Scaling Thermal Properties from the Leaf to the Canopy in the Alaskan Arctic Tundra

Authors: Gersony, Jessica T., Prager, Case M., Boelman, Natalie T., Eitel, Jan U. H., Gough, Laura, et al.

AAAR

Scaling thermal properties from the leaf to the canopy in the Alaskan arctic tundra

Jessica T. Gersony[1,*], Case M. Prager[1], Natalie T. Boelman[2,3], Jan U. H. Eitel[4,5], Laura Gough[6], Heather E. Greaves[4], Kevin L. Griffin[1,2,3], Troy S. Magney[4], Shannan K. Sweet[2,3], Lee A. Vierling[4,5], and Shahid Naeem[1]

[1]Department of Ecology, Evolution, and Environmental Biology, Columbia University, 10th Floor Schermerhorn Extension, 1200 Amsterdam Avenue, New York, New York 10027, U.S.A.

[2]Department of Earth and Environmental Sciences, Columbia University, 557 Schermerhorn Extension, 1200 Amsterdam Avenue, New York, New York 10027, U.S.A.

[3]Lamont-Doherty Earth Observatory, Columbia University, 61 Route 9W, Palisades, New York 10964, U.S.A.

[4]Geospatial Laboratory for Environmental Dynamics, Department of Natural Resources and Society, University of Idaho, 875 Perimeter Drive, MS 1133, Moscow, Idaho 83844, U.S.A.

[5]McCall Outdoor Science School, University of Idaho, McCall, Idaho 83638, USA

[6]Department of Biological Sciences, Towson University, 8000 York Road, Towson, Maryland 21252, U.S.A.

[*]Corresponding author's address: Department of Organismic and Evolutionary Biology, Biological Laboratories–Room 3107, Harvard University, 16 Divinity Avenue, Cambridge, Massachusetts 02138, U.S.A., Jgersony@g.harvard.edu

ABSTRACT

Plants are strongly influenced by their thermal environments, and this influence manifests itself in a variety of ways, such as altered ranges, growth, morphology, or physiology. However, plants also modify their local thermal environments through feedbacks related to properties and processes such as albedo and evapotranspiration. Here, we used leaf- and plot- level thermography on the north slope of the Brooks Range, Alaska, to explore interspecific differences in thermal properties among arctic tundra plants, and to determine if species differentially contribute to plot temperature. At the leaf-level, we found significant differences ($p < 0.05$) for in situ temperatures among the 13 study species. At the plot level, we found that the fractional cover of vascular plant species, lichen, litter, and moss had a significant effect on plot temperature ($p < 0.05$, $R^2 = 0.61$). A second model incorporating thermal leaf properties—in addition to the fraction of vascular plant and other dominant ground covers—also predicted plot temperature, but with lower explanatory power ($p < 0.05$, $R^2 = 0.32$). These results potentially have important implications for our understanding of how individual plant species influence canopy-level thermal properties and how temperature-dependent properties and processes may be impacted by climate change–induced shifts in species composition.

INTRODUCTION

Temperature (usually quantified by soil or air temperature) has been known to greatly influence plant physiology and ecology (Berry and Bjorkman, 1980; Walther et al., 2002; Parmesan and Yohe, 2003; Elmendorf et al., 2012; Gottfried et al., 2012). On a physiological scale, warming experiments us-

ing greenhouses or infrared heaters applied across a range of species and ecosystems have shown that physiological rates, including photosynthetic and respiratory rates, change as a function of air and/ or soil temperature (Hobbie and Chapin, 1998; Zhou et al., 2007; Zhao and Liu, 2009; Heskel et al., 2013, 2014; McLaughlin et al., 2014; Atkin et al., 2015). On a larger, ecological scale, species ranges

are strongly influenced by air temperature—species have evolved to optimize their performance in their respective climate, as demonstrated by evolutionary convergence across phylogenetically unrelated species in climatically similar regions (Mooney, 1977; Beard, 1978; Bunce et al., 1979; Orians and Paine, 1983; Stephenson, 1990; Atkin et al., 2015).

In turn, vegetation not only responds to local thermal conditions, but also influences them through a variety of processes and feedbacks. In high latitudes, models have shown that species with high albedo can decrease local temperatures by means of reflecting, rather than absorbing, relatively more incoming solar radiation than species with lower albedo (Doughty et al., 2011). A species' albedo is a result of differences in physical and biochemical leaf traits (e.g., degree/type of pubescence, foliar pigment concentration, leaf mass per area [LMA]) (Asner, 1998), as well as organismal- and community-level properties such as leaf area index (LAI) (Asner, 1998). High rates of evapotranspiration can also lower local temperatures by allocating more absorbed solar radiant energy into latent, as opposed to sensible, heat flux (Stoner and Miller, 1975; Jones, 1999). Additionally, variation in convective cooling (via altered air-flow dynamics), is determined by differences in physical traits such as leaf angle distribution, leaf thickness and shape, the presence of trichomes, and by variation in canopy architecture (Ansari and Loomis, 1959; Medina et al., 1978; Oke, 1987). As such, to gain a comprehensive mechanistic insight into temperature-dependent processes and properties—such as enzymatically driven physiological processes and species range distributions—an improved understanding of the complex influence of different species on their local microclimate is needed.

