Landscape-Scale Gradients in Vegetation in Denali National Park and Preserve:
A summary of data from 20 study areas

Carl A. Roland
Plant Ecologist
Denali National Park and Preserve
4175 Geist Road
Fairbanks, Ak, 99707

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I. Introduction

We have been collecting vegetation data in Denali National Park according to a randomized multi-stage systematic grid design since 2001 as part of the N.P.S. Vital Signs monitoring program. Our objectives and methods for vegetation monitoring are described in detail in the protocol document for the program (Roland et al, 2004). Since 2001, we have completed sampling of 20 study areas (see Map 1 for locations). Each study area consists of a network of sampling locations - five rows of five permanent vegetation plots, with 500 meters spacing between the plots. These sets of 25 plot study areas are henceforth referred to as “mini-grids” (in contrast to the “macro-grid” that determines the placement of mini-grids on the landscape). Through this work, we have compiled a large data set containing quantitative physical and vegetation data for more than 500 permanent vegetation plots. A set of descriptions and representative photographs for the seven mini-grids measured during 2006 in Denali is provided in Section II of this report.

The Denali vegetation monitoring data set encompasses an extensive geographic area including numerous boreal and alpine sites spread across more than 100 km of longitude and more than 60 km of latitude. This data set thus includes areas of diverse lithologies, divergent ecological histories and extremely variable edaphic conditions including saturated lowland wetlands and ponds, mature forest on permafrost, and steep alpine scree slopes. Disturbance history also varies greatly within and among mini-grids some of these study areas have been partially by burned forest fires within the last decade while others represent very old forests with stand ages in excess of 200 years. Two factors are of critical importance to keep in mind as I describe the data from this program: 1) the location of all of the sample plots is essentially random, based upon a systematic grid with a random seed; and 2) there is considerable ecological variation both within and among all of these study areas.

The vegetation monitoring program sample for Denali is roughly halfway completed at this point (twenty mini-grids have been completed out of a total of 38 planned). This comprehensive (if still preliminary) data set allows us to begin in earnest the process of describing large-scale landscape patterns in Denali and to make inferences about variation in the physical and vegetation parameters we have measured at the landscape-scale. The goal of this report is to communicate selected important examples of these landscape scale results. These results provide an indication of the value of the data collected under this protocol. Of critical importance to understanding these results is that the data is collected within a fully randomized sampling design, so that the patterns we observe in these data and the inferences we make are general ones, valid the across landscape, not simply reflective of the particular sites that we have chosen to install our monitoring plots.

Two primary goals of this program are to effectively sample the major landscape gradients in the study area, and to quantify the relationships between these environmental gradients and the response of vegetation variables. I believe that capturing these baseline ecological relationships is the foundation for detecting and understanding vegetation and other ecosystem changes at a
landscape scale over the long term. The focus of this broad overview is firmly on describing the responses of fundamental vegetation attributes to primary landscape variables. In this document, I will describe the results across all of the 20 mini-grids sampled in Denali thus far for a set of four primary landscape gradients, and the response of six categories of vegetation variables to these gradients.

The primary landscape gradients I will present results for are the following: elevation, slope angle, and permafrost status of soil map unit. I will also examine important secondary gradients in combination with these primary landscape gradients, including soil depth, equivalent latitude, plot azimuth and numerous soil physical and chemical variables.

To quantify and help define the relationships between landscape and vegetation at the large spatial scale represented by this dataset, I will analyze the responses of the following vegetation variables to these primary gradients: vascular plant species richness, cover of selected dominant species, density of trees, the response of different tree species, the stature of live plant biomass (height distribution of live plant cover), and the distribution of dominant vegetation types along the primary landscape gradients. In addition to examining the variation of these vegetation response variables to the primary landscape gradients, I will describe the response of a set of other important physical variables to these large-scale landscape gradients, including several soil parameters (pH, stratum depths, % C, %N, temperature) and mineral cover of soil (rock, gravel, bare).

The essential concept underlying these gradient analyses was the use of post-stratification of the data set according to physical factors that our conceptual models suggest should control variation in the vegetation variables that we have measured. For example, site productivity in interior Alaskan forests (density and basal area of trees) is known to be affected by active layer depth and by elevation. Thus we would expect that if we divide a gradient into segments, and then calculate a mean response for all plots in each of the gradient segments, the relationship between the two variables at a landscape scale will be evident (e.g. a pattern in the response of vegetation values in relation to different levels of the physical factor in a gradient histogram). If there is no such relationship between a physical factor and a vegetation variable, the gradient analyses would show essentially random variation in mean values for vegetation parameter across the physical gradient.

The patterns that emerge from the gradient analyses of the landscape scale data presented here allow us to do two critical things: 1) make informed hypotheses regarding how specific vegetation attributes might be expected to change in response to different scenarios of future changes; and 2) provide an explicit framework to detect any changes as they may occur by comparing the results of gradient analyses from future sampling iterations to the results for the baseline conditions presented here. Understanding how any given vegetation change is occurring across the primary landscape gradients that control vegetation will greatly inform our understanding of the reasons for and consequences of any such changes.

The focus of this summary document is firmly on providing graphical representations of ecological patterns that make the information from this large and complex data set accessible to a wide audience. As a result, I have favored the use of gradient histograms and other visual data
presentations at the expense of providing numerous statistical models that represent the data, in most cases. The type of data summaries presented here are not intended to replace more detailed analyses using inferential techniques, which will be performed as warranted to answer specific questions.

Table One. Twenty mini-grid samples completed between 2001-2006 in Denali National Park and Preserve, Alaska. The locations of these seven sampling areas within Denali are shown in Map 2.

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<tr>
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<th>Number of plots completed in area</th>
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<td>Rock_Cr</td>
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<td>Sandless Lake</td>
<td>Sandless</td>
<td>Boreal</td>
<td>23</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td></td>
<td></td>
<td><strong>468 Plots</strong></td>
</tr>
</tbody>
</table>

II. Study Area Descriptions

The twenty mini-grids that will be treated in this paper are shown in table 1, including the code that is used for each of them (for purposes of brevity) in subsequent graphics, the general landscape character of the study area (transitional mini-grids include both boreal and alpine areas), and the number of plots that were completed in each one. All twenty-five sample points are not always safely accessible for sampling in every mini-grid –e.g. when the point lands on a cliff-face, or in the active channel of a large glacial river.
For purposes of this paper, I will provide general overviews of the seven mini-grids that were sampled in Denali during the 2006 field season. This set of mini-grids encompasses a wide range of the geographic and ecological conditions that have been sampled in the park thus far, and description of the other mini-grids area available elsewhere (Roland et al, 2003, Roland 2006, Project web page - http://mercury.bio.uaf.edu/DenaliLTEM/).

A. Wonder Lake

The Wonder Lake mini-grid was located near the western terminus of the Denali Park Road. It lies primarily on the alluvial terraces on the north side of the McKinley River, south of Wonder Lake (see Map 3). This boreal mini-grid encompassed sites on the newly-deposited active floodplain of the McKinley River, forested areas on old river terraces, and sites in the peaty wetland communities associated with a perennial stream flowing southwest from the benches to the east and above Wonder Lake, and one site on the east-exposed slopes below Wonder Lake (plot 25). The topography was essentially flat, and elevation in this mini-grid averaged 607 meters. The most common vegetation in this area was open white spruce forest (as is visible as dark green areas in the satellite imagery in map 3). We installed and measured plots 8 – 25 in this mini-grid. Plots 1 through 7 were located in river channels and active floodplain and were not safely accessible or permanently mark-able. Representative photos of the landscape in this study area are shown in Plate 1.

B. Kankone Peak

This alpine mini-grid was located along the crest of the Kantishna Hills, near the highest mountain in the range, Kankone Peak. A map of the immediate area is shown in Map 4. This study area was located southwest of Kankone Peak itself, and plots fell on both sides of the crest and included plots on the ridge crest and saddle areas. This mini-grid spanned elevations between 872 and 1332 m, with a mean plot elevation of 1098 m. The area was alpine in character, and most of the plots occurred in tundra or other open alpine habitats, such as open boulder fields and scree, although there were several plots in shrub vegetation at lower elevations in the area. Slope angles for the plots in this mountainous area ranged between 2° and 35°, with a mean plot slope angle of 21°. A conspicuous attribute of the Kankone Peak mini-grid was the large number of seeps and springs that occurred throughout the study area. We installed 21 plots in this mini-grid, but were unable to install four plots due to the fact the points were located in inaccessible areas or in very steep, loose material that would make it unsafe to work. Photos of the landscape in this study area are shown in Plate 2.

C. Bearpaw River

This mini-grid was located 20 km north of the Kankone Peak mini-grid, in the subalpine and lower alpine zone of the Kantishna Hills spanning a ridge that separates the headwaters of the Bearpaw River and Otter Creek (Map 5). This area was characterized by flat and rolling terrain on ridge tops and upper slopes, and steeper slopes lower on the valley walls. The plots spanned elevations from 602 m to 894 m with a mean plot elevation of 781 m. Slope angles for this set of plots ranged from nearly flat (4°) to steeply sloping (31°), with a mean plot slope angle of 12°. The study area was primarily subalpine in character with low shrub tundra being the dominant
vegetation, with patches of alpine tundra in exposed and rocky sites, and tall shrub and open woodland in lower elevation protected or riparian sites. The crew was delayed by one day due to bad weather in getting to the study area, and as a result, three plots were not completed in this mini-grid. A set of representative photos of the landscape in this study area are shown in Plate 3.

