an integrated picture of boreal C and N cycling. The most recent version of the model, which has largely been parameterized with information from studies at the Bonanza Creek Experimental Forest, accurately simulates seasonal and interannual net C exchange of mature Canadian black spruce forests (Fig. 1.3) (Amthor et al. Submitted, Clein et al. Submitted), giving us confidence that the model is a useful tool for extrapolation. We have applied this version of the model to explore the role of the effects of changes in atmospheric carbon dioxide, climate, and fire regime on historical carbon dynamics for Alaska (Fig. 2.14). We are currently incorporating soil thermal and hydrologic dynamics (Hinzman et al. 1996, Romanovsky et al. 1997) into TEM and including additional pools and fluxes as a tool for exploring the consequences of alternative hypotheses concerning the role of root dynamics (H2.1, H2.2), the quality of soil organic matter (H2.2), herbivory (H2.3), and nitrogen dynamics in affecting carbon dynamics through succession. These changes in model structure provides the capability to represent this improved understanding in simulations of regional carbon dynamics. The regional application of TEM driven with historical data sets on climate (theme 1) and on the timing and
Fig. 2.13. In contrast to pronounced decreases in aboveground letter quality and quantity through succession, there are comparatively subtle changes in fine root litter quality and quantity among seres. A) Using the Century model structure (Parton et al. 1987), we envision the possible fates of fine-root derived C to be 3-fold: 1) preserved by low temperatures in relatively labile form in slow or passive turnover pools (cryoprotected), 2) chemically or biologically sequestered into humates, and 3) respired as CO₂ after deposition. While all of these occur, the partitioning of C among these determines the future responsiveness of soil C dynamics to climate variability. B) Using methods pioneered by Trumbore and Harden (1997), we will use laboratory incubations of bomb-derived ¹⁴C as a tracer of C fixed during the 1960's. We expect that cryoprotected organic matter will increase apparent Q₁₀'s, and that the resulting CO₂ will initially be enriched in ¹⁴C. An increase over time in ¹⁴C enrichment during a long-term incubation will suggest that most of the bomb-derived C was sequestered in less-climatically sensitive slow and passive pools.
The location of fire disturbance and subsequent vegetation transitions (theme 3) will allow us to evaluate the relative role of climate and fire regime on regional carbon dynamics in a historical context (H2.4).

Linkage of TEM with other models provides the opportunity to test the integrated response of the boreal forest to changes in climate and disturbance, which is something that we cannot readily achieve with field measurements alone. The representation of biogeochemistry in TEM will be incorporated into the DVM to evaluate interactions between species dynamics (theme 1) and biogeochemistry. Use of the model with historical climate data set (theme 1) provides a test of the climate sensitivity of boreal C cycling (H2.1, H2.2, H2.4). The coupled application of TEM and ALFRESCO (theme 1) enables us to consider the role of vegetation transitions, seed dispersal, fire spread, and fuel dynamics in evaluating the relative roles of climate and fire regime on regional carbon dynamics in the context of projected climate changes (H2.4).

2.9 Theme 3. Landscape controls over changing disturbance regime

Conceptual framework

Our goal in theme 3 is to understand how the processes operating within and among ecosystems on a landscape influence the impact of a changing climate on disturbance regime (Fig. 2.15). There are many stand-level properties related to forest dynamics (theme 1) and biogeochemistry (theme 2) that influence disturbance regime. For example, the probability of fire increases substantially at the turning point when more flammable feather mosses and spruce replace deciduous trees. Conversely, thermokarst probability may be greatest following fire and decline as mosses invade and insulate the soil. Biogeochemistry affects disturbance probability directly. Factors that promote carbon sequestration increase the fuel load to support fire but increase the insulative properties that reduce the probability of thermokarst. Landscape composition and structure also strongly influence disturbance probability by determining the proportion and pattern of disturbance-prone stands on the landscape. For example, disturbance increases the proportion of early successional stands in the landscape (Chapin et al. In press). These stands are both nonflammable and unsuitable for forest harvest, creating a negative feedback to disturbance probability. The patch size of flammable and nonflammable stands on the landscape influences the probability of large fires (Rupp et al. In press, Turner et al. In press). Changes in climate alter disturbance regime in several ways. For example, climate directly affects fire probability through effects on fuel moisture and flammability. Climate affects ignition probability through lightning strike density. Climate might also alter landscape controls over fire regime in other ways, e.g., through drought-induced diminution in the effectiveness of deciduous vegetation as a fire break or changes in successional trajectories. Any significant disturbance could increase the active layer thickness in proportion to disturbance severity. If the active layer thickens to the extent that it does not refreeze the following winter, then the soil regime could become warmer and drier as soils continue to drain during winter, impacting successional dynamics (Theme 1) and local biogeochemical processes (Theme 2). To evaluate our conceptual framework of disturbance, we will test the following hypotheses:

H3.1. Large fires occur only on landscapes dominated by black spruce. Warm dry climate increases the probability of large fires by reducing the effectiveness of deciduous stands as a landscape-scale fire break.

H3.2. The natural fire regime is controlled more by flammability than by ignition, so there is a low correlation between total annual lightning strikes and total annual area burned.

H3.3. Thermokarst is triggered primarily by past disturbance rather than by the direct effect of climate on soil temperature.