While the importance of leaf and air temperatures for plant physiological ecology has been recognized since at least the beginning of the 20th century (e.g., Chandler, 1913), available sampling methodologies have restricted its study to limited spatial extents and resolutions. Studies have mainly focused on either fine-scale point measurements to estimate leaf temperature (e.g., thermocouple measurements; Wilson, 1957) or coarse-scale measurements made by satellite sensors to estimate land surface temperatures and evapotranspiration rates (e.g., MODIS, Landsat, and ASTER thermal sensors; Gillies and Carlson, 1995; Matsushima and Kondo, 2000; Allen et al., 2007; Sobrino et al., 2007; Anderson et al., 2012). However, important interactions between vegetation and climate occur at a variety of scales, such as leaf– (Oke, 1987), whole plant– (Chapin et al., 1979), and community-level scales (Leuzinger and Körner, 2007). Thus, to understand thermal properties ("thermal properties" being defined as an average of the surface temperature of specific leaves or canopies at a point in time) and temperature-dependent processes of an ecosystem, investigation of thermal properties at intermediate spatial scales is required. To our knowledge, no attempt has been made to identify and explore the thermal properties of vegetation across a range of scales and evaluate cross-scale relationships.

Recent advances in thermographic methods allow for sampling across multiple spatial scales. Specifically, the recent development of uncooled thermal imaging sensor arrays configured as affordable handheld thermal infrared cameras—with conversion to temperature precision better than 0.1 °C—have helped facilitate more rigorous understanding of the microclimate of vegetation (Jones 2004). Thermographic imaging systems translate surface thermal infrared (8–15 μm) emissions of complex surfaces into thermographic images from which surface temperatures can be extracted (Jones, 1999, 2004; Leuzinger and Körner, 2007). This allows for spatially explicit quantification of fine-scale variation in vegetation temperature that results from the net influence of a complex variety of factors that determine leaf surface temperature. This technique enables the following: (1) separation of green leaves from nonphotosynthetically active canopy components within each field of view, as opposed to previously employed remote thermal measurements that integrate across the entire field of view, and (2) measurements that are spatially commensurate with the physiological processes that govern ecosystem function. The estimation of surface temperature is derived from measurements of the thermal radiation emitted by the object of interest (Jones, 2004). The algorithms behind the surface temperature estimations correct for the spectral sensitivity of the detector, the emissivity of the surface, the attenuation of radiation throughout the atmosphere, the thermal radiation from external factors that are reflected by the surface of interest, and the thermal

radiation emitted toward the detector by the intervening air (Jones, 2004).

Examples of vegetation-focused thermographic-enabled studies are currently limited, but provide unique insights into vegetation's influence on local thermal environments. For example, Leuzinger and Körner (2007) employed thermographic methods to explore temperature differences between community types (a deciduous canopy and a mixed coniferous and deciduous canopy) in a temperate forest to better understand spatial variation in canopy temperature. They found that mean canopy temperatures differed to varying degrees from air temperatures depending on species composition. However, little is known about how species differ in their thermal properties and how community composition influences canopy-level thermal properties in ecosystems of higher latitudes, such as the rapidly changing Alaskan arctic tundra, where major shifts in species composition as a result of a changing climate are taking place (Sturm et al., 2001; Chapin et al., 2005; Tape et al., 2006; Myers-Smith et al., 2011; Elmendorf et al., 2012; Loranty and Goetz, 2012). Although the biogeochemical implications of these community shifts are well studied (see review: Myers-Smith et al., 2011), resulting shifts in thermal properties of tundra vegetation communities have not been explored.

The arctic tundra is an ideal system to further our general understanding of thermal ecology (the relationships between thermal properties and temperature dependent physiological and ecological processes) for two main methodological reasons. First, tundra canopies are characteristically short (typically 3–23 cm) (Gough et al., 2000), easily enabling top-of-canopy measurements of plot-level temperatures, which removes some of the logistical and economic challenges associated with making such measurements in forested environments. Second, arctic vegetation experiences low drought stress relative to other ecosystems (Billings and Mooney, 1968), which helps eliminate significant temporal variability in physiological properties, such as transpiration rates, which have a significant impact on leaf temperatures.

Here, we employ a combined observational and modeling approach, using in situ thermography at both the leaf and plot (1 m²) scales to test the following hypotheses: (1) Because certain leaf traits (e.g., physiological, morphological, or biochemical) and whole plant traits (e.g., stature/height) influence the surface energy balance of a leaf, plant species will differ significantly in their leaf thermal properties. (2) Due to species-specific leaf thermal properties, as well as those of dominant ground cover components (i.e., moss, lichen, bare ground, rock, water), variation in fractional cover proportions of these ecosystem components will be correlated with plot-level temperature.

