

Structural complexity and land-surface energy exchange along a gradient from arctic tundra to boreal forest

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Abstract.

Question: Current climate changes in the Alaskan Arctic, which are characterized by increases in temperature and length of growing season, could alter vegetation structure, especially through increases in shrub cover or the movement of treeline. These changes in vegetation structure have consequences for the climate system. What is the relationship between structural complexity and partitioning of surface energy along a gradient from tundra through shrub tundra to closed canopy forest?

Location: Arctic tundra-boreal forest transition in the Alaskan Arctic.

Methods: Along this gradient of increasing canopy complexity, we measured key vegetation characteristics, including community composition, biomass, cover, height, leaf area index and stem area index. We relate these vegetation characteristics to albedo and the partitioning of net radiation into ground, latent, and sensible heating fluxes.

Results: Canopy complexity increased along the sequence from tundra to forest due to the addition of new plant functional types. This led to non-linear changes in biomass, cover, and height in the understory. The increased canopy complexity resulted in reduced ground heat fluxes, relatively conserved latent heat fluxes and increased sensible heat fluxes. The localized warming associated with increased sensible heating over more complex canopies may amplify regional warming, causing further vegetation change in the Alaskan Arctic.

Keywords: Leaf area index; Plant functional type; Stem area index; Tree line; Vegetation-climate interaction.

Abbreviations: LAI = Leaf area index; SAI = Stem area index; PFT = Plant functional type; COV = Coefficient of variation.

Nomenclature: Hultén (1968).

Introduction

The climate of the Alaskan Arctic is currently warming more rapidly than at any time in the last 400 years (Overpeck et al. 1997; Serreze et al. 2000). This warming appears to have triggered vegetation changes that include general increases in plant growth observed from satellites (Myneni et al. 1997; Zhou et al. 2001) and expansion of trees and shrubs (Silapaswan et al. 2001; Sturm et al. 2001). Indigenous observations suggest that this shrub expansion is widespread in the North American Arctic (Thorpe et al. 2002). These observations are consistent with warming experiments in which some species or groups of species (plant functional types), especially key deciduous shrub species, have been particularly responsive to recent warming in Alaska (Chapin et al. 1995; Hobbie & Chapin 1998; Bret-Harte et al. 2001) and other arctic sites (Graglia et al. 1997; Shevtsova et al. 1997; Hartley et al. 1999). If species respond differentially to warming, the relative abundances of plant growth forms will likely change through changes in the biomass of existing plants or immigration of new species. In either case, these vegetation changes will alter the structure of an ecosystem and may have consequences for climate by modifying surface characteristics such as albedo, roughness length, and canopy resistance. These changes could feed back to the climate system through alterations in surface energy balance and carbon storage (McGuire et al. 2002; Kittel et al. 2000).

Community differences in biomass and vegetation structure strongly influence surface energy exchange by determining the quantity of energy absorbed and the pathways by which energy is transferred to the atmosphere and soil (Bonan 2002). The energy absorbed depends on the quantity of absorbing surfaces (approximated by leaf area), the albedo (reflectance) of individual leaves, and the complexity of the canopy, which

influences the efficiency with which the canopy traps incoming solar radiation (Oke 1987). Canopy complexity also influences the efficiency and pathway by which absorbed energy is transferred to the atmosphere. The height and density of roughness elements and their structure govern mechanical turbulence and efficiency of convective exchange between leaf and soil surfaces and the atmosphere. The canopy properties also influence, through shading, the partitioning of energy to the ground and the atmosphere.

Despite several key roles of canopy complexity in controlling important aspects of land-atmosphere energy exchange, canopy complexity has rarely been quantified and has never been related to differences in energy exchange among arctic ecosystems. In this paper, we consider canopy complexity to be the combination of vegetation properties such as biomass, cover, height, leaf area index (LAI) and stem area index (SAI). We examined the horizontal component of complexity by looking at the variability in vegetation distribution and the vertical component of canopy complexity by measuring the vertical distribution of leaf and stem biomass. In this paper we describe the compositional and structural differences in the major ecosystem types that characterize the transition from arctic tundra to boreal forest in western Alaska. We then describe several measures of complexity and analyze their relationship to land-atmosphere exchange of water and energy.

Study sites

We studied the transition from arctic tundra to boreal forest near Council (64°53.47' N 163°38.61' W) on the Seward Peninsula, in northwestern Alaska. The climate of the region is warmer and wetter than Alaska's north slope (Fleming et al. 2000). Monthly mean air temperatures in Nome (the climate station closest to the study site) range from -15 °C in January to 11 °C in July (mean 1950-1999; Western Regional Climate Center). Average annual precipitation is 406 mm, including 1549 mm of snowfall. Shrubs (Silapaswan et al. 2001) and trees (Lloyd & Fastie 2002) are currently expanding into tundra on the Seward Peninsula in apparent response to regional warming in the area during the last 40 yr (Barber et al. 1998; Keyser et al. 2000). The sequence of five sites near Council were selected to represent a structural transition from tundra through low shrub, tall shrub and woodland tundras to closed-canopy *Picea glauca* forest, analogous to vegetation transitions that might occur through time in response to warming. The sites were located within 5 km of each other (Fig. 1) and therefore were influenced by the same local climate. Site differences in vegetation reflected variation in topography, soil moisture, soil temperature, and disturbances associated with the 1898 discovery of gold in the region. Human disturbance of these sites appears to have been negligible during the last 80 yr.

