

Chapter 2

**THE ALASKAN TUNDRA:
PLANT AND TERRESTRIAL MICROBIAL
COMMUNITIES IN A CHANGING CLIMATE**

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ABSTRACT

The Alaskan tundra biome is a broad landscape largely distributed along the northern and western boundaries, occupying approximately 300,000 mi², or about one-third of the total land area (570,374 mi²). It is part of the North American tundra biome located at latitudes 60° to 85° North and longitudes 55° to 160° West. The vegetation is largely dominated by moss, small shrubs, and some herbaceous plants. Climate change and global warming have made major impacts in Alaska. During the past 50 years, temperatures increased by an average of ~ 2.0°C, a rate that is twice the U. S. national average for the same period of time. Increasing temperatures and modest changes in precipitation have caused substantial thawing of the moss-rich permafrost, releasing massive amounts of soluble organic compounds that have accumulated over millennia in the form of frozen remains of peat moss that are deposited in strata each growing season. These soluble organic nutrients are utilized by soil microbes, thus increasing their metabolism, altering the composition of the microbial communities, and through increased respiration emitting substantially more CO₂ to the already, heavy-laden concentrations of global atmospheric CO₂. Concurrently, the ecology of Alaskan vegetation is undergoing marked changes, including transitions from largely moss and prostrate shrubs, to increasing invasion by small trees and other erect woody shrubs. Modern research techniques such as use of satellite data, experimental ecological field studies, and laboratory-based modeling and biogeochemical analyses of warming effects on plants and soil microbiota have improved our understanding of how climate change is affecting land plants and the soil microbial communities in the Alaskan tundra. Some current research evidence is summarized, including estimates of future effects on the environment and the consequences for human activity.

INTRODUCTION

Geographically, Alaska is situated at the northern-most part of the North American continent, with a geographic center 63° 50' north latitude, 152° west longitude, approximately 60 miles northwest of Denali; and occupies 586,412 square miles of land area - a total area one-fifth the size of the lower 48 states. Based on landforms, Alaska can be divided into four general physiographic regions (Figure 1): Arctic Coastal Plain (Interior Plains), Rocky Mountain System of Alaska, Central Uplands and Lowlands (Intermontane Basins and Ranges), and Pacific Mountains and Valleys. Further designated regions by latitude (north to south) include the Arctic Coastal Plain, North Slope, Brooks Mountain Range, a central upland dissected by the Yukon River, the massive Alaska Mountain Range, the Pacific Coastal areas and eastern Inside Passage, and the Alaskan Peninsula, and Aleutian Islands of the southwest.

The Alaskan tundra is a broad landscape largely distributed along the northern and western boundaries in the Arctic Coastal Plain, occupying approximately 300,000 mi², or about one-third of the total land area (570,374 mi²). It is part of the North American tundra biome located at latitudes 60° to 85° North and longitudes 55° to 160° West. It lies north of the Rocky Mountain System and slopes gradually toward the Arctic Ocean.



Figure 1. Map of Alaska showing the mountains of the Brooks Range and Coastal N. Slope plains, where extensive tundra is located. Adapted from a State Government of Alaska image (<http://www.adfg.alaska.gov/index.cfm?adfg=viewinglocations.main>).

The Brooks Range Mountains in northern Alaska is a northern extension of the Rocky Mountains. It reaches 600 mi westward from Canada to the Chukchi Sea. Its rugged peaks reach elevations of 9,000 ft in the east, falling to 3,000 ft in the west. A series of rolling plateaus and low mountains, the arctic foothills, borders the coastal plain to the north forming a “polar tundra desert” characterized by a moss-dominated vegetation, and moist tundra-cottongrass tussocks, interspersed with willow-dominated communities along river corridors. Wetlands occupy greater than 83% of the area. It has been a geographic site for substantial recent ecological and climate change research, including the Arctic Long-term Ecological Research (LTER) site located at Toolik Lake (e.g., <http://ecosystems.mbl.edu/ARC/>) on the North Slope. The Toolik Lake area is characterized by continuous permafrost, no trees, a complete snow cover for seven to nine months annually, winter ice cover on lakes, streams, and ocean, and cessation of river flow during the winter. Tussock tundra is the dominant vegetation type, but there are extensive areas of drier heath tundra on ridge tops and other well-drained sites as well as areas of river-bottom willow communities.

Alaska has been dubbed “Climate change ground zero” owing to the marked changes in climate and geography, occasioned particularly by global warming (<http://climatenexus.org/learn/regional-impacts/Alaska-climate-change-ground-zero>). Temperatures are rising at twice the global rate. Alaska has warmed more than 2°C during the past 60 years, including an ~ 3°C increase in average winter temperature – a temperature change nearly half of the change that ended the last ice age. For example, the remarkably warm temperatures at the beginning of 2015 caused early snowmelt and the drying out of the Alaskan landscape, transforming areas of the normally wet and soft surface moss into a dry, brittle to fibrous layer.

This is a review of recent research on the changing environment and ecology of the vegetation, soil microbial communities, and the above- and belowground interactions of microbiota and vegetation in Alaska, with special attention to the tundra. Particular focus is placed on changes in vegetation revealed by satellite imagery and experimental ecological studies examining the effects of warming, soil drying, and changes in soil chemical and physical properties on vegetation and belowground microbial communities. Where appropriate relevant studies obtained from other locales are included to help elucidate findings from the tundra. Observational, real-time studies, of the changing tundra are also included, especially when they contribute to a clearer understanding of results from more indirect means such as satellite data and experimental field and laboratory-based studies. Given the main focus is on observational and experimental research, less attention is given to modeling studies, although this is a field of increasing importance as we endeavor to make better predictions about future scenarios.

There are four sections: Changing Arctic Vegetation, Soil Microbial Communities, Plant and Tundra soil Microbial Interactions, and Conclusions.

CHANGING ARCTIC VEGETATION

Plants are among biota most sensitive to climate, including changing atmospheric and soil conditions. They are directly dependent for their survival and growth on atmospheric and terrestrial resources including, but not limited to, adequate moisture through precipitation and available moisture in the active soil layer, appropriate temperatures within the species

tolerance range, sources of adequate light and concentrations of atmospheric carbon dioxide to support photosynthesis; and for vascular plants, sufficiently deep and nutrient rich soil to support strong and healthy root growth. Within the plant kingdom, tundra plant communities encompass a broad range of plant groups ranging from bryophytes (green moss) to vascular plants. The latter include soft-stemmed herbaceous plants such as sedges, grasses and some indigenous flowering plants, small shrubs such as birch (*Betula*), and small trees, including alder (*Alnus*) and willow (*Salix*). Conifers (evergreen trees) such as black and white spruce (*Picea*) are common in locales suitable for their growth. Lichens (fungal-algal symbioses) are also abundant and significant as sources of food for browsing animals such as caribou (*Rangifer tarandus*), especially in the Arctic during winter. Compared to other biomes, the biodiversity is low with only 1,700 species of vascular plants. The short growing season, and solid permafrost soil (frozen from 10 – 35 in. deep), that thaws only briefly for several months in summer to a shallow depth, prevents strong root development, thus historically limiting large tree growth. With global warming and more extensive thaw of the permafrost, there is a potential for greater incursion of larger vascular plants including taller trees as climate change progresses. Some current evidence of the shifting vegetation scene is presented in the following three sections: Satellite Data and Aerial Observation, Observational Field-based Research, and Experimental Field-based Research. Additional information is presented on the role of wildfires that are occurring increasingly in greater numbers, higher severity, and across a greater area, thus altering the vegetation, ecology, and soil properties of the Arctic.

