Winter Biological Processes Could Help Convert Arctic Tundra to Shrubland

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In arctic Alaska, air temperatures have warmed 0.5 degrees Celsius (°C) per decade for the past 30 years, with most of the warming coming in winter. Over the same period, shrub abundance has increased, perhaps a harbinger of a conversion of tundra to shrubland. Evidence suggests that winter biological processes are contributing to this conversion through a positive feedback that involves the snow-holding capacity of shrubs, the insulating properties of snow, a soil layer that has a high water content because it overlies nearly impermeable permafrost, and hardy microbes that can maintain metabolic activity at temperatures of –6°C or lower. Increasing shrub abundance leads to deeper snow, which promotes higher winter soil temperatures, greater microbial activity, and more plant-available nitrogen. High levels of soil nitrogen favor shrub growth the following summer. With climate models predicting continued warming, large areas of tundra could become converted to shrubland, with winter processes like those described here possibly playing a critical role.

Keywords: tundra, shrubs, snow, microbes, climate change

Transitions in vegetation are nothing new in the Arctic. The geologic record indicates that about 9000 years ago, the region underwent a widespread transformation from a grassland to a tundra ecosystem (Ager 1983). This resulted in the departure or extinction of the large Pleistocene megafauna (Owen-Smith 1987) and the exodus of Paleolithic humans from the Alaskan Arctic (Kunz and Reanier 1994). As recently as 8000 years ago, forests grew along the arctic coast (MacDonald et al. 2000), and the record also tells us that shrubs swept across the tundra several times during the Holocene (Anderson and Brubaker 1993). Now the abundance of arctic shrubs is again increasing, apparently driven by a warming climate. It is possible that we are witnessing the forerunner of another major transition in arctic vegetation.

The evidence for increasing shrub abundance is most comprehensive for northern Alaska. An extensive comparison of old (1940s) and modern photographs (figure 1; Sturm et al. 2001a, Stow et al. 2004) has shown that shrubs there are increasing in size and are colonizing previously shrub-free tundra. In western arctic Canada, increased shrub abundance is also indicated, but there the change has been inferred from the recollections of long-term residents (Thorpe et al. 2002). In central Russia, a transect along the Pechora River has shown a distinct decrease in tundra and a corresponding increase in shrubland (Shvartsman et al. 1999), but for the vast tundra regions of Siberia, there are currently no data on

which to make an assessment. Satellite remote sensing studies (Myneni et al. 1997, Silapaswan et al. 2001, Jia et al. 2003), however, greatly strengthen the case for a pan-Arctic expansion of shrubs. These studies indicate that over large regions of the tundra, leaf area has increased, a change one might expect if graminoids, lichen, and moss were giving way to shrubs.

The expansion of shrubs has coincided with three decades of rising arctic air temperatures. These are now at levels higher than any experienced in the last 400 years (Overpeck

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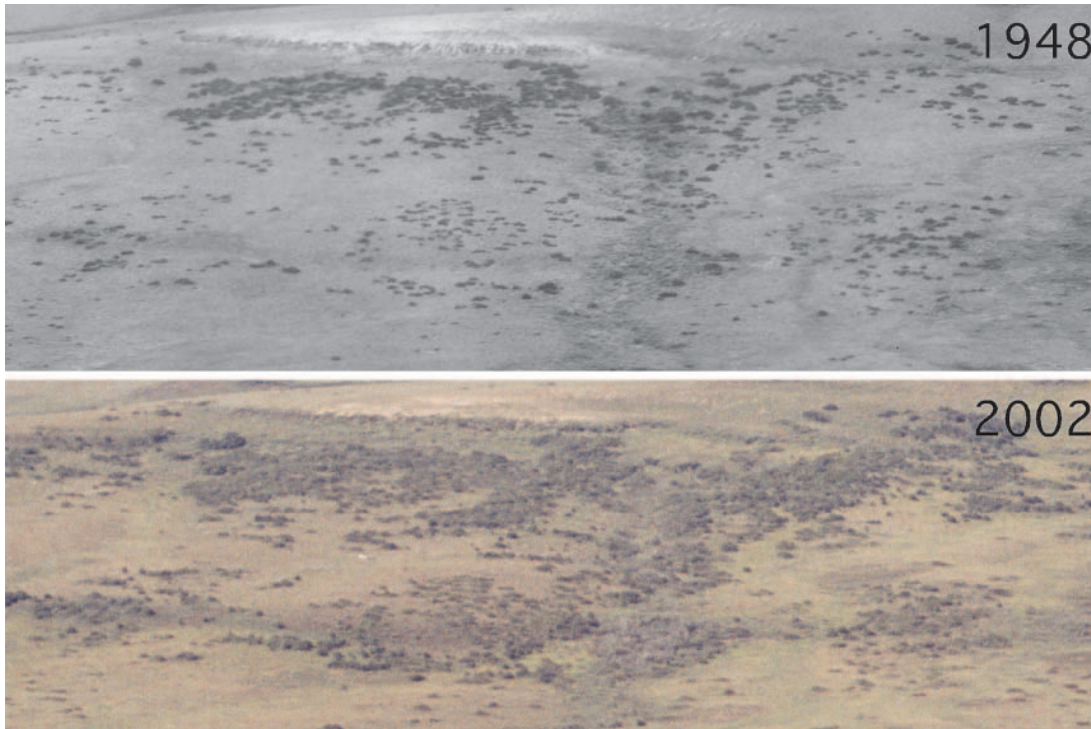
Figure 1. Increasing abundance of shrubs in arctic Alaska. The photographs were taken in 1948 and 2002 at identical locations on the Colville River (68° 57.9' north, 155° 47.4' west). Dark objects are individual shrubs 1 to 2 meters high and several meters in diameter. Similar changes have been detected at more than 200 other locations across arctic Alaska where comparative photographs are available. Photographs: (1948) US Navy, (2002) Ken Tape.

