PLANT SUCCESSION IN THE ARCTIC BROOKS RANGE: FLORISTIC PATTERNS FROM ALPINE TO FOOTHILLS, ALONG A GLACIAL CHRONOSEQUENCE

AND ELEVATION GRADIENT

By

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Abstract

In the wake of rapid glacial retreat, alpine habitats in the arctic are expanding as freshly exposed surfaces become vegetated. Many glaciers in alpine cirques have nearly disappeared, and little is known about the rate of colonization or pioneer communities that develop following deglaciation. Newly developed habitats may provide refugia for sensitive arctic flora and fauna, especially in light of polar warming. To assess this process, vegetation communities developing on two recently deglaciated moraines in the Central Brooks Range were surveyed and compared with communities along a transect spanning both a glacial chronosequence (40-125,000 years since deglaciation) and an elevation gradient (1700-500 m) into the Arctic foothills. Results show that primary succession begins almost immediately following deglaciation. Within forty years fine-grained and rock substrates hosted small communities of 8-13 vascular and nonvascular plant species. Many pioneer taxa, especially lichens, persist into later stages of succession. Overall succession is directional and slow, increasing in species richness for about 10,000 years, after which richness decreases and communities stabilize. This is the first vegetation study on primary succession in the high Central Brooks Range, providing a missing link to a vegetation transect along the Arctic Bioclimatic gradient.

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Statement by Author

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Introduction

The Brooks Range, an Arctic mountain range extending some 1000 km from the Chukchi Sea to the Alaska/Yukon border, presently separates boreal forest to its south from tundra to its north. The Brooks Range has been repeatedly glaciated over the last several million years, and glaciers have deposited numerous moraines and other glacial landforms that are now vegetated. The glaciers remaining in the highest peaks of the Brooks Range have been retreating rapidly over the last several centuries, since the end of the Little Ice Age (LIA), and most are now reduced into high cirques (Figure 1) (Ellis 1978; Pendleton et al. 2015). As these small glaciers disappear and new surfaces are exposed, fresh substrate becomes available for colonization by pioneer plant communities during primary succession. Rapid, recent glacial retreat in the central Brooks Range creates an ideal setting to study the patterns and processes of primary succession in an arctic-alpine environment.



Figure 1. (above) Grizzly Glacier cirque photographed by Jim Ellis in July of 1977. **(below)** The same general scene photographed by the author in July, 2017. Note, these photographs were taken from slightly different distances and locations from the glacier. Red arrows indicate moraine features for comparison of ice mass.

In contrast to the extensive studies of primary succession that have been carried out at lower latitudes, little is known about processes of plant succession in Arctic mountain ranges, despite the fact that these environments are now on the front line of rapid climate changes.

Primary succession affects the process of soil development, alters nutrient cycling, and plant communities formed during this process become the foundations of ecological communities.

Hence changes in vegetation have the potential to create new habitats, accommodate the shifting ranges of animal taxa, and determine biodiversity. In the rapidly changing Arctic, understanding the trajectories and rates of these ecological changes could help us predict and manage the ecological impacts of ongoing climate changes and other disturbances.

Retreating glaciers in the central Brooks Range have left behind a complex mosaic of different substrates ranging from boulder fields to scattered pockets of fine-grained sediment. Course-grained habitats possess a relatively harsh microclimate that is ideal for only a small suite of plants to colonize (e.g., crustose lichens). Fine-grained habitats are more hospitable to a broader range of plants which require deeper soils with increased nutrient and water availability for root establishment. These two habitat types occur on glacial deposits of all ages and at all altitudes (Figure 2), from the crest of the Brooks Range to the foothills abutting the northern slopes.

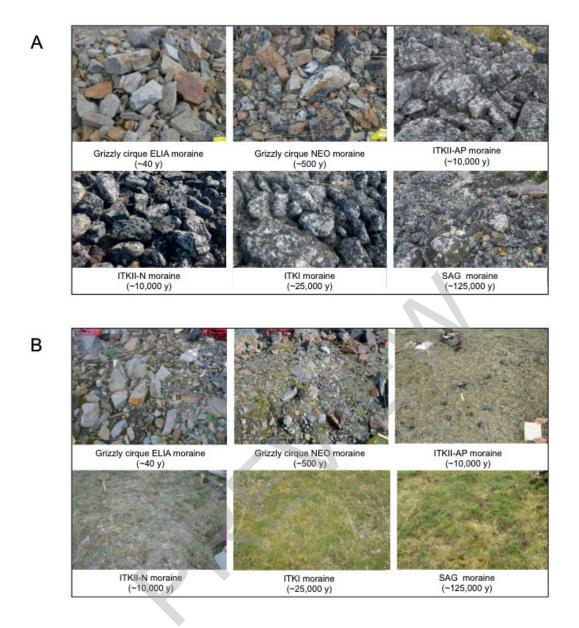


Figure 2. Examples of **(A)** rock and **(B)** fine-grained substrate relevés on each glacial deposit surface in order of the estimated age since deglaciation. For a full set of plot photos see Appendix A.

Arctic environments are inherently more harsh than those at lower latitudes due to colder climate, shorter growing seasons, and generally lower soil fertility (e.g., Svoboda & Henry 1987; Olech et al. 2011). Most arctic plants are adapted to these conditions and are vulnerable to interspecific competition and slight environmental change (see review in Vowles & Björk 2019).

In harsh environments, where inter-specific competition is generally reduced, colonizing plants tend to facilitate later successional plants. Early successional species facilitate later successional species by increasing available nutrients and creating more hospitable microclimate conditions (Svoboda & Henry 1987; Chapin et al. 1994; Callaway & Walker 1997; Anthelme et al. 2014; Reid et al. 2015).