METHODS

Study Site and Field Sampling

All measurements were taken during the 2014 and 2015 summer growing seasons within ~25 km of the Arctic Long Term Ecological Research (ARC LTER) site at Toolik Field Station, located north of the Brooks Range in Alaska (68°38′N, 149°38′W) (Fig. 1). The average July temperature at Toolik Lake is 14 °C, and the annual precipitation at Toolik is 200–400 mm (van Wijk et al., 2005).

For this study, we used 60 1-m² study plots from a range of tundra types surrounding Toolik Lake (n = 20) and Imnavait Creek (n = 40). The plots are distributed along six 100-m-long transects at 10-m spacing intervals in various tundra types: moist tussock tundra (MTT) (30 plots; 1 transect at Toolik Lake and 2 transects at Imnavait Creek), erect shrub tundra (EST) (10 plots; 1 transect at Toolik Lake), and prostrate/dwarf deciduous shrub tundra (PDS) (20 plots; 2 transects at Imnavait Creek). MTT is dominated by tussock-forming and other sedges (*Eriophorum vaginatum* and *Carex bigelowii*), as well as evergreens, mosses, forbs, and short-stature deciduous shrubs (Britton, 1966; Sweet et al., 2015). EST is dominated by tall stature *Betula nana, Salix* spp., and other deciduous shrubs, with a smaller portion of moss, evergreens, and forbs (Shaver and Chapin, 1991; Sweet et al., 2015). PDS is dominated by medium stature *B. nana* and *Salix* spp. as well as graminoids, evergreens, and forbs (water track tundra as described in Chapin et al., 1988; Sweet et al., 2015). These plots were selected because they are representative of the vegetation cover of the study regions (Walker et al., 2005; Sweet et al., 2015). Percent cover of the plots was visually estimated in 2010 and 2011 during peak-greenness (late July)
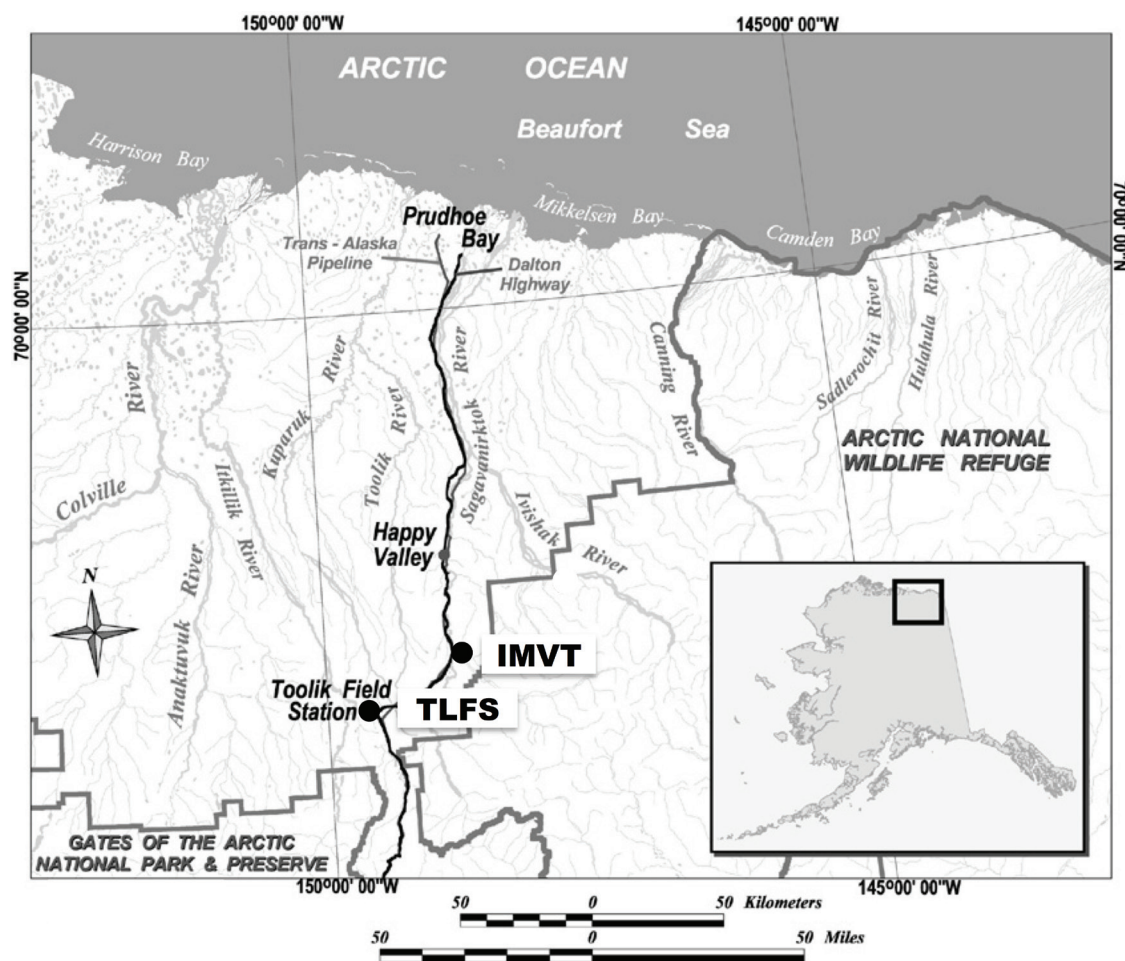
FIGURE 1. Map of the two field sites in arctic Alaska near Toolik Field Station.

through use of a 1-m² frame outlining 20 cm × 20 cm subquadrats (Boelman et al., 2011; Rich et al., 2013); long-term data has shown that there is minimal year-to-year variation in community composition for these community types (Gough and Hobbie, 2003). The vascular plant cover of each plot was on average 62% of the m² plot, whereas the remainder of the plots were covered with lichen, litter, moss, bare ground, and rocks.