Satellite Data and Aerial Observations

The launching of earth-orbiting, data gathering satellites in the mid twentieth century (among them, the first U.S. satellite *Explorer 1*, 1958) opened a new era in Earth observatory capacity, with approximately 1,000 all totaled in operation by the second decade of the twentieth century. Remote sensing satellites are equipped with a variety of data-gathering sensors, including: Optical imaging systems (gathering visible, near infrared, and shortwave infrared data), Thermal imaging systems (for surface temperature), and Synthetic aperture radar (SAR) imaging systems (e.g., gathering vertical relief data). These systems provide major advantages in monitoring and assessing global vegetation patterns that are within the orbiting satellite's geographic data gathering range. The highest resolution instruments provide detail at dimensions of 5 m or less. Two major areas of vegetation analysis research using satellites are reviewed: Changes in vegetation over time, seasonally and across decades, and Vegetation biomass density and geographic coverage. Some emerging evidence of wildfire events and consequences is also reviewed. Naito and Cairns (2011) provide a useful overview of some recent advances in remote-sensing technology and its affordances in arctic vegetation dynamics relative to other major biomes, and their paper provides a potentially useful context for this section. They also make recommendations for future land management policies.

Changes in vegetation over time, seasonally and across decades. Satellite data on changes in arctic vegetation coupled, in some cases, with ground-based evidence has been particularly useful in investigating how vegetation patterns change seasonally and over decadal time scales. On a global basis, Eastman et al., (2013) analyzed a 30-year series (1982-

2011) of data from satellite spectral analyses of vegetation derived from the Global Inventory Modeling and Mapping Studies to detect the presence of trends in seasonality. Over half (56.30%) of land surfaces were found to exhibit significant trends, thus indicating that changes in seasonality are not a rare occurrence. Among these significant trends, almost half (46.10%) belonged to the following three classes of seasonal trends (or evidence of changes). The first significant class (Class 1) accounted for 20.43% of all significantly trending areas, while the second (Class 2) and third (Class 3) most frequent classes accounted for 16.54% and 9.13%, respectively. Class 1 consisted of areas that evidenced a uniform increase in vegetation greenness throughout the year, and was primarily associated with forested areas, particularly broadleaf forests. Class 2 consisted of areas that had evidence of an increase in amplitude of the annual seasonal signal. Thus increases in vegetation greenness in the growing season were balanced by decreases in the brown non-growing season. These areas were found primarily in grassland and shrubland regions. Class 3 was found primarily in the Tundra, as well as Taiga, biomes and exhibited increases in the annual summer peak in vegetation greenness. The results from this broad multi-decadal study for tundra, of special interest here, are consistent with other published observations. These include evidence of large declines in snow cover duration in Tundra Biomes during the 20th century in relation to increases in temperature, which extends the period of time for plant photosynthetic activity (Chapin III, et al., 2005; Euskirchen et al., 2007; Hollister et al., 2005). These observations suggest that seasonal environmental variables may be of particular significance in tundra phenology.

For example, early seasonal effects, such as time of snowmelt onset, in the Arctic can have profound effects on subsequent development of vegetation, depending on the geographic locale. Earlier snowmelt and longer growing seasons due to climate warming have been hypothesized to enhance vegetation productivity (e.g., Zeng et al., 2011). Gamon et al., (2013) used field observations and satellite data to examine vegetation phenology (seasonal cycles) and productivity patterns spatially and temporally for a coastal wet sedge tundra site near Barrow, AK during three growing seasons (2000-2002). Contrary to hypothesized predictions; earlier snowmelt did not lead to increased productivity. Higher elevated sites that became snow free earliest had relatively low evidence of productivity, whereas low-lying regions, that were slow to emerge from snow, reached the highest vegetation productivity by mid-season. Indeed, productivity was associated primarily with precipitation and soil moisture, and secondarily with growing degree days – the latter during this period yielding reduced growth in years with earlier snowmelt. Slight local depressions (typically 10–20 cm in depth) tended to have higher moisture content, often containing standing water for short intervals. These wet locations were dominated by vascular plants, particularly graminoids (e.g., grasses, sedges and rushes), whereas less productive higher, drier locations supported a higher percentage of lichens and mosses. These results point to the importance of combining fine scale and broader scale data gathering in refining predictions about the effects of earlier arctic growing seasons on vegetation productivity. However, the data of Gamon et al., (2013) support emerging evidence from field studies that early-season, local environmental conditions, especially moisture and temperature, are primary factors determining arctic vegetation productivity. For this northern coastal arctic site, growth conditions in the early growing season are mainly influenced by microtopography, hydrology, and regional sea ice dynamics. Predictions are less related to snow melt date or seasonal mean air temperatures, alone. Moreover, this study illustrates the merits of in-situ monitoring of the actual vegetation

responses using field visual observations to obtain detailed information on surface conditions not possible from satellite observations, alone. More generally, studies such as this illustrate the importance of understanding regional variations in climate effects on vegetation dynamics.

As further evidence of regional and topographic effects on vegetation dynamics, Sweet et al., (2015) examined the possible effects of the ongoing increase of deciduous shrub abundance on plant canopy phenology and productivity during the growing and peak seasons in the arctic foothills region of Alaska. Using *in situ* spectral visual data, they compared deciduous shrub-dominated and evergreen/graminoid-dominated, community-level canopy phenology during the growing season. These studies used leaf area index (LAI) as an indicator of vegetation cover. The LAI is a measure of total leaf area of vegetation relative to the basal terrestrial area directly under the vegetation. They used a tundra plant-community-specific leaf area index (LAI) model to estimate LAI throughout the growing season and a tundra-specific net ecosystem carbon exchange (NEE) model to estimate the impact of increased deciduous shrub abundance and its associated shifts in both leaf area and canopy phenology on tundra carbon flux (exchange of CO₂ with the atmosphere). Deciduous shrub canopies reached onset of peak greenness 13 days earlier and the onset of senescence (die back) 3 days earlier compared to evergreen/graminoid canopies. This resulted in a 10-day extension of the peak season.

The combined effects of a longer peak season and the greater leaf area of deciduous shrub canopies almost tripled the modeled net photosynthetic carbon uptake of deciduous shrub communities compared to evergreen/graminoid communities. Moreover, the longer peak season alone resulted in 84% greater carbon uptake in deciduous shrub communities. These results suggest that greater deciduous shrub abundance increases carbon uptake not only due to greater leaf area, but also due to an extension of the period of peak greenness and productivity that prolongs the period of maximum carbon assimilation by photosynthetic fixation of CO₂.

This is consistent with a time series study reported by Potter (2014), based on satellite vegetation coverage data from 2000 to 2010, with the objective to understand landscape-level patterns of vegetation change in ecosystems of interior Alaska. The analyses of data-sets for Alaska vegetation cover types, wetland cover classes, wildfire boundaries since the 1940s, permafrost type, and elevation provided evidence to identify the most likely combination of factors driving regional changes in habitat quality and ecosystem productivity. Approximately 48% of all ecosystem geographic study areas in interior Alaska were identified with significant ($p < 0.05$) positive or negative growing season vegetation coverage trends from 2000 to 2010. Three-quarters of these ecosystem study areas (nearly 110,000 km²) had evidence of significant positive growing season vegetation growth trends. The vast majority of interior Alaska areas with significant positive growing season vegetation growth trends were classified as upland shrub cover. However, in addition, non-forested wetlands (marshes, bogs, fens, and floodplains) were colocated with the shrublands on 13% of that total area. Overall, this evidence supports an hypothesis that temperature effects (warming) have markedly enhanced the rates of shrubland vegetation growth across interior Alaska in recent years.

In addition to seasonal studies, substantial evidence of the greening of the Arctic and expansion of shrublands has accumulated from multi-decadal studies of aerial photographs and satellite data (Bunn and Goetz, 2006; and as reviewed by Myers-Smith et al., 2011).