et al. 1997), and the rate, about 0.5 degrees Celsius (°C) per decade (Chapman and Walsh 1993, Serreze et al. 2000), is five times faster than the global rate of warming (Jones PD et al. 1999). A number of eye-catching environmental changes have been associated with this warming (Sturm et al. 2003), including (a) a reduction in the extent and thickness of sea ice (Parkinson et al. 1999), (b) the retreat of arctic and subarctic glaciers (Arendt et al. 2002), (c) increased annual discharge from large northward-flowing rivers (Peterson et al. 2002), and (d) an Arctic-wide increase in permafrost temperatures (Romanovsky et al. 2002).

With respect to the shrub expansion, it is surprising that most of the documented warming has taken place in winter (January–March; figure 2) and, to a lesser extent, in spring (April–June; Chapman and Walsh 1993, Serreze et al. 2000). Moreover, "spring" in this arctic context means freezing temperatures and a full snow cover through May and often into June. The conventional explanation for shrub expansion is accelerated summer growth, but with arctic warming predominantly affecting winter temperatures, processes outside the normal growing season are certain to be involved. Here we report how arctic soil microbes, buried under an insulating blanket of snow, remain surprisingly active during the frigid arctic winter, producing critical nutrients that the shrubs can utilize the following summer. As the shrubs grow, they trap and hold snow, which better insulates the soil and

the microbes, promoting even more winter activity. Combined, these two mechanisms form a winter feedback system that influences, and perhaps even controls, the transition of the arctic ecosystem from one state to another in response to a changing climate.

A conversion of arctic tundra to shrubland would have many ramifications. It would reduce forage quantity and quality for caribou, which prefer lichens and graminoids over shrubs. This would force the caribou to alter where they graze, which would affect subsistence hunters and the communities that rely on caribou for food. An extensive shrub canopy would also increase the summer sensible heat flux, perhaps by as much as 6 watts (W) per square meter (m^2) (Jason Beringer, School of Geography and Environmental Science, Monash University, Clayton, Australia, personal communication, 14 September 2004), more than twice the global impact of greenhouse gases, which are estimated to be approximately 3 W per m^2 (IPCC 2001). Dark shrubs protruding above the snow would reduce the winter albedo, increasing the solar energy absorbed at the surface. The increased production of woody material would affect the carbon budget. Shrubs allocate carbon to woody stems that have long turnover times compared with annual roots and the leaves of graminoids, so shrub-dominated tundra is likely to assimilate carbon in a different way and store it for a different length of time than shrub-free tundra. With the

Table 1. The five stages of arctic winter and their salient biophysical features (modified from Olsson et al. 2003).

Stage	Sensitivity to change	Salient features
Stage 1: Early snow	High (timing)	Maximum daily temperatures and active-layer temperatures above freezing, development of ephemeral snowpack
Stage 2: Early cold	High (timing and nature)	Daily average and maximum temperatures below freezing, rapid snow buildup, active layer beginning to freeze from the top down
Stage 3: Deep cold	Low	Little new snow accumulation, little or no solar radiation, active-layer temperatures falling, upper active layer completely frozen
Stage 4: Late cold	Low	Active-layer temperatures now in phase with air temperature, air temperature and active-layer temperatures beginning to rise, but active layer still frozen, with limited liquid water
Stage 5: Thaw	High (timing)	Minimum daily temperatures above freezing, snowpack melting, rapidly increasing soil temperatures

production of more woody material and the change in soil moisture levels due to shading, short- and long-term shifts in net carbon exchange and carbon storage would be set in motion (Oechel et al. 2000).

Winter, permafrost, and the active layer

The prolonged cold of arctic winter produces permafrost (perennially frozen ground) and snow that blankets the tundra for two-thirds of the year. These conditions constrain but do not stop biological activity. Significant plant and soil microbial activity continue during three of the five stages of winter that have been identified on the basis of surface and soil conditions (table 1; Olsson et al. 2003). The duration and starting date of these stages vary from year to year, with long-term shifts in stage timing being one of the ways winter can affect the ecosystem state. The asymmetry of winter also constrains above- and belowground biotic activity. The snow buildup is gradual over a period of several months, starting in September, but the melt is abrupt, taking as little as 5 days. As a consequence, the ground cools slowly but warms rapidly. The buildup is offset about 75 days after the summer solstice (June 21), but the melt occurs just a few weeks before the solstice. Plants emerge from the winter snow cover directly into an environment of near-maximum sunlight.