H3.4. The smaller size and greater frequency of disturbance on floodplains than in uplands results in numerous small shrub patches that support greater stability of herbivore populations.
Fig. 2.14. The (a) net carbon flux and (b) changes in carbon stocks relative to 1956 simulated by the Terrestrial Ecosystem Model (TEM) for a boreal forest stand in interior Alaska (longitude = 144.5 W, latitude = 64.0 degrees N) that burned in 1957, and the (c) net carbon flux and (d) changes in carbon stocks relative to 1950 simulated by the Terrestrial Ecosystem Model (TEM) for the entire state of Alaska. Net carbon flux is calculated as net primary production minus heterotrophic respiration minus fire emissions. The dynamics of three simulations are compared: CO2 only, CO2 plus climate, and CO2 plus climate plus fire. For the simulation with fire, burn severity was prescribed as a loss of 23% vegetation carbon to the atmosphere and 36% soil carbon to the atmosphere as fire emissions; these levels are typical for interior Alaska (Kasischke, personal communication). The pattern of fire timing and location was prescribed by the large fire data base for interior Alaska, which begins in 1950. The comparison indicates that the response of stand-level carbon storage to increases in CO2 is highly constrained by nitrogen dynamics, that interannual variability in the response to climate is +/- 0.1 tons per hectare per year, that the stand does not enter positive carbon balance after the fire event until approximately 1970, and that the trajectory of carbon recovery after positive carbon balance is approximately 5 tons per hectare every 20 years. Simulation results are from McGuire et al. (in preparation). The state-wide comparison indicates that the response of carbon storage to increases in CO2 is highly constrained by nitrogen dynamics, that interannual variability in the response to climate is +/- 30 Tg C per year, that CO2 and climate interact to cause positive carbon storage as enhanced nitrogen cycling in response to warming since the 1960s allows vegetation to incorporate rising CO2 into production at a rate of about 50 Tg C per decade, that high fire years can emit as much as 60 Tg C per year, and that the long-term pattern of carbon storage for the simulation with fire is generally tracking the pattern for the simulation with CO2 plus climate. Simulation results are from McGuire et al. (in preparation).
H3.5. Watershed hydrologic and biogeochemical properties are primarily the result of microclimate-disturbance interactions.

Approach

During LTER-3 our study of climate-disturbance interactions will focus on fire and thermokarst, because these disturbance types have increased in response to a warming climate and are common across the Alaskan boreal forest. We will also document patterns of logging at the regional scale and the impacts of flooding and herbivory at the stand scale, as described previously.

Observations of Landscape-Level Pattern and Process

Spatial variation in fire regime. (Verbyla, Kasischke) In the 100 x 100 km Fairbanks Region, we will use remote-sensing imagery to assess the accuracy of maps developed from historical fire records (Kasischke and French 1998). We will develop GIS data layers for pre-fire vegetation, current vegetation, aspect, elevation, weather at the time of the fire, and recorded cause of the fire. We can then estimate fire probability as a function of topography, pre-fire vegetation, and climate (H3.1, H3.2). Lightning from thunderstorms is the dominant fire-starting mechanism for large wildfires in interior Alaska. Using the lightning strike network in Alaska, we will relate fire probability to density of lightning strikes, fuel moisture conditions, vegetation type, and vegetation heterogeneity (H3.1, H3.2). The relationships among these parameters will be the basis of the disturbance modules in the DVM and ALFRESCO.

We will use pre- and post-fire imagery to examine the impact of fire on successional trajectories. For example, we can estimate the probability of post-fire broadleaf versus black spruce vegetation as a function of topographic position, pre-fire vegetation, and fire size. We expect post-fire black spruce to be maintained in areas where mineral soil is not exposed by fire due to low fuel load, cool-moist topographic position, or low fire severity. We expect aspen to invade areas where high fire severity has exposed mineral soil. The results of these analyses will be useful for modeling forest dynamics (theme 1).

Permafrost Dynamics and Thermokarst. (Hinzman and Romanovsky) Fire severity may have a long lasting impact on boreal forest ecosystems through effects on the surface water and energy balances and underlying permafrost. Moderate fires leave the organic surface soil relatively intact, providing the necessary insulation to prevent the underlying permafrost from rapidly degrading. Severe fires that combust the insulative layer and expose the mineral soil beneath improve internal drainage and result in drier surface soil. Any disturbance to the surface layer will increase heat flow through the active layer (the layer of soil above the permafrost that thaws and re-freezes seasonally) into the permafrost. Preserving the surface organic layer is critical to maintaining the thermal integrity of the permafrost. Under the current climatic regime, thermokarst is likely to develop in severely disturbed sites over the warm, ice-rich discontinuous permafrost common in Interior Alaska (Fig. 2.16). We currently have no regional map of thermokarst, so we will use a model developed at CPCRW that simulates topographic patterns of permafrost as a function of climate (Hinzman et al. 1997). This model will be applied to the Fairbanks Region and to the Alaska Climate Transect to estimate regional pattern of permafrost temperatures (and therefore probability of thermokarst—i.e., permafrost temperature > 0°C) for the climates of 1920 (a cool period), 1970 (just prior to recent regional warming), and today. A set of 50-100 sites will be visited to document current permafrost regime to validate the model and test hypothesis H3.3. The age when thermokarst began can be determined from asymmetry of tree rings. Survey transects will be established in the burned forests of the Frostfire experiment in areas prone to thermokarst to detect depressions as they develop and grow. This will enable us to validate heat flow models that predict incipient thermokarst (Hinzman et al. 1997).

On cold sites, the probability of a disturbance exposing mineral soil for establishment of aspen or birch seedlings is low because of high soil water content, cold soil temperatures, and a relatively deep organic horizon. Thus, the regional distribution of black spruce may reflect permafrost distribution. We will apply the permafrost temperature model to the Fairbanks
Fig. 2.15. Hypothesized relationship among processes governing regional and landscape controls over disturbance regime (theme 3). We hypothesize that climate strongly affects both fire and thermokarst and that all disturbances affect biogeochemistry (theme 2). Climate, fire and harvest regime also influence landscape structure, which together with soil moisture (hydrology) influence forest dynamics (theme 1).
Region to predict the probability of black spruce as a function of permafrost. This prediction will then be compared with the actual distribution of black spruce as estimated from satellite remote sensing.

**Hydrologic response to climate and disturbance.** (Hinzman) The watershed studies at CPCRW provide an opportunity to examine the interaction of climate and disturbance on hydrology and biogeochemistry and to integrate these at the landscape scale. There are three intensively studied watersheds, one dominated by north-facing uplands, one dominated by south-facing uplands, and an intermediate watershed that was burned experimentally in 1999 (FROSTFIRE) (Fig. 2.17). These watersheds have a 10-30 yr record of climate and discharge, and a shorter record of stream chemistry. Together they provide a long-term context for measurements of the effects of microclimate (north vs. south-facing watersheds) and disturbance regime (burned vs. unburned) (H3.5). There are two major emphases in the watershed studies: (1) integrated watershed budgets and (2) study of chemical transformations associated with lateral flow. Measurements of stream discharge and chemistry reveal a great deal about the effects of disturbance and microclimate on water balance, erosion, and nutrient transport (integrated watershed budgets). Comparisons of groundwater vs. stream carbon and nitrogen chemistry demonstrate additional controls that are not evident in stand-level measurements. For example, the CPCRW streams show nitrate losses that exceed inputs, which we would not have expected from our stand-level measurements or the literature on temperate N-limited ecosystems (Hedin et al. 1995). We will use isotopic signatures in oxygen, carbon, and nitrogen to quantify ground-water and active layer flow paths and residence times of water as it moves into the stream. These watershed measurements then guide the stand-level measurements needed to understand these nitrogen dynamics (Theme 2).

