



The nature of spatial transitions in the Arctic

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ABSTRACT

Aim Describe the spatial and temporal properties of transitions in the Arctic and develop a conceptual understanding of the nature of these spatial transitions in the face of directional environmental change.

Location Arctic tundra ecosystems of the North Slope of Alaska and the tundra-forest region of the Seward Peninsula, Alaska

Methods We synthesize information from numerous studies on tundra and treeline ecosystems in an effort to document the spatial changes that occur across four arctic transitions. These transitions are: (i) the transition between High-Arctic and Low-Arctic systems, (ii) the transition between moist non-acidic tundra (MNT) and moist acidic tundra (MAT, also referred to as tussock tundra), (iii) the transition between tussock tundra and shrub tundra, (iv) the transition between tundra and forested systems. By documenting the nature of these spatial transitions, in terms of their environmental controls and vegetation patterns, we develop a conceptual model of temporal dynamics of arctic ecotones in response to environmental change.

Results Our observations suggest that each transition is sensitive to a unique combination of controlling factors. The transition between High and Low Arctic is sensitive primarily to climate, whereas the MNT/MAT transition is also controlled by soil parent material, permafrost and hydrology. The tussock/shrub tundra transition appears to be responsive to several factors, including climate, topography and hydrology. Finally, the tundra/forest boundary responds primarily to climate and to climatically associated changes in permafrost. There were also important differences in the demography and distribution of the dominant plant species across the four vegetation transitions. The shrubs that characterize the tussock/shrub transition can achieve dominance potentially within a decade, whereas spruce trees often require several decades to centuries to achieve dominance within tundra, and *Sphagnum* moss colonization of non-acidic sites at the MNT/MAT boundary may require centuries to millennia of soil development.

Main conclusions We suggest that vegetation will respond most rapidly to climatic change when (i) the vegetation transition correlates more strongly with climate than with other environmental variables, (ii) dominant species exhibit gradual changes in abundance across spatial transitions, and/or (iii) the dominant species have demographic properties that allow rapid increases in abundance following climatic shifts. All three of these properties characterize the transition between tussock tundra and low shrub tundra. It is therefore not surprising that of the four transitions studied this is the one that appears to be responding most rapidly to climatic warming.

Keywords

Alaska, arctic, boreal forest, climate change, ecotones, spatial vegetation patterns, spatial transitions, treeline, tundra, vegetation dynamics.

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INTRODUCTION

Comparisons of ecosystems along latitudinal gradients provide an opportunity to document spatial patterns of vegetation community structure and ecological processes that have developed over time in response to long-term environmental conditions. These observations can serve as the basis for developing equilibrium biogeographic models (e.g. Prentice *et al.*, 1992; Epstein *et al.*, 2002) or incorporating long-term behaviour of systems into dynamic vegetation models (e.g. Chapin & Starfield, 1997; Epstein *et al.*, 2000; Kittel *et al.*, 2000; Rupp *et al.*, 2001). Many latitudinal studies have focused on one or a few ecological properties such as vegetation composition (e.g. Bliss, 1995), satellite-derived indices of vegetation (e.g. Jia *et al.*, 2002) or carbon fluxes (e.g. Valentini *et al.*, 2000), although there have been a few recent studies that examined a variety of ecosystem properties along latitudinal gradients (see McGuire *et al.*, 2002; Walker *et al.*, 2003a,b). Here we report a synthesis of information gathered over a 10-year interdisciplinary study (within the NSF program Land–Atmosphere–Ice Interactions, LAII) along a latitudinal gradient from the High-Arctic tundra to the boreal forest. The North American portion of the study spans a latitudinal range of *c.* 30° and a mean annual temperature gradient of *c.* 10 °C,

and therefore includes a variety of vegetation/ecosystem types as well as multiple biomes.

The transitions between the ecosystems found along this gradient are potentially controlled by many factors, including climate, soil substrate changes, topography, and disturbance and may be expressed as either gradual or abrupt spatial changes. Ecosystem properties can differ dramatically from one side of a transition to the other. We focus on spatial transitions, because these often receive less attention in gradient studies than the larger areas of relatively homogeneous properties. More importantly, transitions are places where ecosystems can change dramatically in response to dynamics of some environmental factor, such as climate (e.g. Neilson, 1993; Noble, 1993; Paruelo *et al.*, 1999; Scanlon *et al.*, 2002). In certain cases these transitions reflect abrupt changes with underlying ecological controls, but in other cases they may indicate thresholds in ecological response that reflect the sensitivity of the system to environmental change. An improved understanding of factors controlling spatial transitions may therefore provide insight into ways that a changing environment might trigger vegetation and ecosystem change. These may also be the locations where ecosystem responses to a gradually changing environment are first detected.

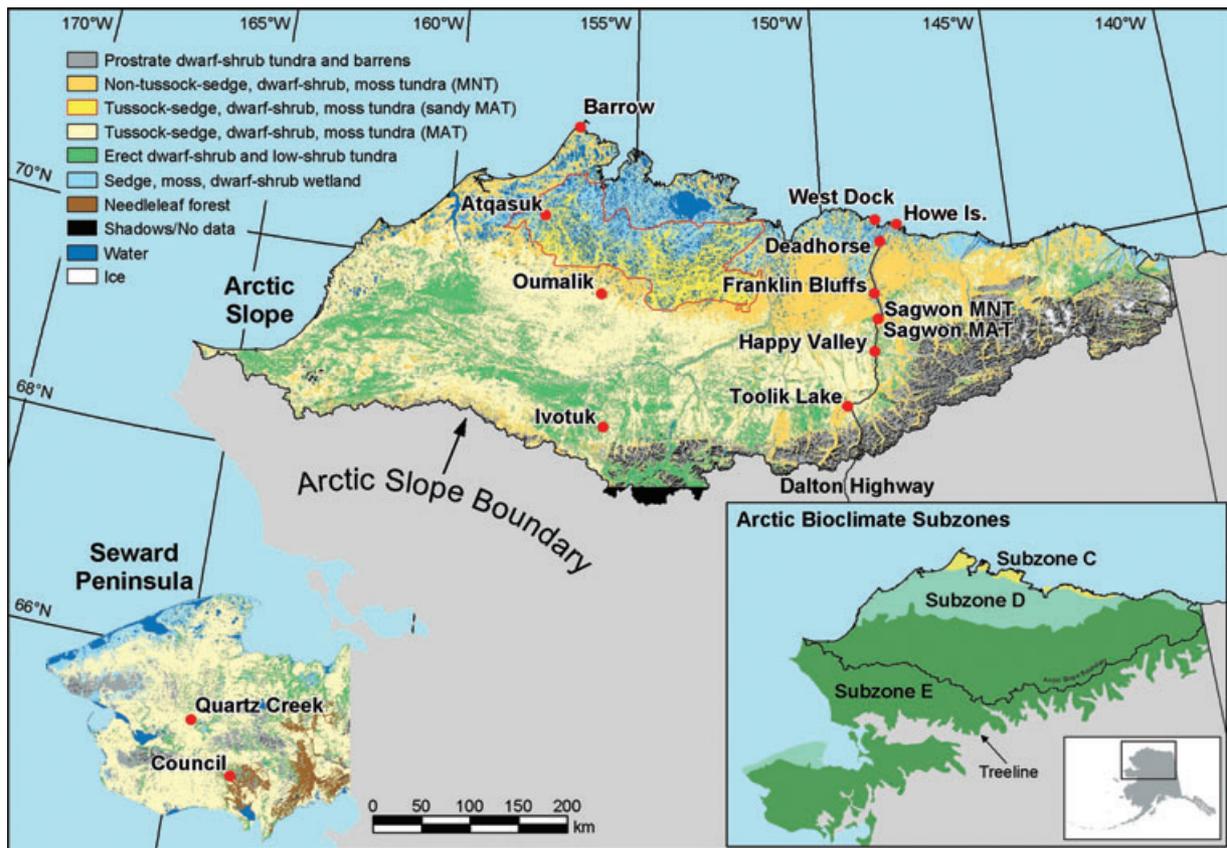


Figure 1 Subzones and transitions of northern Alaska, including important LAII Arctic Transitions of the Land–Atmosphere System (ATLAS) sites. Modified from Walker *et al.* (2003b).

