

28. D. Lizarralde, J. B. Gaherty, J. A. Collins, G. Hirth, S. D. Kim, *Nature* **432**, 744 (2004).
 29. L. A. Coogan *et al.*, *Chem. Geol.* **178**, 1 (2001).
 30. A. Kvassnes, thesis, Woods Hole Oceanographic Institution and Massachusetts Institute of Technology (2004).
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Role of Land-Surface Changes in Arctic Summer Warming

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A major challenge in predicting Earth's future climate state is to understand feedbacks that alter greenhouse-gas forcing. Here we synthesize field data from arctic Alaska, showing that terrestrial changes in summer albedo contribute substantially to recent high-latitude warming trends. Pronounced terrestrial summer warming in arctic Alaska correlates with a lengthening of the snow-free season that has increased atmospheric heating locally by about 3 watts per square meter per decade (similar in magnitude to the regional heating expected over multiple decades from a doubling of atmospheric CO₂). The continuation of current trends in shrub and tree expansion could further amplify this atmospheric heating by two to seven times.

The Arctic provides a test bed to understand and evaluate the consequences of threshold changes in regional system dynamics. Over the past several decades, the Arctic has warmed strongly in winter (1). However, many Arctic thresholds relate to abrupt physical and ecological changes that occur near the freezing

point of water. Paleoclimate evidence, which is mostly indicative of summer conditions, shows that the Arctic in summer is now warmer than at any time in at least the past 400 years (2). This warming should have a large impact on the rates of water-dependent processes. We assembled a wide range of

independent data sets (surface temperature records, satellite-based estimates of cloud cover and energy exchange, ground-based measurements of albedo and energy exchange, and field observations of changes in snow cover and vegetation) to estimate recent and potential future changes in atmospheric heating in arctic Alaska. We argue that recent changes in the length of the snow-free season have triggered a set of interlinked feedbacks that will amplify future rates of summer warming.

Summer warming in arctic Alaska and western Canada has accelerated from about 0.15° to 0.17°C decade⁻¹ (1961–1990 and 1966–1995) (1, 3) to about 0.3° to 0.4°C decade⁻¹ (1961–2004; Fig. 1). There has also been a shift from summer cooling to warming in Greenland and Scandinavia, more pronounced warming in Siberia, and continued summer warming in the European Russian Arctic.

The pronounced summer warming in Alaska cannot be readily understood from changes in atmospheric circulation, sea ice, or cloud cover. Changes in the North Atlantic Oscillation and Arctic Oscillation are linked to winter warming over Eurasia. Variations in the Pacific North American Teleconnection,