Because of the prolonged cold, permafrost (figure 3) forms a nearly continuous layer under the tundra regions of Alaska, Siberia, and northern Canada. Overlying the permafrost is the active layer, made up of strata of organic and mineral soil that thaw each summer and freeze the following winter. Depending on the location and year, maximum thaw depths range from 0.3 to more than 1.0 m. Because the permafrost is nearly impermeable to water infiltration, the active layer is often saturated, far more so than would be expected in the arid arctic climate. Stand-

ing surface water and lakes are ubiquitous. For example, more than 40% of the Arctic Coastal Plain of Alaska is covered by lakes (Sellman et al. 1975), despite low precipitation.

During summer, the active layer warms and thaws from the surface down. In winter, it cools and freezes from the surface down, as the winter cold wave penetrates through the snow and into the ground. It also freezes (albeit more slowly) from the bottom up, chilled by the underlying permafrost. The freezing process proceeds slowly, so it is not until the middle or even the end of winter that the layer is entirely frozen, and in mild winters it may not freeze completely. Even when a particular stratum in the active layer is described as "frozen," a small amount of unfrozen water remains. Adsorption, water–soil particle interactions, and surface tension effects allow unfrozen water to exist at temperatures as low as –40°C (Anderson and Morgenstern 1973, Hinzman et al. 1991). The water is located in thin films (1 to 7 micrometers) that separate soil grains from the ice in pore spaces (Romanovsky and Osterkamp 2000). Depending on soil type, the films can occupy up to 10% of the soil by volume at temperatures between 0°C and –10°C, with thicker films found at higher temperatures and in soils
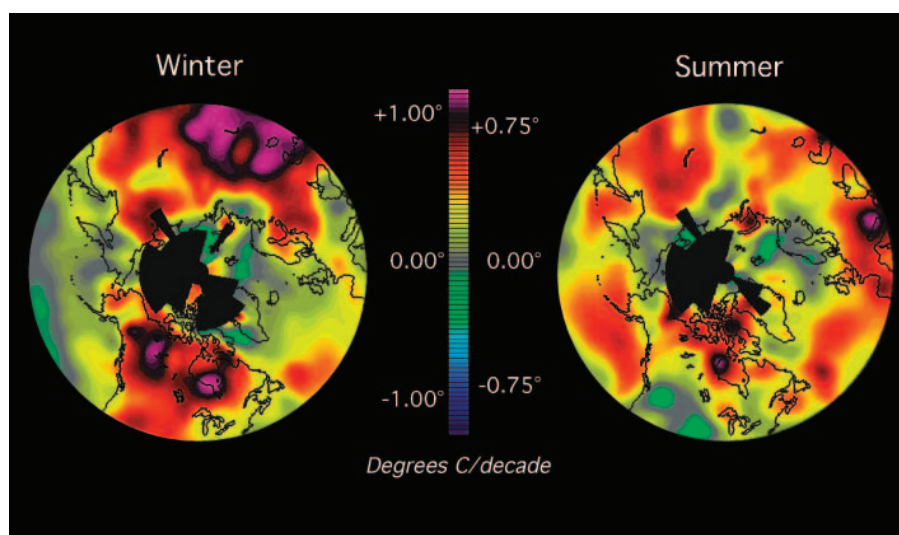

Figure 2. North polar view of the decadal warming in the Arctic in winter (left) and summer (right) for the period 1971 to 2000 (based on Chapman and Walsh 1993, updated at **http://faldo.atmos.uiuc.edu/ARCTIC***).*
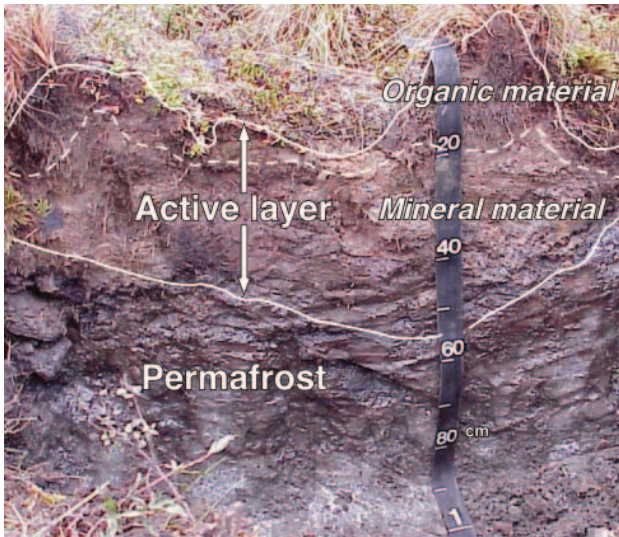
Figure 3. Soil pit profile from arctic Alaska, showing the active layer and the top of the permafrost, which is several hundred meters thick in this location. The hummocky, irregular nature of the interfaces between the layers is the result of cryoturbation, the slow convective overturning of the active layer. Photograph: Gary Michaelson.
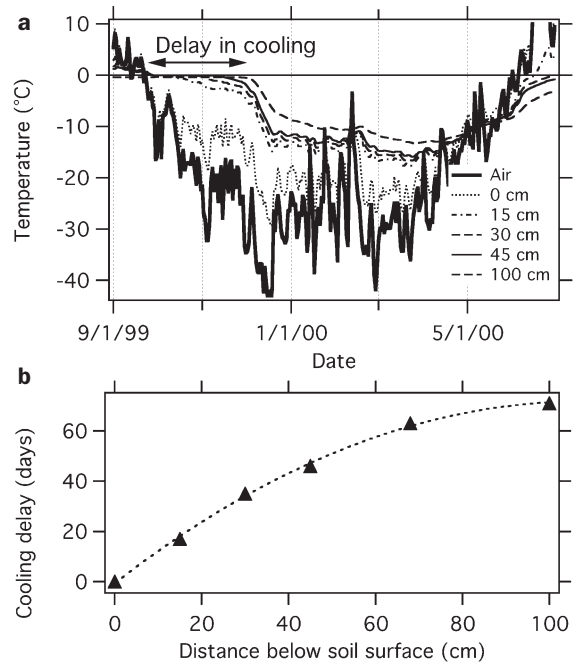