**Landscape Feedbacks from Disturbance Size to Forest Dynamics.** (Walker, Juday, Verbyla, Rexstad). New willow communities that establish following alluvial deposition in the BCEF floodplain are smaller and perhaps more readily colonized by herbivores than are large upland burns. Snowshoe hares are an "edge species" requiring juxtaposition of early successional forage habitat and late successional cover from predators. We will use historic and current color-infrared aerial photography to map shrub patches from the BCEF floodplain and uplands to compare shrub patch size and temporal dynamics and will examine these patches for evidence of herbivore activity. This project links landscape structure (theme 3) to herbivory and forest dynamics (theme 1) to test H3.4.

**Experimental Tests of Controls over Processes**

**Fire.** (Hinzman and Chapin) LTER is now monitoring the impact of the 1999 experimental fire (FROSTFIRE) on forest regeneration (theme 1), carbon stocks and carbon exchange (theme 2), and permafrost dynamics and hydrologic impacts (theme 3) for comparison with pre-fire measurements. See previous sections for details.

**Forest harvest.** (Wurutz) See forest harvest under theme 1.

**Herbivory.** See exclosures and insect outbreaks under theme 1.

**Temporal Scaling**

**Black Spruce-Wildfire Interactions.** (Finney, Edwards, Lloyd, Verbyla) We will improve our temporal resolution of the relationship between vegetation, fire, and climate by analyses of charcoal, pollen, and climate proxies in annually laminated lake sediments (Millspaugh and Whitlock 1995, Clark and Hussey 1996). Macro-charcoal concentrations estimate fires within the lake catchment; micro-charcoal gives a more regional picture. (See theme 1)

**Modeling the Linkage of Pattern and Process**

The interactive effects of climate and landscape structure on area burned will be simulated by ALFRESCO (H3.1, H3.2). Stand-level models can then simulate the resulting effects on stand composition (H1.4, SKOG, DVM), animal population dynamics (H3.4) (Rexstad 1994), soil thermal and hydrologic regimes (H3.3, H3.5) (Hinzman et al. 1998), and biogeochemistry (H2.4; TEM). Together these modeling efforts link our research on disturbance (theme 3) to forest dynamics (theme 1) and biogeochemistry (theme 2).
Fig. 2.16. Thermokarst formation and effects on surrounding vegetation and landscape. Areas with ice-rich permafrost are most vulnerable to thermokarst. The large blue wedges shown in the top frame are lenses of ice that grow and thicken over time. When there is a disturbance to the organic soil layer (the brown layer at the top of the soil section), the underlying ice may begin to melt. Eventually a pond is formed from the saturated soils, which may still have remnant permafrost underneath. The "tipping trees" shown in the lower frame are typical of landscapes that have undergone this process.
2.10 Program integration

We described in previous sections the integration that occurs within each theme (Fig. 2.9, 2.11, 2.15). Here we briefly describe the research connections among the themes (Fig. 2.18), the mechanisms of achieving this integration, and the conceptual issues that our synthesis will address. Climate directly affects virtually all our aspects of the boreal forest (Fig. 2.18), which we document through study of ecological responses to temporal variation (interannual variability, tree-rings, successional change, the pollen record) and spatial variation (topographic and regional) in climate. Forest dynamics (theme 1) responds not only to climate but also to topographic and successional variation in biogeochemistry (theme 2) and to disturbance regime and soil moisture (theme 3). Biogeochemistry is sensitive to climate, forest structure, and disturbance. It affects disturbance regime through its effects on forest structure and feeds back to regional climate through its effect on net carbon exchange and energy balance. Landscape structure and disturbance respond sensitively to climate and forest structure and affect patterns of stand initiation following disturbance (Fig. 2.18). In addition to the strong scientific connections among our research themes, we have several mechanisms that promote scientific integration:

- **Use of common sites and experiments.** By collecting a consistent set of measurements from the same intensive and regional study sites, we have a strong basis for comparisons and synthetic work. Perhaps more important, the use of common study sites facilitates the interaction among scientists and the integration of results from different types of studies.

- **Hierarchical research design.** Each of our study themes requires an understanding of processes at spatial scales ranging from the individual organism to large regions, although each theme has a predominant scale at which most of the research is conducted (e.g., the stand scale for theme 1 and the landscape scale for theme 3). Our choice of intensive and extensive sites is guided by this hierarchical perspective (Walker and Walker 1991), in which we stratify the region into landscape units (north-facing, south-facing, floodplain), each of which contains stands of different successional ages, with additional variability within and among stands of a given age. The long-term temporal perspective is important because the natural range of variability in time-varying processes (climate, disturbance regimes, infrequent events, vegetation dynamics) cannot be captured from studies at a single temporal scale.

- **Modeling Key Research Components.** Our use of a suite of models based on processes that operate at different temporal and spatial scales enables us to incorporate our understanding developed at one scale and explore the logical consequences at other scales. The models provide tools by which each researcher can refine questions about controls over the process which (s)he studies. In this way we explicitly recognize the consequences of these process controls for other components of the system, particularly at large temporal and spatial scales.

- **Synthesis volume.** Our synthesis volume will be a "readable" description of "The Changing Boreal Forest", rather than an edited volume that summarizes only LTER research. The book will explain our current understanding of the structure and functioning of the boreal forest. The necessary cross-referencing among processes and chapters will inevitably improve our understanding of the linkages among processes and scales. The book has been outlined, and serious writing will begin following submission of this proposal.

- **Contributions to Conceptual Issues in Ecology.** Our research is motivated by many of the long-standing and recently developing conceptual issues in ecology (Table 2.1) and directly addresses the application of these issues to understanding of the functioning of the boreal forest. Our synthesis will address three subjects that bridge the subdisciplines of ecology (diversity effects on ecosystem processes, spatio-temporal scaling, and ecosystem sustainability) and which are essential to the application of scientific understanding to ecosystem management. Our research directly addresses each of these areas, providing us with the opportunity to make strong contributions to the theoretical developments in ecology, the integration of ecology with other disciplines, and the application of ecological theory to resolving current environmental problems.