APPROACH

The structural variation in arctic terrestrial ecosystems has been classified into five subzones within polar desert and tundra systems (Walker, 2000; Walker *et al.*, 2002; CAVM Team, 2003). The LAII research encompassed the three southernmost of these five subzones (subzones C, D and E; Fig. 1). The three subzones are distinguished by their dominant shrub type, with subzone C at the northern coast of Alaska characterized by prostrate dwarf shrubs (< 15 cm in height), subzone D in the coastal plains having erect dwarf shrubs (15–40 cm) and subzone E in the foothills of the Brooks Range dominated by low shrubs (> 40 cm). This synthesis focuses on four transitions, two of which can also be subzone boundaries, and another is a zonal boundary. These transitions are:

- 1 the transition between High-Arctic and Low-Arctic systems (subzones C and D);
- 2 the transition between moist non-acidic tundra (MNT) and moist acidic tundra (MAT, also referred to as tussock tundra) (subzones D and E, and also within subzones C, D and E);
- 3 the transition between tussock tundra and shrub tundra (within subzone E);
- 4 the zonal transition between tundra and forested systems (southern boundary of subzone E).

For each transition, we summarize the ecosystem properties (such as vegetation biomass, plant community composition, soil and soil organic matter) and processes (such as fluxes of carbon, water and energy and nutrient cycling) on either side of the transition. We also evaluate the dominant factors controlling the spatial locations of each transition, and assess whether these transitions are abrupt or gradual in space and how the nature of the transition relates to its controlling factors. The overall goal is to describe the spatial and temporal properties of transitions in the Arctic and to develop a conceptual understanding of the nature of these spatial transitions in the face of directional environmental change.

THE TRANSITIONS

High-Arctic–Low-Arctic transition

Ecosystem properties of the transition

Vegetation. The High- to Low-Arctic transition corresponds approximately to the subzone C–subzone D transition and the shift from prostrate dwarf-shrub, herb tundra to non-tussock sedge, dwarf-shrub, moss tundra (CAVM Team, 2003). This transition from High- to Low-Arctic landscapes can represent a dramatic shift between barren and semi-barren regions to predominantly vegetated areas (Bliss, 1997). The change in vegetation cover has significant effects in terms of biological activity and vegetation feedbacks to snow distribution, albedo, and freeze–thaw activity (Bliss, 1995; Walker *et al.*, 2003a,b). The High-Arctic landmass accounts for 31% of the arctic biome (Raynolds *et al.*, unpubl. data.), and the High Arctic is

the only region where truly endemic arctic plant and animal species occur; it is an area that could experience significant changes in response to climate warming.

The transition between High and Low Arctic shows the most dramatic contrast in ecosystem properties of all the transitions that occur within tundra and therefore has played an important role in tundra vegetation classifications. The subdivision of the Arctic into High- and Low-Arctic regions has been used primarily in North America (Bliss, 1988; Bliss & Matveyeva, 1992) but can be extended to the circumpolar Arctic (Bliss, 1995). Recent subzonal divisions of the Arctic classify the High Arctic as subzones A, B and C, and the Low Arctic as subzones D and E (*sensu* Bliss, 1995; Walker *et al.*, 2003a). The transition from High to Low Arctic corresponds to the appearance of ‘southern’ tundras dominated by boreal floristic elements, a wide variety of erect shrub species, well-developed moss carpets and extensive graminoid-dominated tundra. It has also been described as the boundary between the arctic and the ‘hypoarctic’ (with boreal floristic elements), based on floristic distributions (Yurtsev, 1994), and as the northern limit of erect dwarf shrub growth forms (Edlund, 1990; Walker, 2000; Gould *et al.*, 2002, 2003). The transition also represents the separation of predominantly mineral soils in the High Arctic from the presence of more peaty surface horizons in the Low Arctic.

In northern Alaska, the vascular flora of the High Arctic consist largely of graminoids, such as *Carex aquatilis*, *Eriophorum angustifolium*, *Dupontia fisheri* and *Poa arctica*, and prostrate deciduous and evergreen shrubs (e.g. *Salix arctica* and *Dryas integrifolia*, respectively). The transition to the Low Arctic is marked by a change in the dominant graminoid species and the presence of dwarf erect shrubs (Walker *et al.*, 2003b).

Soils. The transition from the High Arctic to the Low Arctic also represents a sharp gradient in the soil environment. The High Arctic has a cold, dry climate as compared with the cold, semi-humid climate of the Low Arctic. The combined effects of low soil moisture and low temperature in the High Arctic lead to low net primary productivity and thus less soil organic matter accumulation than in the Low Arctic. In the High Arctic, chemical weathering of primary minerals is slow, and the soils appear pale greyish brown to grey, indicating only small amounts of iron being released from the primary minerals and weak reduction reactions in soil above the permafrost tables. Leaching is minimal due to low precipitation and the high evaporation caused by nearly constant winds. Thus, soluble salts and carbonates are usually not leached to measurable depths; the soils generally have neutral to slightly alkaline conditions (pH 6.5–8.2) and high base saturation. The soil organic matter accumulates mostly at the surface horizon and shows little incorporation into the subsoils. Thus soil carbon storage is low compared with that of the Low Arctic. There is a twofold increase in carbon stores from the High Arctic to the Low Arctic; the carbon stores of soils from the High Arctic average only 30 kg m⁻² (range: 28–32) as compared with 61 kg m⁻² (range: 36–94) for the Low Arctic (Kimble *et al.*, 1993; Michaelson *et al.*, 1996).

Energy, water and carbon fluxes. No single study has directly compared fluxes of energy, water and CO₂ between High- and Low-Arctic ecosystems in the same region. However, comparisons between studies in High-Arctic ecosystems in Canada (Ohmura, 1984), Svalbard (Harding & Lloyd, 1998) and Greenland (Rott & Obleitner, 1992) and literature from the Low Arctic in other regions (Eugster *et al.*, 2000) suggest emergent patterns. Because of low vegetation cover in the High Arctic, albedo is largely determined by the shortwave reflectance of the soil, which can range from 0.08 to 0.16 in a single location (Harding & Lloyd, 1998) compared with a generally narrower range of values (0.15–0.18) for Low-Arctic tundra (Eugster *et al.*, 2000). Therefore, many High-Arctic sites have a lower albedo than do Low-Arctic sites and absorb a larger proportion of the incoming radiation.

Partitioning among sensible, latent and ground heat fluxes in the High Arctic depends largely on availability of moisture to support soil evaporation and is highly variable among sites (Eugster *et al.*, 2000). Photosynthesis and net primary production can be an order of magnitude lower in High-Arctic systems compared with the Low Arctic, and the net carbon sink may be greater in the Low Arctic at times when regional climate favours net carbon uptake (Miller *et al.*, 1983; Oechel & Billings, 1992; McGuire *et al.*, 2002). CO₂ efflux from soils may be strongly controlled by local-scale variations in temperature, moisture, vegetation and soil organic matter, and the data do not yet exist to make a direct comparison between High- and Low-Arctic systems (see Jones *et al.*, 1999, 2000; Welker *et al.*, 2000).