Figure 4. (a) A temperature record for the air and different depths of soil near Prudhoe Bay, Alaska. (b) The delay in cooling at depth in the soil due to latent heat storage in the ground and snow-cover insulation.

with higher clay contents (Farouki 1981) and lower organic fractions (Hinzman et al. 1991). The presence of these unfrozen films produces a situation analogous to the one found in dry desert soils, where the bulk of the soil environment is inhospitable, but where niche environments are viable for microbes.

The buffered thermal environment of the active layer is, in part, a product of the latent heat barrier associated with soil water freezing. Until the abundant soil moisture trapped above the permafrost freezes, the soil temperature cannot drop below 0°C. This introduces delays in the downward propagation of the 0°C isotherm, which range from just a few days at the soil surface to several months near the base of the active layer (figure 4). For a typical active layer 0.4 m thick, with a liquid water content of 40% by volume, 5 kilojoules (kJ) of latent heat need to be removed from each square centimeter (cm^2) of ground surface before the layer can freeze. Only 0.14 kJ of the heat that needs to be removed is due to the specific heat of dry soil. The snow cover also contributes to the buffered thermal environment in the active layer. Snow, a mixture of air and ice, is an excellent insulator. Its R-values (measuring resistance to heat flow) compare favorably with those of many manufactured insulating materials. For instance, the insulation provided by 0.5 m of arctic snow is equivalent to that of a fiberglass-insulated wall 6 inches (about 15 cm) thick, with an R-value of 20. Measurement and model results (Taras et al. 2002) show that, through its insulating properties, snow attenuates weekly winter air temperature fluctuations by about 40% and daily fluctuations by about 80%. At Franklin Bluffs, 50 kilometers (km) south of Prudhoe Bay,

the average air temperature between 1 November 1999 and 1 May 2000 was –26°C, but the average temperature at 0.3 m depth in the soil was –10°C (figure 4a). The contrast in minimum temperatures was even greater: –45°C in the air compared with –16°C in the soil.

Snow cover, shrubs, and active-layer temperatures

On the windswept tundra, drifting snow is common, and deep drifts often surround and extend downwind from shrubs (figure 5). Where the snow is deeper, soil temperatures are higher because there is more insulation. In fact, as illustrated in figure 6, with sufficiently deep snow, subnivean temperatures can be elevated enough to convert a soil in which there is little or no unfrozen water into one in which unfrozen water films are widespread. In extreme cases, deep drifts can even prevent arctic soils from freezing. Organic debris and leaf litter also tend to concentrate in drifts (Fahnestock et al. 2000), potentially adding a nutrient boost to the same locations where there is a favorable thermal environment for soil microbes.

The snow depth enhancement effect is not limited to individual shrubs or patches of shrubs like those in figure 5. When snow depths from a 100-hectare shrubland in Alaska (1.5-m shrubs) were compared with depths from nearby shrub-free tundra, the snow in the shrubs was consistently deeper (17% to 48%). The deeper snow not only contained more water but also was less dense and therefore a better insulator than the snow on the tundra. The depth difference

Figure 5. A shrub patch that has created a snowdrift in and downwind of the patch. The snow on the tundra behind the patch was about one-fifth as deep as the drift. Photograph: Matthew Sturm.

reflects the enhanced capacity of the shrubs to trap snow, and also a reduction in the amount of sublimation the snow would otherwise have undergone had it been free to blow about (Sturm et al. 2001b, Liston et al. 2002). Up to 40% of the winter snow accumulation can be removed by sublimation if it is not trapped by shrubs (Liston and Sturm 2002).