Satellite data for greening of arctic Alaska (1981-2001) was analyzed by Jia et al., (2003) for three bioclimate subzones in northern Alaska. They reported a 16.9% ($\pm 5.6\%$) increase in peak vegetation greenness across the region corresponding to simultaneous increases in temperatures. Changes in four specific vegetation types, using an 11-yr finer resolution satellite data, showed that the temporal changes in peak and time-integrated greenness were greatest in areas of moist nonacidic tundra. All totaled, these changes in greenness between 1981 and 2001 corresponded to approximately a 171 g m^{-2} increase in aboveground plant biomass.

Sturm et al., (2001) using historic and modern aerial photographs concluded that during the past 50 years of warming, there has been a widespread increase in shrub abundance over more than 320 km^2 of the arctic landscape between the Brooks Range and arctic coast. They examined particularly changes in the three principal deciduous shrubs, dwarf birch (*Betula nana*), willow (*Salix* sp.) and green alder (*Alnus crispa*), as well as changes in treeline white spruce (*Picea glauca*) along the southern edge of the study at the northern base of the Brooks Range. The study area was in a location where human and natural disturbances (leading to successional changes) were minimal, so the authors attributed much of the increase in the abundance of shrubs to the recent change in climate. Moreover, the expanding incursion of vascular woody plants could be a significant contributor to changes in the high-latitude carbon budget, as well as contributing to important changes in the exchange of surface energy. Further studies by Tape et al., (2006) using data spanning 50 years have provided additional confirmation of these trends and provided more detailed vegetation cover changes at the local level. These results are consistent with other time series studies using satellite and aircraft aerial surveys of changes in vegetation in the Beringian Arctic (Bering Sea region). Lin et al., (2012) created multi-temporal high spatial resolution land cover maps for seven locations in the Beringian Arctic and assessed the change in land cover for the period of 1848-2008. Four of the five landscapes studied in Alaska underwent an expansion of drier land cover classes, while the two landscapes studied comparatively in Chukotka, Russia showed an expansion of wetter land cover types.

While there is broad consensus that the vegetation coverage and plant functional types are changing across the arctic landscape, regional differences are clearly to be expected and have been documented. Reynolds et al., (2013) examined 22 years of satellite data in an area of the Northern Foothills of the Brooks Range, analyzing an 823-km^2 area. They found that apparent homogeneous greening, revealed by coarse resolution satellite imagery, was very heterogeneous at finer resolution, with a strong influence due to glacial history. Small, scattered patches with significant increases in satellite evidence of expanded greening occurred throughout the younger, late Pleistocene glacial deposits. On older, mid-Pleistocene deposits, increases occurred in few, larger patches of mostly tussock-sedge, dwarf-shrub, and moss tundra. This is possibly a result of release of nutrients from thawing of ice-rich permafrost. Trends in evidence of greening varied by glacial history, elevation, slope, and the resulting vegetation conditions. The authors conclude that this heterogeneity in response to climate change can be expected throughout much of the Arctic, where complex glacial histories determine existing soil and vegetation characteristics. Further evidence of geographic heterogeneity was reported by Elmendorf et al., (2012) for 158 plant communities spread across 46 tundra locations. They found biome-wide trends of increased height of the plant canopy and maximum observed plant height for most vascular plant growth forms; an increased abundance of litter; increased abundance of evergreen, low-growing and tall shrubs;

and less evidence of bare ground. Although there was evidence of a correlation of increased vascular plant abundance and summer warming, the association was dependent on climate zone, moisture regime, and the presence of permafrost.

Pattison et al., (2015) examined local (plot-level) trends in species composition for field plots in the Arctic National Wildlife Refuge on the coastal plain in NE Alaska from 1984 to 2009 and linked these trends to trends in satellite evidence at fine and coarse scales. During this time, there were few changes in plant community composition. None of the five tundra types that were measured (1. wet sedge and sedge willow, 2. sedge-*Dryas*, 3. tussock and shrub, 4. riparian, and 5. *Dryas* terrace) had increases in total vegetative cover, and deciduous shrub cover in this coastal location exhibited none of the large increases reported elsewhere. Moreover, other studies at sites in northern Alaska (e.g., Tape et al., 2012), found that within tundra vegetation types, shrub expansion appears to be localized to higher resource environments such as floodplains, stream corridors, rocky outcrops, and/or in areas with deeper active layers. Similarly, Verbyla (2008) reported that satellite observations of trends in vegetation between 1982-2003 showed that cold arctic tundra significantly increased in vegetation coverage, while relatively warm and dry interior boreal forests areas consistently decreased. The annual maximum satellite evidence of greening in arctic tundra areas was strongly related to a summer warmth index as reported by Walker et al., (2003) in the next subsection on vegetation biomass.

Vegetation biomass density and geographic coverage. With increasing evidence of a likely expansion of woody shrubs and small trees in some parts of the Arctic, it is also important to study evidence of spatial and temporal patterns in the mass of vegetation (phytomass), plant height, and other ecologically significant metrics related to vegetation abundance and distribution. In this section, particular focus is placed on these functional morphological and anatomical aspects of tundra vegetation.

Detailed analyses of the effects of summer warmth on leaf area index (LAI), total aboveground phytomass (TAP), and density of vegetation greenness estimated by evidence from satellite imagery were made by Walker et al., (2003). Data were collected across the Arctic bioclimate zone in Alaska (extending from the northern boundary southward to the Brooks Range and along the west coast) and extrapolated to the entire circumpolar Arctic. The warmth for plant growth generally increases along the Alaskan bioclimate gradient from north to south. Alaskan phytomass, LAI, and greenness were related to the total summer warmth index (SWI) using statistical regression analyses based on data from 12 climate stations in northern Alaska. SWI = sum of mean monthly temperatures that exceed zero degrees Celsius (C). SWI varies from 9°C at Barrow on the northern edge of the Coastal Plain, AK to 37°C at Happy Valley on the southern edge of the Coastal Plain. Overall, based on the correlations, a five degrees C increase in the SWI is predicted to produce ~ a 120 g m⁻² increase in the aboveground phytomass for zonal vegetation on acidic soil sites, and ~ 60 g m⁻² on nonacidic sites. The distribution of acidic relative to nonacidic sites is related to the time since the last glaciation. Shrubs accounted for most of the increased vegetation on acidic substrates, whereas mosses accounted for most of the increase on nonacidic soils. The LAI was positively correlated with SWI on acidic sites, but not on nonacidic sites. The satellite evidence for green vegetation coverage was positively correlated with SWI on both acidic and nonacidic soils, but coverage on nonacidic parent material was consistently lower than the coverage on acidic substrates. Extrapolation to the entire Arctic using a five-subzonation approach to stratify the circumpolar satellite-derived vegetation coverage and phytomass

estimates showed that 60% of the aboveground phytomass is concentrated in the low-shrub tundra, whereas the high northern Arctic has only 9% of the total. Estimated phytomass densities in five subzones from north to south are 47, 256, 102, 454, and 791 g m⁻², respectively. Based on the statistical evidence, climate warming is likely to result in increased phytomass, LAI, and green vegetation coverage on arctic localized geographic sites. The changes may be most noticeable in acidic areas with abundant shrub phytomass.