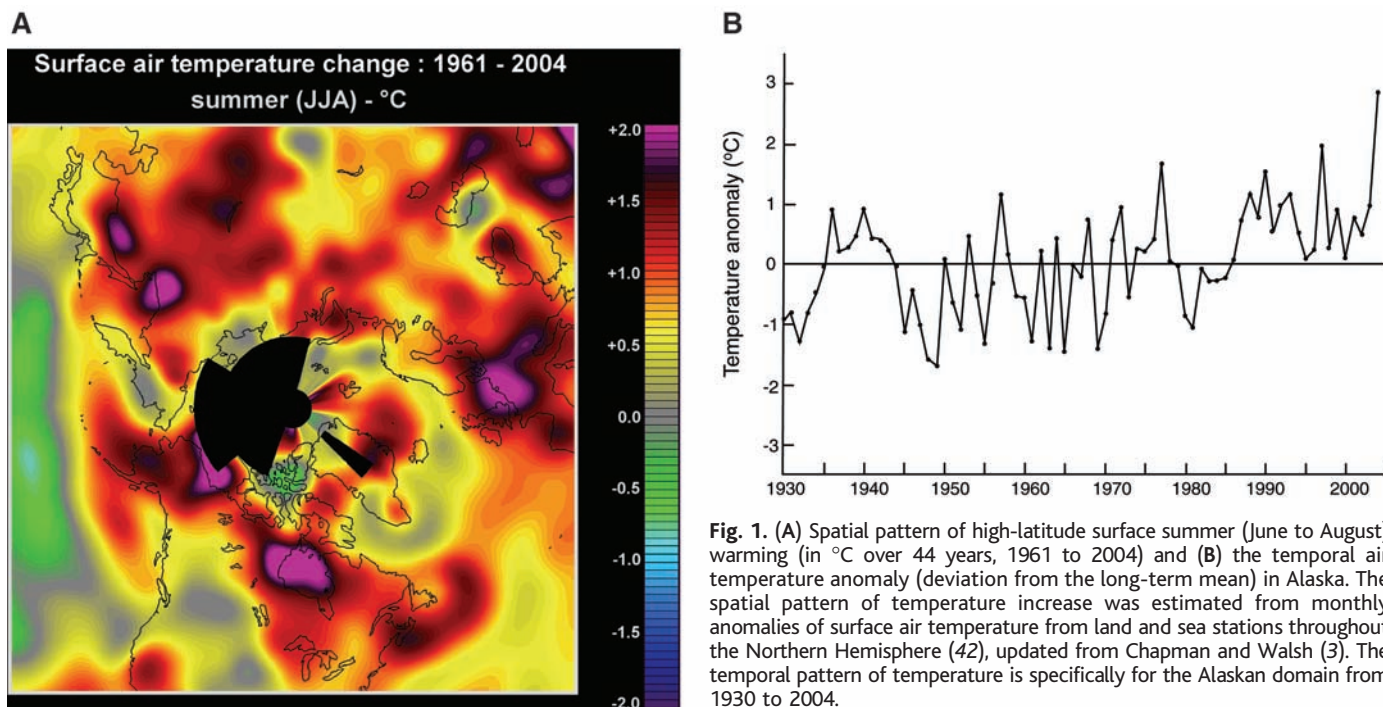


Fig. 1. (A) Spatial pattern of high-latitude surface summer (June to August) warming (in °C over 44 years, 1961 to 2004) and (B) the temporal air temperature anomaly (deviation from the long-term mean) in Alaska. The spatial pattern of temperature increase was estimated from monthly anomalies of surface air temperature from land and sea stations throughout the Northern Hemisphere (42), updated from Chapman and Walsh (3). The temporal pattern of temperature is specifically for the Alaskan domain from 1930 to 2004.

the Pacific Decadal Oscillation, and El Niño–Southern Oscillation have strong impacts on Alaskan winter temperatures, but their influences on summer temperatures are comparatively weak (4–6). There has been a pronounced decline in the extent of summer sea ice, especially north of Alaska and Siberia (1). This implies that solar energy is increasingly augmenting the sensible heat content of the ocean, some of which can then heat the atmosphere over the ocean and adjacent coast (Fig. 2). However, this mechanism fails to explain strong summer warming over interior Alaska (Fig. 1) (7). Further, regional warming trends associated with declining summer sea ice should be more clearly expressed in autumn and winter (8), when much of the additional ocean heat gained in summer will be released back to the atmosphere. The satellite record shows increased summer cloud cover in Alaska (Figs. 2 and 3), similar to patterns described for the circumpolar Arctic (9). The surface cloud radiative forcing in summer over the low-albedo Alaskan land surface tends to be negative, meaning that the decrease in downwelling shortwave radiation to the surface exceeds the increase in the downwelling longwave flux. The consequent reduction in surface net radiation (Fig. 3) would tend to dampen warming resulting from other causes (9).

The summer warming in Alaska is best explained by a lengthening of the snow-free season, causing sensible heating of the lower atmosphere to begin earlier (Fig. 2). Snowmelt has advanced 1.3 days decade⁻¹ at Barrow (coastal), Alaska (10); 2.3 days decade⁻¹ averaged over several (mainly