We examined the effect of a widespread, climatically forced increase in shrub abundance on winter soil microbial activity using two coupled models, one that produces snow depth distributions based on topography and drift-trapping by vegetation (Liston and Sturm 1998) and another that simulates soil temperatures based on the snow depth (Taras et al. 2002). Using the models, we computed the expected number of winter days that microbes are active for a control winter (the present) and for a future state in which shrubs have increased in size and density. For simplicity, we assumed that soil microbes are active as long as the active-layer surface temperature is above –6°C, but that they shut down completely at lower temperatures.

Our focus was the 9000-km^2 Kuparuk Basin, which stretches from the Brooks Range (68.5° north [N]) to the Arctic Coast (70.5° N) near Prudhoe Bay, Alaska. From south to north across the basin, there is a 3°C decrease in winter air temperature (Haugen 1982, Olsson et al. 2002) and a pronounced decrease in snow depth (Liston and Sturm 2002, Taras et al. 2002). Winter lasts 15 days longer near the coast than it does near the Brooks Range (Taras et al. 2002), and the mean and peak wind speeds are also generally higher near the coast (Olsson et al. 2002). As a result, the snow cover in the north-

ern part of the basin is thinner, more windblown, less insulative, and longer lasting than the snow cover in the southern part. Under present-day conditions, temperatures at the top of the active layer decrease from about –6°C in the south to about –20°C in the north (Taras et al. 2002). Not surprisingly, a decrease in both shrub abundance (CAVM 2003) and
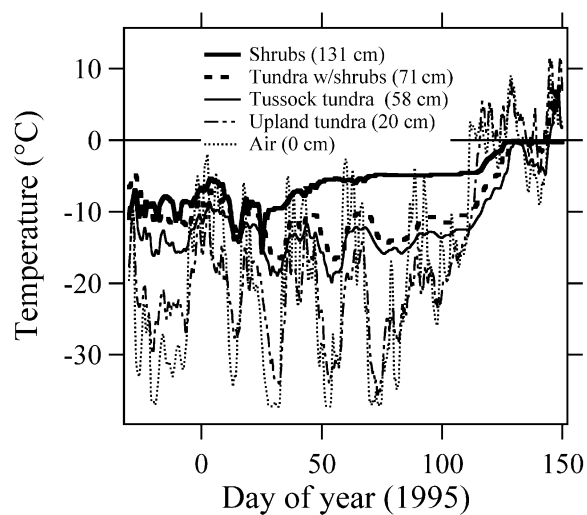

Figure 6. Active-layer surface temperatures as a function of vegetation type, including shrubs. The data are from the Kuparuk Basin in arctic Alaska. The average maximum winter snow depth for each type of vegetation is shown in the key.
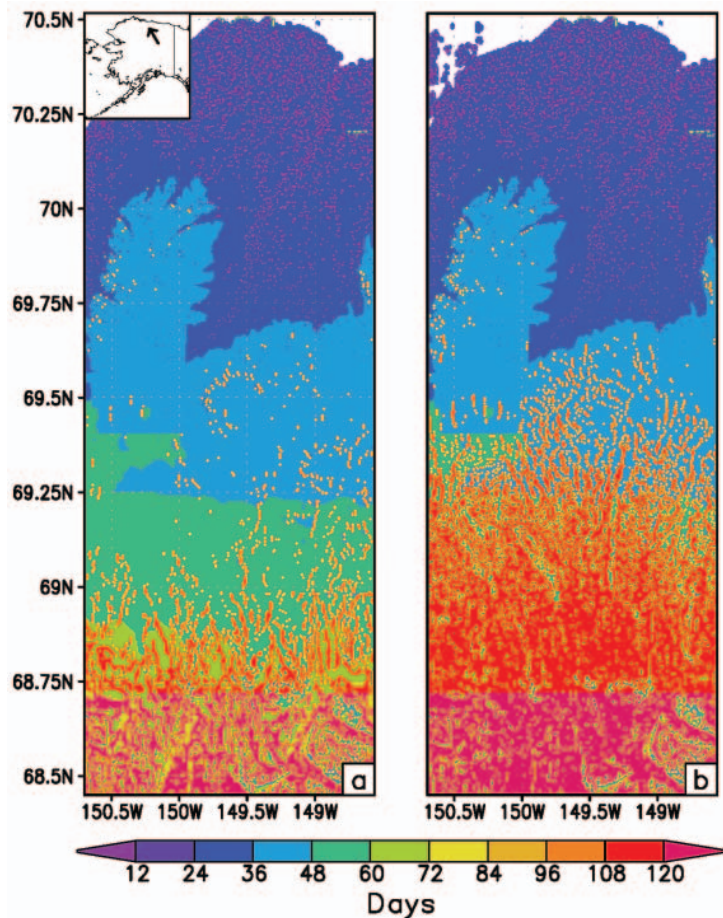
Figure 7. The Kuparuk Basin, showing a proxy index (number of days of microbial activity) for subsurface winter biological activity (a) under present conditions and (b) with projected increases in shrub growth. The index was computed by summing the number of days of the winter that the soil surface temperature is at or above –6 degrees Celsius (Taras et al. 2002). Note the strong latitudinal gradient in this index value. Snow depth increases as a function of vegetation growth, leading to significant increases in the index value, particularly in the middle and southern part of the basin.

winter microbial activity (as inferred from winter soil carbon dioxide [CO_2] efflux rates; Jones MH et al. 1999) are also observed along the same transect.