Nutrients. Nitrogen fixation by cyanobacteria is a key process in High-Arctic ecosystems (Chapin *et al.*, 1991; Chapin & Bledsoe, 1992; Gold, 1998; Dickson, 2000), bringing nitrogen into a system that is strongly nitrogen-limited (Henry *et al.*, 1986). Although nitrogen fixation rates increase rapidly with increasing temperatures, this process can vary by an order of magnitude among sites, and there is no clear evidence from existing data that rates are any different in the High Arctic compared with the Low Arctic. The few studies that have been carried out on nitrogen mineralization in the High Arctic suggest that annual rates may be no different than those found in the Low Arctic (Giblin *et al.*, 1991; Nadelhoffer *et al.*, 1991; Robinson *et al.*, 1995; Hobbie & Gough, 2002), with values on the order of < 1 g N m⁻² annually. Although Chapin (1996) did find peak summer net N mineralization values at Devon Island, Canada to be substantially greater than Low-Arctic values, and it has been shown that organic-rich soils in the Low Arctic can exhibit net N immobilization during the peak of the growing season (Giblin *et al.*, 1991; Jonasson *et al.*, 1993).

Controls on the High-Arctic–Low-Arctic Transition

Climate. Mean July temperatures for the High Arctic are typically < 7 °C, while Low-Arctic mean July temperatures range from 7 to 12 °C. The transition between High and Low Arctic is primarily controlled by climate (Bliss, 1995; Walker,

2000), as the filtering effect of reduced summer warmth in the north constrains the pool of available species and alters vegetation composition and biological activity (Rannie, 1986; Walker, 1995; Callaghan *et al.*, 2001; Walker *et al.*, 2001a,b). Variations in ecosystem properties from High to Low Arctic include those directly controlled by climate (individual species tolerances, enzymatic activity) and those indirectly controlled by climate (e.g. species interactions, nutrient dynamics, soil development and cryoturbation) (Table 1).

Parent material. As the climatic conditions are severe enough that minimal leaching and very weak biogeochemical weathering occur in the High Arctic, the nature of the parent material in the High Arctic exerts a more controlling effect than climate on soil properties. The chemical and physical properties of the soils thus strongly reflect those of the parent material; this is true in both the High Arctic and the Low Arctic. In the Low Arctic, especially on the coastal plains of Alaska, the control of parent material on soils will interact with the controls of drainage and hydrology (Ping *et al.*, 1998; in press).

Topography. The transition from High to Low Arctic varies from gradual to abrupt depending on physiographic features such as mountain ranges, distance from oceans, and substrate congruity. Mountain ranges can compress a climatic gradient, or ocean and ice features can interrupt a continuous gradient to create an abrupt transition. For example, on the Taymyr Peninsula in the Russian Arctic there is a gradual shift from High- to Low-Arctic conditions because the climatic gradient along the landscape is relatively uninterrupted by mountainous or coastal areas (Chernov & Matveyeva, 1997). In contrast, summer warmth patterns in the North American Arctic are strongly affected by the complex mosaic of ice, open water, and large and small islands of the Canadian Archipelago (Edlund & Alt, 1989; Gould *et al.*, 2002), and summer warmth may play a key role in determining the local position of the High- to Low-Arctic transition (Walker *et al.*, 2003a).

Interactions among controls. We are likely to see different responses to climatic change between abrupt and gradual boundaries at the High- to Low-Arctic transition. Expected outcomes as a result of warmer climates and increased growing season length for areas of gradual transition in the High Arctic (e.g. the Taimyr Peninsula) include a northward shift in Low-Arctic ecosystem properties. Local species ranges may expand within the High Arctic, developing a vegetation composition similar to adjacent, Low-Arctic landscapes. One likely effect of warming in the High Arctic will be the development of a moss carpet, which will alter the thermal and hydrological properties of the soil, with consequent effects on permafrost conditions. Current northern oases may see increasing boreal floristic elements and increasing rates of certain ecosystem processes, such as net primary production and nutrient mineralization. Abrupt transitions resulting from mountains or water bodies may respond more slowly to climatic change due to potential

Table 1 Comparison of ecosystem properties between the Low (subzones D–E) and High (subzones A–C) Arctic regions (primarily from ¹ Bliss, 1995 and ² Walker *et al.*, 2003a)

Characteristics	Low Arctic	High Arctic
Environmental		
¹ Length of growing season (months)	3–4	1.5–2.5
¹ Mean July temperatures (°C)*	7–12	2–7
¹ Mean summer precipitation (June–August) (mm)	35–200	25–100
¹ Mean annual precipitation	120–800	60–500
¹ Soil pH (typically)	5–6.5	6–8
¹ Organic layer (cm)		
Lowlands	50–300+	5–50
Uplands	2–20	0–2
Biological		
² Total above ground phytomass (10 ¹² g)†	2208	217
² Above ground phytomass density (g m ⁻²) (typically)†	625	133
¹ Vascular plant flora (<i>n</i>)	700–800	350–400
¹ Dominant vascular plant growth forms	Low, erect shrubs	Prostrate shrubs
¹ Large land mammals (<i>n</i>)	4–8	1–6
¹ Small land mammals (<i>n</i>)	15–30	5–12
¹ Nesting birds (<i>n</i>)	30–100	2–25
¹ Freshwater fishes (<i>n</i>)	10–25	1–9

*Modified from Bliss (1995) to reflect subzonal patterns from Walker *et al.* (2003a).

†Modified from Walker *et al.* (2003a) by combining subzones D–E for the Low Arctic, and subzones A–C for the High Arctic.

n, no. of species.

barriers for species migrations; other areas that may respond slowly are those where the parent material exerts strong controls on plant community composition and productivity.

Any lag in vegetation response to a warming climate will have feedbacks to animal activity at all scales, from megafaunal grazing responses to microfaunal and microbial decomposition of organic matter. Responses for some important large herbivore species (e.g. caribou and muskox) to this mosaic of change in the Arctic will depend not only on vegetation and summer growth, but also on the timing and conditions of snow during the winter. Deeper spring snows or the formation of ice crusts can inhibit access to winter food and affect survival rates.

MNT–MAT transition

The MNT–MAT (also referred to as tussock tundra) transition occurs at the southern boundary of subzone D (near the Brooks Range Foothills–Coastal Plains boundary), where the transition may be controlled by climate; however, the transition can also occur within subzones C, D and E, where it is controlled largely by substrate differences or hill slope position. Distinct soil pH boundaries found in the Arctic produce very different vegetation communities and ecosystem characteristics on either side of the MNT–MAT boundary. One of the most obvious is the boundary between MNT, associated with a soil pH greater than 5.5 and commonly found in subzone D, and MAT on moderately drained Low-Arctic acidic soils (pH < 5.5) within subzone E (Walker *et al.*, 1994, 1998,

2001a). The pH boundaries are primarily controlled by parent material, and MNT systems develop on areas dominated by calcareous loess, late-Pleistocene-age glacial till and limestone deposits (Walker & Everett, 1991). MNT systems are important and significant components of arctic tundra; for example, they cover 22% of the Arctic Slope of Alaska, compared with 28% MAT, 19% shrub tundra and 9% wetlands (Muller *et al.*, 1999).