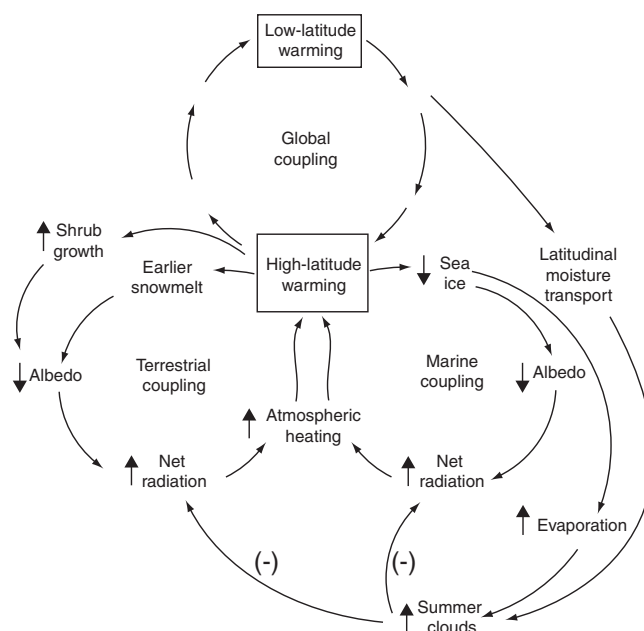


Fig. 2. Diagram of feedback loops that couple climatic processes in arctic Alaska. Arrows linking positive processes indicate a positive effect of one process on another unless otherwise indicated (by minus signs). Quantification of the terrestrial coupling feedback loop is provided in Table 2.

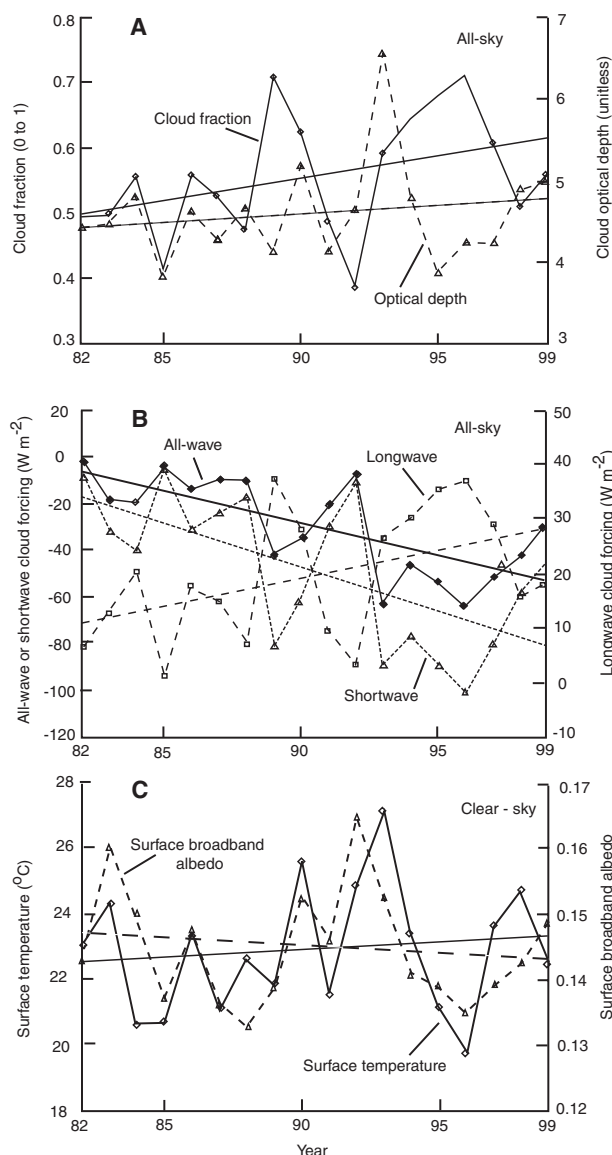


Fig. 3. Satellite record of temporal changes in (A) mean summer (June to August) cloud fraction [slope (S) = 0.0068, P = 0.11] and optical depth (S = 0.0201, P = 0.5); (B) mean summer cloud radiative forcing [net (S = -2.71, P = 0.001), longwave (S = 1.02, P = 0.05), and shortwave (S = -3.73, P = 0.004)]; and (C) clear-sky summer broadband albedo (S = -0.0002; P = 0.6) and surface temperature (S = 0.050, P = 0.6) in arctic tundra on the North Slope of Alaska. Data for the Alaskan domain are drawn from the panarctic data set of Wang and Key (9, 42).