INFRARED THERMOGRAPHY

We made infrared thermography measurements using a FLIR T650sc (FLIR, Nashua, New Hampshire, U.S.A.). In this paper, we assume the emissivity of both individual leaves and plant canopies to be 0.95; the reason for the relatively low emissivity assumption for plant canopies is that arctic canopies have relatively low density (low LAI) (Jones, 2004;

Thompson et al., 2004). However, a potential source of error is the variation in emissivities between different species and canopy types. Plant leaves have been found to have emissivities between 0.92 and 0.99, and an error of emissivity by 0.026 can give rise to a temperature error of 0.66 °C (Jones, 2004; López et al., 2012). All images were processed using the ExaminIR Pro software (FLIR, Nashua, New Hampshire, U.S.A.) and ImageJ (Rasband, 1997–2014) where leaves, plots, or references were each manually traced and the relevant distribution of temperatures was extracted.

For leaf-level measurements, on 6 July 2015 we thermographically sampled 13 of the dominant plant species occurring in our study plots. These species fall into four growth forms (Table 1) and compose 80% of the vascular plant cover in the meter squared study plots. We imaged five individuals of each study species in between 10:00 and 10:30

TABLE 1

Thirteen study species by plant growth form.

Deciduous shrubs	Graminoids	Evergreens	Forbs
Betula nana	*Carex bigelowii*	*Cassiope tetragona*	*Equisetum arvense* *
Salix pulchra	*Eriophorum vaginatum*	*Empetrum nigrum*	*Petasites frigidus*
Salix reticulata		*Rhododendron palustre*	*Polygonum bistorta*
Vaccinium uliginosum			*Rubus chamaemorus*

*Note that *E. arvense* is a pteridophyte but is included in the forb growth form for convenience, as its morphology has characteristics more common with this form than the others.

a.m. from ~20 cm away from the leaf surface. For each of these individuals, we took images of 1–30 sun-lit, attached leaves depending on the size and density of leaves. For example, for *Polygonum bistorta* we imaged and traced one single leaf per individual; for *B. nana* we imaged and traced 5–30 leaves on one branch per individual; for *E. vaginatum* we imaged and traced 5–30 leaves per individual. For each of the five individuals we took four to five images over the course of ~1 minute to account for instantaneous temperature shifts due to slight shifts in environmental conditions. For each individual, the leaf measurements were averaged together, resulting in five data points per study species. These images were not taken from the study plots, but were taken within 1 km of Toolik Field Station. On the sample day, there was no cloud cover (full spectrum range, 285–2800 nm, of solar radiation was 0.313 kW m^{-2}) and the temperature (3 m above the ground) and wind (5 m above the ground) were 22.9 °C and 1.2 m s^{-1}, respectively (Cherry and Cohen, 2014 and 2015). For plot-level measurements, we sampled around solar noon over the course of 2 days (16 and 17 July 2014). On the days of sampling, it was 10.0 and 15.1 °C with wind measurements of 3.1 and 2.1 m s^{-1}, respectively, and consistent cloud cover (full spectrum range, 285–2800 nm, of solar radiation was 0.144 and 0.168 kW m^{-2}, respectively) (Cherry and Cohen, 2014 and 2015). To obtain plot images with a viewing range of 1 m^2, we used a Feather Camera Crane (Lite Pro Gear). In order to capture the proper plot size, depending on the vegetation height, the crane was extended between 3 and 4 m in length. For each study plot (similar to leaf-level), we collected at least two replicate images to account for sudden changes in wind and ambient conditions. The data derived from the replicated images were averaged for each study plot, resulting in one data point for each study plot.

To account for the slight differences in ambient environmental conditions throughout and between the two sample days for plot level, and the impact that these conditions had on the vegetation plot surface temperatures, we used reference images of dry filter paper as it has similar emissivity characteristics as vegetation. Before each set of images, at most 40 min between a study image and a reference image, we took a reference image of a dry piece of filter paper (acclimated to local plot conditions for a minimum of 10 s) from the same height as the study image in order to account for atmospheric humidity and subsequent thermal diffusion and uptake. We calculated normalized plot temperatures by (1) isolating the lowest reference temperature for all plot images across both days, (2) finding the difference between the lowest reference temperature and all other reference temperatures, and (3) subtracting that difference from the associated study images to normalize for changes in ambient temperature and solar radiation between images. This technique successfully normalized our bimodal observations into a normal distribution.