Ecosystem properties of the transition

Vegetation. The transition between MNT and MAT represents the shift between non-tussock sedge, erect dwarf-shrub, moss tundra and tussock sedge, dwarf-shrub, moss tundra (CAVM Team, 2003). MAT is dominated by dwarf deciduous shrubs (including *Betula nana* and *Salix* spp.), evergreen shrubs, tussock sedges (*Eriophorum vaginatum* and *Carex bigelowii*) and acidophilous bryophytes (*Sphagnum* spp., *Aulacomnium* spp. and *Hylocomium* spp.). In contrast, MNT systems rarely have *Betula nana*, generally have fewer evergreen shrubs (*Dryas integrifolia* is a common one however), more diverse and abundant forbs and sedges (mainly *Carex bigelowii*) and minerotrophic bryophytes (*Tomenthypnum nitens* is dominant, and *Sphagnum* spp. are absent) (Walker *et al.*, 2001a; Hobbie & Gough, 2002). Although MNT has greater species diversity (Walker *et al.*, 1994) with twice the number of species per 100 m² in northern Alaska (Walker *et al.*, 2001b), the biomass of MAT is 25–35% greater than that of MNT (Walker *et al.*, 1994, 2003a).

Soils. In Alaska, MAT and MNT soils occur on the northern foothills of the Brooks Range. MNT occurs further north and on exposed slopes where strong winds prevail and often in areas of active loess deposition (Ping *et al.*, 1998). MAT on the Arctic Slope is also often developed on loess material, however for various reasons the pH tends to be more neutral or slightly alkaline in MNT relative to MAT. MAT soil pH tends to increase with depth, indicating that soils are leached; whereas the pH of the MNT soils tends to remain the same or decrease with depth (Ping *et al.*, 1998), indicative of continual input of base cations at the surface (Walker *et al.*, 2001a). Cation enrichment of the soil surface can occur through many processes including eolian and alluvial deposition, and cryoturbation (Walker *et al.*, 2001a). In addition, MNT soils have thinner organic horizons and a significantly thicker active layer than MAT soils (Bockheim *et al.*, 1998). The quantities of clay are similar; however, soils in MNT have significantly more extractable Ca, Mg and total base cations, and significantly less exchangeable acidity and Al than soils in MAT (Bockheim *et al.*, 1998).

MAT has been hypothesized to form as a result of peat formation and ice aggradation on older surfaces, which leads to restricted drainage and a general acidification of the soils (Walker *et al.*, 1994). Colonization of wet soils by *Sphagnum* and other mosses changes the soil chemistry, hydrology and thermal regime of the soil, resulting in peat formation. The soils become acidic as a result of the organic acids contributed by the peat (Ping *et al.*, in press), and once mosses form thick carpets, the soil becomes well insulated, and cryoturbation and the depth of the active layer are generally reduced. The decrease in pH from peat-derived acids in turn favours the growth of more *Sphagnum*, resulting in a positive feedback for the formation of MAT, and it remains acidic until disturbed (Walker *et al.*, 1994).

Recent evidence from Oumalik in western Alaska suggests that the vegetation is initiating the acidification and changing the soil chemistry rather than simply adapting to the soil environment. At this site, both the MNT and MAT vegetation types occur on slightly alkaline soils with base saturation exceeding 90%, with only 8% difference between MAT and MNT (Ping *et al.*, 2000). The transition from MNT to MAT, with increased vegetation cover and decreased cryoturbation is reflected in the carbon stores, with soil carbon contents in MAT nearly double those of MNT (Michaelson *et al.*, 1996). MNT soils also tend to have lower C : N ratios than MAT soils, due to the dominance of grasses and sedges on MNT compared with woody vegetation on MAT (Ping *et al.*, 1998).

Energy, water and carbon fluxes. The major difference between MNT and MAT systems in the energy balance arises from the greater biomass and leaf area index (LAI) in the taller and denser canopies of MAT sites (Walker *et al.*, 1998). Walker *et al.* (2003a) report 35% greater biomass in MAT compared with MNT at Sagwon Hills. The higher LAI in MAT sites shades the surface and reduces energy reaching the ground. In addition, the continuous moss cover and thick organic layers provides greater insulation and reduced heat flux through the

soil (Beringer *et al.*, 2001). Hence, the MNT sites tend to have a greater soil heat flux, 28% greater in one study (Walker *et al.*, 1998), compared with MAT. This greater soil heat flux results in deeper summer thaw (active layer) (Nelson *et al.*, 1997), up to 54% greater depth in MNT sites (Walker *et al.*, 1998).

Although the data are minimal, soil moisture and evapotranspiration were not significantly different between MNT and MAT at Sagwon Hills (Walker *et al.*, 1998). The greater LAI and biomass at MAT sites, however, result in about twice the gross photosynthetic uptake and three times the respiration of MNT and an overall greater net carbon gain during summer (Walker *et al.*, 1998, 2003a,b). There is a much greater accumulation of carbon over time at MAT sites. Methane efflux was also six times greater in the more anaerobic soils of the MAT sites compared with the MNT sites (Reeburgh *et al.*, 1998; Walker *et al.*, 1998).

Nutrients. Further understanding of the changes in nitrogen availability across the MNT–MAT transition is still necessary. Although there is greater microbial activity and more decomposed organic matter in MNT soils (Walker *et al.*, 2001a), the MAT sites at Toolik Lake, Alaska, exhibit higher rates of net N mineralization (Hobbie & Gough, 2002), and higher soil and plant N and K concentrations (Bockheim *et al.*, 1998; Hobbie & Gough, 2002). Patterns of cation cycling are more consistent across the transition, with lower cation exchange capacity, lower exchangeable base cations, and lower soil and foliar Ca concentrations in MAT compared with the MNT sites (Bockheim *et al.*, 1998; Hobbie & Gough, 2002). This occurs because the humic acid-rich soils of MAT leads to greater leaching losses of cations, which reduces the availability of minerals and nutrients, particularly calcium, for plants (Walker *et al.*, 2001a).

Controls on the MNT–MAT transition

Climate. A warmer climate in the future may reduce the extent of MNT systems, as loess sources become vegetated, cryoturbation becomes less intense and MAT proliferates (Walker *et al.*, 2001a). There are also climatically related controls exerted by interactions between snow and shrubs. MAT systems have a higher proportion of shrubs, which tend to trap more low-density snow and insulate the soil. The increased snow cover and greater winter soil temperatures may promote further shrub growth within MAT (Sturm *et al.*, 2001a). We expect that northward shifts in the boundary between MNT and MAT would occur only over century to millennial time scales as a result of climatic warming, because of the slow rate at which soil-forming processes (the dominant control) respond to climate. An alternative scenario of colder and drier future climate with shallower snow pack may promote the formation of frost boils and cause continual movement of non-acidic mineral material to the surface. In addition, loess deposition from the dry river valley sources would increase soil alkalinity and further the development of MNT across the landscape (Walker *et al.*, 1998).

Parent material. The spatial nature of the MNT/MAT transition is dictated by substrate controls and will be abrupt where MNT develops on limestone deposits or late-Pleistocene-age glacial till deposits. On areas dominated by calcareous loess, the influence of non-acidic substrates may be gradual as seen in transects along the Arctic Slope where soil pH decreases with distance away from the non-acidic loess source (Walker & Everett, 1991). However, the MNT/MAT boundary will often remain distinct where a pH threshold is reached that allows acidophilous mosses such as *Sphagnum* to become established, marking and accentuating the boundary between MNT and MAT.

Parent material is critically important in determining whether a site will be MNT or MAT. When the parent material is eolian in nature, elevation can also be a factor. For instance, in the southern foothills of the Arctic Slope, higher elevation slopes are primarily MAT, possibly due to reduced loess deposition at the higher elevations and higher precipitation (Ping *et al.*, 1998). The age of the parent material also plays a role; older loess sediments have lost carbonates and are relatively more acidic than younger carbonaceous sediments (Ping *et al.*, in press). Hence, on the Arctic Slope, the patterns of different substrates are related to the input of calcareous loess, balanced by losses due to marine, fluvial, eolian, cryogenic, glacial and thaw lake processes over time (Ping *et al.*, 1998). It should also be noted that within subzone D on the coastal plain of northern Alaska, there is an MNT-MAT boundary at the edge of a Pleistocene sand sea (Carter, 1981); these acidic sands support a diminutive version of MAT, with relatively short dwarf-shrubs.