- **Diversity-function relationships.** Test of the turning points concept provides an explicit test of ways in which species traits influence ecosystem processes (Chapin et al. 1998). Most previous tests have been with short-term experiments in herbaceous communities (Tilman and...
Fig. 2.17. Effects of fire severity on vegetation and permafrost. Fire severity will impact successional (theme 1) and biogeochemical (theme 2) processes and long-term landscape evolution (theme 3). The short and long-term impacts of a disturbance such as a forest fire will be greatly influenced by the degree of fire severity. After a severe burn, the surficial organic soil is completely removed, leaving the underlying permafrost sensitive to thermal degradation. A talik, or unfrozen zone above the permafrost and below the seasonally frozen soil, may allow internal drainage to continue year round ultimately yielding warmer and drier soils.
Downing 1994, Tilman et al. 1996, Hooper 1998, Hooper and Vitousek 1998). The DVM incorporates the documented effects of species or functional types on biogeochemistry and disturbance (Chapin et al. 1996a, Chapin et al. 1996b) and can be used to simulate the long-term consequences (Coffin and Lauenroth 1990, Kittel et al. In press) of various scenarios of climate, fire, and management. Our studies of diversity (H1.3) explicitly test causes of landscape and regional patterns of diversity.

Spatio-temporal scaling. Scaling is a pragmatic problem because scientists have been unable to incorporate critical processes (e.g., cloud nucleation and disturbance spread) at large temporal and spatial scales. It is of fundamental theoretical interest because processes that are observed at large scales are often the patterns to be explained at smaller scales (Allen and Starr 1982, Walker and Walker 1991, Allen and Hoekstra 1992), raising questions about the consequences of processes at spatial and temporal scales other than those at which they are measured. Virtually every question addressed by the BNZ LTER is considered at a broad range of temporal and spatial scales, and our modeling is explicitly aimed at linking processes across scales, so we expect to contribute substantially to understanding of the linking of processes across scales.

Ecosystem sustainability. The sustainability of ecosystems depends on the interactions among negative feedbacks that retain the system in its current state and positive feedbacks that push it toward a new state (DeAngelis et al. 1986, DeAngelis and Post 1991, Chapin et al. 1996c). The strong directional changes in virtually all determinants of ecosystem functioning (climate, soil resources, biota) threaten the future sustainability of the biosphere (Vitousek 1994, Walker et al. 1998).

Our long-term goal of BNZ LTER research is to develop the scientific understanding necessary to assure the sustainability of the boreal forest (Chapin and Whiteman 1998).

Integration with other research programs. The BNZ LTER has chosen to focus on the interaction of climate and disturbance, as these affect the functioning of the Alaskan boreal forest. We extend this research by seeking additional outside funding (Table 2.5) and attracting collaborators who build on and contribute to our LTER research (Table 2.7). Research that is essential to understanding of the boreal forest but beyond the funding capabilities of the LTER includes (Tables 1.2, 2.5, 2.7):

1. Process studies of fine root and mycorrhizal dynamics (Ruess), organic N uptake (Kielland), microbial C dynamics (Schimel), soil C turnover (Harden, Schuur), fire behavior (Sandberg), insect outbreaks (Raffa), vertebrate population cycles (Rexstad), permafrost dynamics (Romanovsky), river runoff (Hinzman), land-surface feedbacks to climate (Lynch, Chapin), boreal forest and the global C cycle (McGuire)
2. Regional comparisons with the boreal forests of Canada (Apps, Gower) and Russia (Zimov, Fukuda) and with other LTER sites.
3. Human dimensions of the boreal forest, including timber harvest (Wurtz), and fire control (Chapin, Naylor).
4. Patterns of change including genetic diversity (Cook, Denton), biodiversity (Walker), species migration (Sveinbjornsson, Lloyd, Juday, Starfield), disturbance regime (Kasischke), land cover (McGuire, Melillo), climate (Chapin, Lynch), and social processes (Naylor).
5. Model development at scales ranging from populations (Malmstrom, Rexstad) to landscapes (Starfield) to regions and the globe (McGuire, Melillo, Harden).
Fig. 2.18. Summary of the BNZ LTER research program. Research integration within each theme is described in Figs. 2.9, 2.11, and 2.15. Successional changes in N supply (theme 2) affect species composition and biomass (theme 1) and vice versa. Stand composition and landscape structure affect ecosystem exchanges of water, energy, and CO2, which in turn affect regional climate. Disturbance both affects and is affected by forest composition. Soil moisture (hydrology) affects forest composition and biogeochemistry. Specific measurements being made to document these effects are shown in Table 2.4.
Table 2.7. Research by BNZ affiliate scientists (non-BNZ PIs) that integrates with BNZ research. The research by BNZ affiliate scientists is closely coordinated with BNZ LTER research but is directed by non-LTER PIs.