Model results (figure 7a) indicate under present-day conditions a tenfold decrease in the number of days that subsurface microbial activity takes place between the Brooks Range and the coast. This strong gradient is primarily the result of the snowfall gradient across the basin. Increasing the shrub height and abundance by 31% for moist tundra, 18% for moist–wet tundra, 6% for wet tundra, and 4% for shrublands (the amount of the increase dropping proportionately in those areas where shrubs are already affecting the snow depth or where the soil is too wet for shrubs; Liston et al. 2002) produced up to a 60-day increase in the number of days of winter soil microbial activity (compare figure 7a with figure 7b). The largest changes are in the middle of the basin. In the north, the change is limited because the soils are wet and

shrubs are unlikely to grow. In the south, they are limited because the shrubs are already tall and abundant. The results highlight that winter soil microbial activity is about equally sensitive to climate gradients and to changes in shrub cover. Changes in either factor can have a significant effect on the duration of winter activity and therefore affect the potential buildup of nutrients in winter.

Arctic microbial activity in winter

It is now well established that microbial (bacterial and fungal) respiration continues in arctic soils through the winter (Kelley et al. 1968, Zimov et al. 1993, Oechel et al. 1997, Fahnestock et al. 1999, Welker et al. 2000), along with nitrogen mineralization (Giblin et al. 1991, Grogan and Jonasson 2003, Weintraub and Schimel 2003). These activities are known to continue even in soils cooled to –10°C (Flanagan and Veum 1974, Clein and Schimel 1995, Mikan et al. 2002, Michaelson and Ping 2003), though for much of the winter the active layer is at a higher temperature (figures 4, 6, 7). Belowground plant biomass has been suggested as an alternate source of the observed respiration (Grogan et al. 2001), but this view is not widely held. Measured winter efflux rates range as high as 400 to 500 milligrams (mg) carbon as CO_2 per m^2 per day, though more typically they are 20 to 50 mg carbon as CO_2 per m^2 per day. Even the lower rates are sufficient to determine whether the ecosystem is a net sink (because of summer storage) or a net source to the atmosphere when extended over the long winter (Oechel et al. 1997). The efflux rates are closely linked to soil temperature (and unfrozen water content), and are higher where there are shrubs and deeper snow (Fahnestock et al. 1999).

An unusual shift in microbial substrate use takes place as arctic winter progresses and soil temperatures drop below freezing. The microbes living in the organic matter–rich surface soil begin to use less plant detritus and to rely more heavily on dissolved substrates and recycled microbial biomass and products. Our data indicate that the proportion of carbon respired from the microbial biomass and product pool roughly doubles, from 7% to 14% of the total respired carbon, as arctic soils freeze (figure 8a). Even though this substrate change is not very large in terms of carbon sourcing, it represents an important shift from nitrogen-poor plant detritus to nitrogen-rich microbial substrates of higher quality (Michaelson and Ping 2003) that may have bearing on the increasing abundance of shrubs. The shift helps ensure that higher rates of net nitrogen mineralization continue as soil temperatures drop (figure 8b). Interestingly, the shift occurs above 0°C (figure 8a).

The mechanism underlying the shift is not clear. We would have expected the shift to occur as the soil froze and the soil water system changed from a continuous water web to a set of discontinuous unfrozen water films. Following this transition, the microbes would have access only to (a) internal

resources, (b) dissolved substrate in the unfrozen films, and (c) substrate recycled from dying organisms (cryptic growth; Chapman and Gray 1986). Cut off from the plant and soil polymers they rely on during the summer (Michaelson and Ping 2003, Weintraub and Schimel 2003), the microbes would be expected to shift their use to the materials available in the water films. However, the shift occurs before the soil freezes, indicating that the change is due to some other physical or physiological mechanism, possibly one related to the dynamics of cellulytic or lignolytic enzymes.

More directly related to shrubs, the substantial winter microbial respiration rates that have been observed are known to be aided by cryoturbation, the slow convective overturning of the active layer due to freeze–thaw heaving and settlement (figure 3). This process moves near-surface soil organic matter of relatively high quality into subsurface layers where it can be worked on by microbes during more of the winter. It is quite effective. Arctic Alaskan soils contain as much organic matter in subsurface layers as they do in surface organic horizons (Michaelson et al. 1996). Because these deeper layers stay warmer for a longer period of time (figure 4), and because they have a higher silt content, they contain unfrozen water films that are thicker and more abundant than those higher in the soil column (Romanovsky and Osterkamp 2000). The highest respiration rates in soil at below-freezing temperatures are found in subsurface layers containing the largest proportion of cryoturbated organic matter. Notably, the water-soluble organic substrates in mineral soils under shrubs are of higher quality than those found under tussock tundra (Michaelson and Ping 2003), one more reason why microbial action is enhanced where shrubs are more abundant.