Disturbance. Frost scars, or frost boils, are unique cryogenic disturbance agents in the Arctic (Walker *et al.*, 1994). Also known as non-sorted circles, these frost scars are small areas (0.5–1.5 m diameter) of highly disturbed mineral soil created by freeze–thaw processes (Washburn, 1956; Walker *et al.*, 1994). The area of non-sorted circles is significantly greater in MNT than in MAT, and it is thought that cryoturbation plays an important role in maintaining MNT in Arctic Alaska (Bockheim *et al.*, 1998). Recent investigations, however, indicate that although frost boils in MAT are masked by vegetation cover, they are still actively heaving in the winter due to the formation of ice lenses in the soil and settling in the summer with melt (Ping *et al.*, 2002).

The alkalinity of soils is controlled on the coastal plain and northern foothills by a combination of loess and cryoturbation (Walker & Everett, 1991). The high degree of frost heaving within MNT soils continually exposes mineral soil, brings calcareous subsoils to the surface and prevents the build-up of thick organic horizons (Walker *et al.*, 1998, 2001a). Under these conditions *Sphagnum* spp. that ultimately result in soil acidification cannot establish (Ping *et al.*, 1998), and MNT systems can become stable in the presence of disturbance. Some of the dominant MNT species such as *Dryas integrifolia*, however, are particularly sensitive to disturbance (Walker & Everett, 1991), making them vulnerable as well. MNT can also

occur on hill slope shoulders and hill crests within MAT where there is high frost heave activity or drainage of mineral-rich water from upslope areas.

Tussock tundra–shrub tundra transition

Ecosystem properties of the transition

Vegetation. The boundary between tussock tundra and shrub tundra represents the shift from tussock sedge, dwarf-shrub, moss tundra to either erect dwarf-shrub tundra or low shrub tundra (CAVM Team, 2003). We focus here largely on the transition to low shrub tundra. This transition occurs in irregularly shaped patches within subzone E of northern Alaska and the Seward Peninsula (Walker, 2000). Low shrub tundra can also be the dominant vegetation in subzone E, as seen in parts of the Seward Peninsula, south-western Alaska, and especially in the Arctic of European Russia. The greatest difference across the boundary from tussock tundra to low shrub tundra is the change in canopy complexity due to increased vegetation cover, height and LAI of the deciduous shrubs (McFadden *et al.*, 1998; Eugster *et al.*, 2000; J. Beringer *et al.*, unpubl. data; Thompson *et al.*, 2004). The boundary between the two tundra types involves increases in the abundance and biomass of deciduous dwarf birch (*Betula nana* L.) and willow (*Salix pulchra* Cham.) shrubs. In tussock tundra, the deciduous shrubs are one of three major vascular functional types, sharing canopy dominance with tussock-forming sedges and evergreen shrubs. In low shrub tundra the deciduous shrubs dominate the canopy (Shaver & Chapin, 1991). The presence of a taller deciduous shrub canopy reduces biomass of evergreen shrubs, graminoids and non-vascular plants (Chapin & Shaver, 1996).

Soils. Soil characteristics change in parallel with vegetation at the transition from tussock tundra to low shrub tundra. The organic layer under the low shrub tundra is shallower (3–10 cm) than in tussock tundra (*c.* 20 cm) (Ping *et al.*, 1998), due in part to the reduced cover of mosses, especially peat-forming *Sphagnum* mosses. Carbon and nitrogen pools are smaller, and C : N ratios are lower, in the organic layer of the low shrub tundra soils than in tussock tundra soils (Ping *et al.*, 2000). Winter soil temperatures are also substantially warmer beneath shrubs, because the snow trapped by shrubs is deeper and denser and has lower thermal conductivity than snow in tussock tundra (Sturm *et al.*, 2001a). This may explain the greater winter CO₂ flux from soils in low shrub tundra than in tussock tundra (Fahnestock *et al.*, 1999).

Although site differences in slope and aspect may account for some of the soil differences between tussock and low shrub tundra, long-term experiments suggest that shrubs can affect soil properties. After a 20-year nutrient addition in tussock tundra, a dense shrub canopy developed and the organic layer was reduced (M. Mack *et al.*, unpubl. data). These changes were determined more strongly by plant community composition dynamics than by fertilization directly (Shaver *et al.*, 2001).

Energy, water and carbon fluxes. Albedo generally decreases with the development of the shrub canopy because the taller shrubs are more effective at scattering and trapping incoming solar radiation. In addition, the canopy masks the more reflective components of the tundra such as lichens and standing dead leaves of graminoids. Typical tussock tundra albedos are 0.2 compared with shrub tundra of 0.15 (Eugster *et al.*, 2000). The lower albedo found over low shrub tundra increases the net radiation over these areas relative to less shrubby tundras, driving increased fluxes of heat and moisture (J. Beringer *et al.*, unpubl. data).

The higher leaf and stem area associated with a denser shrub canopy also increases shading of the ground and soil, which reduces the ground heat flux and increases the amount of energy available for partitioning into heat and moisture fluxes to the atmosphere (McFadden *et al.*, 1998; J. Beringer *et al.*, unpubl. data). Canopy shading decreases soil water evaporation to a greater extent in low shrub tundra relative to tussock tundra, where evaporation can occur freely from the moss layer at the surface. Evapotranspiration from the shrub ecosystem is therefore driven more strongly by transpiration.

Because of low ground heat fluxes, the fraction of net radiation partitioned to sensible heating of the air is higher in shrub tundra relative to tussock tundra (J. Beringer *et al.*, unpubl. data). Greater heating of the atmosphere will be found over areas of shrub tundra, with estimates of sensible heating from modelling and field studies that vary from 3.4 to 7.1 W m² (Chapin *et al.*, 2000a,b). This increased sensible heating is substantial on a unit ground-area basis in the context of other forcings on climate such as a doubling of CO₂, calculated to be a heating equivalent of 4.4 W m².

The energy balance across the spatial transition from tussock tundra to low shrub tundra during winter and spring is altered by spring snow sublimation, albedo and evapotranspiration. Modelled increases in shrub density led to a 20% increase in winter snow depth, decreasing sublimation and increasing snow pack at the time of spring melt. These feedbacks to the winter moisture budget affected both timing and magnitude of snowmelt (Liston *et al.*, 2002). In a regional field study of the effects of shrubs on snowmelt, J. Beringer *et al.* (unpubl. data) found that the onset of spring melt occurred up to a week earlier in shrub-dominated sites compared with tussock tundra sites. The protrusion of stems through the snow acts to absorb energy and hasten snow melt. Shrub density was as important as 3.6° of latitude (or 400 km) in determining melt dates (J. Beringer *et al.*, unpubl. data).

Total aboveground live biomass typically ranges between 75% and 100% greater in shrub tundra compared with tussock tundra, whereas aboveground net primary production can range from being similar to c. 100% greater in shrub tundra (Shaver & Chapin, 1991; Shaver *et al.*, 1996; S. Riedel *et al.*, unpubl. data). Soil and ecosystem respiration do not vary consistently between tussock tundra and shrub tundra (Shaver *et al.*, 1996; Jones *et al.*, 1999), although winter soil respiration rates have been shown to be greater in shrub sites compared with sites without shrubs (Fahnestock *et al.*, 1999).