STATISTICAL METHODS

We used several statistical approaches to analyze the various data sets in this study. Observed and predicted plot temperatures, as well as leaf temperatures, were tested for normality in distribution and homogeneity of variance with the Shapiro-Wilks and Bartlett tests (grouped by transects for plot level and by species for leaf level), respectively. If

data were significantly non-normal or did not have homogeneity of variance, data were transformed (squared) prior to analysis.

To test species and growth-form level differences in leaf temperature we used a one-way analysis of variance (ANOVA); these differences were further explored with a Tukey Honest Significant Difference (HSD) test. For the growth form temperature comparisons, we ran a mixed model with "species" as a random effect. If the random effect was not significant, we omitted it from the model.

The relationships between canopy composition and plot temperature were tested for statistical significance by fitting a multiple regression model with the 13 study species' fractional cover and the fractional cover of bare ground, moss, water, rocks, lichen, and litter as independent variables and observed plot temperature as the dependent variable; the model was simplified through an Akaike Information Criterion (AIC) selection and as a result certain ground covers were removed. Furthermore, we used this multiple regression model to predict plot temperatures in which certain growth forms were dominant. We also tested this model specifically on MTT study quads to better understand the role of *E. vaginatum* in that community type; for this, we ran an additional AIC selection test.

We also used linear regression to quantify the relationship between observed plot temperature and predicted plot temperature (PPT). PPT was calculated for each study plot by weighing each of the study species' leaf-level temperature by their fractional cover in that respective plot. The key difference between PPT and the plot temperatures predicted by the previous model is that leaf temperatures are taken into consideration in PPT, whereas they are not considered in the previous multiple regression model. The coefficient of determination (R^2) as well as the root-mean-squared error of prediction (RMSE) were used as our model fit statistics. Further, we expanded this model into a multiple linear regression, which, in addition to using PPT as an independent factor, also incorporated the percent cover values for both nonvascular plants (moss and lichen) and other dominant ground cover components (bare ground, water, rocks, and litter). The expanded model was simplified through an AIC selection test. We tested this model on the various community types to better

understand its robustness, and ran an AIC selection test for each community type.

For these linear regressions with observed temperature as the dependent variable, we also explored linear regressions that used the principal components of the ground cover types, as opposed to the raw cover data, to account for the possibility that the ground cover types were well correlated. If the principal component models explained more variance than the multiple regression models, the principal component models would be used.

All statistical analyses were performed in R 3.1.1 (R Core Team, 2014). The hydroGOF package was used for obtaining the RMSE, and the LMERtest package was used for the mixed modeling analysis. Differences and relationships were considered significant at $p < 0.05$. In all analyses, because the ground cover was expressed fractionally, we used the arcsine square root transformation of the cover types.

RESULTS

Leaf-Level Measurements

There were significant species-level differences in temperatures ($p < 0.05$). The range of average observed leaf temperatures for all species was between 22.74 and 27.19 °C, with a mean of 24.96 °C and standard error of 0.55 °C (Fig. 2). Deciduous shrubs were significantly cooler than all other growth forms ($p < 0.05$); forbs were significantly cooler than evergreens and graminoids ($p < 0.05$); lastly, evergreens and graminoids were not significantly different from one another ($p > 0.05$). The random effect of "Species" was omitted from the growth-form model because it was not significant.

Plot-Level Ground Cover Model

Our multiple regression modeling results suggest that plot temperature can be predicted by ground cover (Table 2). The model that explained the most variance included the transformed fractional cover of *B. nana, Cassiope tetragona, Empetrum nigrum, E. vaginatum, Rubus chaemomorus, Salix pulchra, Salix reticulata, Vaccinium uliginosum,* lichen, litter, and moss ($p < 0.05$; $R^2 = 0.61$; standard error: 0.77; degrees of freedom: 45) (Table 2). The significant independent variables in the regression model were the transformed
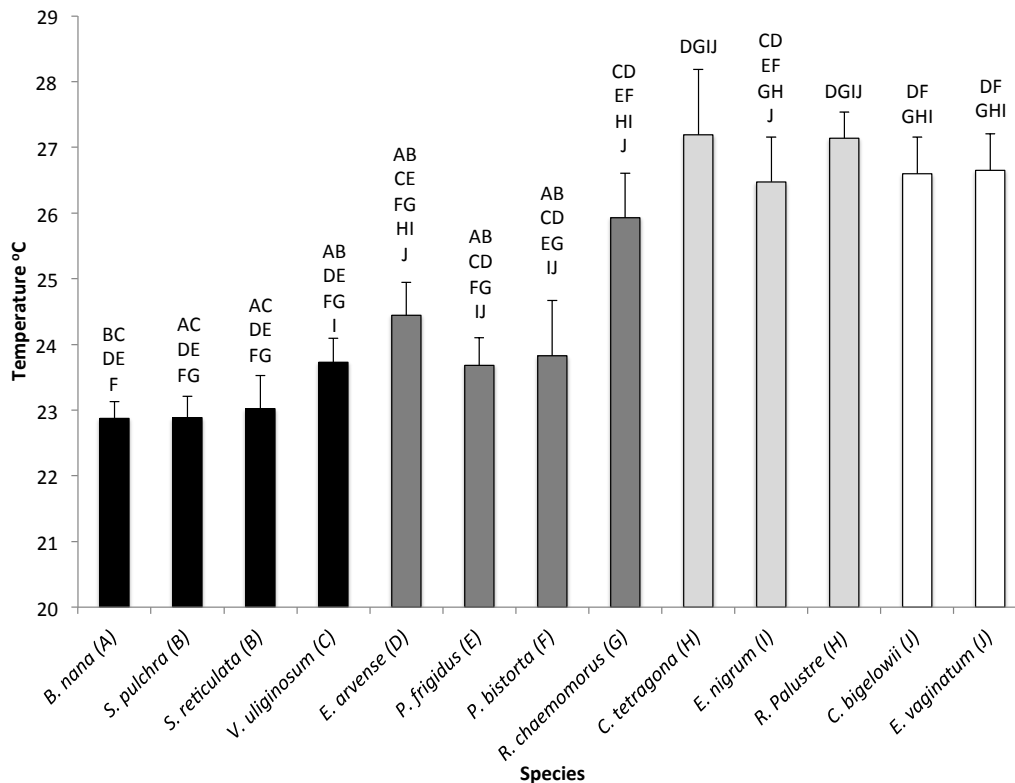
FIGURE 2. Leaf temperatures of the 13 study species. Black: deciduous shrub; dark gray: forb; light gray: evergreen; white: graminoid. Letters illustrate which species are not significantly different from one another.