The tundra site was located on the floodplain of the Niukluk River (Fig. 1) with permafrost near the surface. Active thermokarst development in the site is leading to sparse moist depressions with sedges (*Eriophorum angustifolium*). The site featured large patches of lichens (*Cladonia mitis* and *C. rangiferina*) and *Sphagnum* hummocks. Sedges and low evergreen shrubs comprised most of the vascular biomass (Table 1). The low shrub site was located on a moderate (9°) SSW-facing slope (Fig. 1). Lichens and low evergreen shrubs dominated microsites with a thin organic layer, whereas taller deciduous shrubs and sedges dominated stripes with deeper organic and mineral soils (Table 1). The tall shrub site was located on a well-drained (6°) S-facing slope (Fig. 1). Tall (> 2 m) *Betula glandulosa* and *Salix* spp. shrubs dominated the canopy with smaller deciduous shrubs, forbs and mosses in the understorey (Table 1). The disturbance history of this site is unknown, but it is close to an area mined for gold around 1900, and ditches and pipes used in mining were found near the site. The woodland site was located in a moderately drained (5°) ESE-facing broad creek valley and featured tall (> 2 m) *Betula glandulosa* and *Salix* spp. shrubs with a low density of *Picea glauca* (Table 1). Permafrost was found underlying the site. The site was located close to the town of Council, but historic photographs from the height of the gold-mining era

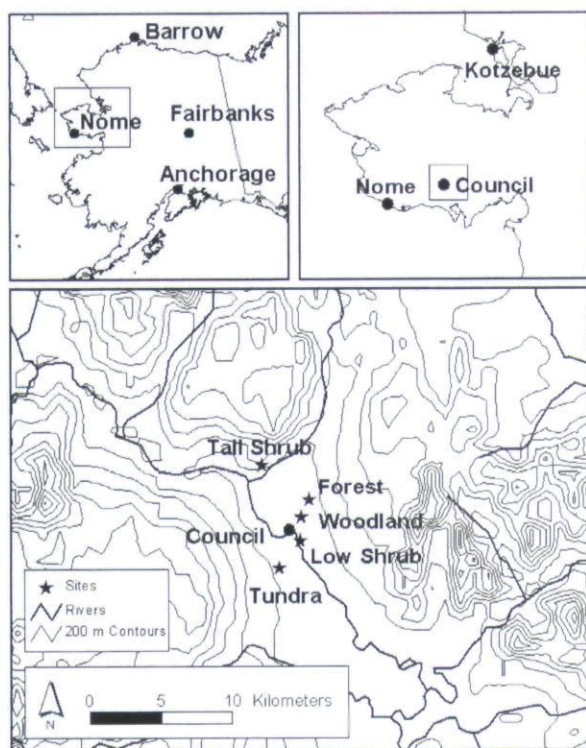


Fig. 1. Location of Council and Council sites.

Table 1. Cover of uppermost leaves in the understorey class and cover of non vascular plants in ground classes organized by canopy class and plant functional type (PFT). Data are means \pm standard error ($n = 10-12$). Letters signify a significant difference between sites at the $\alpha = 0.05$ level based on a significant MANOVA followed by a Ryan-Einot-Gabriel-Welsch multiple range test. nd = PFT absent from site. The cover of canopy shrubs and trees (tall shrub, woodland, and forest sites) are not included.

Canopy class/PFT	Cover (hits per quadrat)				
	Tundra	Low shrub	Tall shrub	Woodland	Forest
Understorey					
Deciduous shrubs	14.3 \pm 3.5	24.8 \pm 5.8	26.5 \pm 5.1	10.0 \pm 4.0	16.5 \pm 5.2
Evergreen shrubs	28.3 \pm 4.7 a,b	33.9 \pm 5.5 a	12.7 \pm 5.7 b,c	3.1 \pm 1.8 c	19.0 \pm 4.6 a,b,c
Forb	1.2 \pm 0.5 c	2.6 \pm 0.8 c	15.7 \pm 4.2 b,c	33.7 \pm 7.2 a	29.5 \pm 6.0 a,b
Grass	nd	2.0 \pm 1.6	15.1 \pm 2.9	33.1 \pm 8.5 a	13.9 \pm 3.0
Sedge	23.7 \pm 4.0	11.5 \pm 3.2	23.0 \pm 4.0	13.4 \pm 4.5	27.7 \pm 3.1
Total	67.5 \pm 6.5	81.1 \pm 12.1	90.8 \pm 11.5	93.27 \pm 12.3	105.9 \pm 10.6
Ground cover					
Lichen	38.5 \pm 10.2 a	41.6 \pm 10.6 a	6.6 \pm 3.3 b	0.2 \pm 0.1 b	11.6 \pm 4.2 b
Non-Sphagnum moss	26.9 \pm 7.4 b,c	17.2 \pm 5.2 c	43.2 \pm 5.1 b	19.0 \pm 5.0 c	76.0 \pm 5.6 a
Sphagnum	24.0 \pm 4.6 a	1.3 \pm 0.7	nd	nd	nd
Total	87.3 \pm 5.01 a	59.3 \pm 9.8 b	49.8 \pm 4.4 b	19.2 \pm 4.9 c	87.6 \pm 6.6 a