In addition to satellite visual evidence, Light Detection and Ranging (LiDAR) technology has recently been evaluated as a potential tool to estimate the tundra's vegetation composition and physical structure. LiDAR remote sensing - either from satellite, aircraft or on the ground - measures distance from sensor to a target object (e.g., a shrub) by emitting a laser beam that illuminates the target and analyzing the time it takes for the light to bounce off of the target and return back to its source (sensor location). Greaves et al., (2015) use ground-based LiDAR techniques to estimate biomass and leaf area of two dominant, low-stature (<1.5 m tall) arctic shrub species (*Betula* and *Salix*) in 24 (0.64 m²) subplots established in northern Alaskan tundra (Toolik Lake). They found that LiDAR is a promising technology to monitor the biomass of woody plants such as woody shrubs and small trees that are increasingly invading previously moss-rich tundra, expanding on results of prior passive, spectral remote sensing techniques that were used to estimate dynamics in plant biomass (e.g., Boelman et al., 2003, 2005, 2011). For example, they found strong relationships between total harvested biomass and total leaf dry mass ($R^2 = 0.93$), and between leaf dry mass and leaf wet area ($R^2 = 0.99$). In this way, Greaves et al., show that their LiDAR based approach yields aboveground biomass and leaf area estimates for low-stature shrubs at fine spatial scales (sub-meter to ~50 meters) with the fidelity required to monitor small but ecologically meaningful changes in tundra structure. Importantly, this field-based study is the first to suggest that airborne LiDAR may indeed prove useful in detecting ongoing and expected changes in the tundra's 3-D vegetation structure. Greaves et al., results were comparable to results from previous studies linking TLS metrics to vegetation biomass in other biomes, including broad-leaved and conifer trees (Ku et al., 2012; Lin et al., 2010; Olsoy et al., 2014; Vierling et al., 2012). Beck et al., (2011) mapped shrub cover on the north slope of Alaska using satellite remote sensing images to distinguish between and map (>1m) and short shrub presence at a high spatial resolution (<5 m grid cell size) in different parts of the geographic region observed. The data were statistically transformed to yield maps of total- and tall-shrub cover, expressed as a percent of the total surface area. Data were also collected by direct observation of the coverage of the two groups of shrubs in the field, and the final shrub cover maps generated from their statistical analyses corresponded well with the field measurements ($r^2 = 0.7$). The resulting maps compared favorably with existing vegetation type maps previously published for the study area. More specifically, their shrub cover maps predicted that shrubs were present in 86% of the mapped area, with 78% of the area having a cover of $\geq 10\%$, and 54% having a cover of $\geq 50\%$. Overall, the maps showed that shrubs are nearly ubiquitously present on the North Slope of Alaska. They occurred in all but the wettest area, with low-lying wetland areas on the coastal plain of the North Slope having the lowest shrub cover. Tall shrub presence was predicted in 29% of the mapped area, with 18% having a cover of $\geq 10\%$, and 3% having a cover of $\geq 50\%$. For overall patterns, the map indicated a general east-west gradient of increasing shrub cover; tall shrub cover particularly was evident on the North Slope of Alaska. Moreover, further north on the North Slope, tall shrubs become more restricted to favorable topographical conditions such as stream channels and floodplains.

However, tall shrub cover over areas > 50% was rarely observed when total shrub cover was $\leq 60\%$. These data are consistent with the evidence of geographic variability reported in the final portions of the prior section on temporal changes in vegetation (e.g., Elmendorf et al., 2012; Pattison et al., 2015; Raynolds et al., 2013; Tape et al., 2012; Verbyla, 2008).

Field-Based, Direct Observations

Satellite and other remote-sensing technology provide broad scale coverage of vegetation changes in the Alaskan tundra with varying detail depending on fine-scale resolution, but detailed studies of plant morphology, physiology and other biological aspects of importance in vegetation dynamics at site-levels are currently best studied by direct data gathering in the field. To augment the review of remote-sensing studies presented above, some illustrative field-based studies are included here. Some general published sources can be consulted as a context for this section (e.g., Callahan and Jonasson, 1995; Chapin III et al., 2005; Epstein et al., 2004; Hufnagel and Garamvölgyi, 2014; Post et al., 2009; Walter, 2004).

Seasonal studies using direct observation at various sites in Alaska have provided some general insights into climatic forcing functions on vegetation composition and diversity. For example, observations of vascular plants, bryophytes and lichens in sub arctic tundra by Makoto and Klaminder (2012) indicated that soil frost disturbances are important for maintaining successional gradients over several centuries within the arctic landscape at small spatial scales (<3m). Moreover, they predict that the termination of soil frost activity as a result of future warmer winters may result in a loss of micro-sites having young vegetation communities with high plant diversities, and a subsequent establishment of mature shrub-dominated plant communities. However, Frost et al., (2013) show that increasing shrub dominance is not occurring as a simple function of regional climate trends, but is also a function of cryogenic disturbances associated with small, widely spread patterned-ground landscapes throughout the Arctic. Based on evidence that temperature seasonality (S-T), i.e., the difference between summer and winter temperatures, is diminishing over time with warming of northern lands, Xu et al., (2013) using a combination of remote sensing and land-based data report that trends in the timing of initiation, termination and performance of photosynthetic activity, tied to threshold temperatures, may alter vegetation productivity or modify vegetation seasonality (S-V) over time. The observed diminishment of S-T and S-V indicates a significant latitudinal shift equatorward, from more northern to southern limits, during the past 30 years in the Arctic. With continued warming, they predict that an additional S-T diminishment equivalent to a 20° equatorward shift could occur this century, and more attention is needed to determine the impact that this may have on the environment and ecosystem services.

Seasonal warming also can have major affects on topography and localized soil conditions. Continued warming trends affect plant growth directly, but also can have indirect affects through changes in nutrient availability and soil structure. Warming can cause permafrost to thaw and thermokarst (ground subsidence) to develop. This can alter the structure of the ecosystem by altering hydrological patterns within a site and driving changes in the composition of vegetation (e.g., Osterkamp et al., 2009). Schuur et al., (2007) examined a natural gradient of permafrost thawing in three Alaskan tundra sites. They found that vascular plant biomass shifted from graminoid-dominated tundra in the least disturbed site to

shrub-dominated tundra at the oldest, most subsided site. The intermediate site, however, was co-dominated by both plant functional groups. Patterns of productivity for vascular plants followed the changes in biomass, whereas nonvascular moss productivity was especially important in the oldest, most subsided site. Across all sites, graminoids were most evident on the cold, dry microsites; whereas, the moss and shrubs were associated with the warm, moist microsites. Total nitrogen within green plant biomass differed across sites, suggesting that there were increases in soil nitrogen availability where permafrost had thawed.

Arndal et al., (2009) studied seasonal variation in gross ecosystem production, plant biomass, and carbon and nitrogen pools in five high arctic vegetation types (*Cassiope*, *Dryas*, *Salix* heath, grassland, and fell). Large differences were observed in seasonal growth and production within and among vegetation types. Mosses contributed considerably to the total C and N pool in grassland, fen, and *Salix* heath. The fell, with highest pool of leaf N, leaf chlorophyll, and moss N, was the most productive vegetation type in terms of gross ecosystem production (GEP), despite the lowest total biomass. Across vegetation types, leaf biomass, leaf N, and moss N pool size substantially influenced GEP. Within most vegetation types, GEP correlated with leaf N. This is correspondent with the notion that N may limit plant production in many high arctic ecosystems. The timing of the peaks in C and N pools in leaves did not coincide with that in the mosses and in woody tissues. With continued warming and shifts in plant functional types across arctic sites, there also may be unpredictable changes in the nutrient dynamics and plant productivity as exemplified by this research.

Shifting vegetation patterns also have a ripple effect throughout arctic ecosystems affecting wildlife (e.g., Marcot et al., 2015), including birds (Boelman et al., 2014; Fossøy et al., 2014; van Oudenhove et al., 2014; Wild et al., 2015), and other animals important as human food sources, such as caribou and other large and small mammals (Gustine et al., 2014; Joly et al., 2012; Nicolson et al., 2013; Wheeler et al., 2015; Vors and Boyce, 2009).

Field-Based, Experimental Studies

Field-based observational studies have provided a sound framework for more detailed experimental studies on climate change in arctic tundra ecosystems. Some long-term experimental field research stations have been established in the Arctic, especially in the north coastal plain, including the International Tundra Experiment (ITEX), and the Arctic LTER suite of experiments near Toolik Lake, Alaska. Some of the major findings from these experimental studies are summarized here.