fractional cover of *E. vaginatum, R. chaemomorus, S. reticulata,* litter, and moss ($p < 0.05$) (Table 2). The parameter estimates suggest that if everything else is held constant, an increase in *E. vaginatum, R. chaemomorus, S. reticulata,* litter, or moss would result in a decreased plot temperature (Table 2). Plot temperatures ranged from 12.67 to 17.95 °C, with a mean of 15 °C and standard error of 0.16 °C. Specifically in MTT study quads, we found that the model remains significant with a strong explanatory power ($p < 0.001$; $R^2 = 0.61$; standard error: 0.75; degrees of freedom: 20), and the coefficient remains negative (–5.94) for *E. vaginatum* (data not shown).

Using the multiple regression model that was based on the study quads from all community types, we found that in a modeled scenario in which the percent cover of *B. nana* and *S. pulchra* (two of the dominant deciduous shrubs; Bret-Harte et al., 2001) both composed 50% of the ground cover, the predicted plot temperature was 17.05 °C (95% prediction interval between 14.82 and 19.28 °C; data not shown). In a scenario in which percent cover was entirely (i.e., 100%) composed of *E. vaginatum* (a

dominant graminoid; Bret-Harte et al., 2001), the predicted plot temperature was 14.46 °C (95% prediction interval between 11.49 and 17.43 °C; data not shown).

Plot-Level Ground Cover and Leaf Temperature Model

There was no significant relationship between PPT (based on percent cover and leaf temperatures) and observed plot temperature ($p > 0.05$; $R^2 < 0.1$; RMSE > 5; data not shown). After adding nonvascular plant ground cover, the predictive model became significant and explained 32% of the variance in temperature ($p < 0.01$; $R^2 = 0.32$; standard error = 1.021; degrees of freedom: 53) (Table 3). The multiple regression that explained the greatest amount of variance included PPT and cover of water and lichen. The only significant independent variable in this multiple regression was lichen cover ($p < 0.05$); water cover and PPT were not significant (Table 3).

When used on the various community types, this model had a range of explanatory power. For MTT,

TABLE 2

The results of a multiple regression exploring the impacts of ground cover of vascular plants and non-vascular plant ground cover on observed plot temperature. Model $R^2 = 0.611$; $p < 0.01$; standard error $= 0.77$; degrees of freedom $= 45$. Bold denotes a significant variable.

Plot temp~	Parameter estimate	*P*-value
Betula nana	−1.424	0.159
Cassiope tetragona	1.799	0.166
Empetrum nigrum	−1.600	0.157
Eriophorum vaginatum	**−3.890**	**0.002**
Rubus chaemomorus	**−3.154**	**0.001**
Salix pulchra	−1.176	0.186
Salix reticulata	**−6.719**	**0.042**
Vaccinium uliginosum	1.683	0.093
Lichen	1.647	0.083
Litter	**−4.048**	**0.001**
Moss	**−3.037**	**0.009**

TABLE 3

The results of a multiple regression where the dependent variable was observed plot temperature and independent variables were predicted plot temperature (PPT) (based on fractional cover of dominant vascular plants and species-specific leaf temperatures), proportion of plot consisting of standing water, and proportion of plot consisting of lichens. Model $R^2 = 0.32$; $p < 0.01$; standard error $= 1.021$; degrees of freedom $= 53$. Bold denotes a significant variable.

Plot temp~	Parameter estimate	P-value
Predicted plot temperature (PPT)	−0.2950	0.107
Water	−4.2748	0.056
Lichen	**4.5403**	**<0.001**

the model with the best explanatory power (PPT and bare ground as independent variables) increased in explanatory power ($p < 0.01$; $R^2 = 0.44$; standard error $= 0.9$; degrees of freedom $= 26$), when compared to the explanatory power of the model on all of the study quads. However, for the other two community types (EST and PDS) the model was not significant (data not shown).