indicated vegetation on the site that was similar to that which occurs presently. The forest site was flat (3°) and faced ESE (Fig. 1). The forest canopy species was *Picea glauca* with an understorey of tall *Salix* shrubs. Low shrubs, forbs and mosses formed a near-continuous ground cover (Table 1). A 1901 photograph showed that a majority of the site had been cut in about that year, and tree cores indicate that the forest is approximately 100 years old (A. Lloyd & C. Fastie pers. comm.).

Methods

Biomass and horizontal/vertical complexity

Within each site, we selected a large homogeneous area of vegetation that met eddy covariance requirements of fetch and slope (Balocchi & Meyers 1998). In $100\text{ m} \times 100\text{ m}$ sampling grids centered on an eddy covariance tower, we measured a variety of vegetation characteristics such as cover, height, biomass, leaf and stem area index in 10-12 randomly selected $20\text{ cm} \times 50\text{ cm}$ quadrats of the understorey and $1\text{ m} \times 1\text{ m}$ quadrats of the tall shrub overstorey, where present. All sampling occurred at the time of peak above-ground biomass, between mid July and mid August. Tall shrub, understorey and ground cover were measured using a point frame. In this study, cover is the uppermost leaf hit of each species at each point, which is a variation on point-framing methods used in other tundra studies (Arft et al. 1999; Shaver et al. 2001) (Table 1). The coefficient of variation (COV) of canopy cover provides an estimate of the horizontal complexity in the ecosystem. Horizontal complexity is greatest in sites with a discontinuous canopy or patchy distribution of

cover or biomass. *Picea* density was measured in the woodland and forest sites by counting stems in a subsample of $10\text{ m} \times 10\text{ m}$ plots in the grid (42 in the woodland site and 25 in the forest).

For the canopy PFTs we measured the height of *Picea* trees using an inclinometer and recorded the height of the top leaf for the tall shrubs. For the understorey species, height was recorded at the uppermost height where the vertical pin of the point frame intercepted the plant, therefore the height represents the average height of individuals in the quadrat. We measured the depth of live biomass for the ground cover PFTs.

Above-ground vascular plant biomass was harvested to the top of the moss or lichen layers, which were collected separately. We used an allometric equation ($386 * \text{DBH}^2 * 0.001$) developed for *Picea* in interior Alaska (J. Yarie pers. comm.) to estimate the total spruce biomass. Mosses and lichens were harvested at the level of the depth measurements. Plant biomass was oven-dried at 60°C for at least 48 hr and weighed.

Leaf and stem area index

We made site-wide measurements of the leaf area index (LAI) using a Licor 2000 Optical Plant Canopy Analyzer by sampling every 10 m within the grid (121 points). For the tall shrub layer, we measured stem area index (SAI), i.e., the number of stems intersected by a pin dropped from the top of the canopy to the ground surface, as our measure of stem density. Our measure of SAI therefore represents the vertical complexity of the tall shrubs.

Surface energy and moisture exchange measurements

In the center of each vegetation grid we measured radiation, microclimate and water and energy exchange using eddy covariance technique. The methods are described in detail in Beringer et al. (subm.). Net radiation represents the balance between incoming and outgoing radiation. Net radiation is strongly controlled by albedo, the proportion of incoming shortwave radiation reflected by the ecosystem. The absolute magnitude of the fluxes at each site is affected by seasonal variation in incoming radiation and variability in the climate drivers. The sites were measured at different times, therefore in order to compare the sites, we normalized all values to a reference site (the tundra site), which was measured continuously during summer. We then constructed ratios to examine the relative partitioning to ground, latent and sensible heating fluxes among sites.

Results

Total above-ground biomass ranged nine-fold from tundra site to forest (Table 2). The dominant plant functional type shifted across the sites. Biomass was dominated by lichens and mosses in the tundra site, by low deciduous shrubs in the low shrub site, by tall shrubs in the tall shrub site and in the woodland site and by trees (*Picea*) in the forest.

Canopy and shrub overstorey biomass

Picea accounted for 85% of the above-ground biomass in the spruce forest, with tall shrubs (mainly *Salix*) contributing another 7% of above-ground biomass (Table 2). In contrast, the deciduous shrub canopy contributed less than 1% of total biomass in the tundra site. At intermediate sites there was a more even distribution of biomass among overstorey PFTs. At the woodland site, for example, the overstorey canopy still accounted for most (65%) of total biomass, and the above-ground biomass was shared among the three canopy groups (*Picea*, *Betula* and *Salix*). At the tall shrub site, the canopy PFTs contributed 80% of the above-ground biomass, with *Betula* accounting for 68% of canopy biomass and *Salix* the remainder. At the low shrub site, the canopy (primarily *Betula*) accounted for 39% of above-ground biomass.