Nutrients. Differences in litter decomposition among growth forms are large relative to abiotic effects such as temperature (Hobbie *et al.*, 2000). Production of leaf litter in shrub tundra is much higher, decreasing the residence time of nutrients in vegetation, compared with tussock tundra. Shrub tundra has higher nitrogen mineralization rates than tussock tundra (Giblin *et al.*, 1991). The differences in species composition across this transition are likely to have a strong effect on nutrient fluxes in these systems (Shaver *et al.*, 2001).

Controls on the tussock tundra–shrubs tundra transition

Climate. The location of low shrub tundra correlates with summer temperatures, with the boundary between tussock tundra and low shrub tundra occurring at approximately the 10 °C mean July isotherm (Walker, 2000). However, the distribution of shrubs along hillslopes and riparian areas suggests that summer temperature is not the only factor controlling the transition between tussock tundra and shrub tundra. In addition to summer temperature, hydrology, fluxes of nutrients along streams, and winter snow conditions can give rise to the same transition.

Slight increases in shrub density and height lead to a deeper winter snow pack (Sturm *et al.*, 2001a), and a positive snow–shrub feedback in which the deeper snow pack leads to enhanced shrub growth and further snow trapping. With a transition to low shrub tundra come changes in species composition and vegetation structure, decreases in soil organic layers, changes in soil temperatures and alterations of nutrient cycling. Mechanisms of this feedback include protection from winter desiccation, greater winter insulation and increased summer soil moistures. Warmer winter soil temperatures enhance decomposition and could lead to increased nutrient availability, which promotes further shrub growth (Sturm *et al.*, 2001a).

Topography. Shrub tundra is found in a variety of landscape locations. In the northern part of subzone E, it is found in riparian areas and on south-facing hill slopes of intermediate grade. In warmer parts of subzone E, shrub tundra is sometimes the zonal vegetation, particularly in areas with discontinuous permafrost. Where the shrub tundra occurs along river or stream channels, the transition between the riparian shrub tundra and other tundra types in adjacent areas can be abrupt; whereas the transition is more likely to be gradual, where the shrub tundra occurs on hillslopes (Walker *et al.*, 1994). At broader spatial scales the boundary between tussock tundra and areas of low shrub tundra (located further to the south in the foothills of the Brooks Range) is detectable with remote sensing (Muller *et al.*, 1999). The gradual transitions along hill slopes and climate gradients suggest that distributions could change rapidly in response to climatic change due to vegetative expansion of shrubs.

Interactions among controls. Overall, the boundary between tussock tundra and low shrub tundra is largely controlled by temperature with secondary feedbacks through soil moisture

and winter snow conditions. Temporal transitions at this boundary could occur on decadal time scales for several reasons. First, the mechanism for change is the growth of deciduous shrubs that are already present on both sides of the transition. Secondly, some species of deciduous shrubs quickly respond to environmental change. In tussock tundra, for example, a 3 °C summer warming with greenhouses caused an increase in shrub biomass in about 10 years (Chapin *et al.*, 1995). Some shrubs, such as *Betula nana*, have the capacity to quickly increase the number of structural branches, through elongation of pre-existing short shoots (Bret-Harte *et al.*, 2001). *Betula* can also support substantial secondary growth and therefore grow taller and increase in biomass (Bret-Harte *et al.*, 2002). Pollen evidence from paleoecological studies suggests that *Betula* also expanded during the warm, early Holocene (Brubaker *et al.*, 1995). Nitrogen fertilization experiments have led to a dramatic increase in *Betula nana* (Shaver *et al.*, 2001), and climatic warming, which could increase nitrogen mineralization in soils, may have a similar effect.

Shrubs in the Alaskan Arctic have increased their abundance in response to climate warming over the last few decades, both by expanding across landscapes and by increasing biomass where they already exist (Sturm *et al.*, 2001b). On the Seward Peninsula, Silapaswan *et al.* (2001) found that expansion of shrubs on hillslopes and along riparian corridors had occurred over a 10-year period.

Tundra–boreal forest transition

Ecosystem properties of the transition

Vegetation. This transition represents a major zonal boundary, as it corresponds to a dramatic shift in plant physiognomy and the stature of the dominant growth form. The presence or absence of trees is what largely distinguishes tundra from boreal forest. On the Seward Peninsula in Alaska, for example, most of the species present in the shrub tundra communities that abut treeline forests are also present in the understory of the forested areas. The transition from tundra to forested vegetation therefore typically involves gradual changes in tree density and morphology. The width of the treeline ecotone can vary substantially among sites (Fig. 2). In western Alaska, two general types of tundra–forest ecotones are common. Along major river drainages, dense spruce forests occupy floodplain surfaces, whereas tussock tundra or low shrub tundra typically occupies sites off of the active floodplain. These river drainage settings give rise to abrupt treelines, where the distance from continuous forest to the tree species limit may be < 50 m. These sites generally lack an area of small, growth-stunted trees, and in many cases the continuous forest limit, treeline, and tree species limit coincide (Sveinbjornsson, 2000; Sveinbjornsson *et al.*, 2002). The abruptness of these boundaries probably reflects the overwhelming influence of permafrost on vegetation distribution in these settings. The active layer is likely to be very deep (or permafrost may be

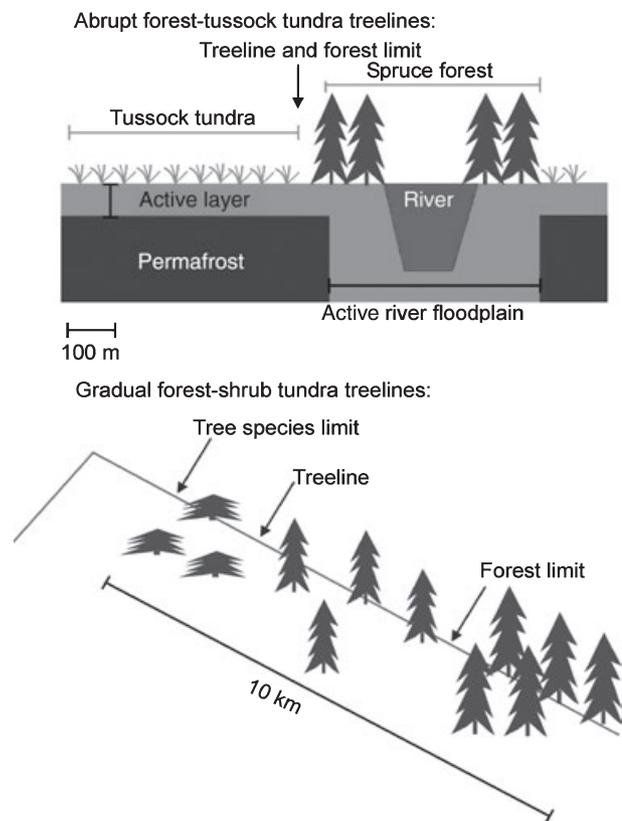


Figure 2 Structure of two major types of treeline in arctic Alaska.

entirely absent) within the active river floodplains, but active layer thickness declines rapidly off of the river floodplain. The abrupt vegetation gradient may therefore reflect an equally abrupt gradient in the influence of permafrost. In upland areas, the forest-tundra ecotone is generally very broad, and in certain places the transition from tundra to continuous forest stretches over 10 km or more. Where forest abuts shrub tundra, there is generally not an area of growth-stunted trees, but in more wind-exposed sites, where forest yields to low alpine tundra, stunted trees are common beyond treeline.