D. Mount Healy Ridge

This alpine mini-grid was located on the south slopes of the high ridge of the outer Range that runs to the east from the Savage River; equidistant between the Rock Creek mini-grid and the Primrose Ridge mini-grid (Map 6). The Mt. Healy study area was the steepest, had the highest mean elevation and contained the greatest topographic relief of any mini-grid yet sampled. The average plot elevation in the Mt. Healy min-grid was 1388 meters, with a range in plot elevation of between 1160 meters at plot 3 and 1734 meters at plot 25. This majority of this area was characterized by steep, barren alpine slopes, especially in the three northern rows of points. Plots in the southern two rows of plots were generally more vegetated, with tall shrubs in the riparian areas, gullies, and lower slopes (plots 1 and 3), and open alpine tundra with scattered low shrubs in the slopes and ridges (plots 2, 4, 5, and 10). The area was precipitous, and traveling between points was challenging. In fact, because of the extremely steep, loose character of the substrate in this area, we were unable to sample seven of the points in this mini-grid. However, these unsampled plot locations were almost entirely barren of plant cover and covered with recent slide debris or located in precipices. Photos of the landscape in this study area are shown in Plate 4.

E. Primrose Ridge

This alpine mini-grid is located on the high ridge just west of the Savage River (see Map 7), known as Primrose Ridge for the large population of Primula eximia that occurs there. Primrose Ridge mini-grid was first installed and measured in the summer of 2002 as part of the pilot project for this program and it was fully remeasured during 2006, giving us two iterations of data for this alpine study area. Primrose Ridge is noteworthy because it has considerable amount of rolling and flat topography at high elevation, which is unusual in the Alaska Range. Large contiguous areas of moist to wet graminoid-herbaceous tundra have developed on these flat surfaces, with shrub tundra in the sloping terrain at lower elevations, dry Dryas fellfield in exposed areas and prominences, and rocky scree and tundra on steep side slopes. The mean elevation for the plots in this mini-grid was 1277 m with a range in elevation from 1002 m at plot 24 to 1454 m at plot 11. Mean slope angle for this mini-grid was 17° with a range of slope from flat (0° at plot 12) to very steeply sloping (37° at plot 16). All of the plots in this mini-grid were accessible and installed during both sampling iterations. Photos of the landscape in this study area are shown in Plate 5.

F. Bear Creek

This boreal mini-grid is located in the true basin lowlands west of the Kantishna Hills on level and rolling terrain on alluvial terraces and loess-laden hills north of Bear Creek (Map 8). Much of this study area is occupied by ponds and saturated wetland areas, interspersed with boggy black spruce forest and willow shrub riparian areas. The few low ridges and knobs that emerge
from the flat wetlands support well-drained white spruce and birch forest, especially on southerly aspects. Mean elevation of the 25 plots we measured in this study area was 158 m, and elevations only spanned 21 m of plot elevation, from 153 meters at plot 9 and 174 meters at plot 19. The mean plot slope angle was 1.5°, with a range of 0° at numerous plots to 10° on the knoll plot 13. A notable attribute of his mini-grid was that a large part of southwestern portion of this area burned in 1996. Ten of the plots in this mini-grid were located in areas that were burned during the 1996 fire, including plots 1 through 5; 8 – 10; and 14 - 15. The most common vegetation types in this mini-grid included black spruce woodland and open forest on permafrost (with birch-ericaceous understory) and open wetlands (both graminoid and shrubbed). Burned plots had higher cover of graminoids and in some cases standing water. Photos of the landscape in this study area are shown in Plate 6.

G. Sandless Lake

This boreal mini-grid was located east of Sandless Lake, in the interior basin lowlands west of the Kantishna Hills 20 km east of the Bear Creek mini-grid (Map 9). This mini-grid is similar to the Bear Creek mini-grid in some respects: there were several ponds and considerable area supporting black spruce bog vegetation. In addition, part of this study area was also burned fairly recently (1996). A key difference between these two boreal study areas was the predominance of open sedge wetland areas in Bear Creek, which were not prevalent in the Sandless Lake study area. This decreased abundance of open sedge wetlands in Sandless Lake is related to the greater topographic variation in this area; whereas Bear Cr. was largely flat with a few prominences, the ponds in the Sandless Lake area were located in topographic depressions, without adjacent large flat expanses. Three of the points in this mini-grid were not sampled because they landed in a pond. Elevation of the plots in this mini-grid was higher, on average than for the Bear Creek mini-grid with a mean plot elevation of 201 m. Plots ranged in elevation from 183 m at plot 10 to 217 m at plot 16. The mean slope angle was 6°, with a range of slope angles of nearly flat (1 degree at plot 9) to moderately sloping (25° at plot 13). Photos of the landscape in this study area are shown in Plate 7.

III. Results

I present the results of this work organized first by the physical gradients considered here (elevation, slope, permafrost status), and secondly by the vegetation variables that I analyzed for this report: patterns in species richness and biogeographic affinities of the vascular flora, cover of dominant species, stature of the vegetation (vertical arrangement of biomass), overall tree density, tree species distribution, tamarack mortality, and distribution of the dominant vegetation types within the sample. Each of the vegetation variables is a section of the report. Within each of these results sections, I examine the responses of the vegetation variable to each of the three physical gradients – elevation, slope angle, and permafrost status. In cases where it is warranted, I present two-factor gradient analyses that show the simultaneous response of vegetation variable to two environmental gradients.
A. Physical gradients on the landscape of Denali

In this section I present the summary results for a set of physical and soil factors measured in 467 permanent vegetation plots in the 20 mini-grid samples treated for this report. Specifically, I show how these factors varied in relation to the three primary landscape gradients that I am examining for this report: elevation, slope angle and permafrost status of soil map units.

1. Elevation

The most important primary landscape gradient affecting the biota of this mountainous park is elevation. Elevation affects nearly all aspects of the ecosystem because of the myriad influences on microclimate and geomorphology related to increasing elevation, including increased precipitation, decreasing air temperatures, shorter growing season, different soil-forming conditions and weathering regimes, increased geomorphic disturbance and related phenomena.

The twenty mini-grid sample we have accomplished thus far effectively samples elevations between 153 m and 1734 m (Fig. 1 shows a dot-plot of all plot elevations, arranged by mini-grid). Note that there is a gap in the landscape elevation representation between about 250 to 450 m elevation (between the Sandless and LE Fork samples in figure 1). This gap exists because Bear Creek and Sandless Lake were the first two mini-grids to be sampled in the true basin lowlands west of the Kantishna Hills. This minor gap in elevation representation will be closed as we install the other plots within this area.

Figure 2A shows the sample sizes (number of plots) in each of the 200 m segments of the elevation gradient. The remaining gradient histograms in figure two show the results of single-factor gradient analyses of the variation the mean responses of several landscape traits in relation to the elevation gradient. These gradient analyses show expected correlations such as increasing mean slope angle with increasing elevation, and (slightly) decreasing air temperature at the time of sampling with increasing elevation (Fig. 2). It is worth noting that mean values for equivalent latitude (henceforth referred to as $EQ$) apparently declined slightly with elevation on this gradient. $EQ$ is an index of solar radiation that integrates, slope, aspect and latitude to yield a value (in degrees) that represents the latitude at which a flat surface would receive an equivalent amount of annual solar radiation as the surface in question (all other things being equal). Thus high numbers (the maximum $EQ$ value is 90°) represent areas towards the poles (thus low radiation sums) and low values represent areas towards the equator, the absolute minimum value thus being 0° (thus relatively high radiation sums). This reflects that there is a slight tendency of the alpine areas in this particular sample to be more south-exposed than north-exposed (on average). This same trend can be seen in the gradient shown in Fig. 2E that shows a decline in mean deviation of plot aspect with due south along this elevation gradient (although there were many north exposed plots in all of the categories).

As expected, many soils variables varied strongly with plot elevation across this data set according to these elevation-gradient analyses (Fig. 3). The mean response of the following soils variables appeared to increase monotonically with increasing elevation: soil pH, soil temperature at 10 cm depth at time of sampling, coarse fraction of the soil (>2mm), sand percent of soil fine fraction, rock cover of ground and gravel cover of ground (Fig. 3). These gradient trends all
reflect increased geomorphic disturbance and the greater influence of bedrock that is related to
the primacy of slope and cryoturbation processes in the alpine zone. A slight trend in increased
mean soil temperatures in high elevation study sites could potentially be the result of higher solar
radiation received by south-sloping surfaces (prevalent at high elevation in this dataset), and also
perhaps the lingering effects of increased winter insulation of alpine soils by generally deeper
average snowpack observed in the alpine zone.

In contrast, the mean responses of the following soils variables showed apparent monotonic
decreases with increasing plot elevation: soil moisture, soil carbon and nitrogen percentages, silt
percent of soil fine fraction, and depth of the organic layer (Fig. 3). These gradient responses
reflect the greater productivity and accumulation of organic matter in boreal areas of the
landscape, and the increase in soil moisture associated with both increased water holding-
capacity of organic-rich soils and the higher proportion of wet areas of the landscape in flat or
rolling lowland terrain. It is worth noting that major regime shifts in climate would change these
primary gradient signatures. For example a warming and drying interior Alaska cause the
conversion of peatlands to forest or to open dry scrub plant communities. Several parameters
showed somewhat variable mean responses to elevation gradient, including litter depth, living
mat depth, soil depth, and percent bare ground, likely due to localized differences (Fig. 3). For
example, soil depth is controlled by different factors in different landscape segments; in the
alpine it is principally a function of depth to bedrock, whereas in boreal lowlands it is controlled
primarily by the depth to permafrost (depth of the active layer). These multiple causal factors for
a single measured variable may thus complicate simple gradient responses.

2. Slope angle

Slope angle strongly affects the geomorphic regime of a site and interacts with aspect and
latitude to control the radiation budget of a landscape surface (along with the attributes of the
local horizon). Plot slope angles in this sample ranged between flat (0° slope) and very steep
(54°; see a dotplot for all observed values of slope angle in Fig. 4). There was considerable
variation both within and among mini-grid samples with respect to slope angle, except for some
of the lowland mini-grids located in the basins that were essentially level over large areas. There
was also a general positive correlation between mean elevation of a study area and mean slope
angle, which is to be expected because mountainous areas tend to be dominated by sloping
terrain and thus have steeper slopes, on average. However, there were numerous plots with low
slope angle in the high elevation areas represented by this sample, and steep slopes in the
lowland areas (see Fig. 5).