Understorey biomass

Understorey biomass differed less strongly across sites compared to canopy biomass and was distributed across sites in a greater diversity of plant functional types. Understorey biomass was greatest in the low shrub site but remained substantial in all sites (Table 2). Deciduous and evergreen shrubs co-dominated the understorey in all sites except the tall shrub and woodland, where deciduous shrub biomass exceeded evergreen biomass. Sedges accounted for a substantial proportion (19%) of understorey biomass in the tundra, and grasses and forbs both accounted for a similar proportion (16-19%) of understorey biomass in the woodland site.

Table 2. Total above-ground biomass of major plant functional types (PFT) in five ecosystems ranging from tundra to forest. Data are means \pm SE ($n = 10-12$). Statistics and abbreviations as in Table 1.

Canopy class/ PFT	Above-ground biomass (g.m ⁻²)				
	Tundra	Low shrub	Tall shrub	Woodland	Forest
Canopy					
<i>Picea</i>	nd	nd	nd	882.0 \pm 162.7	4454.0 \pm 194.3
<i>Betula</i>	3.8 \pm 2.6	428.2 \pm 141.7 a,b	1142.8 \pm 383.8 a	1069.0 \pm 407.2 a	6.1 \pm 4.4 b
<i>Salix</i>	nd	2.5 \pm 2.3	529.2 \pm 199.0 a,b	884.5 \pm 298.3	312.0 \pm 143.2 a,b
Understorey					
Deciduous shrubs	42.8 \pm 15.1	276.7 \pm 75.8 a	101.5 \pm 25.1	59.3 \pm 31.7	42.1 \pm 14.0
Evergreen shrubs	55.2 \pm 13.2	159.7 \pm 24.8 a	38.7 \pm 19.2	5.5 \pm 3.6	56.2 \pm 19.5
Forb	6.5 \pm 3.2	6.2 \pm 2.8	13.2 \pm 4.0	19.0 \pm 4.7	13.2 \pm 2.4
Grass	nd	1.5 \pm 0.8	4.5 \pm 1.1	21.2 \pm 8.2 a	5.1 \pm 1.4
Sedge	24.5 \pm 4.2 a	12.9 \pm 3.5 a,b	8.6 \pm 3.0 b	7.5 \pm 3.1 b	13.1 \pm 3.5 a,b
Ground cover					
Lichen	197.7 \pm 84.7	162.4 \pm 52.6	42.7 \pm 20.9	1.9 \pm 1.3	81.2 \pm 62.2
Non-Sphagnum moss	71.6 \pm 17.9 b	52.2 \pm 24.2 b	203.8 \pm 41.6 a	50.6 \pm 19.1 b	224.6 \pm 1.4 a
Sphagnum moss	179.5 \pm 54.3 a	1.5 \pm 1.0	nd	nd	nd
Total	581.6	1103.8	2085.0	3000.5	5207.6

Table 3. Canopy and understorey heights and ground cover depths. Data are means \pm SE ($n = 10-12$). Statistics and abbreviations as in Table 1.

Canopy class/PFT	Vegetation height and Ground cover depth (cm)				
	Tundra	Low shrub	Tall shrub	Woodland	Forest
Canopy					
<i>Picea</i>	nd	nd	nd	730 \pm 0	620 \pm 80
<i>Betula</i>	9.9 \pm 4.6	34.75 \pm 5.99	82.8 \pm 12.0	85.0 \pm 14.5	15.4 \pm 17.4
<i>Salix</i>	nd	nd	81.7 \pm 15.9	97.7 \pm 13.2	119.5 \pm 2.5
Understorey					
Deciduous shrubs	8.4 \pm 0.9	15.5 \pm 4.6	11.1 \pm 1.5	15.6 \pm 2.2	7.0 \pm 1.2
Evergreen shrubs	5.7 \pm 0.8	7.2 \pm 9.8	5.4 \pm 0.9	6.85 \pm 1.1	5.74 \pm 0.7
Forb	4.2 \pm 0.9	8.07 \pm 0.68	22.3 \pm 4.9 a	10.1 \pm 1.2	5.49 \pm 0.5
Grass	nd	44.4 \pm 4.4 a	6.6 \pm 1.4 c	31.2 \pm 2.1 b	6.64 \pm 0.3 c
Sedge	25.4 \pm 0.2 b	33.3 \pm 3.5 a	5.8 \pm 0.7 b	28.2 \pm 1.5 a,b	8.1 \pm 1.2 c
Ground Cover					
Lichen	4.6 \pm 0.8 a,b	1.7 \pm 0.4 c	1.7 \pm 0.7 c	6.0 \pm 0.0 a	1.78 \pm 0.4 c
Non- <i>Sphagnum</i> moss	2.1 \pm 0.3 a	0.9 \pm 0.8 b	1.4 \pm 0.3 a,b	2.1 \pm 0.4 a	0.74 \pm 0.3 b
<i>Sphagnum</i>	1.3 \pm 0.2	2.5 \pm 0.8	nd	nd	nd

Ground-cover biomass

The biomass of ground cover, which consisted of non-vascular plants, was greatest in the tundra site and least in the woodland site (Table 2). Lichens and non-*Sphagnum* mosses were important in all sites except the woodland, where lichens were negligible. *Sphagnum* biomass, which was very high at the tundra site, comprised little or none of the ground cover in the other sites. Lichens and non-*Sphagnum* mosses showed complex patterns of distribution across sites, and were not clearly correlated with canopy biomass.