At low altitudes in the Arctic, habitats on even slightly raised topographic features (e.g., moraines, kames & pingos), can reflect plant communities found in the alpine. For example, many of these communities are dominated by non-vascular plants such as lichens and bryophytes (Olech et al. 2011), whereas lowland communities at lower latitudes tend to be dominated by vascular plant growth forms (Chapin et al. 1994; Lang et al. 2012). Certain plant growth forms are commonly found in both Arctic and Arctic-alpine habitats, but are less common at lower latitudes such as plants that grow in low cushions or mats. This growth form allows for facilitation of neighboring species as well as self-proliferation by increasing soil accumulation, nutrient availability and regulating microclimate conditions (Reid et al. 2015). Therefore, along an Arctic glacial chronosequence and elevation gradient, the effect of altitude on plant community formation may be buffered by distinct environmental similarities between lowland and alpine sites.

Globally, the Arctic is at the forefront of climate change impacts, which are particularly amplified by loss of sea ice in the Arctic Ocean (Hinzman et al. 2005; Wendler et al. 2010; Bhatt et al. 2010). However, the impacts and severity of climate change vary across Arctic regions, and warming is having more drastic impacts on plant communities at lower altitudes. This is due in part to direct effects on frozen ground containing ice-rich permafrost (e.g., thermokarsting and cryoturbation; Olech et al. 2011; Walker et al. 2015), which is less common in the arctic-alpine,

than in tundra communities at lower altitudes. Low altitude sites are also more impacted by the expansion of shrubs (shrubification) across the tundra, which is limited in the arctic-alpine by environmental conditions such as cooler and shorter growing seasons, lower soil quality, and generally less substrate stability (Cornelissen et al. 2001; Lang et al. 2012; Vowles & Björk 2019). Anthropogenic disturbance (e.g., road construction & infrastructure development) is also more common at lower elevations, often reducing or changing habitat, resulting in similar impacts on vegetation communities as warming such as increased flooding, alteration of microtopography, and loss of organic layer (Walker et al. 2015) . Differences between alpine and lowland environments in the Arctic will likely result in warming under current conditions to be beneficial to alpine communities by causing alpine vegetation to proliferate and increase in floral biodiversity, and harmful to lowland communities causing a loss in habitat and floristic diversity (Carlson et al. 2014). Identifying rates and patterns of community development during primary succession in the arctic-alpine is important for understanding how communities respond to change. Contrasting early successional plant communities with plant communities on similar substrates at lower altitudes is important for predicting how young communities will develop over time, and what environmental factors drive development.

By comparing the present-day vegetation on two common habitat types across a glacial chronosequence and elevation gradient, I assessed the effects of altitude, time, and environment on the nature of plant communities and the trajectory of succession. This research is based on two main goals focusing on primary succession in the arctic-alpine and successional processes over the course of 125,000 years and 900m in altitude: 1.) document community development of new alpine habitat in a recently deglaciated cirque. 2.) use older glacial deposits at varying elevations to form an understanding of how pioneer plant communities develop over time.

These goals were substantiated by addressing two major objectives: 1.) determine what plant species are pioneer colonizers, what communities they form and at what general pace colonization takes place. 2.) determine how long plant communities undergo succession along this transect, how communities change, and what major environmental factors drive these changes.

Background

Study Area and Geology

The Brooks Range is part of the physiographic division known as the Arctic Mountains province consisting of mountains and hills generally around 2,000 m above sea level (a.s.l.) carved from Paleozoic and Mesozoic sedimentary rocks (Wahrhaftig 1965). Underlying bedrock in the Brooks Range is composed chiefly of Paleozoic (345-600 million years) limestone, shale, quartzite, slate and schist, with granitic intrusions in some of the higher regions (Wahrhaftig 1965). The Atigun Pass area is a complex mixture of highly resistant Kanayut Conglomerate, sandstone, shale, and limestone (Ellis 1978; Mull & Adams 1989) and includes the glacial deposits that were analyzed as the alpine relevés in this study.

The Arctic Foothills province is divided into the northern and southern foothills. The southern foothills are between 370 and 1070 m above sea level, characterized by irregular buttes, knobs, mesas, and east-trending ridges intervening with undulating tundra plains (Wahrhaftig 1965). They are underlain by diverse sedimentary rocks of Devonian to Cretaceous age with mafic intrusions (Wahrhaftig 1965). These Southern foothills (hereafter referred to as "foothills") abut the northern slope of the Central Brooks Range and include the glacial deposits that were analyzed as the lowland relevé locations in this study.

Glacial history

During the Pleistocene, large valley glaciers developed in the Brooks Range (Wahrhaftig 1965). The grinding action of these glaciers enlarged valley heads into cirques and steepened mountainsides leaving jagged ridges (arêtes) and spires (Wahrhaftig 1965). Three major glacial advances occurred in the central Brooks Range during the last 200,000 years: the Sagavanirktok River (SAG; 125,000-150,000 yr), the Itkillik I (ITKI; 50,000-70,000 yr), and the Itkillik II (ITKII; 10,000-25,000 yr) (Table 1, Figure 3; Hamilton & Porter 1975; Ellis 1978). All three of these advances involved valley glaciers descending out of the Brooks Range into the adjacent foothills where they deposited sweeping moraine systems and extensive outwash terrains below 800 m. After retreating into high cirques during the early Holocene (ca. 11,000-8000 years ago), glaciers underwent a series of minor Neoglacial re-advances starting ca. 4000 years ago that deposited prominent end moraines in cirques above 1800 m a.s.l.. The final Neoglacial advances of cirque glaciers took place during the Little Ice Age (LIA) (ca. AD 1250-1850). Little Ice Age advances left end moraines located inside those deposited during their maximum Neoglacial advances (Hamilton & Porter 1975; Ellis 1978).