<table>
<thead>
<tr>
<th>Project</th>
<th>PI</th>
<th>Agency</th>
<th>Start</th>
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<tbody>
<tr>
<td>Climate</td>
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<tr>
<td>Meteorological processes</td>
<td>Ishikawa</td>
<td>JAMSTEC</td>
<td>1997-</td>
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<tr>
<td>Regional climate modeling (veg. Feedbacks)</td>
<td>Lynch, Wu</td>
<td>NSF</td>
<td>1997-</td>
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<tr>
<td>Theme 1</td>
<td></td>
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<tr>
<td>Forest population dynamics model (SKOG)</td>
<td>Malmstrom</td>
<td>NASA</td>
<td>1998-</td>
</tr>
<tr>
<td>Genetic diversity of Alaskan biota</td>
<td>Cook, Denton</td>
<td>UAF</td>
<td>1998-</td>
</tr>
<tr>
<td>Alaska tree-ring transect</td>
<td>Jacoby, D’Arrigo</td>
<td>NSF</td>
<td></td>
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<tr>
<td>Proposed</td>
<td></td>
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<tr>
<td>Fire effects on mycorrhizae</td>
<td>Helm</td>
<td>NSF</td>
<td>1999-</td>
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<tr>
<td>Geographic patterns of fungal diversity</td>
<td>Laursen</td>
<td>UAF</td>
<td>1998-</td>
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<td>North American boreal vegetation map</td>
<td>McDonald</td>
<td>NASA</td>
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<td>Theme 2</td>
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<td>Holocene C and N cycling (fire effects)</td>
<td>Harden</td>
<td>USGS</td>
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<td>Post-fire N retention (15N addition expts)</td>
<td>Mack</td>
<td>NSF</td>
<td>1999-</td>
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<td>Fire effects on atmospheric C budgets</td>
<td>Randerson, Neff</td>
<td>Cal Tech</td>
<td>1999-</td>
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<td>Remote sensing of canopy N</td>
<td>Zimmermann</td>
<td>IARC</td>
<td>1999-</td>
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<tr>
<td>Watershed nutrient dynamics</td>
<td>Shibata</td>
<td>NASA</td>
<td>1998-</td>
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<tr>
<td>Inventories of boreal soil carbon</td>
<td>Ping</td>
<td>NASA</td>
<td>1998-</td>
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<tr>
<td>Land-cover change and the global C cycle</td>
<td>Melillo</td>
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<td>Veg. effects on soil 14C turnover after fire</td>
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<td>1999-</td>
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<td>Theme 3</td>
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<tr>
<td>Experimental burns in Alaska and Siberia</td>
<td>Fukuda</td>
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<td>Fire behavior modeling</td>
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<td>Boreal tree-line modeling (climate/fire effects)</td>
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<td>NASA-JPL</td>
<td>1994-</td>
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<td>Urano</td>
<td>NASA</td>
<td>1998-</td>
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<td>1999-</td>
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<td>Other regions</td>
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<td>Canadian and circum-boreal Carbon budgets</td>
<td>Apps</td>
<td>Can FS</td>
<td>1995-</td>
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<td>Siberian boreal C and CH4 emissions</td>
<td>Zimov</td>
<td>Russian SF</td>
<td>1995-</td>
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<tr>
<td>BOREAS follow-up (carbon balance)</td>
<td>Gower</td>
<td>NASA</td>
<td>1998-</td>
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<td>LTER national network, especially</td>
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<td>Arctic LTER</td>
<td>Hobbie, Shaver</td>
<td>NSF</td>
<td>1987-</td>
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<td>HJ Andrews LTER</td>
<td>Swanson</td>
<td>NSF</td>
<td>1987-</td>
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</table>
Section 3  Literature Cited in Sections 1 and 2


Cater, T. C., and F. S. Chapin, III. In press. Differential species effects on tree seedling establishment in boreal post-fire succession: Resource competition or modification of microenvironment? Ecology


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Ryan, M. G., D. Binkley, and J. H. Fownes. In press. Age-related decline in forest productivity: pattern and process. Advances in Ecological Research


Ecosystems


Section 4 Site management

The Bonanza Creek LTER project is jointly funded by NSF and by the U.S. Forest Service (through the Pacific Northwest Experiment Station). Over the past four years BNZ has undergone a substantial change in leadership and organization as a result of the closure of the Institute of Northern Forestry (the USFS Experiment Station in interior Alaska) and the retirement of the lead PIs for both the NSF (Van Cleve) and the Forest Service (Viereck) components of BNZ. Following the closure of INF, PNW established a new Cooperative Forestry Research Unit at the University of Alaska Fairbanks, which provides a continuing Forest Service presence in the BNZ LTER. In the two years since our previous proposal, several changes have solidified the BNZ leadership. Stuart Chapin and Marilyn Walker, the co-directors of the BNZ LTER, have moved to the University of Alaska, with Chapin as a UAF faculty member and Walker as the USFS unit leader. Both co-directors now focus their research primarily on the BNZ LTER sites, with their major effort directed toward the integration of the research program described in this proposal.

BNZ LTER has two intensive research sites: The Bonanza Creek Experimental Forest (BCEF) is within the Tanana State Forest and is managed by the PNW Cooperative Forestry Unit through a renewable 50-yr lease. The Caribou-Poker Creek Research Watersheds (CPCRW) was added to the BNZ LTER program during LTER2 because it is the major site of hydrologic and aquatic research in interior Alaska. It includes lands under the jurisdiction of the University of Alaska and the Alaska DNR. The BNZ LTER manages BCEF and CPCRW, with general policy issues addressed by the BNZ executive committee and detailed management overseen by the site manager and the staff responsible for the long-term monitoring at BCEF and CPCRW.

The Forest Service and NSF-sponsored 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 NSF and USFS components. The PIs (Chapin and Walker) are jointly responsible for ensuring that all research conducted at Bonanza Creek and CPCRW is in the best interests of the long-term research program in these sites. A site manager (currently being recruited) deals with daily management issues (Fig. 4.1). 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. Decisions about scientific direction of the LTER are made at five levels.