In general, the apparent strength of the gradient responses between slope angle and the suite of
landscape and soils parameters was less than the strength of the gradient responses that were
observed for these parameters relative to elevation (compare Fig. 3 to Fig. 7). In most cases this
was likely due to the greater influence of elevation on these variables as compared to slope.
However, it should also be noted that the distribution in the number of plots among the seven
slope angle categories (sample size) was less even than was the case for the sample size
distribution among the elevation categories, with 38 percent of the plots in the data set falling in
the lowest slope angle category (see Fig. 6).
There was a strong, apparently monotonic positive response of mean soil pH, mean soil temperature, mean percent rock cover, and mean percent gravel cover to increasing elevation (Fig. 3) in this data set. The data for slope angle show a similar, yet less distinct and consistent positive response for mean values of these variables across the gradient in slope angle (Fig. 7). Similarly, the negative gradient response for mean values of soil moisture, soil carbon, soil nitrogen, and organic layer depth across the gradient of increasing slope angle was apparently weaker than the gradient response observed for elevation (compare Fig. 3 and Fig. 7).

Due to the autocorrelation in the dataset between slope angle and elevation, it was important to parse the relative contributions of elevation and slope angle in controlling these soils variables across this large data set. To do this, I performed a set of two-factor gradient analyses by using a three by three slope by elevation matrix and calculating the mean response for each variable in each of nine cells defined by levels of slope angle and elevation (see three-dimensional histograms showing the results of these analyses in Fig. 8).

The two-factor gradient graphs show apparent variations in the relative strength of these two landscape variables in affecting mean values for soils traits. For example, both percent coarse fraction of soil and soil temperature both appeared to show strong positive correlation with both increasing elevation and increasing slope angle (Fig. 8 A & B). The two-factor gradient analysis for soil pH, on the other hand, suggests that this variable responded primarily to elevation. Conversely, increases in the mean percent rock cover was apparently primarily related to increases the slope angle of a plot across this data set, as might be expected. Two-factor gradient graphs for organic layer depth and for depths of the live mat showed apparently strong negative response to both increasing elevation and to increasing slope angle.

3. Permafrost status of soils map units

A soil survey map of Denali was recently completed (Clark and Duffy 2005). One part of this map consisted of GIS polygon data for which numerous landscape and ecological variables (such as ecoregion, life zone, permafrost status) were assigned to each map unit polygon based upon field observations and aerial photo-interpretation by the study authors. I performed a spatial join using ArcInfo software that assigned this suite of map unit variables to each of the plots in this data set, based upon which soil map unit in which the plot was located. Each map unit was characterized as to its permafrost status – continuous, discontinuous, sporadic, and none (not-rated). I used map unit permafrost status as a categorical variable, and calculated mean responses for all of the variables across each of these categories to determine whether the plot data showed a response to the permafrost gradient. Analyzing the plot-based monitoring data in the context of the polygon-based soils map provides a useful way to “scale-up” the plot data to the entire landscape. If we see detect patterns in the variation of key physical and vegetation parameters based upon these attributes, we can potentially extrapolate the changes (or stasis) that we measure as additional sampling iterations occur using this spatial data set. In addition, this framework allows us to make spatially-explicit estimates for the quantitative measurements made on the plot network.

The plots in the data set were more or less equally distributed across the three most common permafrost types in the interior region of the park – sporadic (163 plots), discontinuous (146
plots) and continuous (146 plots; Fig. 9A). There were only 13 plots in the “not rated” or none category – which is usually bedrock areas in the high mountains.

The gradient patterns revealed by the analysis of plot data in relation to soil map unit permafrost status were clear and potentially provide an excellent tool for detecting changes in vegetation based on permafrost degradation going forward. There were several evident gradient responses between the landscape variables (Fig. 9) and increasing intensity of permafrost: 1) the mean plot azimuth deviation from due south was highest in the continuous permafrost category and lowest in the no permafrost category (that is plots in continuous permafrost soils units were, on average, more north-facing) and as a corollary, mean equivalent latitude (EQ) showed the same trend. EQ is an index of solar radiation that integrates slope, aspect and latitude to yield a degree value – the latitude at which a flat surface would receive the same amount of annual solar energy. Thus high values represent polar regions (low solar radiation receipts) and low values represent equatorial regions (high solar radiation receipts). Unsurprisingly, mean elevation and slope angles showed an apparent decreasing trend with increasing intensity of permafrost across this data set.

Strong monotonic gradient responses characterize almost all of the relationships between map unit permafrost status and the mean values for measured soil variables (Fig. 10). These gradient analyses indicate a positive correlation trend between permafrost intensity and mean soil moisture, soil carbon and nitrogen, and the depth of litter, live amt and organic layers. In contrast, soil pH, temperature, coarse fraction percentage, sand percentage and the percent cover of rock, gravel and bare ground all showed monotonic decreases with increasing permafrost intensity of the soil map units (Fig. 10). In future sample iterations we will use the post-stratification shown here to parse this spatially extensive data set to specifically address questions of whether large-scale changes in vegetation are occurring due to changes in permafrost conditions, as has been predicted to occur. If such widespread changes occur, the mean responses of measured variables across this gradient should change.

B. Vegetation Responses to Landscape Gradients

In this section I present the results of numerous analyses performed to investigate the relationship between primary landscape gradients and variation in selected important vegetation parameters. The goal of these analyses was to determine whether the plot network captured the important gradients controlling selected vegetation variables, and to create a framework for understanding how we will detect changes through time in this spatially-extensive dataset using the concept of post-stratification. Underlying the my extensive use of post-stratification is the hypothesis that change in vegetation will best be detected by examining mean responses along these primary physical gradients because change will be expressed differently in different landscape segments.

1. Landscape Gradients in the Diversity of Vascular Plant Species

Species composition and the community species diversity are fundamental attributes of the botanical resources of our parks. A particularly important attribute of Alaska’s natural
vegetation is that the patterns of species composition and species richness that we observe are strictly the result of natural processes operating at geologic time scales. It is important to realize that this is not the case for most of the earth’s surface. Much of the natural vegetation even the large, relatively “pristine” national parks in the western U.S. is contaminated with exotic species and many plant communities there are the result of biological invasion and human activity, rather than strictly natural processes. This situation has major implications for conservation of these park units and considerable effort and financial resources are dedicated to mitigating the ecological consequences of these perturbations each year.

The undisturbed character of our vegetation is a precious resource that should be safeguarded. It allows us a unique window into the processes and ecological histories that have created these patterns. Introductions of exotic species in combination with ecological upheavals due to climate change present real dangers to this natural heritage. A primary objective of this program is to quantify these baseline patterns with our plant communities and to detect whether any changes are occurring to these baseline conditions over time. Early detection of changes in patterns of species diversity, were they to occur, would represent real opportunities to anticipate potentially grave impacts to our parks botanical resources.

a) Response to Elevation Gradient

A simple linear regression of log [vascular plant species number] on plot elevation for this data set reveals a rather surprising result: a very highly significant, positive relationship between plot species number and elevation (r-squared = 0.357; p<0.000001; n = 465; Fig. 11). Examining the dotplot of species number by mini-grid (mini-grids are arranged in order of increasing elevation on the x axis) we see the same underlying pattern – although there is substantial variation both within and among these study areas in plot species richness, there is a clear increasing trend in the species richness of a plot with increasing elevation (Fig. 12). All of these species were native to Alaska.

I performed a gradient analysis of mean plot species richness by parsing all of the plots in the data set into 200 m increments of elevation and deriving the mean species richness for all plots across each of these gradient segments (Fig. 13; note that this gradient analysis is identical to those shown for physical and soils variables in Fig. 2 and Fig. 3). This analysis reveals a somewhat more nuanced picture of the relationship between these two variables – mean plot species richness does indeed rise precipitously with elevation up to the 1200-1400 m category, but then apparently declines somewhat for elevations above this level. It should be noted, however, that there were only twelve plots in the highest elevation category, and it is possible that sampling variation resulting from low sample size for this elevation category might thus unduly influence this picture. These twelve plots were generally located in very active slide areas, thus few stable slopes were represented in this segment of the gradient for the current sample.

This pattern of species richness represents a significant result and runs counter to a body of literature regarding the relationship between elevation and species richness. I investigated this surprising relationship between species richness and elevation further by asking whether these clear differences in plot species number across the elevation gradient represented real differences
in plant diversity among these elevation zones, or were simply an artifact of greater “species-packing” in the high elevation zones. That is, because individual alpine plants are much smaller, on average, than those in lowland areas this relationship could possibly be related to our plot size, rather than to an important underlying pattern of diversity on the landscape. If such were the case, we would expect overall species richness aggregated over groups of numerous plots to be higher in the lower elevation zones, indicating higher turnover of species among plots over larger areas and a thus higher overall number of species in the lowlands.

The species richness patterns in response to elevation were definitively not related primarily to plot size, but rather reveal a true gradient in species diversity at a landscape scale within the dataset (see Fig. 14 and Fig. 15). The lowest number of plots in a single cell of this gradient analysis was 12 (in the > 1400m category – see Fig. 2). I analyzed the data to yield the mean number of unique vascular plant species observed across all possible sets of 12 plots for each of the elevation strata (12 plots represents 2400 m² of sampled area = 200 m² x 12). The results of this analysis are shown in Figure 14. Note that the gradient pattern in species richness was actually substantially more pronounced at this larger area sampled – with the 1200 and 1400 m categories containing nearly three times the mean number of species per 2400 m² as the lowest elevation category (< 400 m).