Henry and Molau (1997) and Oberbauer et al., (2013) summarized some of the major findings from the ITEX studies. The ITEX research used open-top chambers (OTCs), consisting of enclosing sides with an open top that permits ambient insolation, while also controlling temperature and regulating snow depth. Some of the major findings for vascular plants are presented. The OTC treatments increased mean near-surface temperatures by 1-3°C during the growing season, simulating predictions from global circulation models. All of the species investigated responded to the temperature increase, especially in phenology and reproductive variables. However, these short-term responses were differentiated, and no general pattern in type or magnitude of response was noted for functional types or phenology class. In general, responses were similar among sites, although the response magnitude tended

to be greater in high arctic sites. Early snowmelt increased carbon:nutrient ratios in plants, suggesting that sustained growth and reproductive responses to warming will depend on nutrient supply. Moreover, increased carbon:nutrient ratios in litter could buffer nutrient cycling, and hence plant growth.

To obtain baseline data on natural variations in tundra climate on vascular plant responses, ITEX control data obtained from natural sites outside of the OTCs were used to test the phenological responses to background temperature variation across sites spanning latitudinal and moisture gradients. Overall, the analyses did not show an advance in phenology. Instead, temperature variability during the years sampled and an absence of warming at some sites resulted in mixed responses. Seasonal, phenological transitions of high arctic plants clearly occurred at lower heat sum thresholds than those of low arctic and alpine plants. Heat sum threshold is the initial temperature value required to sustain a plant response during the remaining season, such as leaf flushing in spring. However, sensitivity to temperature change was similar among plants from the different climate zones. Plants of different communities and growth forms differed for some phenological responses. Heat sums associated with flowering and greening appear to have increased over time. These results point to a complex suite of changes in plant communities and ecosystem functions in high latitudes and elevations as the climate warms, and also points to some of the challenges of adequately simulating natural environmental changes in experimental studies.

Borner et al., (2008) reported more detailed data on ITEX experiments where the effects of increased winter snow depth, and thus decreased growing season length, were examined on the phenology of four arctic plant species (*Betula nana*, *Salix pulchra*, *Eriophorum vaginatum*, and *Vaccinium vitis-idaea*), including seasonal nitrogen availability in arctic snowbed communities. Increased snow depth had a major effect on the temporal pattern of first snow-free date in spring, and plant bud break, and flowering; but did not affect the rate of plant development. By contrast, snow depth had a large qualitative effect on N mineralization in zones with deep snow, causing a shift in the timing and amount of N mineralized compared to the control ambient snow zones. Nitrogen mineralization in deep snow zones occurred mainly overwinter; whereas, N mineralization in ambient snow zones occurred mainly in spring. Concentrations of soil dissolved organic nitrogen (DON) were approximately five times greater than concentrations of inorganic nitrogen (DIN) and did not vary significantly over the season. Based on these results, the authors predicted that increases in the depth and duration of snow cover in arctic plant communities will likely have minor effects on the rate of plant phenological development, but potentially large effects on patterns of N cycling.

Rumpf et al., (2014) further examined the effect of snow regimes (snow cover depth and duration) by experimentally manipulating snow regimes using snow fences and shoveling. They assessed above ground size of eight common high arctic plant species weekly throughout the summer. Plant growth responded to snow regime. Air temperature sum during the snow free period was the best predictor for plant size. Plants in early snow-free treatments without additional spring warming were smaller than controls. Responses varied among species to the effects of deeper snow with later melt-out. Moreover, no generic trends were detected when responses were categorized by growth forms or habitat associations, thus indicating the importance of examining species-level responses to some of these snow regime variables.

Using a combined approach of snow fencing and experimental warming in OTCs Wharen et al., (2005) examined the effect of changes in winter snow cover at Toolik Lake, Alaska. OTCs, paired with unwarmed plots, were placed along snow gradients for each experimental and control areas that were adjacent to snowdrifts. After eight years, the vegetation of the two sites, including that in the control plots had changed significantly. At both sites, the cover of shrubs, live vegetation, and litter, together with canopy height, had all increased; while lichen cover and diversity had decreased. At the moist site, bryophytes decreased in cover, while an increase in graminoids was almost entirely due to the response of the cottongrass sedge *Eriophorum vaginatum*. The snow addition treatment particularly affected species abundance, canopy height, and diversity; whereas, the summer warming treatment had few measurable effects on vegetation. However, the latter must be interpreted in the context that the natural interannual temperature fluctuation at these sites was considerably larger than the temperature increases within OTCs ($< 2^{\circ}\text{C}$). Snow addition also had a greater effect on microclimate by insulating vegetation from winter wind and temperature extremes, modifying winter soil temperatures, and increasing spring run-off. Most increases in shrub cover and canopy height occurred in the medium snow-depth zone (0.5–2 m) of the moist site, and the medium to deep snow-depth zone (2–3 m) of the dry site. Deciduous shrubs, particularly *Betula nana*, increased in cover at the moist tundra site, while evergreen shrubs decreased. These differential responses may be explained, in part, by the larger production to biomass ratio in deciduous shrubs, combined with their more flexible growth response under changing environmental conditions. At the dry site, where deciduous shrubs were a minor part of the vegetation, evergreen shrubs increased in both cover and canopy height.

On a broader scale, Van Wijk et al., (2003) used meta-analysis to examine the results of the Arctic LTER experiments near Toolik Lake, Alaska, including some comparative data from Abisko, Sweden; with special emphasis on aboveground biomass responses of different arctic and subarctic ecosystems to experimental fertilization, warming and shading. The results for Toolik Lake are reviewed here. While there were some consistent trends, site-specific differences were noted as reported in other tundra experimental research. Aboveground plant biomass, particularly the biomass of deciduous and graminoid plants, responded most strongly to nutrient addition. In contrast, evergreen shrubs showed a significant negative overall response to fertilization, although this was caused entirely by a strong decline of the biomass. The biomass of mosses and lichens decreased as the biomass of vascular plants increased. The decreased response of the non-vascular species is probably caused by an inhibition in growth by a combination of shading from the dense upper canopy of *Betula nana* and burial by vascular plant litter. As reported in other tundra warming studies, *Betula nana* increased its dominance and replaced many of the other plant types. The warming without fertilizer addition did not lead to any significant responses among the different vascular plant types, and shading did not lead to significant effects in any group of the vascular plants. In general, these results are consistent with other experimental studies, where fertilization has a greater effect on vascular plant biomass than warming. Moreover, there were also large site-specific differences within each region. The variations in response patterns show the need for analyses of joint data sets from many regions and sites, in order to uncover common responses to changes in climate across large arctic regions in comparison to regional or local responses.

Some additional results of experimental studies of vegetation responses to changing climate variables include the following: herbaceous plant and shrub communities (Bret-Harte

et al., 2008; Chapin III et al., 1995; Gough and Hobbie 2003; Hessel et al., 2014; Jagerbrand et al., 2012; Klady et al., 2011; Lang et al., 2012; Mack et al., 2004; Marchand et al., 2005; McLaughlin et al., 2014; Shaver et al., 2001), and trees (Hobbie and Chapin, 1998; Hofgaard et al., 2010; Moyes et al., 2013).

Fire Consequences

Some illustrative studies on fire effects in the tundra are reviewed. While there is good evidence of increasing invasion of woody vascular plants in susceptible regions of the Arctic; wildfires are reported to be more frequent, increasingly severe, and of larger spatial extent due in part to warming and drier conditions. However, fire effects on tundra ecosystems are poorly understood and sometimes difficult to quantify in remote regions where a short growing season seriously limits ground data collection. Kolden and Rogan (2013) used satellite coarse-resolution remote sensing to quantify wildfire burn severity of the 2007 Anaktuvuk River Fire in Alaska, the largest tundra wildfire that has been recorded on Alaska's North Slope. The satellite data were processed to provide broad scale evidence of surface, subsurface, and comprehensive burn severity. They analyzed the burn relative to three temporal periods: Pre-fire period, Initial Assessment post-fire (pre-green up), and Extended assessment post-fire (post-green up). The pre-fire situation consisted of low-lying herbaceous material (including grass tussocks) on less productive sites, or continuous dwarf shrub canopy normally <1 m in height on more productive sites. Bare soil was not a component of the pre-fire scene in this ecotype, as an organic horizon of decomposing biomass covered the mineral soil. As a result of the burn, the landscape was marked by localized zones with standing water, burned and saturated char and black soil surfaces, and patches (sub-meter to several meters in area) of unburned or only partially consumed non-photosynthetic vegetation, consisting primarily of grasses from prior growing seasons. Moreover, the organic horizon was consumed in a spatially variable pattern up to a meter in depth. At one year post-burn, data showed a decrease in severity, including added photosynthetic vegetation. Tussock sedges regenerated during summer in some of the most severely burned sites, in general indicating rapid vegetation regeneration on the burned site at this locale.