Soils. Soil properties do not vary in a consistent fashion across the tundra–forest ecotone. The position of treelines associated with river floodplains is often closely tied to the location of permafrost, and trees in these sites are generally restricted to areas underlain by well-drained and relatively warm alluvium. Sites away from the active river floodplain are typically underlain by cold, poorly drained soils with shallow active layers and are dominated by tussock tundra. With the exception of situations like these, however, treeline position does not often correspond with abrupt changes in soil properties. Sveinbjornsson (2000) found that soil moisture was slightly higher above treeline (e.g. in tundra) than at treeline, but concluded that such differences in soil moisture were minor compared with differences between valley bottom sites and mountain sites.

Soils formed in upland tundra generally are poorly drained, so the active layer is reduced, as indicated by the dominantly grey colour and strongly mottled soils of the upper active layers. Cryoturbation is so strong that nearly 40% of the pedon carbon is in the upper permafrost. In shrub tundra to forest transitions, such as those on the Seward Peninsula, there is no permafrost present.

As the land cover grades from tundra to forest, there is generally improved drainage, from poorly drained to imperfect or somewhat poorly drained soils. Due to the drainage improvements, the upper soil mineral layers become more aerated with increased oxidation of iron-bearing minerals. The soil colour appears pale yellow to pale brown, and only the lower active horizons appear reduced. In the forest, there is evidence of increased leaching in that there is a Bs or Bsh horizon that designates the presence of alluvial Fe or Al-humus complexes. Most notable is the bright colour in the B-horizons of the forest soils that indicates an increased degree of weathering (i.e. oxidation). This is further supported by relatively high amounts of extractable Fe, indicating the presence of weatherable iron products, mostly goethite and cristobalite (C.L. Ping *et al.*, unpubl. data).

From tundra to forest, there is decreased acidity in the O horizons but increased acidity in the underlying mineral horizons. The increased acidity is accompanied by increased exchangeable aluminium. The base saturation also decreases along the transition resulting from the major bases, mainly Ca and Mg, being replaced by H and Al. Due to the improved drainage and increased temperature in forest sites, the total pedon carbon store decreases relative to tundra, especially in the permafrost-free areas.

Energy, water and carbon fluxes. Forest tundra has greater roughness length, lower summer albedo and substantially lower winter albedo than does shrub tundra (Lafleur & Rouse, 1995; Chapin *et al.*, 2000a,b; Rouse *et al.*, 2000). Continuous boreal forest has an even lower albedo than forest-tundra (Betts & Ball, 1997; J. Beringer *et al.*, unpubl. data). These differences lead to greater net radiation and sensible heat fluxes over forest compared with tundra (J. Beringer *et al.*, unpubl. data).

Both Chapin *et al.* (2000b) and Sturm *et al.* (2001a) highlighted the importance of shrub presence in altering ecosystem processes, demonstrating that the presence of some woody plants makes a measurable difference in fluxes of energy and nutrient cycling. The degree to which energy fluxes, for example, change along the tundra-forest ecotone may depend strongly, therefore, on the nature of the adjacent tundra vegetation. Treelines along river floodplains, where dense forests yield abruptly to tussock tundra vegetation, may exhibit much steeper gradients in energy, water and nutrient fluxes than upland treelines, where forest yields to shrub tundra vegetation that may be more similar in terms of energy flux and effect on snowpack.

Few carbon cycling comparisons exist between boreal forest and shrub tundra; however, northern forests tend to be sinks

for atmospheric CO₂, whereas tundra has been found to be either sources or sinks, with the sinks having magnitudes less than those of boreal forest (Lafleur, 1999; Chapin *et al.*, 2000b; Lafleur *et al.*, 2001; Rouse *et al.*, 2002). Increases in CO₂ flux from soil to atmosphere in tundra appear to be strongly related to the degree of soil dryness, with drier soils producing greater soil CO₂ fluxes (Chapin *et al.*, 2000b; Lafleur *et al.*, 2001; Rouse *et al.*, 2002).

Nutrients. Soil nutrient availability is often lower in tundra than at treeline (Nadelhoffer *et al.*, 1992). These differences are probably primarily a consequence of reduced mean soil temperatures in tundra areas compared with forests. Changes in soil nutrient availability may be highly sensitive to the relative importance of soil temperature (which tends to reduce decomposition rates in tundra relative to forest soils) and litter quality (which may increase decomposition rates in shrub tundra relative to coniferous forests). Less inorganic nitrogen availability in tundra relative to forests may lead to greater use of soil organic nitrogen directly by tundra shrubs compared with the evergreen trees of boreal forests (Schulze *et al.*, 1994).

Controls on the tundra-boreal forest transition

Climate. On a circumboreal basis the position of treeline falls largely within the July maximum temperature isotherms of 10 and 12 °C (Hare, 1950; Larsen, 1974). The location of treeline also corresponds reasonably well with the position of the arctic front (e.g. Sveinbjornsson *et al.*, 2002). Paleocological studies have demonstrated repeatedly that the positions of both arctic (e.g. Spear, 1993; MacDonald *et al.*, 2000; Lloyd *et al.*, 2002) and alpine treeline (e.g. Denton & Karlén, 1977; Lloyd & Fastie, 2002) have shifted synchronously with climate in the past, providing further support for the hypothesis that treeline is determined by some effect of temperature.

Although spatial and temporal correlations point to an important role for climate in determining the position of treeline, the mechanistic basis of those correlations remains largely unknown. Temperature is likely to affect reproduction in treeline forests, both by influencing the amount of energy available for reproduction and by restricting the availability of favourable microsites for germination. Temperature effects on reproduction at treeline have been particularly well documented in Canadian treeline sites dominated by black spruce (*Picea mariana*). Black & Bliss (1980), for example, found that both seed production and seed germination were limited in black spruce (*Picea mariana*) populations at treeline in north-western Canada, and Sirois (2000) found that the production of viable seeds by black spruce declined along a poleward latitudinal transect in eastern Canada.

Low temperatures at treeline also affect tree growth, as indicated by the prevalence of lower growth rates in trees at and north of (or above) treeline compared with similar individuals within areas of continuous forest (e.g. Sveinbjornsson, 2000 and references therein). The absence of trees

north of and above treeline may therefore represent a failure to maintain an adequate carbon balance in the face of low growth during the growing season and high tissue loss due to winter injury (e.g. Wardle, 1981).

Although the effects of temperature on the growth and distribution of treeline trees are relatively clear, there is increasing evidence that the distribution of spruce in Alaska may also respond to moisture availability. Rising temperatures in the twentieth century have led to decreased growth in white spruce at treeline for both interior and western Alaska (Lloyd & Fastie, 2002), particularly in dry, continental areas. Therefore, the effects of temperature on tree performance at treeline may be strongly modified by moisture availability.

Differences in energy fluxes (Chapin *et al.*, 2000a) between tundra and forest ecosystems may lead to regionally important climate feedbacks at the tundra–forest transition, as greater near-surface atmospheric warming over boreal forest regions may act as a positive feedback on forest vegetation. The relative importance of these feedbacks, however, remains uncertain. Bonan *et al.* (1992) and Foley *et al.* (1994) concluded that expansion of boreal forest could initiate measurable climate feedbacks as a result of albedo differences between tundra and forest ecosystems. Recent measurements of energy fluxes in ecosystems throughout the Arctic, however, have suggested that feedbacks associated with differences in vegetation types within regions (e.g. shrub-tundra vs. tussock tundra) were more pronounced than differences between boreal and arctic regions (Chapin *et al.*, 2000b).

Parent material. Although substrate characteristics generally do not vary systematically along the tundra-forest ecotone, substrate conditions are likely to be extremely important in determining the position of treeline along major river drainages. The position of treeline in these locations appears to be closely associated with the limit of permafrost; permafrost-free floodplain surfaces are dominated by relatively dense forests, while adjacent permafrost-rich sites are dominated by moist acidic or shrub tundra (e.g. Fig. 2).