To examine differences in species : area relationships across the elevation gradient over larger areas of the landscape, I calculated mean species area curves for each of these elevation strata for all of the plots in each (because there are different numbers of plots in each stratum, the total amount of area sampled varies among strata). Figure 15 shows these mean species:area accumulation curves for the entire data set parsed into seven elevation strata. Note the striking differences in species accumulation curves among these elevation strata: at the 9400 m² point, for example, (mean number of unique species observed aggregated across 47 plots- noted by the black vertical line in Fig. 15) the two most species-rich elevation strata (1000 to 1200 m and 1200 to 1400 m) had mean species richness of 258 and 245 species respectively as compared to the two lowest elevation strata (less than 400 m and between 400 - 600 m) which had 108 and 104 species respectively – fewer than half the number of species over this very large amount of sampled area.

b) Responses to Slope and Elevation Gradients

Figure 16 shows the results of a two-factor gradient analysis of mean plot vascular plant species richness for the simultaneous response of this variable to elevation and slope angle across this dataset. Elevation is apparently the more important independent variable, but there is also a trend towards higher species richness in the highest slope category for each category of elevation. Mean plot species richness in >20° category was 4.1 species higher than for the <10° category for the less than 750 m elevation stratum, this difference was 5.47 and 3.44 species per plot for the 750 to 1000 m and greater than 1000 m elevation categories respectively.

The smallest sample size for any of the cells in this two-factor gradient analysis presented above was 7 plots (for the high slope angle/low elevation category). To examine species richness on a larger scale than simply mean number of species per plot, I calculated the mean number of unique species observed in all possible sets of 7 plots for each of the cells in this two-factor
gradient analysis. The results of this analysis are shown in Figure 17. The essential pattern in mean species richness revealed for averaging across 7 plots (1400 m² of area) was essentially identical to that of the mean 200 m² plot species richness analysis – there was approximately three times the number of species in the high elevation, steep slope angle stratum as in the low elevation, low slope angle stratum in both analyses.

c) Response to Permafrost Gradient

The highest mean plot species richness was observed in the sporadic permafrost category with 33.49 species per plot across 165 plots (Fig. 18). The lowest species richness was observed in the continuous permafrost stratum which had a mean species richness of 16.51 across 146 plots, less than half the number of species per plot than the plots located in soils units with sporadic permafrost. Permafrost sites in interior Alaska are species-poor, and usually dominated by a few widespread boreal plant taxa capable of germinating and growing in this environment.

The pattern of species richness observed for mean number of species per plot held true when we considered total species richness across 146 plots (which represents a sample area of 29,200 m² (Fig. 19). A total of 350 species were observed in the 146 plots located on soils map units that were rated as sporadic permafrost, whereas only 171 vascular plant species were observed in the 146 plots located in soil map units rated as continuous permafrost; there were a total of 301 vascular plant species observed in plots located on soil map units rated as having discontinuous permafrost.

2. Landscape Gradients in the biogeographic affinities of vascular plant species

To further investigate important aspects of the biodiversity of the Park landscape that these findings reveal, I examined how different components of overall plant diversity responded to the elevation gradient (Fig. 20). Each species in the program database has been assigned with a variety of attributes, including their global geographic range, and important biogeographic characteristic. I calculated the mean species richness for each of the five primary geographic range categories represented in our flora, which are:

1) Amphi-Beringian – species occurs on both sides of the Bering Strait, with a distribution that is limited to North America and Eurasia, and is roughly centered on Beringia.
2) Alaska-Yukon endemic – species only occurs in Alaska, Yukon Territory and adjacent areas.
3) Circumpolar – species occurs on all circumpolar continents, including in Greenland and European and Asian segments of Eurasia
4) Incompletely Circumpolar – species occurs on all but one circumpolar continent, usually either absent from Greenland and the European or Asian segments of Eurasia (many of species in this group are circumboreal plants absent from arctic regions).
5) North American – species whose range occurs only in North America (sometimes with satellite populations on Greenland also)
a) Responses to Elevation and Slope Gradients

The results of this gradient analysis show that the species groups with the strongest positive gradient response in species richness to increasing elevation were for Amphi-Beringian species and Alaska-Yukon endemic species (Fig. 20). In fact, Alaska-Yukon endemics were the only group with the highest mean species richness in the highest elevation category (>1400 m). Furthermore, the results of a two-factor gradient of Alaska-Yukon endemic plant species richness in repose to elevation and slope angle (identical to the total vascular plant species analysis shown in Fig. 18) show a very strong increase in endemic species richness to both slope and elevation at the spatial scale including seven plots (1400 m²; see Fig. 21). Mean number of Alaska-Yukon endemics across all possible sets of seven plots (1400 m²) was more than 20 times higher in the steepest, highest elevation category as compared to the lowest slope angle, lowest elevation category (8.31 endemic species per plot vs. 0.40 endemic species per 1400 m²).

c) Responses to Permafrost Gradient

Areas located in areas of the landscape with continuous permafrost were generally quite species-poort, with low mean species richness per plot (Fig. 22). This low diversity was particularly true for taxa with Amphi-Beringian and Alaska-Yukon endemic geographic distributions. These two categories of species had markedly increased species richness with decreasing intensity of permafrost of soils unit – both of these species-groups were least species-rich (on average) in continuous permafrost and had highest mean species richness in the plots located on non-permafrost soils map units (Fig. 22).

3. Landscape Gradients in the Cover of Dominant Species

A primary objective of this monitoring program is to detect changes in the cover of dominant species at the landscape scale. We assume that if significant changes in the cover of dominant species were to occur on the Park landscape in response to (for example) climate change, then these changes would occur differently in different segments of the primary landscape gradients that control the abundance of these species. For example if warming were to increase shrub growth, we would expect that to be hypothetically particularly evident in at least three areas of the landscape:

1) The middle to upper-elevation zones of the Park at the boundary where shrub growth currently declines with increasing elevation;
2) In cold permafrost zones where tall shrub growth is currently limited by cold and wet soils conditions;
3) In wetland areas where shrubs are currently excluded by saturated soils and drying and warming facilitates shrub encroachment into open sedge wetlands.

The rate, vertical structure, and species composition of each of these trajectories of change would differ markedly depending upon landscape context and current vegetation. Nonetheless, all three of these trajectories of change (which have already been documented in Alaska to varying
degrees and with varying types of data), if they were to occur at a landscape scale, would have profound implications for the biota of Denali.

Thus under this scenario of landscape change we would expect a “migration” of peak cover percentages for shrub species towards the left (higher elevation categories) in these gradient graphs. The primary task for the first iteration of sampling, then, is to establish and quantify these important vegetation-landscape relationships, and determine the most important factors that control species abundances on the current landscape.

I identified a set of 15 dominant species for analysis that included the vascular plant taxa that were dominant (in terms of highest mean percent cover in the vegetation) over different sections of the elevation gradient (these species are shown in table 2). The goal of these analyses was to determine the gradient responses of dominant plant species to the primary landscape gradients.

Table 2. List of dominant species according to their general zone of dominance along the gradient of elevation captured by this data set.

<table>
<thead>
<tr>
<th>Widespread dominant species</th>
<th>Lowland dominant Species</th>
<th>Mid-elevation dominant species</th>
<th>Alpine dominant species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carex bigelowii</td>
<td>Eriophorum vaginatum</td>
<td>Alnus viridis</td>
<td>Dryas octopetala</td>
</tr>
<tr>
<td>Ledum decumbens</td>
<td>Ledum groenlandicum</td>
<td>Betula nana</td>
<td>Cassiope tetragona</td>
</tr>
<tr>
<td>Vaccinium uliginosum</td>
<td>Picea mariana</td>
<td>Empetrum nigrum</td>
<td>Festuca altaica</td>
</tr>
<tr>
<td>V. vitis-idaea</td>
<td></td>
<td>Picea glauca</td>
<td>Salix reticulata</td>
</tr>
</tbody>
</table>

Fig. 23  Fig. 24  Fig. 25  Fig. 26

a) Responses to Elevation Gradient

Results of the single-factor gradient analyses of species cover in relation to elevation for these 15 dominant species are shown in figures 23 through 26. In general the species cover data from this data set showed a strong (even remarkable) correspondence with theoretical literature on simple species distributions in relation to single environmental gradients. Specifically, 11 of the 15 dominant species analyzed here, the majority showed a generally unimodal, more or less normal distribution of mean percent cover along the elevation gradient, or a semi-truncated version of a normal distribution. Two of the remaining three species (Ledum groenlandicum and Picea mariana) showed a highly left-skewed distribution of percent cover in relation to elevation gradient (high percents at low elevation) and one (Cassiope tetragona) showed a right-skewed cover signature in relation to elevation. This provides an indication that our plot network has
effectively captured the responses of these species in terms of cover to this important landscape gradient.

Four species were dominant over a wide range of the elevation gradient encompassed by this sample but had highest cover percentages in the low elevation gradient segments: Carex bigelowii, Ledum decumbens, Vaccinium uliginosum and V. vitis-idaea (Fig. 23). Three species showed a left-skewed distribution pattern in relation to elevation gradient were dominant in low elevation sites (Fig. 24): Eriophorum vaginatum, Ledum groenlandicum, and Picea mariana. The set of species that were dominant in the middle of the elevation gradient (with highest mean cover occurring between 600 and 100 m segments) included Alnus viridis, Betula nana, Empetrum nigrum, and Picea glauca (see Fig. 25). The four species in the group of alpine dominants were Dryas octopetala, Cassiope tetragona, Festuca altaica, and Salix reticulata (Fig. 26).

b) Responses to Slope and Elevation Gradients

Cover of the dominant species in this study area showed varying responses to the combined influences of elevation and cover across this data set, as expected. Cover of certain species, such as Carex bigelowii and Ledum decumbens (Fig. 27 A, B) had strong negative responses in mean percent cover to both increasing elevation and increasing slope angle. Other dominants, including the tundra species Cassiope tetragona showed positive responses in mean cover to both of these landscape gradients (Fig. 27 C, D). Species such as Alnus viridis and Picea glauca showed an apparent increase in mean cover in the steeper slope angle strata while having variable response to the elevation gradient (Fig. 27 E, F). Alder (Alnus) was particularly abundant in the subalpine zone at mid-elevations.

c) Responses to Permafrost Gradient

The set of fifteen dominant taxa displayed variable responses to the permafrost gradient captured in this sample. Interestingly, all of the most common and widespread vascular plant species in the park, including Vaccinium uliginosum, V. vitis-idaea, and Carex bigelowii, among others showed highest cover in the soil map polygons with ‘continuous permafrost, and showed a more or less monotonic decrease in mean cover with decreasing intensity of permafrost (Fig. 28). These are predominantly boreal species with reduced cover in high elevation areas.