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coastal) stations (10); 3.6 days decade⁻¹ in the northern foothills of the Brooks Range (11); 9.1 days decade⁻¹ for the entire Alaskan North Slope [calculated from the satellite data set of Dye *et al.* (12)]; and 3 to 5 days decade⁻¹ for the region north of 45°N (12). Similarly, spring soil thaw has advanced 2.0 to 3.3 days decade⁻¹ over North American and Eurasian tundra (microwave satellite) (13) and leaf-out date has advanced by 2.7 days decade⁻¹ in Alaska (model estimate) (14) and by 4.3 days decade⁻¹ in North America above 40°N (satellite record) (15). We calculate that the observed snowmelt advance of about 2.5 (1.5 to 3.5) days decade⁻¹ in the Alaskan Arctic increases the energy absorbed and transferred to the atmosphere per decade by about 26 MJ m⁻² year⁻¹ [3.3 W m⁻² (Table 1)]. This regional decadal change is comparable (per unit of area) to the global atmospheric heating associated with a doubling of atmospheric CO₂, which is projected to occur over multiple decades.

Since 1950, the cover of tall shrubs within Alaska's North Slope tundra has increased 1.2% decade⁻¹ (from 14 to 20% cover) (16, 17). The widespread nature of shrub expansion is supported by indigenous observations (18) and satellite-derived vegetation indices (15, 19, 20). A meta-analysis of field warming experiments at 11 arctic sites showed that increasing summer temperature by 1° to 2°C [which is the magnitude observed in Alaska in the past 20 to 30 years (Fig. 1B)] generally triggers in-

creased shrub growth within a decade (21), which is consistent with (i) observations of recent shrub expansion (16), (ii) the paleorecord of Holocene shrub expansion during warm intervals (22), and (iii) greater shrub abundance at the warm end of latitudinal gradients (23). Although shrubs increase the amount of absorbed radiation and atmospheric heating, we estimate that they account for only about 2% of the recent warming caused by land-surface change, because of the small area over which documented shrub expansion has occurred to date (Tables 1 and 2).

At the arctic treeline, white spruce (*Picea glauca*) has both expanded into tundra and increased in density within forest tundra regions of western Alaska (24). Although the treeline is stable in some areas of Alaska, the majority of studied sites show a treeline advance (25). Climate warming promotes forest expansion by creating disturbed sites for seedling establishment in ice-rich permafrost (26) and promoting the growth of seedlings (27) and (in general) mature trees (28). We calculate that 11,600 km² (2.3% of the treeless area) has been converted from tundra to forest in the past 50 years, based on extrapolation of observed rates of forest expansion [2.55 km in lowlands and 0.1 km at the treeline in the past 50 years] (25) to the entire forest-tundra transition zone in Alaska. Although conversion to forest increases absorbed radiation and atmospheric heating 4.7-fold just before snowmelt and by 25% in mid-

summer, we estimate that this vegetation change accounts for only about 3% of the total warming caused by land-surface change, because of the small areal extent (0.5% decade⁻¹) of the vegetation change (Tables 1 and 2). On cloud-free summer days, satellites detect only a weak trend toward reduced broadband albedo and increased surface (skin) temperature over arctic Alaska (Fig. 3), which is consistent with our conclusion that recent vegetation change has caused relatively little regional summer heating.

Although the increased length of the snow-free season is the main cause of summer warming observed to date, the increasing abundance of shrubs and trees is likely to contribute disproportionately to future summer warming. The change in atmospheric heating from before to after snowmelt is much larger in low-statured tundra vegetation than in shrub and forest vegetation that masks the snow surface (Table 1). Our calculations show that if vegetation changes become more widespread, the effects of vegetation would increase substantially, while those of season length would proportionately diminish (Table 1) (29). How likely are these vegetation changes to occur? The conversion of arctic tundra to spruce forest never occurred during previous Holocene warm intervals (22) and is unlikely to be extensive in the current century because of time lags associated with migration (30). Shrub expansion could occur quickly, however, because small shrubs are already present in most tundra areas (23).