We used the linear regression models with the raw cover data instead of the principal components of the raw cover data because the model with principal components explained less of the variance than the models that incorporated the raw cover data. Each of the principal components explained a relatively small proportion of variance, suggesting that there was not a strong correlation between types of ground cover (data not shown).

DISCUSSION

Interspecific Differences in Leaf-Level Temperature

Our study found that plant species common to this arctic tundra system showed significant interspecific variability in leaf temperatures, which is consistent with our first hypothesis. Deciduous shrub and forb species had significantly cooler leaf temperatures than evergreen and graminoid species. This finding supports previous work from the arctic tundra in which leaf-trait values cluster by growth form (e.g., Oberbauer and Oechel, 1989, Johnson and Tieszen, 1976). Given that rates of plant physiological processes are strongly temperature dependent (Berry and Bjorkman, 1980), the interspecific variation in leaf temperatures observed here suggests that different species may be experiencing different in situ operating temperatures for physiological processes, which may influence operating physiological rates, even when in similar regional climates. Further, below 35 °C, temperature-induced changes in photosynthetic rates are reversible (e.g., there is no permanent damage to the physiological infrastructure) for most plants. When temperatures are above 35 °C, however, there may be irreversible damage to various enzymes in the photosynthetic system (Berry and Bjorkman, 1980). The Intergovernmental Panel on Climate Change reports that by 2100 temperatures for the Alaskan Arctic will increase between 2 and 9 °C (Stocker, 2014). Currently, the average temperature for the area is 14 °C (van Wijk et al., 2005). Therefore, there is potential for the average temperature to be 23 °C by 2100. However, for 2015 the maximum temperature reached at Toolik Field Station was 26 °C on 6 July at 17:00 (Cherry and Cohen, 2014 and 2015). This maximum for 2015 was 12 °C above the average. Therefore, if we assume that the variability of temperatures will remain similar and if we use the predictions from the extreme climate change sce-

nario model (RCP 8.5), the maximum temperature for 2100 would be exactly 35 °C. Therefore, this suggests that species with warmer leaves—such as the sun-lit evergreen and graminoid species in our study—may experience greater physiological stress as accelerated arctic warming continues (McElwain et al., 1999).

Here, we observed that the temperature of the leaves of deciduous shrubs is closely tied to the temperature of the atmosphere (deciduous shrub average: 23.13 °C; temperature of atmosphere during sampling: 22.9 °C; Fig. 2), whereas evergreen and graminoid plants are warmer than the atmosphere by more than 3° (evergreen average: 26.9 °C, graminoid average: 26.6 °C; Fig. 2). These findings are supported by Jarvis and McNaughton's explanation of plant canopy-atmosphere decoupling (Jarvis and McNaughton, 1986). Canopy height and complexity greatly influence the coupling of plant canopy and atmospheric conditions by altering airflow (Lambers et al., 2008); for example, pine wood canopy conditions are found to be largely coupled to the atmosphere (Whitehead et al., 1984) and grasslands are found to be decoupled (McNaughton and Jarvis, 1983). Increasing structural complexity causes eddies of air to penetrate the canopy, homogenizing the leaf conditions and the atmospheric conditions (Lambers et al., 2008). Therefore, in this present study, the environmental conditions of plants with increasing structural height and complexity (i.e., deciduous shrubs) are expected to be more closely tied to the atmosphere, and the environmental conditions of plants with decreasing structural height and complexity (i.e., evergreens and graminoids) are expected to be less closely tied.

In addition to canopies, coupling between individual leaf conditions and the atmosphere can also be explored. The degree to which leaf conditions are coupled to atmospheric conditions is influenced by the boundary layer and the stomatal conductance of the leaf (Jarvis and McNaughton, 1986). The boundary layer of a leaf is dictated by a variety of leaf characteristics such as leaf size and morphology (Monteith and Unsworth, 1990; Nobel, 1991; Schuepp, 1993; Martin et al., 1999). Boundary layer increases in size with increasing size of leaf (Miller et al., 1976; Nobel, 1991). The larger the boundary layer, the more decoupled the conditions at the leaf surface are from the atmosphere. Another component influencing the magnitude of coupling is stomatal conductance. If stomatal conductance is extremely high (e.g., ∞), the water vapor pressure deficit condition (the difference between saturated vapor pressure and actual vapor pressure) at the leaf surface (VPD_L) is less coupled to the environment because VPD_L will become zero even if there are changes in evaporation rate caused by changes in the atmospheric water vapor pressure deficit (VPD_A) or changes in the boundary layer. In other words, as stomatal conductance increases, coupling between VPD_L and VPD_A has a greater capacity to decrease (Jarvis and McNaughton, 1986). The observed conditions of graminoids and deciduous shrubs, namely that graminoids have narrow leaves and low stomatal conductance when compared to deciduous shrubs in the Arctic (personal observation; Oberbauer and Oechel, 1989), suggest that the leaf microenvironment of graminoids should be more closely tied to the environment (as was shown in the modeled leaf temperatures of Miller et al., 1976).