Alpine and subalpine dominants such as Alnus viridis and Dryas octopetala are occur in much reduced abundance in the cold, wet lowlands soils. One dominant species with considerable cover in the lowlands that showed a gradient signature of reduced cover in soil map units with permafrost was white spruce (Picea glauca). This conforms with expectation of white spruce as a species most typical of warmer areas of the landscape, including river terraces and south-exposed slopes.
4. Landscape Gradients in the cover of different growth form classes within the vegetation

We have organized the project database and statistical summary routines to allow species-level data, such as those that are presented above, to be seamlessly aggregated and summarized according to a variety of plant attributes, such as growth form or species geographic range, for example. These species attributes are stored in a table in the relational database and organized to allow using these attribute values in place of species names in analyzing the project data. Top provide and example of the utility of this, I present a set of gradient analyses showing the variation in the cover of different growth form classes below.

The purpose of this section is to provide an example of the utility of organizing cover data collected by this program according to growth form. Thus I will not go into great detail showing all growth-form data for all of the gradients. Instead I have chosen three pairs of “growth form” elements from cover transect data. I will present the results of single-factor gradient analyses (for elevation, slope and permafrost status) for each of these three pairs of growth form elements.

a) Response to Elevation Gradient

Mean cover of bryophytes and lichens showed clearly different responses to the gradient in elevation captured by this sample (Fig. 29). Mean bryophyte cover is essentially constant across the elevation categories in the boreal zone (less than 800m), and declines monotonically from a maximum mean cover of 60% in the 600-800 m category to a low of 10% in the > 1400 m category. Lichen cover, in contrast varied very little from a mean value of approximately 13 percent across all the elevation categories below 1200 m, but had slightly higher cover in the high alpine categories (26 percent in 1200-1400 m and 20 percent in > 1400 m category). Shrub cover showed a left-skewed distribution in mean cover around the maximum value of 54% in the 800-1000 m, with higher cover values in the low elevation than high elevation (mean cover of 30% in the <400m category vs. 1% in the >1400 m category (Fig. 30). These observations are in accord with our general perception of maximum shrub cover in the subalpine zone and adjacent uplands. Shrub cover is displaced by competition from trees in the lowlands, and is limited by harsh microclimatic condition in the high elevation areas.

The response of dwarf shrub cover across this gradient, on the other hand, was more variable with a roughly bimodal distribution (two peaks in abundance values). This (putative) bimodal abundance pattern likely corresponds to two distinct species-groups of dwarf shrubs, a lowland group including Oxycoccus microcarpus and Andromeda polifolia and an alpine group including Dryas spp. Cassiope tetragona, and several dwarf Salix species (Fig. 30). Highest dwarf shrub cover was 29 %, which was observed in the 1200-1400 m category, whereas lowest mean dwarf shrub cover was 9% in the >1400 m category.

We have also categorized non-plant species elements of cover into categories representing “growth forms” for example – bare mineral soil, gravel and rock cover are summed into a category called “mineral cover” and flowing and standing water are summed into a category called “water cover”. The results of the single-factor gradient analyses of these two cover
categories showed (predictable) dramatic increases in mineral cover of the ground surface with elevation, and decreases in the water cover of the ground surface with elevation (Fig. 31).

b) Response to Slope Gradient

Mean cover of bryophytes was essentially constant across all of the slope categories until the 24° to 30° category, where it declined to a mean of 38% from a mean of 54% in the 18° to 24° slope category (Fig. 32). Lowest bryophyte cover was 25%, and was observed in the highest slope category (unsurprisingly). Mean cover of lichens was similar across the entire gradient, with the highest value observed in the highest slope category, at 23%.

The only gradient response of mean shrub cover to slope angle that was apparent was a decline in cover in the two steepest-slope categories (which had mean cover of 24% and 26.5 respectively; Fig. 33). Dwarf shrub cover was essentially constant across the gradient in slope angle in the dataset, varying around an overall mean of about 20% cover, with no apparent general response across the gradient. It should be noted that individual species of dwarf shrubs show strong responses to the gradient, it is only the case that in aggregate, this class of species did not vary perceptibly in mean cover in response to slope angle (Fig. 33).

Mean mineral cover of the ground surface increased strongly with increasing slope angle, reflecting the importance of geomorphic disturbance in steep areas of the landscape (Fig. 34). Water cover was essentially limited to the lowest slope angle category, although traces did occur across the slope gradient (from rivulets in alpine areas in steepest categories).

c) Response to Permafrost Gradient

Moss is a crucial element in the formation of permafrost in the boreal region, insulating the soil from summer warmth. Thus these results confirm an expected pattern showing highest bryophyte cover in the plots located in soil map units with continuous permafrost (mean cover of 63%; Fig. 35). The lowest bryophyte cover was observed in the “none” permafrost category (7%). Mean cover of lichen appeared to decline with decreasing intensity of permafrost status, although this was not a pronounced trend, with values for all categories within one standard error of each other, except for none, which was apparently reduced lichen cover (5%; Fig. 35).

Mean cover of shrubs was highest in the discontinuous permafrost category (45%) but was essentially the same across this gradient (Fig. 36). Plots located in soils units without permafrost had lowest mean shrub cover (2%), likely because these were high-elevation plots. Dwarf shrub cover showed an essentially identical pattern to that of shrubs across this gradient, except with reduced absolute cover percentages, and relatively higher cover in the None category than was observed for shrub cover (12% dwarf shrub cover vs. 2% shrub cover in this category; Fig. 36).

There was a strong positive gradient response of mean mineral cover to decreasing permafrost intensity, as expected; because very little mineral material is exposed in densely vegetated permafrost areas of the landscape (Fig. 37). Mineral cover is abundant in disturbed areas less likely to have permafrost, such as river corridors, slopes and escarpments. Standing water cover
did not vary appreciably across this gradient, except it was absent from plots located on units with no permafrost (Fig. 37).

5. Landscape Gradients in the Stature of Vegetation

Vegetation stature is a fundamental aspect of the ecosystem and is important in terms of the types and rates of primary productivity and in defining the habitat for almost all species of wildlife, especially birds. Changes in vegetation stature would be expected from a variety of different stressors to park ecosystems. The most obvious such change would be from climate change. The effects of climate change have widely been postulated to have significant influences on the distribution of trees and shrubs, with both expansion and contraction of forest hypothesized for different landscape segments and trajectories of climate change. Clearly any landscape-scale changes in the structure of vegetation have substantial implications for all of the Park’s biota, from moose to mosquitoes.

The cover transects that we measure in each permanent vegetation monitoring plot allow us to characterize the vertical arrangement of live plant cover across the landscape and thus to analyze the landscape gradients that are important in controlling vegetation stature. In this section, I present the results of some of these analyses for this 20 mini-grid data set.

a) Response to Elevation Gradient

Elevation is clearly the major factor in controlling the stature of vegetation on the Park landscape. Forest and other tall-statured vegetation are much more common in the lowlands, and absent from high elevation areas. However there are several factors that confound the strict correlation of monotonic increases in tall-statured plant cover with decreasing elevation. There are three types of habitats that occur in the lowland areas of the Park that generally do not have tall-statured forest vegetation: 1) areas with solidly-frozen permafrost; 2) early successional areas, such as post-flood or post-fire communities; and 3) wetlands with saturated soil or standing water conditions.

There are three graphs shown in figure 38 representing gradient analyses of percent live plant cover in three height categories above the ground: less than 50 cm, between 50 cm and 200 cm and greater than 200 cm across the elevation gradient represented by this sample. Note that the only substantial trend in the low height stratum (<50 cm) is the strong diminution of cover in the highest category of elevation (>1400 m), which is the result of increased geomorphic disturbance and overall reduced plant cover due to harsh climatic conditions of the high alpine zone. Mean cover for this stratum for all of the other elevation categories ranges between 51 and 69 percent, with the means generally all within one standard error. In the two taller height strata, cover declines in lower elevation height categories. In the 50-200 cm height stratum, mean percent cover drops off markedly in the in the 1200-1400 m elevation category, and in the greater than 200 cm vegetation stratum, mean percent cover drops off in the 1000 –1200 m elevation category.
These trends in cover by height stratum along the elevation gradient shown in figure 38 are less marked than might be expected. One major reason for this is the high number of lowland plots in the Toklat Basin on solidly-frozen permafrost that were accomplished as a part of this sample – many of these plots supported low-statured open tussock vegetation that reduces the mean cover of plots in the two lowest elevation strata. Another reason is that the two lowest elevation mini-grids in the sample (Bear Creek and Sandless Lake) were both affected by recent fires, this drastically reducing the amount of tall-statured vegetation in almost half of these plots.

b) Responses to Elevation and Soil Depth Gradients

I evaluated the contributions of two important physical variables in controlling the stature of vegetation cover by performing a two-factor gradient analysis, parsing the dataset jointly by soil depth (representing the depth of the active layer) and elevation (see Fig. 39 and Fig. 40). Plots located in areas with deep active layers (>50 cm) in the lowlands had roughly six times the mean live plant cover in two taller height-strata as compared to plots located in areas with the shallowest active layers (< 25 cm); 19 percent mean live plant cover in the > 200 cm stratum for plots with active layers (> 50 cm) as compared to 3 percent mean live plant cover in plots with <25 cm active layer. For the 50 – 200 cm height stratum, this difference was 25 percent to 4 percent.

c) Response to Permafrost Gradient

Soil attributes related to permafrost attributes including depth of the active layer were an important factor in controlling the stature of the vegetation in this data set, along with elevation. Figure 41 shows the results of two two-factor gradient analyses of mean live plant cover in relation to permafrost category of soil unit and elevation for two vegetation height strata (50-200 cm above the ground and > 200 cm above the ground). Once again, note the monotonic increase in mean live plant cover with decreasing intensity of permafrost (from continuous to sporadic), for both vegetation height strata. Also, the trend of decreasing live plant biomass cover with increasing elevation for these height strata is evident. Presumably, if permafrost degradation occurs through warming of the soil, the strong apparent constraints imposed on stature of plant growth in the continuous permafrost areas will be released. Thus we would expect that if we re-created identical histograms to these based upon the data from a future iteration of sampling, they would exhibit a markedly different gradient signature between elevation, soil polygon and stature of live plant cover. Changes in this fundamental relationship would have numerous important effects on ecosystem function and wildlife habitat.