Canopy height

Canopy height is often used as a surrogate of canopy complexity in studies of energy exchange because height correlates closely with roughness length, the aerodynamic property that partly determines the efficiency of convective exchange between the canopy and the atmosphere (Oke 1987). Canopy height ranged from 0.10 m in tundra to 7.3 m in the woodland site (Table 3). Average *Picea* height was 15% less (6.2 m) in the forest than in the woodland (7.3 m). Average height of *Betula* shrubs was very similar between the shrub and woodland sites (0.83 and 0.85 m, respectively). Average height for *Salix* increased from 0.82 m in the tall shrub site to 0.98 m and 1.2 m in the woodland and forest sites, respectively (Table 3).

Canopy cover

Detailed measurements of canopy cover showed a different pattern of canopy complexity than would be inferred from site differences in canopy height. The forest had more continuous tree cover than the woodland

(see density measurements below). The tall shrub layer had a nearly continuous cover of leaves that was identical (92%) between the tall shrub and woodland site (Fig. 2). However, the lower coefficient of variation (COV) in the woodland site compared to the tall shrub site (32% and 38% respectively) suggests a smoother canopy in the woodland site. In the tall shrub site, *Betula* accounted for 56% of the tall shrub cover and *Salix* accounted for the remainder. In the woodland site the proportional contribution of tall shrub species to total cover was the reverse (43% *Betula*, 57% *Salix*) (Fig. 2). The canopy cover of tall shrubs in the forest site was much lower (39%) and had a higher COV (77%) than in the shrub-dominated sites, reflecting a sparser distribution and greater horizontal complexity of tall shrubs in that site. *Salix* accounted for almost all (94%) of the tall-shrub cover in this site (Fig. 2).

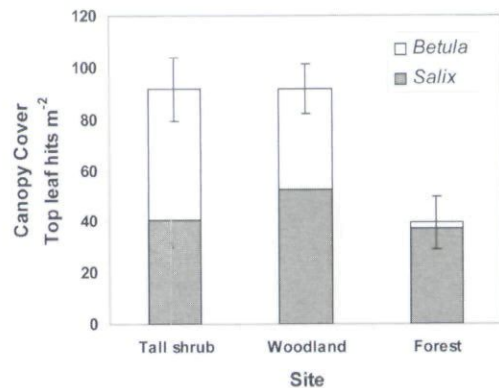


Fig 2. Canopy cover of *Betula* and *Salix* shrubs measured with a point frame. Hits on the top leaf of each species determine canopy cover. Data shown are mean and standard error.

Understorey density

Total understorey density, which is approximated by measurements of cover, tended (non-significantly) to increase along the gradient from tundra to forest (Fig. 3, Table 1). The coefficient of variation for total density was also similar among sites. The low shrub site had the greatest variability (COV 52%) indicating greater horizontal heterogeneity, and the tundra site had the lowest (COV 32%). These patterns are roughly similar to those described above for biomass and could reflect restriction of understorey deciduous shrubs to the least shaded sites (tundra, low shrub, and tall shrub) and the concentration of forbs and grasses to the more productive sites (tall shrub, woodland, and forest). A MANOVA test at the $\alpha = 0.05$ level followed by a Ryan-Einot-Gabriel-Welch multiple range test was used to evaluate height differences among sites. For most functional types, heights were similar across sites (Table 3). The height of the low deciduous and evergreen shrubs did not vary significantly across the gradient of sites ($F_{4,37} = 2.28, p > 0.0794$) ($F_{4,38} = 0.97, p > 0.4350$), suggesting that their morphology was relatively insensitive to shading. Sedges and grasses, with their vertical leaf structure and low stem allocation are at the top of the canopy, deciduous shrubs are intermediate, and the more shade-tolerant evergreen shrubs are at the bottom of the canopy. Forbs are variable in their canopy position, due to site differences in species composition.

Ground cover

Non-vascular plants covered most of the ground surface in the tundra and forest sites, 50%-60% of the ground surface in the low shrub and tall shrub sites and less than 20% in the woodland site (Table 1). The variability among sites in the ground cover was much greater than in the understorey (Fig. 3). The woodland

site had the greatest COV (84%), reflecting its sparse distribution of mosses and lichens. The low shrub site also had a highly variable distribution of ground cover (COV 57%). The ground cover distribution was less complex in the tall shrub, forest and tundra sites, reflecting their more continuous distribution of mosses and lichens.

Ground cover was deepest in the tundra site, and slightly shallower in the low shrub site and forest site. Lichens were deepest in the woodland site. Neither moss functional group varied significantly in depth between the tundra and low shrub site (Table 3).