Shrubs trigger several feedback loops that influence their expansion rate. Shrub growth is stimulated by nitrogen (N) supply (31, 32), so shrub expansion would be accelerated if N cycling rates increased through either increased N concentrations in litter (33) or winter soil warming due to snow accumulation beneath shrubs (34, 35). Given observed winter temperature dependence (Q_{10}) (36), the 3° to 10°C warmer winter temperatures observed beneath shrubs should enhance N mineralization by about 170 mg of N m⁻² year⁻¹, a 25% increase in annual N mineralization, which could support an increase in plant production of about 15 g m⁻² year⁻¹ (37). Alternatively, the shrub expansion rate would decline if the increased C:N ratio of the more woody litter (38) or soil cooling due to summer shading (39) reduced N cycling rates. N addition triggers shrub dominance (31) and soil carbon (C) loss (32), and shrub dominance correlates with higher winter respiration (40) and smaller soil C pools (41), suggesting that the positive (stimulatory) biogeochemical feedback loop predominates (32).

We have shown that summer warming in the Alaskan sector is occurring primarily on

Table 1. Observed changes per decade in summer atmospheric (atmos.) heating (by latent plus sensible heat flux) in Alaskan tundra and potential future changes if arctic tundra were completely converted to shrub tundra or spruce forest. The observed changes are subdivided into changes due to the longer snow-free season and those due to the increased areal extent of shrublands and forest. Also shown is the change in heating associated with a doubling of atmospheric CO₂.

Cause of change	Atmos. heating		
	(MJ m ⁻² year ⁻¹)*	(% of total)	(W m ⁻²)†
Observed change in atmos. heating over tundra (per decade)			
Due to snowmelt advance‡	25.53	95	3.28
Due to vegetation change			
Shrub expansion	0.59	2	0.08
Forest expansion	0.88	3	0.11
Total change	27.00	100	3.47
Maximum potential change in atmos. heating over tundra			
Due to complete conversion to shrubland			
Effect of snowmelt advance‡	19.48	28	2.51
Effect of shrub expansion	49.50	72	6.37
Total change	68.98	100	8.88
Due to complete conversion to forest			
Effect of snowmelt advance‡	10.60	5	1.36
Effect of forest expansion	190.80	95	24.54
Total change	201.40	100	25.90
Atmos. heating change caused by doubling of atmos. CO ₂ §			4.4

*Data are from Table 2. †Heating averaged over a 90-day snow-free season. ‡Due to an observed advance in the date of snowmelt of 2.5 days decade⁻¹. §(43).

Table 2. Changes from pre-snowmelt to midsummer in the energy budget of tundra, shrubland, and forest in arctic Alaska. Also shown is the observed change in energy budget (per decade) and the potential future change if arctic tundra were completely converted from tundra to shrubland or forest (42). R_s , incoming shortwave radiation; R_n , net radiation.

Energy budget parameter	Vegetation type		
	Tundra	Shrub	Forest
Pre-snowmelt (June)			
Albedo	0.8*	0.6*	0.20†
R_n (% of R_s)	27*	39*	59†
Atmos. heating (% of R_n)‡	38*	61*	82†
($MJ\ m^{-2}\ day^{-1}$)§	2.46	5.71	11.61
Post-snowmelt (June)			
Albedo	0.17	0.15	0.11
Net radiation (% of R_s)	64.4	63.9	71.8
Atmos. heating (% of R_n)	82	88	92
($MJ\ m^{-2}\ day^{-1}$)§	12.67	13.50	15.85
Summer (July)			
Albedo¶	0.17 ± 0.01 (5)	0.15 ± 0.002 (7)	0.11 ± 0.004 (10)
Net radiation (% of R_s)¶	64.4 ± 0.6 (8)	63.9 ± 0.9 (6)	71.8 ± 4.2 (8)
Atmos. heating (% of R_n)¶	82 ± 3 (11)	88 ± 2 (7)	92 ± 2 (18)
($MJ\ m^{-2}\ day^{-1}$)#	8.45	9.00	10.57
Observed change in atmos. heating over tundra (per decade)			
Due to snowmelt advance			
Atmos. heating ($MJ\ m^{-2}\ year^{-1}$)**	25.53	19.48	10.60
Due to vegetation change			
Change in area (% of original area)††	-1.66	1.20	0.46
Atmos. heating ($MJ\ m^{-2}\ year^{-1}$)‡‡	0	0.59	0.88
Potential future change in atmos. heating over tundra due to complete vegetation conversion			
Due to snowmelt advance			
Atmos. heating ($MJ\ m^{-2}\ year^{-1}$)**	-	19.48	10.60
Due to vegetation change			
Change in area (% of original area)§§	-	100	100
Atmos. heating ($MJ\ m^{-2}\ year^{-1}$)‡‡	-	49.50	190.80