Overall, the Anaktuvuk River fire burned 1,039 square kilometers of the Alaskan Arctic Slope with serious consequences for changes in the soil and ecosystem carbon content (Mack et al., 2011). The tundra ecosystems lost $2,016 \pm 435$ g carbon m^{-2} in the fire, an amount two orders of magnitude larger than the annual net carbon exchange through photosynthesis by plants and CO₂ emissions due to respiration and other sources in undisturbed tundra. Sixty percent of this carbon loss was from soil organic matter, and radiocarbon dating of residual soil layers revealed that the maximum age of soil carbon lost was 50 years. In proportion to the entire burned area, the fire released approximately 2.1 teragrams of C to the atmosphere, an amount similar in magnitude to the annual net carbon sink for the entire arctic tundra biome averaged over the last quarter of the twentieth century. Further documentation of the Anaktuvuk River fire behavior and burn severity is provided by Jones et al., (2009).

The persistence of post-burn, long-term effects following tundra wildfires was reported by Barrett et al., (2012) at a time 17 years after a tundra fire on the North Slope of Alaska. Fire-related changes in vegetation composition were assessed from remote-sensing imagery

and ground observations of the burn scar and an adjacent comparative control site. Early-season remotely sensed imagery from the burn scar exhibited a low vegetation coverage compared with the control site. However, the late-season evidence is slightly higher. The satellite data of vegetation coverage indicated a quick recovery, reaching the range of pre-fire levels three years after the burn, with occasional spikes that were much higher. After five years of recovery, the maximum growing season evidence of vegetation greening was elevated in the burn scar although there was no difference in the average extent compared with pre-fire levels. The burned sites had 86% and 91% ground cover, whereas the control site had 100% vegetation cover. The ground cover composition in the burned sites was distinct from that of the control. The latter was composed primarily of *Salix*, leaf litter and, to a lesser extent, *Eriophorum vaginatum* (cottongrass) and other graminoids. Although *E. vaginatum*, *Salix* spp. and litter were major components of the burned site, moss and *Betula nana* were considerably less abundant. In addition to grasses, ground cover typically found in the burned site, but not the control, included *Ledum palustre* (an evergreen shrub in the heath family: Ericaceae), forbs, fireweed (*Chamerion angustifolium*) and open ground.

In a similar designed study, Narita et al., (2015) reported on the recovery of tundra vegetation and the depth of permafrost thaw on the Seward Peninsula, Alaska, the site of a wildfire in 2002. As in the study by Barrett et al., vegetation in the burned site was compared to an adjacent unburned tundra site five to 10 years post-fire. Effects of the fire on the vegetation varied among species and were spatially variable at the stand scale. Notably, the cover of evergreen shrubs, bryophytes, and lichens remained drastically decreased five years after the fire and had not recovered even 10 years after the fire. However, the cover of graminoids, especially *E. vaginatum*, and of the deciduous shrub *Vaccinium uliginosum* increased. The depth of permafrost thaw increased, and its spatial pattern was related to vegetation structure; specifically, deeper thaw corresponded to graminoid-rich areas, and shallower thaw corresponded to shrub-rich areas. As the *E. vaginatum* cover increased, the thaw depth recovered to that of the unburned area, and the spatial variation had disappeared 10 years after the fire. Further evidence of physical short-term changes after a tussock tundra fire on the Seward Peninsula is presented by Liljedahl et al., (2007).

Further chronological evidence of burn recovery was documented by Racine et al., (2004) who also studied a tundra fire and vegetation change on the Seward Peninsula, Alaska, but in this case along a hillslope where the recovery was not so pronounced as at the site studied by Narita et al., In this study, prior to the fire in 1977, soils and vegetation ranged from poorly drained moist tussock-shrub tundra on the lower slopes to well-drained dwarf shrub tundra on the back slope and very poorly drained wet sedge meadow on the flat crest. The vegetation was sampled on the slope before the fire and at eight sites following the fire at irregular intervals from one year to 25 years. Short-term recovery, during the first decade, was dominated by growth of bryophytes, sedges, and grasses from both regrowing sedge tussocks and seedlings. However, during the second and third decade, and by 24 years after the fire, evergreen (*Ledum palustre*) and deciduous shrubs (mainly *Salix pulchra*, willow) expanded markedly. Indeed, the shrub cover was generally higher than before the fire! Upslope on the better-drained and more severely burned tussock-shrub and dwarf-shrub tundra sites, willows (mainly growing from seed) became established during the first 10 years after the fire, and appeared to have grown rapidly during the subsequent 15 to 20 years. However, *Sphagnum* moss and fruticose lichens showed little or no recovery after 24 years at any site, except for *Sphagnum* moss in the wet meadow site. Additional evidence of slow recovery of lichens on

burned caribou range in the Alaska tundra has been reported by Jandt et al., (2008), including evidence of poor recovery after as much as 25 years post burn. Further evidence of the severity and consequences of Alaskan wildfires are reported by Rocha and Shaver (2011), Bret-Harte et al., (2015), and Loboda et al., (2013).

Beyond the tundra sites reviewed here, increasing evidence of the effects of wildfires on tree stands and woody plants has also been reported for a variety of forested sites in Alaska (e.g., Kaischke et al., 2002; Lloyd et al., 2007; Yarie, 1981).

PLANT AND TUNDRA SOIL MICROBIAL COMMUNITIES

Plants have a dynamic relationship with soil microbial communities (bacteria, fungi and protists). The microbes, especially in close vicinity of plant roots, increase the fertility of the soil by making essential plant nutrients more accessible through remineralization (Adl, 2003; Clarholm, 1981, 1989; Koller et al., 2013). Likewise, plant roots secrete organic nutrients utilized by fungi and bacteria for growth, and in turn the bacteria at the base of soil microbial foodwebs provide prey for protists, such as amoebae and flagellates (Adl, 2003; Anderson and McGuire, 2013; Darbyshire, 1994). Some larger amoebae also prey on fungi (Old and Darbyshire, 1978, 1980). Climate change, especially global warming, is expected to have major effects on the composition and life activities of tundra soil microbes. Some recent evidence is presented first, followed by implications for plant-microbe interactions under conditions of warming in the tundra.

Global Warming Effects on Tundra Soil Microbial Communities

Bacteria. One of the most immediate effects of global warming is permafrost thaw and its consequences on microbial community structure and function, especially for bacteria. Deng et al., (2015) investigated soil bacterial and archaeal communities using molecular genetic techniques across a permafrost thaw gradient at different depths in Alaska during a thaw progression over three decades. Based on 97 samples, corresponding to 61 known classes and 470 genera, they reported that soil thaw depth and the associated soil physical-chemical properties had predominant impacts on the diversity and composition of the microbial communities. Both richness and evenness of taxa in the microbial communities decreased with soil depth. Acidobacteria, Verrucomicrobia, Alpha- and Gamma-Proteobacteria dominated the microbial communities in the upper horizon; whereas, abundances of Bacteroidetes, Delta-Proteobacteria and Firmicutes increased towards deeper soils. There were less effects of thaw progression in microbial communities in the near-surface organic soil, probably due to greater temperature variation. Thaw progression decreased the abundances of the majority of the associated taxa in the lower organic soil, but increased the abundances of those in the mineral soil, including groups potentially involved in degradation of recalcitrant C compounds (Actinomycetales, Chitinophaga, etc.). The changes in microbial communities may be related to altered soil carbon sources by thaw progression. Overall, this study revealed different impacts of thaw in the organic and mineral horizons and suggests the

importance of studying both the upper and deeper soils while evaluating microbial responses to permafrost thaw.