Leaf area index and Stem area index

LAI increased across the vegetation gradient from tundra to forest (Table 4). The pattern of increase was different from that of biomass, with the greatest increase from tundra to tall shrub and relatively minor increases from the tall shrub to forest, where biomass increased most dramatically.

Stem density or SAI provides a measure of the density of roughness elements, another structural attribute of vegetation that influences convective exchange with the atmosphere. The density of *Picea* trees increased 20-fold from the woodland site ($54.8 \text{ ind. ha}^{-1}$) to the forest ($1090 \text{ ind. ha}^{-1}$). In the tall shrub layer, combined SAI of *Betula* and *Salix* decreased along the vegetation gradient from tall shrub to woodland to forest (3.2, 2.8, and 0.94, respectively) (Table 4). The forest showed the greatest coefficient of variation of SAI among plots (COV 87%), the woodland showed the least (COV 39%), and the tall shrub site was intermediate (COV 54%). *Salix* accounted for 38%, 44%, and 96% of the SAI in the shrub, woodland, and forest sites, respectively (Fig. 4) and was slightly less than its proportional contribution to canopy cover because of its greater leaf allocation than *Betula* (Fig 3).

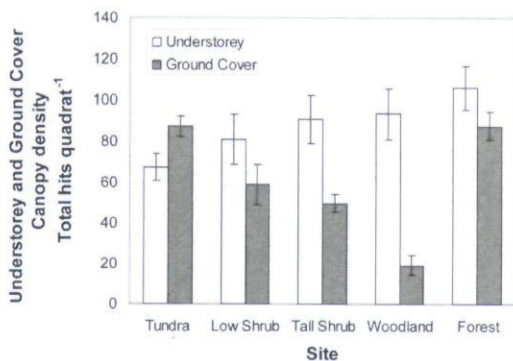


Fig. 3. Understorey and ground cover canopy density for all sites with mean and standard error bars shown.

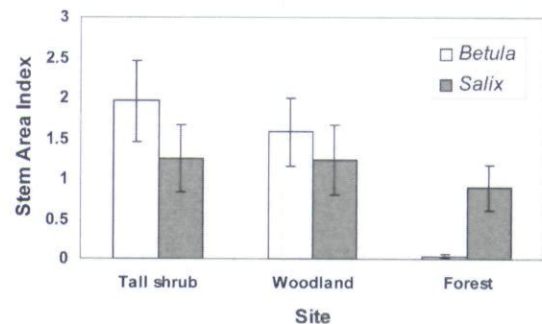


Fig. 4. *Betula* and *Salix* stem area index (SAI) for the sites with a tall shrub component to the canopy. Mean and standard error shown. Units for SAI are $\text{m}^2 \cdot \text{m}^{-2}$.

Discussion

Energy absorption

The patterns of biomass and canopy complexity that we documented had important consequences for land-surface energy exchange characteristics measured by Beringer et al. (subm.) in the same sites. Albedo decreased dramatically along the vegetation gradient from tundra to forest (Table 4). Site differences in albedo correlated closely with total above-ground biomass (Fig. 5a) and with LAI (Fig. 5b).

Albedo responded most sensitively to changes in biomass at low levels of biomass (Fig. 5a), although the relationship is only slightly different from linear. This suggests that masking of the reflective ground cover of lichens and of standing dead leaves of sedges contributes strongly to site differences in albedo in open communities (tundra to low shrub site to shrub sites). Albedo decreased with increasing LAI (Fig. 5b). This relationship is expected from theory because increments in biomass and leaf area increase the probability that radiation reflected from one canopy element will be absorbed by another rather than being reflected back to space (Oke 1987). The greater diversity of functional types and associated vertical canopy complexity at sites with high LAI could also contribute to their low albedo. Our data suggest that both masking of the ground surface and canopy complexity contribute to site differences in albedo, and that the relative importance of these mechanisms depends on canopy biomass and LAI. Patterns of albedo across the Council sites were similar to those in other tundra and boreal sites (Table 4) (Betts & Ball 1997; McFadden et al. 1998; Baldocchi et al. 2000).

Site differences in vegetation composition, vertical and horizontal complexity and albedo drive site differences in net radiation (the energy absorbed by the ecosystem). Sites with high above-ground biomass, LAI, and low albedo absorb more solar energy than sites with low values of these parameters (Table 4). These site differences in net radiation are important because they determine the