* (44, 45). † (46, 47). ‡ Measured sensible (H) plus latent heat (LE) fluxes (% of R_n). § Calculated as $R_s \times (R_n/R_s) \times (H + LE)/R_n$, assuming average R_s at snowmelt at Barrow, Alaska ($24\ MJ\ m^{-2}\ day^{-1}$) (44). || Assume values after snowmelt are the same as those measured in midsummer. ¶ (46–48) (number of sites is shown in parentheses). # Calculated as $R_s \times (R_n/R_s) \times (H + LE)/R_n$, assuming summer average R_s at Toolik Lake, Alaska ($16\ MJ\ m^{-2}\ day^{-1}$) (49). ** Change in daily atmospheric heating ($MJ\ m^{-2}\ day^{-1}$) (post-snowmelt – pre-snowmelt) \times 2.5 days of snowmelt advance per decade. †† Change per decade in observed areal extent of each vegetation type. ‡‡ Change in daily heating due to vegetation change (new vegetation – original vegetation) \times 90-day season \times change in areal extent. §§ Assume 100% conversion to the new vegetation type.

land, where a longer snow-free season has contributed more strongly to atmospheric heating than have vegetation changes. This heating more than offsets the cooling caused by increased cloudiness. However, the high temperature sensitivity of several feedback loops, particularly those associated with shrub expansion, suggests that terrestrial amplification of high-latitude warming will likely become more pronounced in the future. Improved understanding of the controls over rates of shrub expansion would reduce the likelihood of unexpected surprises regarding the magnitude of high-latitude amplification of summer warming.

References and Notes

1. M. C. Serreze et al., *Clim. Change* **46**, 159 (2000).
 2. J. Overpeck et al., *Science* **278**, 1251 (1997).

3. W. L. Chapman, J. E. Walsh, *Bull. Am. Meteorol. Soc.* **74**, 33 (1993).
 4. S. Corti, F. Molteni, T. N. Palmer, *Nature* **398**, 799 (1999).
 5. K. E. Trenberth, J. W. Hurrell, *Clim. Dyn.* **9**, 303 (1994).
 6. B. Hartmann, G. Wendler, *J. Clim.*, in press.
 7. J. C. Comiso, *J. Clim.* **16**, 3498 (2003).
 8. Arctic Climate Impact Assessment, *Impacts of a Warming Arctic* (Cambridge Univ. Press, Cambridge, 2004).
 9. X. J. Wang, J. R. Key, *Science* **299**, 1725 (2003).
 10. R. S. Stone, E. G. Dutton, J. M. Harris, D. Longnecker, *J. Geophys. Res.* **107**, 4089 (2002).
 11. F. S. Chapin III et al., unpublished data.
 12. D. G. Dye, *Hydrol. Process.* **16**, 3065 (2002).
 13. N. V. Smith, S. S. Saatchi, J. T. Randerson, *J. Geophys. Res.* **109**, D12101 (2004).
 14. A. R. Keyser, J. S. Kimball, R. R. Nemani, S. W. Running, *Global Change Biol.* **6** (suppl. 1), 185 (2000).
 15. L. Zhou et al., *J. Geophys. Res.* **106**, 20069 (2001).
 16. M. Sturm, C. Racine, K. Tape, *Nature* **411**, 546 (2001).
 17. K. Tape, thesis, University of Alaska Fairbanks, Fairbanks, AK (2004).
 18. N. Thorpe, N. Eyegetok, N. Hakongak, Kitikmeot Elders,