1. Chapin and Walker are jointly responsible for the continuity and quality of long-term measurements of the BNZ LTER as co-directors of the BNZ LTER (Fig. 4.1). They meet weekly to discuss important issues.
2. A national advisory committee provides guidance on effectiveness of the general research directions of the BNZ LTER program. This group will meet once in year 4.
3. Chapin and Walker make major policy decisions governing the direction of the overall LTER program, with the advice of a 6-member executive committee (Ruess, McGuire, Valentine, Viereck, Verbyla, and Hinzman in LTER3). These decisions include budget allocation, integration among research components within LTER, linkages between LTER and other research programs, data management policy, etc. To date, all issues have been decided by consensus of this group. If this group cannot reach consensus, the PI (Chapin) will make the decision. The BNZ executive committee convenes monthly in meetings that are open to all BNZ LTER scientists. At these meetings we discuss any issues of concern plus an in-depth discussion of a topic of general interest. This meeting format proved productive in the preparation for this renewal proposal.
4. A theme leader who is a member of the LTER executive committee (Fig. 4.1, Table 4.1) coordinates integration within each of the three research themes. Within each theme there are specific research components for which an LTER scientist is responsible. These groups make most of the day-to-day scientific decisions about how to conduct the research within individual components. Broader issues are brought to
Fig. 4.1. Management structure of the BNZ LTER. The BNZ co-directors (Chapin and Walker) are responsible for (1) maintaining the long-term integrity of the research sites, (2) directing the scientific program of the BNZ LTER, and (3) ensuring the relevance of the research program to national and international scientific issues. Decisions concerning site integrity of our permanent study sites (BCEF and CPCRW) are made by the LTER co-directors, with input from land management agencies. The LTER site manager addresses daily issues affecting site integrity. The LTER Science Program is described in Table 4.1 of the proposal text. The BNZ actively participates in the national LTER network. It addresses the concerns of the USFS through the Northern Forestry Cooperative Unit, directed by Walker and funded by the USFS. We receive periodic advice from our National Advisory Committee about how best to address major conceptual and environmental issues in ecology. The BNZ LTER has become the hub of ecological research in the Alaskan boreal forest but depends on non-LTER research to develop more comprehensive understanding of the boreal forest. This research includes (1) long-term research conducted by state and federal agencies, (2) non-LTER-funded research by BNZ PIs, and (3) research directed by non-LTER PIs, which is affiliated with BNZ LTER research. The PI of each affiliated research program receives all the LTER group communications about BNZ issues and is invited to participate in our annual symposium. These BNZ affiliates are effectively part of the BNZ program if they receive funding for their research from non-LTER sources.
the monthly meeting of the executive committee. The involvement of many PIs in multiple research components plus the oversight by the executive committee guarantees coordination across the research components.

5. All BNZ scientists (PIs, staff, and students) meet twice annually. In early winter we hold a 2-day symposium/workshop where each BNZ scientist presents research results (day 1; see the BNZ website for abstracts) and where we discuss overall BNZ LTER issues and interactions with agencies (day 2). We invite representatives of relevant agencies, biological consulting companies, and public advocacy groups to this symposium. In LTER3 we will also meet in the spring to coordinate details of the summer field research.

Each investigator is allocated a separate budget (Table 7.1, budget justification). Every two years each investigator must submit a progress report that includes major findings, a listing of data sets 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 executive committee. If more frequent budgetary adjustments are necessary, these will be made annually at the time of budget submission to NSF. We have made substantial changes in budget allocation among existing projects and changes in personnel since the last mid-point site-review to adjust for research performance and the changing needs of the program. 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, and other critical 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, etc). This budgetary process has worked well so far.

Due to retirements, we have confronted the issues of maintaining continuity and allowing gradual evolution of a long-term research program. When the two lead PIs of BNZ LTER2 retired simultaneously, the University of Alaska and the Forest Service, as the two lead institutions, brought in new PIs, one of whom (Chapin) had been a co-PI in LTER1 and had helped write the LTER2 proposal. Where possible, we have brought in new investigators to overlap with departing PIs for at least a year (e.g., Kielland’s replacement of Bryant). In cases where overlap of personnel has not been possible we provide interim oversight of the project and develop a strategy for continuation. For example, following Oswood’s retirement in July 1999, Joan Braddock (an aquatic microbiologist) has assumed oversight of the aquatics project (with continued input from Oswood), until the UAF faculty position in aquatic ecology is filled (anticipated July 2000), at which time we will decide how best to provide leadership to the aquatic ecology component of the BNZ program. The aquatic ecology program has been a productive and essential component of our research, and we intend to maintain a strong program in this area.

We encourage non-LTER investigators to conduct research at BNZ in three ways: (1) LTER inter-site comparisons (Table 1.2), (2) other collaborations with LTER scientists (Tables 2.5 and 2.7), and (3) independently initiated research projects in BCEF or CPCRW (Table 2.7). We established a group of LTER affiliate scientists (Table 2.7, Fig. 4.1), who collaborate closely with LTER investigators but are not funded by the LTER program. We provide logistic and travel assistance to LTER affiliates and other collaborating scientists, to the extent possible.
Table 4.1. Subdivision of responsibilities in the BNZ LTER and their relationship to LTER network core research areas. The name in bold has primary responsibility for the design, implementation, quality control, and analysis of this component of the research.

**Major research themes: Walker and Chapin**

- **Climate:** Hinzman, Romanovsky, and Chapin
  - Theme 1: Forest dynamics: Walker and Kielland
    (LTRC area: Populations of key organisms)
  - Vegetation dynamics and diversity: Walker, Juday, and Wurtz
  - Mammals: Kielland, Rexstad, Doak
  - Insects: Raffa, Illman, and Werner
- **Theme 2: Biogeochemical processes:** Ruess, Valentine, and Boone
  (LTRC core areas: primary production, organic accumulation, nutrient cycling)
  - Biomass and NPP: Ruess and Sveinbjornsson
  - Herbivory: Kielland and Werner
  - Soils processes: Valentine, Boone, Ruess, and Kielland
  - Net ecosystem carbon exchange: Chapin and McGuire
  - Aquatic biogeochemistry: TBN
  - Theme 3: Disturbance and landscape processes: Verbyla and Hinzman
  (LTRC core area: disturbance regime)
  - Hydrology and watershed biogeochemistry: Hinzman
  - Landscape fire dynamics: Kasischke and Verbyla
  - Forest harvest: Wurtz and Valentine

**Scaling and Integration:** McGuire, Finney, Walker, and Chapin

- **Modeling:** McGuire
- **Remote Sensing and GIS:** Verbyla and Walker
- **Paleoecology:** Finney, Lloyd, Juday, and Mann
- **Human dimensions:** Chapin and Juday

**Education and outreach:** Sparrow

**Program-Agency Liaison:** Wurtz and Kielland

- ADF&G, USFWS: Kielland
- DOF: Wurtz
- AFS, USGS: Hinzman
- LTEM: Rexstad

**Data Management:** Blodgett and Walker

**Site Management:** TBN and Chapin

**Collections:** Boone

- Plant and soil sample archival: Boone
- Herbarium: Walker
- Animal tissues: Cook

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*aFunded by Schoolyard supplement

bFunded by Univ. of Alaska Museum*
Section 5  Data and information management

5.1  Goals and objectives of data management

Information management at the BNZ LTER site is constantly evolving to implement new ideas and technology, as they mature. The primary goal of data and information management at our LTER site is to insure the long-term security and usability of data sets collected at our site. To reach this goal, a data management system has been developed with the following elements:

1. Documentation: Standardized documentation of data sets allows both current and future users of the data to understand the data and its origins.
2. Quality Control: Quality control seeks to insure the validity and integrity of data and metadata.
3. Access: User-friendly access to data sets allows those that need the data to locate and retrieve them in a readily usable form.
4. Security: Establishment and enforcement of procedures for protecting against loss or damage to data sets via natural disaster, theft, or any other destructive means.