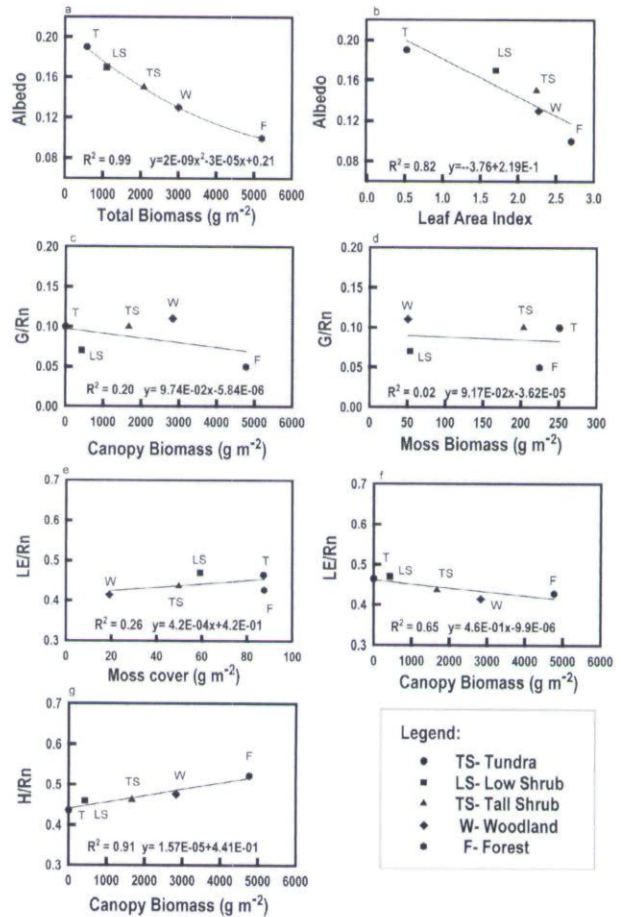


Fig. 5. (a) Regression of total biomass on albedo; (b) LAI regressed on albedo; (c) Moss (combined *Sphagnum* and non-*Sphagnum* types) biomass regressed on fraction of net radiation (Rn) partitioned to ground heat flux (G); (d) Regression of ground heat fraction and canopy biomass; (e) Relationship of moss biomass to latent heat flux fraction (LE); (f) Canopy biomass regressed on latent heat flux; (g) Total biomass regressed on sensible heat flux (S). Units for flux ratios are $W \cdot m^{-2} / W \cdot m^{-2}$.

energy available for transfer to the atmosphere and soil (Oke 1987; Beringer et al. subm.). Available net radiation was very similar in all sites with the exception of the

Table 4. Leaf Area Index (LAI), shrub Stem Area Index (SAI) albedo, net radiation and fraction of net radiation partitioned into sensible, latent and ground heat fluxes. Flux and LAI values from Beringer et al. (subm.). Numbers in brackets are values reported by Eugster et al. (2000) for comparable arctic and subarctic ecosystems. nd = parameter not measured in those sites. Units for flux fractions are $W \cdot m^{-2} / W \cdot m^{-2}$.

Site	LAI	SAI	Vegetation structure and energy partitioning values				
			Albedo (midday mean)	Net radiation ($W \cdot m^{-2}$)	Ground heat flux fraction	Latent heat flux fraction	Sensible heat flux fraction
Tundra	0.52	nd	0.19 [0.155]	94.2	0.10 [0.11-0.24]	0.46 [0.40-0.55]	0.44 [0.22-0.42]
Low shrub	1.70	nd	0.17 [0.155]	92.1	0.07 [0.11, 0.13]	0.47 [0.38, 0.44]	0.46 [0.46, 0.55]
Tall shrub	2.24	3.22	0.15 [0.16]	104.1	0.10 [0.10, 0.21]	0.44 [0.33, 0.48]	0.46 [0.48, 0.51]
Woodland	2.27	2.82	0.13 [0.13, 0.125]	123.8	0.11 [0.06, 0.12]	0.41 [0.28, 0.45]	0.48 [0.49, 0.60]
Forest	2.70	0.94	0.10 [0.11]	118.5	0.05 [0.09]	0.43 [0.58, 0.38]	0.52 [0.38, 0.47]

forest site, which had a 20% greater net radiation. The greater amount of net radiative energy available at the surface at the forest site will likely amplify differences in energy partitioning in this site.

Energy partitioning

Site differences in energy balance depend on the partitioning of energy between ground heat flux, and convective latent and sensible heat fluxes to the atmosphere. The fraction of net radiation partitioned into ground heat flux is controlled by canopy shading, the insulative properties of the ground cover, and the temperature gradient within the soil, which is strongly influenced by presence or absence of permafrost. No vegetation characteristic that we measured (canopy biomass, canopy cover, moss biomass, moss cover, LAI) showed a significant regression relationship with ground heat flux, indicating that no single vegetation property that we examined accounted for site differences in ground heat flux (Fig. 5c, d). It seems likely that ground heat flux responds to some combination of factors. Among our five sites, shading and/or the thermal gradient created by presence of permafrost appeared more important than moss biomass or moss type in controlling ground heat flux. We conclude this based on the following observations. First, ground heat fluxes were high in the two sites with permafrost (the tundra and woodland sites), which suggests that the presence of permafrost contributed substantially to ground heat flux in sites where it was present. Second, the site with the most radiation reaching the moss surface (tundra) had intermediate partitioning to ground heat flux whereas the site with the least radiation reaching the moss surface (the forest) had the lowest ground heat flux, indicating that shading does not, by itself, control ground heat flux but could be a contributing factor.