Further evidence of impacts of changing soil physical-chemical properties on bacterial communities was studied by Campbell et al., (2010), especially with respect to the likely influence of increased deposition of reactive nitrogen that accompanies changing patterns of precipitation and permafrost thaw. Substantial losses of C were previously reported after long-term nutrient additions in moist acidic tundra (MAT) soils on the North Slope of the Brooks Range, Alaska, possibly due to the enhanced respiratory activity of more active bacteria (Mack et al., 2004). To assess the possible role of bacterial communities in these C losses, Campbell et al., utilized molecular genetic analyses coupled with community-level physiological profiling to describe changes in MAT bacterial communities after short- and long-term nutrient fertilization. They analyzed soil from four sets of paired control and fertilized MAT soil sites. Bacterial diversity was lower in long-term fertilized plots. Long-term fertilization also was correlated with shifts in the utilization of specific substrates by microbes present in the soils. The combined data indicate that long-term fertilization produced a significant change in microbial community structure and function. This was linked to changes in C and N availability and shifts in aboveground plant communities.

Additional evidence of increased carbon loss from humic soil substances (HS) due to bacterial action in subarctic tundra soil (Council, AK) was reported by Park et al., (2015) using experimental microcosms. The quantity of humic acids (HA) decreased to 48% after a 99-day incubation at 5°C as part of a biologically mediated process. Bacterial community analysis showed that during the microcosm experiments, the relative abundance of bacteria and archaea (methane-producing microbes: “methanogens”) particularly increased, suggesting their involvement in HS degradation. Furthermore, using 122 strains of HA-degrading bacteria cultured from nearby sites, the authors reported increasing HS-degradation rates in parallel with rising temperatures in a range of 0°C to 20°C, with most notable increase occurring at 8°C compared to 6°C. Overall, the results indicated that, although microbial-mediated HS degradation occurred at temperature as low as 5°C in tundra ecosystems, increasing soil temperature caused by global climate change could substantially increase HS degradation rates. Furthermore, if the thawing period is extended, degradation activity could also increase, thereby directly affecting nearby microbial communities and the plant rhizosphere environments surrounding plant roots.

Effects of global warming in the Arctic also have been studied with respect to the combined responses of bacteria and fungi (e.g., Wallenstein et al., 2007). Fungal and bacterial community structure in tussock, inter-tussock and shrub organic and mineral soils at Toolik Lake, AK were evaluated using molecular genetic techniques. The soil communities were sampled and analyzed at the end of the growing season in August 2004 and also just after the soils thawed in June 2005. Although tussock and inter-tussock soil communities were very similar at the phyla level, the communities differed substantially between vegetation types. Across sampling dates, the communities were relatively stable at the phyla and subphyla levels, but differed significantly at finer phylogenetic scales. Acidobacteria dominated tussock and inter-tussock bacterial communities, while Proteobacteria dominated shrub soils. This is consistent with previous reports that shrub soils contain an active, bioavailable C fraction, while tussock soils are dominated by more recalcitrant substrates. Concurrently, tussock fungi communities had higher proportions of Ascomycota than shrub soils, while Zygomycota were more abundant in shrub soils. Increasing evidence of greater shrub

abundance in warmer and drier arctic sites suggests that soil microbial communities and their functioning are likely to be altered by continued climate change.

Fungi. Specifically, with respect to fungi in the Arctic, Timling and Taylor (2012) reviewed recent molecular data and concluded that there is comparatively high fungal diversity in arctic soils, with simultaneously no evidence for lower species richness at higher latitudes. Moreover, laboratory analyses of tundra soil fungal C-biomass indicates it is approximately an order of magnitude greater than bacteria, the next most abundant microbial taxa in most soils. For example, Anderson and McGuire (2013) reported tundra soil fungal C-biomass of 5 to 11 mg g⁻¹ soil dry weight compared to 20 to 120 µg g⁻¹ for total bacteria. The dominant fungi, and particularly ectomycorrhizal-forming fungi (ECM), appear to be cosmopolitan species. More particularly, community composition is altered under experimental warming, although arctic fungi are capable of growth at sub-zero temperatures. Melanized forms are frequent and host specificity is low. Experimental research on the effects of soil warming on tundra fungal communities (e.g., Gemi et al., 2015; Morgado et al., 2015; Semenova et al., 2015) has indicated that certain species of ECM and other fungal groups are favored by warming and may become more abundant, while many other species may go locally extinct due to direct or indirect effects of warming. Differences are also observed in moist tundra compared to dry tundra. There is a greater change in community composition in moist tundra, but less in the dry tundra. In general, species-level differences in responses to warming need to be considered more carefully. Moreover, such shifts in fungal community composition may also affect nutrient cycling and soil organic C storage as reported above for bacteria.

Moreover, other long-term warming studies of ECM associated with *Betula* shrubs (Deslippe et al., 2011) demonstrated opposing effects of long-term warming and fertilization treatments on ECM fungal diversity. Warming increased, and fertilization decreased, the diversity of ECM communities. They showed that warming leads to a significant increase in high biomass fungi with proteolytic capacity, especially *Cortinarius* spp., and a reduction of fungi with high affinities for labile N, especially *Russula* spp. In contrast, fertilization treatments led to relatively small changes in the composition of the ECM community, but increased the abundance of saprotrophs. Consequently, these data suggest that warming profoundly alters nutrient cycling in tundra, and may facilitate the expansion of *B. nana* through the formation of mycorrhizal networks of larger size.

Protists (e.g., amoebae and flagellates). Among the major bacterial predators in soil ecosystems, naked amoebae and heterotrophic flagellates are the most abundant, including those in tundra soils (e.g., Anderson 2014a). Given the importance of the soil microbial communities in ecosystem services, especially the critical link of protists between bacteria and higher biota in soil food webs, there is remarkably little current research on global warming and its effects on tundra soil protists. Indeed, much of the present literature is largely very recent (e.g., Anderson 2008, 2010, 2012, 2014b) and some of it is summarized here. In general, the densities of bacteria and protists in moss-rich tundra soils are comparable to organically rich soils elsewhere; e.g., bacteria (10⁸-10⁹ g⁻¹soil dry wt.), heterotrophic nanoflagellates (10⁵-10⁷ g⁻¹soil dry wt.), naked amoebae (10³ g⁻¹soil dry wt.), and testate amoebae enclosed by an organic or mineral test (~10² g⁻¹soil dry wt.). In general, the higher the level in the trophic hierarchy, the larger the size of the protist, with some testate amoebae near the top in the size range of hundreds of microns.

Presently, we have less information on how global warming will affect the taxonomic composition and community structure of tundra soil protists compared to research on their physiological ecology, and role in the biogeochemical carbon cycle. The latter is of critical importance, because the amount of respiratory CO₂ released by soil microbial communities can be substantial, thus increasing atmospheric CO₂ and exacerbating the greenhouse effect. Also, bacterivorous protists can sequester carbon consumed from bacteria during predation, thus passing it up the food chain, and controlling bacterial biomass and bacterial respiration, a major source of soil microbial respiratory CO₂. Overall, based on laboratory studies of respiratory CO₂ release with increasing temperature, the Q₁₀ (rate of increase in respiration for each 10 deg. C rise in temperature) on average is very close to 2.0. That is, the metabolic activity of the soil microbes, in general, tends to increase by two times, for each 10 degree Celsius rise in temperature. Predictions of total CO₂ emissions from soil microbiota is expected to increase as global warming causes increased warming and thawing of the permafrost soil in the Arctic, resulting in release of organic compounds that can be used by the microbiota for respiration.