Disturbance. The role of disturbance in affecting the position or dynamics of the tundra-forest ecotone remains largely unknown based on empirical data. The two disturbances most likely to affect treeline are fire and thermokarst. Fires certainly occur at treeline, although their frequency is probably substantially lower (every 1000 years or more) than in the central boreal forest (Kasischke *et al.*, 2002). Fire may have two opposing effects on treeline dynamics. First, fire may reduce regeneration by killing mature trees and thus reducing seed rain. Payette & Fillion (1985) have hypothesized that late Holocene fires in eastern Canada led to widespread deforestation because the availability of viable seed was too limited to allow regeneration. Models of treeline dynamics suggest that the rate of treeline advance in a warming climate is highly sensitive to fire regime, as fires reduce seed rain and thus forest regeneration (Rupp *et al.*, 2000a,b; Lloyd *et al.*, 2002). Secondly, fire may improve regeneration at treeline by

reducing competition with tundra vegetation and providing favourable microsites for germination. The relative importance of these two potentially opposing effects remains unknown.

Although fire is probably the most important large-scale disturbance at the tundra-forest boundary, thermokarst disturbance may affect treeline dynamics in areas where the position of treeline is associated with the presence and absence of permafrost. On the Seward Peninsula in Alaska, for example, spruce has invaded tussock tundra since the early 1900s in areas that have been severely affected by thermokarst, but not in adjacent undisturbed areas (Lloyd *et al.*, 2002, 2003). In such areas, treeline may exhibit highly nonlinear responses to warming, as an advance of spruce into tundra may be contingent upon melting of permafrost. In general, disturbance is probably important in modifying the rate of response of trees at treeline to climate, but should not be considered, in most cases, as a control over the position of the tundra–forest transition.

There is abundant evidence that past changes in climate have been associated with shifts in the position of treeline, and indeed warming that began in the late 1800s has been associated with an advance of treeline in western Alaska (Suarez *et al.*, 1999; Lloyd *et al.*, 2002) and interior Alaska (Lloyd & Fastie, 2002). The major uncertainties associated with predicting responses of treeline tree populations to future warming involve the role of moisture availability and disturbance (by fire or thermokarst). Both factors may contribute to strong nonlinearities in future response to warming (Calef *et al.*, in press).

SUMMARY AND CONCEPTUAL FRAMEWORK

In summary, our observations of the four major ecosystem transitions between High-Arctic tundra and boreal forest in Alaska suggest that each transition is sensitive to a unique combination of controlling factors (Table 2). The transition between High and Low Arctic is sensitive primarily to climate, whereas the MNT/MAT transition is controlled to a greater degree by soil variables such as parent material, permafrost and hydrology, as these are modified by regional scale processes such as glaciations and loess deposition, and the balance between finer-scale disturbance and vegetation succession. The MAT/shrub tundra transition appears to be responsive to several factors, including climate, topography and hydrology. Finally, the tundra/forest boundary responds primarily to climate and to climatically associated changes in permafrost.

There were also important differences in the demography and distribution of the dominant plant species among the four vegetation transitions that we studied. The shrubs that characterize the MAT/shrub tundra transition can achieve dominance potentially within a decade, whereas spruce trees often require several decades to centuries to achieve dominance within tundra, and *Sphagnum* colonization of non-acidic sites at the MNT/MAT boundary may require centuries to millennia of soil development. The continuous distribution of shrubs across the MAT/shrub tundra transition will further

Table 2 Relative importance of environmental factors on ecosystem transitions

	Rate of change [†]	Relative importance for transitions*			
		High/Low Arctic	MNT/MAT	Tussock/shrub tundra	Tundra/forest
State-factor controls					
Climate	M-F	H	M	H	H
Parent material	S	L	H	L	L
Topography	S	M	L	H	L
Disturbance	S-F	L	H	L	M
Environmental interactions					
Permafrost/active layer	M-F	L	H	M	H
Hydrology and snow	M-F	M	H	H	M
Properties of dominant plant species					
Time to dominance		M	S	F	S
Continuity of abundance across transition [‡]		I	A	C	A

*H, high; M, medium; L, low.

[†]F = 0–10 years; M = 10²–10³ years; S = 10⁴+ years.

[‡]C, continuous; I, intermediate; A, abrupt.

facilitate rapid vegetation response at this transition. Current information on the vegetation changes between High and Low Arctic is not yet comprehensive enough to make such assessments regarding the temporal dynamics of this transition.

Together these differences in apparent controls over spatial patterns of system properties and the responsiveness of the dominant plant species provide a conceptual framework for predicting vegetation sensitivity to temporal changes in climate. We suggest that vegetation will respond most rapidly to climatic change when (i) the vegetation transition correlates more strongly with climate than with soil variables, (ii) dominant species exhibit gradual changes in abundance across spatial transitions, and/or (iii) the dominant species have demographic properties that allow rapid increases in abundance following climatic shifts. All three of these properties characterized the MAT/shrub tundra transition. Of the four transitions that we studied, this is the one that has shifted most rapidly in response to experimental warming (Chapin *et al.*, 1995; Sveinbjornsson, 2000; Hobbie & Gough, 2002; Sveinbjornsson *et al.*, 2002) and recent regional warming (Sturm *et al.*, 2001b; Lloyd & Fastie, 2002), and it has also responded rapidly to post-glacial warming (Brubaker *et al.*, 1983).

At the opposite extreme, transitions controlled by soil development are likely to change slowly, which could explain the compositional stability of the MNT vegetation to experimental warming (Hobbie & Gough, 2002). Recent data, however, may call into question the stability of MNT, as remotely sensed indices of vegetation greenness have increased more in MNT over the past two decades than other tundra vegetation types (Jia *et al.*, 2003; Stow *et al.*, 2004). There is no evidence at this point of rapid, decadal species composition changes in MNT. Paleoecological data suggest that changes from MNT to MAT vegetation have occurred at timeframes on

the order of thousands of years; however these changes occurred during a rather gradual early- to middle-Holocene climatic change (Oswald *et al.*, 1999; Oswald *et al.*, 2003). Based on the spatial patterns and demographic properties of the vegetation at treeline, we expect that the forest limit will respond sensitively to climate, but more slowly than the MAT/shrub tundra transition.

While we are less clear about the High- to Low-Arctic transition, Epstein *et al.* (2000) suggest that changes in vegetation in the High Arctic as a result of warming may be constrained by low quantities of soil organic matter. It is reasonable, however, to expect relatively large changes to the presently very sparse vegetation in the High Arctic. Small increases in the summer mean temperature will result in major changes to the total accumulated warmth (e.g. thawing degree days) available for plant growth. This could cause major changes in mosses and sedges and eventually lead to peaty soil surface horizons and a rapid paludification in some areas of the High Arctic.

One of the most difficult challenges in projecting vegetation dynamics to climatic change has been the development of rules for vegetation responses to climate. Many models of vegetation change are based on either assumptions of equilibrium relationships to climate (e.g. Prentice *et al.*, 1992) or physiological responses to climatic change (e.g. Kittel *et al.*, 2000; Sitch *et al.*, 2003). Our observations of ecosystem transitions from High-Arctic tundra to boreal forest suggest that the dynamics of these transitions can provide useful clues for predicting large-scale patterns and rates of vegetation change. We suggest that an enhanced understanding of vegetation transitions in space can improve our ability to predict patterns and rates of vegetation response to future changes in climate.

The synthesis presented here provides a comprehensive view of the changes in northern ecosystems along a latitudinal

gradient, the spatial transitions that occur between these ecosystems and a conceptual framework regarding how these transitions might change over time with dynamics in environmental forcing. With this information, hypotheses regarding ecosystem dynamics could be posed and tested with observations and/or field experiments.

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