Additional important goals for data management include the following:

1. Facilitating the process of getting data from the field into the data management system.
2. Training users in the use of the network, the web, and the data management system.
3. Enabling or improving both intra-site and inter-site communications and networking.
4. Network and systems administration and technical support.
5. Researching new ideas and technology that would benefit the site.

5.2 Historical Perspective

Initial efforts in data management at BNZ focused on developing an infrastructure for the data management system and documentation of projects and data sets. Standardized forms for documenting overall projects and individual data sets were available as printed forms or electronic files. In 1994 we transferred our data base to the World Wide Web (WWW) to increase its accessibility to the scientific community. In 1997 we implemented the use of a shareware relational database, MSQL, to allow information to be organized according to the needs of the user, rather than only in the way it was entered.

5.3 Current System

The system: The current BNZ data management system is housed on a Sun Spare server 3000. All metadata that have been submitted to the data management system are on line and accessible via the BNZ web server. All our current data sets are publicly accessible via this server. Server accesses have increased over time as both our available data and online usage in general have increased (Figure 1.3). All data are stored in ascii files, and metadata are stored in MSQL database tables. Currently there are five tables in the MSQL database: bibliography, project description, data description, site description, and personnel. Data files are stored in a hierarchical structure based on the PI, or an overall subject such as climate.

Documentation: Standard online forms for documenting projects, data sets, sites, and personnel are accessible via the WWW to researchers with the required password. These forms are filled out and submitted to a temporary storage area for data management review. Once reviewed, data management submits the forms into the main BNZ MSQL database, and the information becomes universally available via the WWW. Project description records describe the overall project. Data-set description records describe an individual data set, which can be made up of one or more files of the same structure and content. Site description records provide a detailed description of an individual research site. Personnel records describe an individual. Logical links can be made between each of the various tables to provide various ways of looking for information.

Quality control: Quality control is the responsibility of the PI who submits the data set to the BNZ data management system. PI's rely on various methods for quality control, including
plotting, visual inspection, and programmatic range checking. The data manager subjects each data set to range checking and reports the extreme values for each data set back to the PI prior to placing the data set on line.

**Access:** Our data management policy is to place all data on line within 1-2 years of collection. Currently all our on-line data sets are available to the scientific community without restriction. However, there will occasionally be circumstances where restricted access may be desirable (e.g., locations of endangered species, time-series data to be used in a dissertation). These exceptional cases of restricted access require approval of the BNZ executive committee and in most cases will revert to unrestricted access within 2-3 years after collection.

Access to Bonanza Creek data is made via our WWW server. We provide logical links between tables to allow different ways of getting to information. Data files must be accessed via the data description form, which describes the data set in detail. To get to a data description form, you may go through the project description table, the personnel table or the data description table.

**Security:** Data reside on individual PI's computer system, and on the Bonanza Creek server. Data on the server is backed up weekly to 8mm tape. Two copies of the backup are created, one of which is stored off-site. The server is located in a secure area behind a combination-locked door.

**Role of data manager.** Darrell Blodgett, the BNZ data manager, plays several key roles in our LTER site. (1) He is responsible for the maintenance and security of the data base. (2) During LTER3 he will interact with researchers during the entire scientific process—from the initial planning of sampling designs and field data collection to archiving and distribution of long-term data. The purpose here is to make data archival an integral part of data collection and analysis. (3) He takes a proactive role in searching out and modifying appropriate software to facilitate ease of data entry and use on our web site. (4) As system administrator, he troubleshoots and solves problems of networking the computers of LTER scientists. (5) He works with other LTER data managers to improve the networking capabilities of the network. For example, he worked with the climate committee to develop a way to harvest climate data from individual sites so that climate data could be retrieved and centralized on LTER-network climate data base and is currently taking the lead in developing a similar LTER-network system for harvesting other LTER site information.

**Procedures to ensure each investigator places data on line.** Our major mechanism of getting individual investigators to place data on line is to ingrain in each scientist a sense of responsibility for public archival of data and to make the process as easy and beneficial to the investigator as possible. Compliance with this responsibility is an important aspect of our internal review process, when we reallocate budgets among projects every two years. Investigators who refuse to archive their data cannot receive continued LTER funding.

5.4 Future developments

Our information system will continue to evolve as new ideas, technology, and software tools become available. Our efforts up to this point have emphasized hardware infrastructure, documentation, access, and security. Quality control will continue to be the charge of the researchers, although we will add a data-screening process to flag extreme values in the data. Additional new efforts in the next 4 years will be to increase the number of data sets on line and to increase the ease of access and usability of these data sets. We will also develop and regularly update summary data sets that are likely to be of frequent interest (climate, biomass, NPP, species diversity, etc.).

**More data sets on line:** We now have about 100 distinct data sets on line (Table 1.3), and long-term data sets are kept as current as possible. Nonetheless there are additional LTER data sets, primarily related to short-term observations and experiments, that must be placed on line. This will receive increased emphasis in LTER3 and will be an important component of our interim project evaluation and re-budgeting process.

A new emphasis in LTER3 will be to identify relevant environmental, ecological, historical, and social-science data sets for Alaskan boreal forest that have not been collected by
LTER and to find the most expedient way to make these available to ecologists. The options that we will pursue are (in order of preference) (1) to develop web links to other web sites where these data sets are archived (e.g., maps of Alaskan climate, soils, and vegetation, developed jointly by the BNZ LTER and the EROS data center of USGS and maintained on the EROS web page), (2) to provide technical advice and encouragement to agencies to develop their own long-term data bases (to which we would develop web links), as we are doing with the Denali National Park monitoring program (see outreach), or (3) to offer the service of the BNZ web site as a repository for important non-LTER ecological data (see outreach). This incorporation of non-LTER data sets into the BNZ data base is part of our new effort to build strong linkages with other research units in Alaska, such as Forest Inventory of USFS. We have designated an LTER PIs to be responsible for developing linkages with each agency (Table 4.1) and will explore the availability of appropriate data sets and determine how best to increase the accessibility of these data to the general community. Our first priority is simply to identify the nature and contact location of important data sets; in addition, we will facilitate their availability via WWW, as time and resources permit.