A winter biophysical feedback loop

A positive feedback loop links snow, shrubs, soil, and microbes (figure 9). Active-layer temperatures in and around shrubs are higher than in shrub-poor locations (figure 6), resulting in enhanced winter microbial activity (figure 8) that persists through more of the winter. This results in more net nitrogen mineralization during winter (Schimel et al. 2004) and higher shrub leaf nitrogen content in summer. It also lowers the leaf carbon–nitrogen ratio, which may increase the decomposability of the leaf litter. For tundra, manipulation experiments (Chapin et al. 1995), point frame studies (Arft et al. 1999), and studies of latitudinal gradients in plant community composition (Bliss and Matveyeva 1992) indicate that where there are more nutrients, shrub growth is favored over that of other tundra plants. Larger and more abundant shrubs (figure 1) trap more snow (figure 5) and reduce winter sublimation losses, leading to deeper snow cover and still higher soil temperatures (figure 6).

The feedback loop was suggested (Sturm et al. 2001b) on the basis of colocated snow depth and shrub height measurements, but several links in the loop were speculative when it was first introduced. These links are now better established. They include evidence (a) that the microbes have access to substrate and unfrozen water through most of the
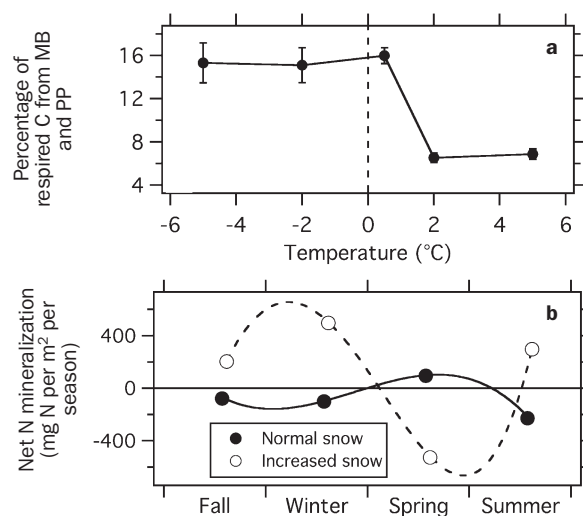

Figure 8. (a) Shift in microbial substrate use with temperature. Above 0 degrees Celsius (°C), the microbes metabolize nitrogen-poor plant detritus, but below 0°C they rely more on nitrogen-rich microbial products. (b) Winter decomposition and nutrient mineralization for an area where the snow depth has been artificially enhanced compared with a control plot where it has not. Abbreviations: C, carbon; MB, microbial biomass; N, nitrogen; PP, product pool.

winter, (b) that as a result, microbial activity continues at below-freezing soil temperatures, (c) that the activity is due in part to a shift in substrate use by the microbes, (d) that even though winter rates of activity are lower than those of summer, the cumulative impact is a substantial contribution to the annual total because of the length the winter, and (e) that increasing the winter snow depth (i.e., accumulation in and around shrubs) produces greater net nitrogen nutrient mineralization (Schimel et al. 2004).

One link in the feedback loop remains untested. Does increased net winter nitrogen mineralization result in enhanced summer growth of shrubs? Summer fertilization of tundra leads to enhanced shrub growth (Chapin et al. 1995), so if winter-produced nutrients remain in place and are available to the plants the following growing season, the loop in figure 9 is closed. Do the nutrients stay put? During the spring thaw, active sheet wash and runoff could potentially strip off or redistribute these nutrients. Because of the rapid nature of the thaw, however, arctic soils are typically still frozen during peak runoff. Moreover, most of the winter nutrient production takes place at depth in the active layer and is likely to be protected from redistribution. Initial indications based on studies using nitrogen-15 (Bilbrough et al. 2000) also suggest that tundra plants can acquire soil nitrogen while the ground is still snow covered. We therefore think that the snow–shrub–soil–microbe feedback loop is contributing to the expansion of shrubs in the Arctic (figure 1; Sturm et al. 2001a) and may help explain why this expansion has coincided with winter warming (figure 2).
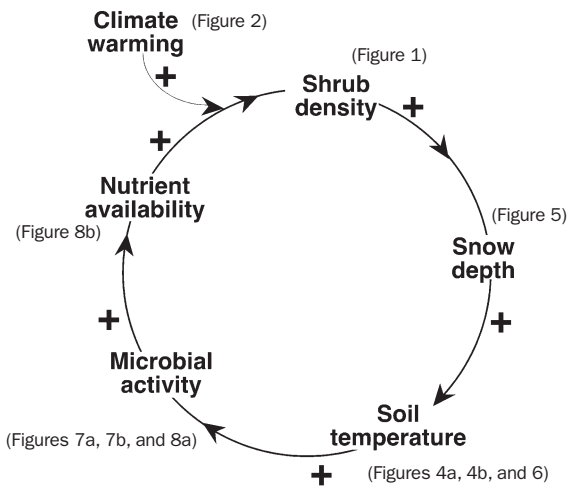
Figure 9. The snow–shrub–soil–microbe feedback loop (based on Sturm et al. 2001b).