6. Landscape Gradients in the Density of Trees

The presence of trees in a landscape represents a qualitative shift in vegetation – from open to forested landscapes. The establishment of trees in an area implies large changes in patterns of primary productivity, quantum shifts in local wind patterns, changes in the albedo of the landscape and mechanisms of heat transfer between atmosphere and the ground, among many others. Because of its central importance, monitoring tree abundance is a crucial element of this monitoring program. One way that we do this is by quantifying the density of trees by censusing and measuring all individuals above breast height (1.37 m) and mapping all trees > 12 cm in
diameter in all plots. This allows us to generate estimates of density and basal area of trees, by species and condition class at a landscape scale.

I identified three primary size-classes of individuals for the tree measurements in this program: Trees – individuals with a diameter at breast height (dbh) of 12 cm or greater; Saplings – individuals with dbh of less than 12 cm, and seedlings – individuals that are less than 1.37 m tall (thus 0 dbh). Density of individuals in these three size-classes varied greatly both within and among the mini-grid samples in this dataset (Fig. 42). Study areas located in the lowlands predictably contained plots with the highest live and dead tree densities (trees being individuals with dbh >12 cm). The study areas containing plots with the highest densities of tree-sized individuals were of two types: those with sloping terrain in warm, southerly exposures (East Chitsia, Wigand, Rock Creek, Bear Creek and Middle Teklanika) or study areas with substantial floodplain or river-terrace habitat (Wonder Lake, Middle Teklanika, and Rock Creek,). The study areas with the highest densities of dead individuals in the tree size class were as follows: Bear Creek, Sandless Lake, Wonder Lake and East Chitsia. Mortality in the Bear Creek and Sandless mini-grids was attributable to recent fires that killed trees in those areas. Mortality of trees in the East Chitsia and Rock Creek min-grids occurred in plots with the oldest, mature forest with large trees dying due to density-dependent factors and pathogens.

In general, the mini-grids with the highest numbers of plots with high live sapling densities (individuals <12 cm, >0 cm dbh) were located either in burned areas (Bear Creek, Sandless; Fig. 42) or in mini-grids with considerable flat or gently sloping lowland grids with large areas of continuous permafrost (Wigand, West Toklat and Middle Teklanika R). These “saplings” represent relatively mature black spruce that do not reach a large stature in cold, wet soil conditions of continuous permafrost. Plots with high numbers of dead saplings were only observed in the two mini-grids within this sample that were recently burned – Bear Creek and Sandless (Fig. 42). High sapling mortality in these two study areas was caused by fire.

The highest plot seedling densities in this sample were observed in Bear Creek and Sandless mini-grids (more than 50000 stems / ha; see Fig. 42). These high seedling densities were, in general, located in plots that were affected by the recent fires in these two study areas. Plots with intermediate seedling densities were observed in the East Chitsia, West Toklat and Middle Teklanika River mini-grids. These plots were located in areas where either slope or fluvial processes created open areas for establishment of relatively large number of tree seedlings. Plot seedling density is potentially a very important monitoring tool, for it implies at least the potential for very large structural changes in the vegetation over short spaces of time, particularly in study areas with low overall tree density currently.

a) Response to Elevation Gradient

Mean density of tree-sized individuals was highest in the 600-800 m elevation category for both live and dead individuals (Fig. 43). Mean live and dead sapling densities, on the other hand, were highest in the less than 400 m elevation category, and declined monotonically with increasing elevation, with no trees in the plots above 1000 m elevation (Fig. 43). Mean seedling densities were four times higher in the less than 400 m elevation stratum than in any of the other strata, seedling densities were virtually zero in the strata above 1000 m elevation (Fig. 43).
b) Response to Elevation and Soil Depth Gradients

The results of two-factor gradient analyses of tree, sapling and seedling densities on elevation and soil depth show strong patterns that suggest that these two-factors play a substantial role in controlling tree density at the landscape scale (Fig. 44). The mean value for tree density in the low elevation, deep soils category was higher by a factor of two as compared to any other category in this gradient analysis.

c) Response to Permafrost Gradient

Mean density for individuals in the >12cm size class was highest in the plots sporadic permafrost category, with a very similar mean density value in the discontinuous permafrost category (Fig. 45). The lowest density was in the continuous permafrost category with a much lower density of individuals reaching this size class. Mean density of saplings, on the other hand, was more even across these categories, with essentially identical values (given high variability in density values) across the gradient (Fig. 46). Mean density of seedlings was highest in the continuous permafrost category, at least in part because the two mini-grids with plots in recent burns (and thus extremely high seedling densities) were located in this landscape category (Fig. 47).

7. Landscape Gradients in the Distribution of Tree Species

In this section I examine the differences in density patterns among the various individual tree species observed in this sample. These data allow us to understand the differing habitat preferences and distribution patterns of tree species at a landscape scale, which in turn allows us to make informed predictions about how landscape change might differentially affect these important species. In addition, if we detect different responses of these species to the primary landscape gradients in future sampling iteration, this will be important information for understanding how change is affecting the Park landscape.

a) Response to Elevation and Soil depth Gradients

There were clear differences in the density of the primary tree species on the Park landscape in response to these landscape gradients. For the purposes of this summary, I will present the results of two-factor gradient analyses of three tree species densities in response to elevation and soil depth to illustrate the types of differences we have observed in the data set.

The results of the three two-factor gradient analyses of tree-size class densities for these three species (white and black spruce, and aspen) are shown in figure 48. (8) Three primary differences among the gradient signatures for these species emerge from an examination of these analyses: 1) white spruce had an overall higher density in the large size classes across all gradient segments as compared to the other two species (note that virtually no aspen in this size-class, > 12 cm, occurred in this sample); 2) black spruce were clearly confined to lower elevation strata than white spruce; and 3) tree-sized individuals of both white and black appeared to occur in the highest densities in deeper soils (>50 cm mean soil depth) and in low elevation (< 750 m).
This likely reflects sites of higher productivity associated with deeply thawed soils in river bars and southerly-exposed slopes in the warmer boreal lowlands.

The patterns in tree species density that are revealed from the two-factor gradient analyses of the sapling-size class data for these three tree species are different than for the tree-size class data (compare Fig. 48 to Fig. 49). First, black spruce density is clearly concentrated in the sapling size class in this data set, with density of 1049 black spruce stems per hectare in the cell defined by elevations of less than 750 m and soil depths between 25 and 50 cm (Fig. 49). Secondly, there are markedly different responses to the soil depth gradient among these three species that relate directly to the varying environmental tolerances and competitive abilities of each species. Aspen, a species normally associated with warm hillsides and river bars, shows the strongest positive density response to increasing soil depth (=active layer depth) with zero individuals observed in the plots in the 0 to 25 cm soil depth category and a mean density of 864 stems per hectare in the deep soil category. Interestingly, peak black spruce sapling densities were observed in the middle soil depth category. This likely reflects two dynamics: 1) competitive exclusion of black spruce from the deeper active layer areas with warmer and drier soil (note the high density of white spruce trees in this category in Fig. 48), and; 2) exclusion from the 0 to 25 cm soil depth category due to cold, wet and generally inhospitable growing conditions in the sites with very shallow active layers.

c) Response to Permafrost Gradient

Mean density of tree-sized individuals was variable among soil map unit permafrost categories for the four primary tree species observed in this sample of twenty mini-grids (Fig. 50). Density of white spruce was highest in the map units categorized as having sporadic or discontinuous permafrost. Highest mean density of black spruce, conversely, was observed in the continuous permafrost category, as was the mean density of Alaska birch (Betula neoalaskana).

Sapling densities were highest in the continuous permafrost category for black spruce, Alaska birch, and quaking aspen (Fig. 50). The highest mean sapling density for white spruce, conversely, was observed in the group of plots located in map units categorized as having discontinuous permafrost (Fig. 50). Similarly, mean seedling densities for black spruce and birch were apparently highest in the continuous permafrost map units, whereas white spruce seedling densities were highest in the sporadic permafrost category. One reason for the very high mean seedling density in the continuous permafrost units is that the two mini-grids that were burned (and thus had very high post-fire seedling densities).

8. Tamarack (Larix laricina) mortality

Tamarack (Larix laricina) occurs only sporadically in the lowlands of Denali National Park (and interior Alaska generally), usually in low-lying areas with cold, wet soils also occupied by black spruce. A major outbreak of the larch sawfly (Pristiphora erichsonii) that peaked in the mid-to late 1990’s affect populations of this tree around the state and resulted in mortality of these trees in many locations. We observed larch in five mini-grid study areas during this study (Bear Creek, Bearpaw, East Chitsia, Sandless Lake, and Wigand Creek). I analyzed the plot data from
this study to determine whether larch trees in this study area showed patterns of mortality that indicate the population was affected by the recent sawfly outbreak.