Ease of data access and usability. We will continue to pursue our current efforts to improve availability of user-friendly data entry, quality control, and plotting programs so as to facilitate the documentation and archival of data sets by LTER investigators. By providing user-friendly data analysis tools, we hope to provide an environment that facilitates analysis, cross-comparison, and synthesis so that each investigator will want to put their data on line quickly to analyze it, rather than feel it is an obligation that they must fulfill.
Section 6  Outreach efforts

The BNZ LTER has substantially expanded its efforts at outreach in the areas of K-12 education, development of formal ties with other research programs, museums and agencies, and organization of science symposia. We are searching for a site manager, one of whose responsibility will be to augment our outreach to the general public.

Education

As part of the LTER schoolyard program, we have added a new PI (Elena Sparrow) to direct our K-12 education efforts. We have teamed up with two ongoing science education programs, GLOBE (NASA) and Partners in Science to train science teachers in 15 Alaskan towns and villages. LTER funding enabled six Fairbanks elementary and high school teachers to be added to the program. We have initially focused attention on teachers in close proximity to our LTER site to explore how best to integrate education with our research program.

In addition to the formal LTER schoolyard program, individual LTER PIs have taught short courses for secondary school science teachers from rural Alaska (Oswood and Bryant), developed web-based curricula in long-term ecological monitoring (Verblyea, Sparrow, and Juday), worked in rural schools to describe the LTER science program (Lloyd), taught about LTER science in local environmental summer camps for grade school students (Rexstad), involved high school students in LTER research projects (Ruess and Chapin), taught lessons in climatology and helped establish climate and soil monitoring stations in local schools (Hinzman), and acted as judges for the local elementary and secondary school science fairs (many PIs).

Ties with other LTER sites

The BNZ provides a logical comparison with many other LTER sites, particularly the vegetation types that are immediately north (Arctic [ARC] LTER site) and south (HJ Andrews [HJA] LTER site). We have worked closely with these two sites to develop programs that will maximize the opportunities for comparative studies. A joint proposal with the ARC site seeks funding for the Alaska Climate Transect. Our intention is to understand Alaska as a regional system in which the boreal forest and tundra are linked by many common biotic components and by the atmosphere. We are developing museum collections and a sample archive that will serve both the ARC and BNZ sites. With HJA we are developing common protocols in studies of hydrology, vegetation feedbacks to climate, and designs for regional study of biodiversity.

Ties with Alaskan long-term ecological research programs

Our LTER science symposia and active solicitation of collaborations with agencies have created closer links with several long-term ecological research programs in Alaska. We are assisting the Long-Term Ecological Monitoring (LTEM) program of the National Park Service in developing a web-based data archive similar to the BNZ database. The BNZ LTER and LTEM will use the same regional sampling protocols, hierarchical vegetation classifications, and climate monitoring programs. Two LTER investigators (Rexstad and Juday) also work in the LTEM, providing direct communication between the two programs.

Collaborative arrangements provide the LTER access to population and habitat data from the Alaska Department of Fish and Game (ADF&G). We are developing a GIS database of previous forest harvests with the Alaska Division of Forestry (DOF). We worked with the EROS data center of USGS to develop statewide maps of climate, vegetation, and other variables at the 1-km scale (Table 1.1). The BNZ LTER collaborated with the Alaska Fire Service (AFS), a section of BLM, to burn a 740 ha watershed in CPCRW in July 1999 (FROSTFIRE). As follow-up, the LTER initiated regular seminars allowing interchange between scientists from LTER and agencies (AFS, ADF&G, DOF, etc.). An explicit objective of these seminars is the development of models that link climate, fire, post-fire succession, and wildlife habitat. AFS has offered to do additional prescribed burns to meet LTER science needs. Our long-term goal is to identify and make accessible all the long-term data bases in Alaska that are useful for ecological modeling.
We provide links to agency web sites where data are available, provide on our web site a list of data sets and contact information, or will post these data on our web site, as a last resort.

**Ties with museum collections**

Using LTER supplement funding, we have worked with the University of Alaska Museum to develop collections of plants (herbarium specimens and tissue collections), insects, and vertebrates that provide both a long-term record and a broad spatial record of genetic and species diversity of Alaska. We have also initiated discussions with them about how to proactively design the optimal long-term collections program, rather than to be passive recipients of specimens that are brought to the museum. We anticipate a strengthening of this tie with the Museum, as we strengthen the biodiversity component in our regionalization studies.

**Involvement in forest management issues**

In 1997, we held a workshop on the ecological role of forest harvest in interior Alaskan forests. This workshop presented perspectives from state and federal land managers, native groups, commercial interests, and ecologists. We developed a conceptual model of the role of human activities as an integral component of the boreal forest and determined that, in the next two decades, human decisions about fire control would have much greater impact on the boreal forest than would forest harvest. We seek external funding to explore the role of humans as components of the Alaskan regional system. We plan a second symposium on forest harvest.

Wurtz occupies the Forest Science seat on the Citizens' Advisory Committee for the 1.7 million-acre Tanana Valley State Forest. Juday has participated in training sessions for the Alaska Division of Forestry, the Bureau of Land Management, and the National Park Service. Several LTER scientists have contributed to articles sponsored by the Society of American Foresters in the local newspaper and to the occasional newsletter "Forest Science Notes" published by the UAF Dept. of Forest Science.

**Outreach to the general public**

LTER scientists (Juday, Romanovsky, Chapin, and others) have been interviewed by numerous radio and television stations (NBC, CBS, ABC, public television and radio, Danish Broadcasting System) and newspapers (New York Times, local Alaskan newspapers) about the impact of global warming on boreal forests. Juday was an invited speaker in the Congressional Seminar series, sponsored by U.S. Global Change Research Program, Washington. The audience included members of Congress and staff, constituencies involved in U.S. global change policy, and agencies involved in global change research. NOVA film crews interviewed LTER scientists and filmed the FROSTFIRE experimental burn as part of a major television series on the ecological role of fire. Hinzman led four public meetings to explain the science of the Frostfire project.