One model, based on laboratory evidence (Anderson, 2008, 2010), is that at 20°C, (approximate high summer temperatures in the tundra) the amount of CO₂ emitted to the atmosphere could increase from about 1 Kmol CO₂ km⁻² soil h⁻¹ to more than 3 Kmol km⁻² soil h⁻¹ during early spring conditions when the soil thaws from 5 cm depth to 15 cm depth. During summer when the microbial communities are more abundant, the emissions could be ~ four times as great. As reported in the above section on bacteria, altered C sources in the soil may significantly affect microbial community structure and function, including changing nutrient patterns, thus affecting both microbes and plants that depend on the nutrients. Moreover, the fate of soil-released respiratory CO₂ is of critical importance. If aboveground increase in plant production is sufficient, it may partially or completely offset the release from soil by fixing the CO₂ into organic compounds and plant biomass during photosynthesis (e.g., Anderson, 2013; Chapin and Shaver, 1996; Heskell et al., 2013; Sweet et al., 2015).

Above- and belowground interactions of plants and soil microbial communities. With increasing evidence of the expansion of herbaceous plants and especially shrubs and small trees into the arctic tundra, major changes can be expected in the dynamics of the interaction of the aboveground vegetation with the belowground microbial communities, especially the effect of roots on the soil physical structure and chemical composition. Increasing atmospheric CO₂ concentrations and increased warming, resulting in enhanced plant photosynthesis, also can elevate organic compounds translocated to the roots where some are released as root exudates. Root exudates include glucose, amino acids, tricarboxylic acids, and other small molecular weight organic compounds in addition to larger molecular weight products such as mucopolysaccharides and other gelatinous secretions, especially at the root tip. Organic root exudates, especially in the very thin soil layer surrounding the roots (rhizosphere), serve as organic nutrients that enhance bacterial growth and production. In turn, protists grazing on the bacteria proliferate in the CO₂-driven, organically enriched, soil environment (e.g., Anderson and Griffin, 2001; Rønn et al., 2002; 2003; Treonis and Lussenhop, 1997). Leaf fall and litter also contribute to organic enrichment of the soil and may particularly provide particulate organic C resources for fungi and other decomposers (Adl, 2003). Increased densities of microbial communities in organically enriched soil are expected to produce higher emissions of respiratory CO₂, thus potentially contributing to higher atmospheric loading of CO₂. Current laboratory-based studies on the effects of soluble

organic compounds on tundra soil microbial respiration indicate that pulsed release of small molecular weight compounds into the soil produce a transient spike in respiration lasting on the order of an hour or more with increased CO₂ release (Anderson, 2012).

For example, glucose enrichment of tundra soil produced a pronounced two- to three-fold increase in respiration above basal rate, which declined over four hours to baseline levels. However, less than 1% (w/w) of glucose-C supplement was respired during the respiratory spike. A more substantial amount of the glucose-C became incorporated in microbial biomass. Although respiratory response to pulsed glucose-C was minimal, the overall mean basal rate at 20°C after one week ranged between 4 and 6 nmol min⁻¹ g⁻¹ soil, indicating a significant assimilation and respiration of constituent soil organic C. Respiratory CO₂ emissions were greater in summer than in early spring soil samples, probably related to more robust densities of microbiota that develop during the warmer summer months. Further research is needed on the synergistic or antagonistic effects of changing climate and edaphic variables among tundra environments, including permafrost thawing and nutrient release, plant responses to global warming, and the responses of soil microbes in a changing tundra climate. Some further published sources on issues of above- and belowground interactions in high latitude environments may be of interest (Bardgett and Wardle, 2010; Gough et al., 2012; Grogan and Chapin, 2000; Steiglitz et al., 2006).

CONCLUSION

Together, field-based and remote-sensing studies have decisively documented that the arctic tundra vegetation is changing. With warmer temperatures, longer growing seasons, and in some cases drier conditions, more productive, woody vegetation is becoming more dominant on the tundra, at the expense of formerly moss-rich and graminoid-dominated tundra environments. These changes are also bringing less favorable conditions for lichen growth and herbaceous plants. This is due especially to shading by the canopies of the woody plants, cover by litter fall, and drier conditions; thus reducing the lichen and herbaceous plant biomass in many areas of the tundra. Herbaceous plants and lichens are a major source of food for caribou, the lichens are especially important in winter, and diminishing supplies may impact the health, geographic distribution and population of caribou. Woody plants also may be impediments for some ungulates in reaching foraging sites. Bird species, especially migratory birds that reproduce in the Arctic and smaller mammals (e.g., voles, lemmings and ground squirrels), are increasingly adversely affected by the changing environment. Amidst this general scenario, however, there are locales where these major changes are less evident, and the topography, hydrographics, and nutrient regimes of varying tundra locales contribute substantially to local differences in the vegetation response to a changing climate.

Changes in the aboveground vegetation also can produce favorable, and in some cases unfavorable, effects on belowground microbial communities, including bacteria, fungi and protists. Increased herbaceous and woody vegetation can provide more organic nutrients for microbial communities in addition to the release of organic compounds from thawing permafrost soil. Warmer growing conditions and higher concentrations of atmospheric CO₂ enhance plant productivity and CO₂-fixing photosynthesis, providing more organic compounds that are translocated to the plant roots. Organic exudates from the roots provide

nourishment for bacteria and fungi. Bacteria are prey for protists (amoebae and small flagellates) at the base of soil food webs, and this can enhance the transfer of carbon compounds to higher trophic levels in the food web hierarchy. However, increased metabolism by soil microbes also yields higher emissions of respiratory CO₂ from soil to the atmosphere, and unless there is a compensatory uptake of the CO₂ by the increasingly denser vegetation, the net excess of atmospheric CO₂ may further exacerbate the greenhouse effect and global warming, particularly given the massive area of the circumpolar tundra. In some cases, permafrost thaw and increased precipitation leads to water logging of the moss-rich soil. While this potentially provides a favorable environment for growth of some soil protists, water logging can also lead to anaerobic conditions that suppress metabolism and prevent aerobic respiration resulting in less CO₂ emissions. However, anaerobic conditions favor the proliferation of methanogenic microbes (e.g., archaea) that produce methane, a much more powerful greenhouse gas than atmospheric CO₂. Drier conditions occurring in some locales may reduce respiratory CO₂ release, but favor more wildfires that disastrously destroy the metastable moss-rich environment that has persisted for millennia. In some cases, a reasonable recovery may occur within decadal time intervals; but in other cases, the scares last far longer, with much less favorable environments for plant growth or the success of indigenous and migratory animals, including birds.

The extent of these changes for human communities and human activities such as agriculture, game for hunting-dependent communities, and recreational resources that are important to the economy of some arctic regions, are not fully understood (e.g., Beaumier et al., 2015; Nicol and Heininen, 2014; Parkinson and Birgitta, 2014). However, there are sufficient early warning signs that the environmental changes have consequences for humanity that are more than of scientific interest, and locally may be more significant than broad geographic surveys can fully capture at the present time. In some locations, the thawing permafrost leads to major changes in surface topography, including thermokarst; and in some coastal regions, massive land subsidence threatens entire communities that are gradually sliding into the sea.

The changing climate of the Arctic is more than of local significance. Broad changes in surface conditions including changing snow cover patterns and effects on albedo, warming that alters the thermal balance of the tundra atmosphere, and increasingly less coastal sea ice, have ramifications for climate change globally. The Arctic is intricately linked with changing climate regimes worldwide. The manifold consequences of climate change in the Arctic (“Ground zero”) for our habitable global environment are only beginning to emerge; and much more substantial research is needed to fully understand the consequences of these changes for the future of humanity on planet Earth.

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