The pattern in tamarack mortality for the five mini-grids where it was observed was clearly markedly different than for any other species for these same areas (Fig. 51). Whereas dead individuals outnumbered live ones for all size classes of tamarack, live individuals greatly outnumbered dead ones for all of the other tree species in all of the size classes (although only conifers are presented in figure 51). These larch mortality data likely capture the results of the larch sawfly outbreak in the northern lowlands of Denali. This represents a real test of the ability of this sampling program to detect changes in mortality in an uncommon tree species in this study area.

9. Landscape Gradients in the Distribution of Dominant Vegetation Types

We used the Alaska Vegetation Classification to classify the vegetation of each of the permanent plots that was installed for this program (Viereck et al 1992). Vegetation types are recognizable as discrete assemblages of plant species that share common dominant species and structural characteristics that often occur in association with particular landforms or terrain features. For example, open balsam poplar forest is a vegetation type commonly encountered on river terraces in interior Alaska. It represents a specific successional stage following flood disturbance in certain areas. There is a characteristic set of species that we expect to occur in this vegetation type on the current landscape. Classifying a particular area of vegetation according to a system such as the Alaska Vegetation Classification provides a shorthand way of summarizing a variety of variables simultaneously. In reference to monitoring, changes in both the relative and absolute abundance of individual species within the vegetation may accumulate over time to then produce “quantum” changes to a new vegetation type. This occurs constantly in our landscapes through the process of ecological succession (generally observed as a cyclical process).

Other, more directional changes in species composition and abundance may occur through time that actually produce new and different vegetation types on the landscape (as has occurred repeatedly through geological time). One possible mechanism for this is climate change that produces new combinations of environmental conditions than were previously extant, thus stimulating new and different combinations of species and thus new vegetation types. Vegetation types or communities thus represent “snapshots” in time of particular species assemblages resulting from the collection of individualistic responses of local plant species to their environment, and interactions among these species. According to best evidence, a vegetation type or specific assemblage of plant species does not represent a stable biological entity in the long term. Thus while I believe it is useful to describe and categorize changes in vegetation types on the landscape over time for various purposes, I also would stress that our direct measurements of the individual vegetation attributes should detect important changes in the vegetation prior to relatively drastic changes that produce quantum changes in vegetation type (except in the case of wholesale disturbance, such as fire, flood, or mass movement events such as landslides).
There were ten vegetation types at level three of the Alaska Vegetation classification that were observed in at least ten of the permanent vegetation plots in this data set. Figure 52 shows the distribution of these ten most common vegetation types among 5 strata of elevation (the histogram presents the percent of plots in the elevation category where the given type was observed, thus it is a frequency histogram normalized for the number of plots in the elevation categories).

The most common vegetation type in this study area overall was 2C2 – Open low scrub, which was observed in 34% of all plots measured in this dataset (Fig. 52). The most common expression of this structural type is open-low birch-ericaceous scrub in cold, wet permafrost soils, dominated by *Betula nana*, *Carex bigelowii*, *Ledum decumbens*, *Vaccinium uliginosum* and *V. vitis-idaea*. This type is very common from the lowlands into the subalpine zone in gentle to rolling slopes. Note that this type occurred in relatively high frequency in all of the elevation categories below 1000 m elevation (Fig. 52). The other type that occurred in high frequency in the lowlands was Open Needleleaf Forest, which was observed in 30 percent of the plots below 400 m in elevation. The most common expression of this structural type was open black spruce woodland in permafrost situations, with the understory frequently dominated by the suite of species listed above for Open Low Scrub. Woodland Needleleaf forest (1A3), another relatively common lowland type, was quite similar in composition to the Open Needleleaf Forest, although with less tree cover.

The three alpine tundra types (2D1 – Dryas Dwarf Scrub, 2D2 – Ericaceous Dwarf scrub, and 2D3- Willow Dwarf Scrub) occurred in roughly equal frequency in the elevation stratum higher than 1000 m, each of these was observed in about 20 percent of the 137 plots in this stratum (Fig. 52). The other common alpine type in this data set was 7B3 – Barren Scree and Talus, which was observed in 15 percent of the plots above 1000 m in elevation. This was particularly common in steep areas in the Mount Healy, Tributary, and Gorge Creek mini-grids.

IV. Discussion and Conclusions

We are approximately at the mid-point of establishing the permanent sampling plot network for the landscape-scale vegetation monitoring program for Denali National Park and Preserve. Data from the first iteration of sampling represent the baseline to which data from future sample iterations will be compared. Thus detecting change (the primary reason for this monitoring program) awaits further sampling iterations. However, the baseline data provide a wealth of detailed quantitative information regarding vegetation-landscape relationships that represent a unique data set for understanding these relationships in the Park. For example, these data have revealed several significant attributes of landscape patterns in biodiversity that would be very difficult or impossible to quantify using other methods.

A foundation of this monitoring program is effectively sampling the primary physical gradients that control variation in the vegetation at the landscape and meso-scales with our plot network. In order to determine whether we have met this criterion, it is necessary to fully explore the data on an ongoing basis to determine two primary facets of this issue:
1) Were the physical gradients effectively and completely sampled;
2) Do these physical gradients appear to be important in controlling the vegetation variables that we have chosen to monitor?

To determine whether the sampling design has effectively sampled the gradients, I have examined the ranges of variation in the primary variables to determine whether there were gaps in the data for these gradients (such as the gap between 200 m and 400 m in the elevation gradient shown in Fig. 1). To demonstrate the importance of these physical gradients in controlling variation in monitored variables of the vegetation, in a clear and visual way, I performed a large number of gradient analyses of the entire data set. I discuss the results of these analyses below.

**Species richness**

The results of this study show a strong pattern of increasing vascular plant species richness with elevation up to the 1200 m to 1400 m level. Species richness was found to decline somewhat in the small group of plots measured above this elevation zone, but was still quite high relative to low elevation areas of the landscape. The alpine zone is clearly the most floristically diverse area for vascular plants in this landscape, both in terms of species richness per unit area and for total species richness across large areas (see species: area curves in Fig. 15). This result runs directly counter to a substantial body of empirical and theoretical literature that has taken up the issue of species diversity along elevation gradients (Whittaker, 1960; Hamilton, 1975; Whitaker and Nerling, 1975; Schmida and Wilson, 1985; Gentry, 1988; Oddland and Birks, 1999; Kessler, 2000; Grytnes and Vitaas, 2000; ). Many investigators of this question found that elevation and species richness were inversely correlated with species richness showing a monotonic decrease with elevation (Hamilton, 1975; Schmida and Wilson, 1985; Gentry, 1988; Kitayama, 1992; Vazquez and Givnish, 1998; Odland and Birks, 1999; Grytnes, 2003; Fosaa, 2004). In considering species richness patterns in relation to elevation, some authors have suggested that the diminution of species richness with elevation is a general rule equivalent to global pattern of decreasing species diversity with increasing latitude (MacArthur, 1972; Simpson, 1983; Brown, 1988; Begon et al 1990; Rohde, 1992; Stevens, 1992). Many investigators have observed a “humped” relationship of species richness with elevation where species richness is highest at some intermediate elevation (Whittaker, 1960; Whitaker and Neiering, 1975; Lieberman et al, 1996; Kessler, 2000; Grytnes and Vitaas, 2002; Grytnes, 2003).

The pattern in species richness in Denali does not conform well to the hypothesized reasons for observed “humped” relationship of species richness to elevation (see Grytnes et al, 2006). This hypothesis suggests that satellite populations of low-elevation species that occur above treeline are responsible for small increases in species richness at mid-elevation stations. These data show consistent monotonic increase of per plot and total species richness well into the alpine region, with presumably a steep drop-off in richness as the region of permanent rock and ice is reached (we have captured the beginning of this drop-off with the current data set showing strong declines in mean and total species richness above 1400 m in elevation, although with limited sample size to date).
We have observed a novel pattern in the response of plant species diversity to elevation with this dataset. This pattern likely relates to the unique biogeographic circumstances of interior Alaska relating to Pleistocene ecological history of the region. Specifically, the pool of species adapted to tundra and other open environments is considerably larger than the pool of species adapted to boreal forest and scrub communities due to the repeated winnowing of boreal taxa from the landscape during glacial advances over the course of the Pleistocene. During glacial intervals there were no forests in this region, and many boreal species likely vanished from the landscape or were restricted to small areas. Boreal species have returned during the interglacial period, but the forests and related boreal habitats are relative newcomers to this landscape. The primary stable refugium on the current landscape for the larger pool of species that occupied interior Beringia during the full glacial is the alpine zone – e.g. tundra and associated environments. Conditions there are perhaps considerably more similar to the climatic “norm” over the past two million years than any other area of the current landscape. Boreal environments, on the other hand, are relatively new to interior Alaska, having developed over the past 12,000 years or so.

The data for the biogeographic elements of the flora would seem to confirm this observation, with plants endemic to Alaska and with an Amphi-Beringian distribution showing the strongest positive gradient response to elevation compared to all other groups. These are presumable groups of species groups that were well-represented in the Pleistocene landscapes of Beringia. Their distribution pattern suggests that they likely were present in full-glacial landscapes because endemics are restricted to this area, and Amphi-Beringian taxa have evolutionary roots in Asia and likely crossed into North America during full-glacial periods when the Bering Land Bridge was exposed.

These results have major implications for the conservation of our endemic flora and for plant biodiversity in the Park generally. In the context of tree and shrub encroachment due to climatic warming there is clearly a potential for loss of alpine habitats. With the loss of alpine habitats, there is a clear potential for negative impacts to the overall biodiversity of the Park landscape, as well as loss of rare endemic species restricted to open alpine areas. Of course it is unknown what the potential and/or rate of establishment of “new” habitat for the alpine flora could be under a warmer climate. One factor potentially limiting the upward migration in elevation of many tundra plants is the very steep, geomorphically- active and soil-less character of areas currently above the elevation limit for tundra.