Discussion and implications

Recent shrub expansion and invasion has been observed in semiarid grasslands and tallgrass prairies (Schlesinger et al. 1990, Archer et al. 2000, Lett and Knapp 2003, McCarron et al. 2003). While disturbance (grazing) or suppression of disturbance (fire) has played a role in establishing the shrubs in these lower-latitude ecosystems, climate-driven biological feedbacks similar to those described here have ensured that, once established, the shrubs have thrived. For example, Schlesinger and colleagues (1990) found that the introduction of shrubs in semiarid grasslands led to a localization of water and other soil resources under the shrubs, which had a positive feedback effect analogous to our results (figure 9). In a way that is eerily similar to the drifting of snow around shrubs on the tundra, they also found that the wind eroded material from the spaces between shrubs. This further differentiated the resources available to the vegetation. Lett and Knapp (2003) found that canopy shading, not soil source enrichment, maintained shrub dominance after shrubs were introduced to the tallgrass prairie. In both cases, however, positive feedbacks associated with a change in plant functional type (from low graminoids to erect and stiff shrubs) ensured the shrubs' success.

The competitive advantages of arctic shrubs are not limited to their physical architecture. They also have the highest potential for resource uptake of all the arctic plant functional groups, and they produce some of the most rapidly decomposable litter (Shaver et al. 1996). This is why within 10 years of a disturbance of the tundra by tracked vehicles, the disturbed areas are covered by shrubs, and why warmed and fertilized plots experience a relative explosion of shrubs (Chapin et al. 1995). With these attributes, shrubs are poised to take advantage of the current climate warming more readily than the other tundra plants. It may also explain why there have been several widespread expansions of shrubs

during the Holocene (Anderson and Brubaker 1993). What is less certain is how the current expansion might proceed, and whether it will actually convert the tundra into a shrubland. Shaver and colleagues (1992) have pointed out that the initial response of a tundra ecosystem to a change in climate is likely to be quite different from the response over decades or centuries. As the expansion of tundra shrubs continues and the shrubs occupy more of the landscape, canopies will thicken, leading to summer shading and a myriad of other effects that could produce fundamental changes in soil conditions. These could modify the winter feedback processes we have described here.

One aspect of the arctic tundra system that argues for more extensive rather than less extensive change is that the system is particularly susceptible to change because of the roles played by snow and permafrost in determining the soil conditions and microbial activity. Small shifts in ambient conditions (temperature, snow depth, or both) could produce large changes in the amount and distribution of unfrozen water in the soil and in the duration and timing of biological activity (figures 7, 8). This, in large measure, is because the system is balanced at the freezing point of water. This sensitivity is mirrored in Antarctica, where a whole cascade of terrestrial ecosystem changes has been observed in response to 20 years of cooling (Doran et al. 2002).

In table 2, by contrasting present-day tundra with shrubby tundra, we suggest some of the ecosystem changes that might ensue if shrub abundance continues to increase. The table is by no means comprehensive, but it does suggest that there would be important hydrologic, energy balance, and carbon budget ramifications. Changes in the carbon budget are likely to have global implications. Increased release of winter carbon due to greater soil microbial activity would compete with increased fixing of carbon in the form of woody plants to produce a balance that is difficult to predict. Of potentially greater impact, however, would be a secondary effect of a tundra-to-shrubland conversion: alteration of the thermal regime of the permafrost. This alteration could liberate large stores of carbon that are currently frozen and not participating in the carbon cycle (Michaelson et al. 1996). Not everything would change, of course. Wet meadow tundra is unlikely to turn shrubby, and places like Fenno-Scandia, where the tundra is already fairly shrubby, are likely to see only limited change. Still, a shrubby Arctic would be a markedly different place from the present-day Arctic covered by tundra.

The Arctic is locked in the grip of winter for two-thirds of the year, but biological activity continues to take place during that time. The results presented here suggest that these winter biological processes may be playing a crucial role in transforming the tundra landscape into shrubland. These results also challenge the view that plant community composition is controlled solely by competitive interactions during the growing season. If we want to predict how the current changes will play out in the future, and assess the ramifications of these changes, we are going to need year-round studies that link summer and winter biological activity.

Table 2. Key differences in properties between shrubby and nonshrubby tundra.

Properties	Nonshrub tundra	Shrub tundra
Snow depth/duration	Shallower/shorter	Deeper/longer; more snow runoff
Albedo	Higher	Lower
Summer active-layer depth	Deeper	Shallower (because of shading)
Summer active-layer temperature	Warmer	Cooler
Soil temperature	Higher in summer, lower in winter	Lower in summer, higher in winter
Nutrient (nitrogen) cycling	Faster	Slower
Carbon cycling	Faster	Slower
Caribou forage access and quality	Higher	Lower
Winter CO_2 flux	Lower	Higher
Summer CO_2 exchange	Lower	Higher

CO_2, carbon dioxide.

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