in *The Earth is Faster Now: Indigenous Observations of Arctic Environmental Change*, I. Krupnik, D. Jolly, Eds. (Research Consortium of the United States, Fairbanks, AK, 2002), pp. 201–239.
 19. C. S. Silapaswan, D. L. Verbyla, A. D. McGuire, *Can. J. Remote Sensing* **27**, 542 (2001).
 20. G. J. Jia, H. E. Epstein, D. A. Walker, *Geophys. Res. Lett.* **30**, : 2067 (2003).
 21. A. M. Arft et al., *Ecol. Monogr.* **69**, 491 (1999).
 22. L. B. Brubaker, P. M. Anderson, F. S. Hu, in *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*, F. S. Chapin III, Ch. Körner, Eds. (Springer-Verlag, Berlin, 1995), pp. 111–125.
 23. H. E. Epstein et al., *J. Biogeogr.* **31**, 1917 (2004).
 24. A. H. Lloyd, T. S. Rupp, C. L. Fastie, A. M. Starfield, *J. Geophys. Res.* **107**, 8110 (2003).
 25. A. H. Lloyd, *Ecology*, in press.
 26. A. H. Lloyd, K. Yoshikawa, C. L. Fastie, L. Hinzman, M. Fraver, *Permafrost Periglacial Processes* **14**, 93 (2003).
 27. S. E. Hobbie, F. S. Chapin III, *J. Ecol.* **86**, 449 (1998).
 28. J. M. Szeicz, G. M. MacDonald, *J. Ecol.* **83**, 873 (1995).
 29. J. A. Foley, J. E. Kutzbach, M. T. Coe, S. Levis, *Nature* **371**, 52 (1994).
 30. T. S. Rupp, F. S. Chapin III, A. M. Starfield, *Clim. Change* **48**, 399 (2001).
 31. M. S. Bret-Harte, G. R. Shaver, F. S. Chapin III, *J. Ecol.* **90**, 251 (2002).
 32. M. C. Mack, E. A. G. Schuur, M. S. Bret-Harte, G. R. Shaver, F. S. Chapin III, *Nature* **431**, 440 (2004).
 33. F. S. Chapin III, G. R. Shaver, *Oecologia* **77**, 506 (1988).
 34. M. Sturm et al., *J. Clim.* **14**, 336 (2001).
 35. M. Sturm et al., *Bioscience* **55**, 17 (2005).
 36. C. J. Mikan, J. P. Schimel, A. P. Doyle, *Soil Biol. Biochem.* **34**, 1785 (2002).
 37. G. R. Shaver, F. S. Chapin III, *Ecol. Monogr.* **61**, 1 (1991).
 38. S. E. Hobbie, *Ecol. Monogr.* **66**, 503 (1996).
 39. J. P. McFadden, F. S. Chapin III, D. Y. Hollinger, *J. Geophys. Res.* **103**, 28947 (1998).
 40. J. T. Fahnestock, M. H. Jones, P. D. Brooks, D. A. Walker, J. M. Welker, *J. Geophys. Res.* **103**, 29023 (1998).
 41. G. L. Michaelson, C.-L. Ping, J. M. Kimble, *Arct. Alp. Res.* **28**, 414 (1996).
 42. Materials and methods are available as supporting material on Science Online.
 43. J. T. Houghton et al., Eds., *Climate Change 2001: The Scientific Basis* (Cambridge Univ. Press, Cambridge, 2001).
 44. S. L. Dingman et al., in *An Arctic Ecosystem: The Coastal Tundra at Barrow Alaska*, J. Brown, P. C. Miller, L. L. Tieszen, F. L. Bunnell, Eds. (Dowden, Hutchinson and Ross, Stroudsburg, PA, 1980), pp. 30–65.
 45. M. Sturm, T. Douglas, C. Racine, G. E. Liston, *Biogeosciences* **110**, 10.1029/2005JG000013 (2005).
 46. H. P. Liu, J. T. Randerson, J. Lindfors, F. S. Chapin III, *J. Geophys. Res. Atmos.* **110**, D13101 (2005).
 47. J. Beringer, F. S. Chapin III, C. D. C. Thompson, A. D. McGuire, *Agric. For. Meteorol.* **168**, 10.1016/j.agrformet.2005.05.006 (2005).
 48. W. Eugster et al., *Global Change Biol.* **6** (suppl. 1), 84 (2000).
 49. F. S. Chapin III, W. Eugster, J. P. McFadden, A. H. Lynch, D. A. Walker, *J. Clim.* **13**, 2002 (2000).
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 Methods
 References

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