**Abundance of Dominant Species**

A unique attribute of this sampling design is that it allows us to make unbiased estimates of the absolute abundance of individual species at a landscape scale, using identical plot methodology across the Park from the lowlands through the high alpine zone. We are able to directly estimate which species are the most abundant in different segments of the park landscape, and model how the cover of individual dominant species responds to environmental gradients using unbiased data. Much of the species modeling that occurs at a landscape scales relies on data from numerous different studies that used different plot sizes and sampling configurations, or relies on very coarse estimates derived from visual estimation of cover over large areas (these data are often of variable or unknown quality and accuracy).
The unbiased models of species abundance that we will create based upon successive sampling iterations will be important tools for detecting changes in park vegetation over time. Direct statistical comparisons of cover from identical transect methodology in identical locations across time allow for us to see whether a particular species is changing either in individual plots or in different segments of the landscape gradients. What makes these gradient models so crucial to detecting and understanding change is the fact that the overall mean cover of a species in the plot network may not change over time, even though large changes may be occurring on the landscape. For example, white spruce has been shown to have opposite responses to climate warming in different segments of the landscape, depending on the relevant limiting factors (which change with location). Warming has likely resulted increased growth and reproduction of white spruce in areas where short season or cold conditions limit its abundance (treeline situations) but decreased growth rates in lowland areas where drought and competition for water are the primary limiting factors (Wilmking, ). Thus one can easily envision a scenario where mean spruce abundance remains constant across the entire set of plots, but its gradient signature of abundance in relation to elevation changes dramatically.

The gradient analyses of cover that I performed for this report document patterns of abundance that conform to expectations of informed observers of park landscape. For example, it comes as no surprise that black spruce (Picea mariana) is a primary dominant species in lowland areas of the park landscape, that Vaccinium uliginosum is abundant across the landscape, ort that Dryas octopetala is the most abundant alpine species in this area. These general patterns represent common knowledge to ecologists in interior Alaska. The significant thing about these data is rather that we have rigorously measured and quantified the specific abundance patterns of these species in relation to these gradients, so that if these fundamental patterns change through time we can detect it quantifiably (not just notice it through keen observation). After all, in 50 years the “common knowledge” about the landscape among current ecologists will not be available to those assessing the monitoring data.

**Abundance of Growth form Classes**

Species-based inferences such as those discussed above may not be the most appropriate attribute of interest for some monitoring questions. Instead, certain questions are best approached combing data across groups of species that share a similar important attribute such as growth form (tree, shrub, dwarf shrub, forb, graminoid, fern, lycophyte, moss, Lichen, etc…). For example, for many vegetation attributes that define wildlife-habitat, the species within a given growth-form class are more or less interchangeable. Nesting habitat for passerine birds, for instance, is frequently defined by the shrubbiness of an area, without regard to the species composition of the shrubs – alders or willows serve their needs equally well. Because changes in the abundance of individual species may not be informative in some cases we have developed the capability of combining measured values for species into informative groups.

Another valuable reason for assessing changes across groups of species is that a strong ecological change occurring on the landscape (such as shrub invasion of wetlands) may be a function of the parallel gradient responses of numerous species that, taken individually, are not detectable or significant, but taken as a group are highly significant. Given natural variation, for example, a statistical analysis that showed an increase of 5 % cover of several shrub species (e.g.
Myrica gale, Chamaedaphne calyculata and Salix fuscescens) across all plots located in wetland meadows across two sample iterations, may not yield a significant result for these species individually. However, an identical statistical analysis of the 15% increase in shrub cover in aggregate for the same group of wetland plots (sum for increases across these three species) across the same sample interval that may yield a highly significant result.

The examples of gradient responses presented here (shrubs, dwarf shrubs, mosses and lichens, mineral and water cover) reflect large-scale patterns in the abundance of these elements on the landscape. For example, it comes as no surprise that absolute abundance of moss decreases with elevation and slope across the landscape, or that mineral cover of the ground surface increases in steeper slopes and higher elevation. I believe that examining patterns in the abundance of growth forms will likely be more informative in smaller spatial scales than the data presented here because at this scale, we are combining cover values of so many species together that some of the strong and ecologically relevant local patterns are swamped by combining values of species with very different habitat requirements. This is illustrated by the gradient response in “dwarf shrub” category presented here. In contrast to trees, there are many dwarf shrubs in our flora that are adapted to various conditions and microclimates so that the strong species-level responses to gradients vanish when the data are combined using this category. If the area of consideration is restricted to the meso scale (one or a few adjacent mini-grids) analysis of the growth form data for this component is more meaningful and ecologically informative.

Stature of the Vegetation (vertical structure)

Vegetation stature (the vertical arrangement of live plant biomass) is a crucial element of the vegetation at all spatial scales because it defines the habitat for many animal species, and strongly affects important physical factors including patterns of snow accumulation, boundary-layer heat transfer, distribution of solar energy at the ground surface, local wind patterns, and albedo, among others.

The transition from dwarf tundra to scrub and scrub to forest each represent “quantum” transitions in the ecosystem for both habitat character for birds and wildlife and for vegetation influences on physical attributes of a site. It is likely that warming climate will elicit major changes in the vegetation structure along all three of the gradients considered here, which are all related to physical control over vegetation stature related to soil temperature and growing season length. We can expect the peak in the 50 cm to 200 cm cover that is currently in the 800 – 1000 m elevation category (subalpine zone) to both increase in and move to the right of this gradient graph with warming temperatures. Similarly, changes in the intensity and extent of permafrost would likely affect the gradient signatures for this set of plots both in the soil depth and permafrost unit gradients.

Thawing permafrost would likely have variable effects in the near term with formation of thermokarsts in ice-rich permafrost actually reducing vegetation stature in some areas, while in areas with less ice-rich permafrost seeing increases in tree and shrub growth and thus increasing vegetation stature in other areas. Regardless of the actual direction of the response, it seems very
likely that parsing the data set using these gradient techniques will be informative for detecting any changes in this variable,

**Tree density and the Distribution of Tree Species**

A change from an open landscape to a forested one represents a major shift in the ecosystem because trees tend to affect all aspects of primary productivity because of the altering of the competitive balances for light and other resources. It also influences important aspects of the management of a landscape because of the concerns about fire and the alteration of habitat for mammals that influence human subsistence and recreational uses.

Issues surrounding the response of elevational treeline to climate change were the foundation of the original Denali prototype Long Term Ecological Monitoring Program (LTEM). Three sets of three replicate plots were installed for that program in the Rock Creek watershed of Denali National Park to monitor changes in vegetation in three elevation zones (boreal, treeline and alpine) in 1992. The data that we have acquired during this program (since 2001) have shown the importance and value of a landscape-scale approach in contrast to the localized watershed approach taken for the LTEM program.

Specifically, there is considerable variability in both the elevation and character of treeline habitats on the Park landscape, and there are numerous gradients other than elevation that are important in affecting the location of treeline. The cool and moist edaphic conditions found in north-facing slopes of grids such as Upper Sushanna and Lower Stony Creek show much lower mean tree densities, even though they are lower in elevation (see Fig. xx).

The strong gradients in tree density at a landscape scale in response to two simple, easily measured variables – soil depth and elevation observed in this dataset is a significant finding. This strong relationship suggests that changes in active layer depth due to increased summer temperatures, over time, will lead to detectable responses in these gradient signatures. In this scenario for potential change, both one of the predictor variables (soil depth) and the response variable (tree density) would potentially be changing over time. Thus for future analyses to detect changes, we would run these gradient analyses assigning plots to strata based upon their membership in the gradient segments from soil depth measurements form the first sample iteration (results presented here, see Fig. XX through Fig. XX). In this way we will be able to assess some of our hypotheses regarding changes in the density of trees based upon two sample iterations.

**Tamarack Mortality**

Detecting trends in the mortality of tree species on the landscape is an objective of this monitoring program. These data show that, at least for the case of larch sawfly-induced Tamarack mortality, the design is capable of meeting this objective. The results from the five grids where tamarack was observed allowed us to see the markedly different patterns in mortality of this species in comparison to all other tree species in the sample (Fig. XX). That we were able to detect this elevated mortality at a landscape scale for tamarack is particularly significant.
because this species is uncommon and has an idiosyncratic and spotty distribution on the landscape. Thus if we can detect changes in mortality for this species, it should be possible for all the trees species we encounter.

**Distribution of Dominant Vegetation Types**

As changes in the abundance and distribution of plant species accumulate over time, one net result will be changes in the distribution of vegetation types on the landscape. This change occurs continually through successional processes, but changes in climate and/or artificial stressors could cause directional change through time. For example, areas historically occupied by dwarf birch scrub in the subalpine may be permanently transformed into boreal forest with warming of the climate.

The primary value of tracking changes in the distribution of discrete vegetation types in this program is twofold: 1) often vegetation types are used in wildlife habitat modeling (as opposed to quantitative species abundance data) so this increases the utility of the data for integration in other studies; and 2) we can use remotely-sensed data or aerial photos to map vegetation types and thus to scale-up information from the plot-based data (points) to polygons.

**Conclusions**

The data presented in this report reflect measurements made at 467 plots distributed over a very wide geographic area that represents large differences in habitat from lowland bogs and recently burned sites in the boreal zone to barren scree near summits in the alpine zone. This dataset is unique in Alaska’s parklands because the data for such a large area were collected according to identical protocols with identical plot configurations according to a randomized design. Thus we can make unbiased estimates for a large number of parameters using rigorously collected quantitative data. These data represent the baseline to which information from subsequent sampling iterations will be compared. This information also represents a deep well that can be used to inform the scientific community, land managers, and the public about the ecosystems of the Park.

It is important to recognize the strength of the relationships that we have documented between variation in vegetation and a set of physical variables. If this same sampling design was instituted in many other areas of the world (outside of polar regions), we would likely see considerably diminished responses along the gradients as compared to those I have presented here. This is because of the primary importance of environmental factors in controlling the vegetation at this high latitude, due to the importance of climate and solar angle. In other areas of the world, the relative contributions of physical factors and biotic interactions in controlling plant community patterns is very different, with an increase in the importance of biotic interactions relative to physical factors.
V. Literature Cited