Finally, contrary to our expectation that moss biomass would reduce ground heat fluxes, the tundra site, which had the most insulative ground cover (*Sphagnum*; Beringer et al. 2001a) and greatest moss biomass, did not have the lowest ground heat flux (Fig. 5d). The presence of permafrost in this site appeared more important than moss biomass or moss type in controlling summer ground heat flux. Over the longer term, mosses may be an important factor contributing to the presence of permafrost because they are more effective in reducing heat input to soils in summer (due to abundant air spaces) than in winter (when ice conducts heat effectively through mosses from the soil to the atmosphere).

Our ground heat flux values were generally within the range reported by Eugster et al. (2000) (Table 4). Previous studies (summarized in Eugster et al. (2000)) concluded that partitioning to ground heat fluxes is generally

negatively correlated with LAI. However the correlation among the Council sites was not as strong as suggested by the literature, perhaps because the Council sites varied in presence/absence of permafrost, which was not the case in previous comparisons. It should be noted that ground heat flux, which is measured at several single points, is not strictly comparable to net radiation measured across a broad footprint (Mayocchi & Bristow 1995).

Latent heating should be controlled by both the surface evaporation from mosses and soil and evapotranspiration from the vascular canopy. Across the Council sites, the evaporative fraction was nearly constant. Contrary to our expectations, the fraction of net radiation partitioned to latent heat flux (the evaporative fraction) showed a weak relationship with moss cover (Fig. 5e) and decreased slightly along the gradient of increasing biomass (Fig. 5f). Mosses evaporate freely as long as they are moist and their contribution to latent heating is determined by the net radiation they receive. As the vertical complexity of the canopy increases, the mosses at the ground surface are increasingly shaded, reducing ground surface evaporation. On the other hand, total vascular transpiration increases as canopy leaf area increases. The combined effect of decreasing ground evaporation and increasing transpiration across the sites is that the evaporative fraction appears nearly constant. However, under conditions of moisture stress, increasing stomatal resistance results in decreased transpiration from the canopy. In the Council sites, drying of the surface and air in summer during our measurement period decreased partitioning into latent heating in the forest site. However, the absolute value of the latent heat flux was greater due to greater available energy (net radiation minus the ground heat flux). The partitioning of net radiation into latent heat fluxes that we observed in the Council sites was lower for shrub tundra and higher for the forest sites compared to values reported for similar vegetation types in other arctic and boreal ecosystems (Eugster et al. 2000) (Table 4), probably because the forest at Council had a denser canopy than those studied in other forest-tundra comparisons (Rouse 1984; McFadden et al. 2003).

The fraction of net radiation partitioned into sensible heat flux correlated very strongly with biomass (Fig. 5g). Decreasing ground heat fluxes combined with the little variation in latent fluxes meant that along the gradient from tundra to forest an increased proportion of net radiation was available for sensible heating. The biggest increase in sensible heating occurred between the woodland and forest sites, which suggests that development of a full *Picea* canopy was important in enhancing convective efficiency because a well-developed canopy has more turbulence and more efficient turbulent transport.

Conclusions

Our measurements of vegetation characteristics (biomass, density, height LAI and SAI) show that there are multiple dimensions to the site variation in canopy complexity. Changes in this complexity across the gradient resulted from both the addition of the new functional type (tall deciduous shrubs and *Picea*) across the gradient and interactions among the functional types. The addition of a full spruce canopy had the greatest effect on the tall shrubs, leading to a 60% reduction in total shrub biomass. This effect was strongest on the *Betula* shrubs, which were virtually absent from the forest site. In the ground-cover layer, the addition of tall shrubs and *Picea* reduced the *Sphagnum* mosses; however total ground cover was fairly similar across the sites. Even in the understorey, where total biomass and cover were relatively similar across the sites, there was a complex pattern of change in abundances within and among functional types. This suggests that the functional types are responding to site characteristics other than to just canopy development, e.g. differences in nutrient cycling. For example, forbs and grasses had higher biomass and cover in the high-biomass sites (tall shrub, woodland, and forest), where nutrients were presumably more available than in the low shrub and tundra sites.

Changes in canopy complexity affected net radiation at each site and its partitioning into ground and convective fluxes. Albedo decreased and net radiation increased from tundra to forest. It was difficult to determine the relative influence of moss biomass and canopy cover on ground heat fluxes due to the confounding effect of permafrost presence and absence in the sites. Latent heat fluxes appeared to be better correlated with the development of a leafy canopy than the presence of mosses. Increasing canopy complexity, particularly increasing biomass had a strong relationship with sensible heat fluxes.

The warming associated with the increased sensible heating over more complex canopies could have local effects, including feedbacks to biogeochemical processes (enhanced decomposition and production). Accelerated nutrient cycling could favour deciduous shrubs over types with slower nutrient turnover. Other regional effects of changes in energy partitioning could include changes to the disturbance regime such as increased fire frequency, and more flammable vegetation types, as well as more frequent insect outbreaks (Lloyd et al. 2003). Localized warming above ecosystems with a tall, complex canopy may feedback to regional climate by warming the boundary layer (Beringer et al. 2001b). Our results lend further evidence to the complexity of the interactions between vegetation changes due to an increasing canopy complexity and other ecosystem char-

acteristics, such as the presence of a moss layer, or permafrost in determining the changes to surface energy and moisture balance.

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