Given this understanding of leaf/canopy-atmosphere coupling, our observations support the claim that the temperatures of leaves in this study may be more influenced by canopy-atmosphere coupling than leaf-atmosphere coupling forces, due to the fact that we found that the temperature conditions at the deciduous shrub surface, when compared to the graminoid surface, were more closely tied to the environment. However, forbs are an exception to this conclusion—we found that many of the low-lying forbs are closely tied to the environment. This finding does not support the theory that canopy-atmosphere coupling is the driving dictator of leaf temperature and suggests that there may be a complex interaction occurring between the influence of canopy structure and leaf characteristics on plant-atmosphere coupling and/or that other factors may also be influencing leaf temperature.

Another factor to consider is evaporative cooling. Stomatal conductance, in a context outside of leaf-atmosphere coupling, should also be considered because conductance in the context of evaporative cooling is known to play a role in controlling leaf temperature (Ansari and Loomis, 1959; Medina et al., 1978; Oke, 1987). Oberbauer and Oechel (1989) found that leaf-level stomatal conductances are lowest for evergreens, intermediate for forbs and graminoids, and highest for deciduous shrubs.

This observed pattern supports our findings, in the context of latent-heat loss.

While we identify canopy-atmospheric coupling and evaporative cooling as key drivers of leaf temperature, other factors are also known to influence leaf temperature (Martin et al., 1999; Doughty et al., 2011). In trying to understand the complex parameters influencing leaf temperature, we ran a leaf energy budget model with leaf temperature as the output (Appendix text and Tables A1 and A2). This model provided leaf temperatures that were inconsistent with our observed leaf temperatures, further shedding light on the complexity of factors influencing leaf temperature (Appendix text). We assume that leaf level temperature is dictated by a suite of interactions between canopy height and structural complexity, leaf size, leaf orientation, stomatal conductance, albedo, surrounding environmental temperature (e.g., tussock/surrounding community temperature and soil temperature/permafrost depth) and other leaf traits, such as trichome density (Ehleringer, 1989; Martin et al., 1999; Doughty et al., 2011).

## Influence of Canopy Composition and Leaf Temperature on Canopy Temperature

In partial support of our second hypothesis, we were able to predict plot temperatures based on fractional cover of vascular plant ground cover and other dominant ground cover components ($p <$ 0.01; R^2 = 0.61; Table 2). Extrapolating our plot-level ground cover model to modeled community types, our results show that if there is a shift from a completely graminoid dominated community to a completely shrub dominated community, the temperature of the plot would increase by 2.59 °C. By illustrating the importance of species cover for plot temperature, our findings support previous studies that suggest that a climate change–induced shift in communities could play a key role in altering the tundra's energy balance (Loranty et al., 2011), as well as energy dependent properties and processes, such as arthropod and microbial habitation (Pincebourde and Woods, 2012).

In juxtaposition to our second hypothesis, inclusion of leaf temperatures in our model, interestingly, did not improve the predictive power—

in fact, predictive power (i.e., R^2) decreased from 0.61 to 0.32. However, it is important to note both that (1) the model had more explanatory power in the MTT community type when compared to the other community types, and (2) for the EST and PDS communities, medium to large stature shrubs are more common than in MTT communities (Britton, 1966; Shaver and Chapin, 1991; water track tundra as described in Chapin et al., 1988). These observations suggest that, generally, properties of canopies other than leaf level temperature are dictating canopy temperature, and, specifically, properties associated with increasing canopy structural complexity may be a dominant cause of the leaf-temperature model breakdown—including the influence of canopy architecture on canopy-atmosphere coupling and the influence of total aboveground biomass on absorbed irradiance and canopy shading (Stoner et al., 1978; Oke, 1987; Friedl and Davis, 1994; Beringer et al., 2005).

Additionally, there were discrepancies between spatial resolutions (species-specific leaf temperatures vs. the temperatures of communities dominated by that respective species). These discrepancies further support the claim that properties of canopies other than leaf-level temperature are dictating canopy temperature. To illustrate the point of observed discrepancies between spatial resolutions, while we found that *E. vaginatum* had warmer leaves relative to other study species, a higher percent cover of this species was associated with lower plot temperatures when looking at all tundra types, as well as specifically MTT sites. This is inconsistent not only with our own leaf-level findings, but also with our thermographic images that illustrate that graminoid-dominated tundra appeared warmer than adjacent shrub-dominated tundra (Fig. 3). Further, this finding is also inconsistent with the finding of Chapin et al. (1979) that *E. vaginatum* tussocks were 6–8 °C warmer than surrounding intertussock areas. Additionally, Miller et al. (1984) also found that infrared loss from tussock areas was higher than from intertussock areas in a modeled scenario. Chapin et al. (1979) attribute this temperature difference between tussocks and intertussock areas to the fact that, relative to prostrate intertussock vegetation, tussocks have a protruding and bulbous physical structure (which increases the amount of inter-
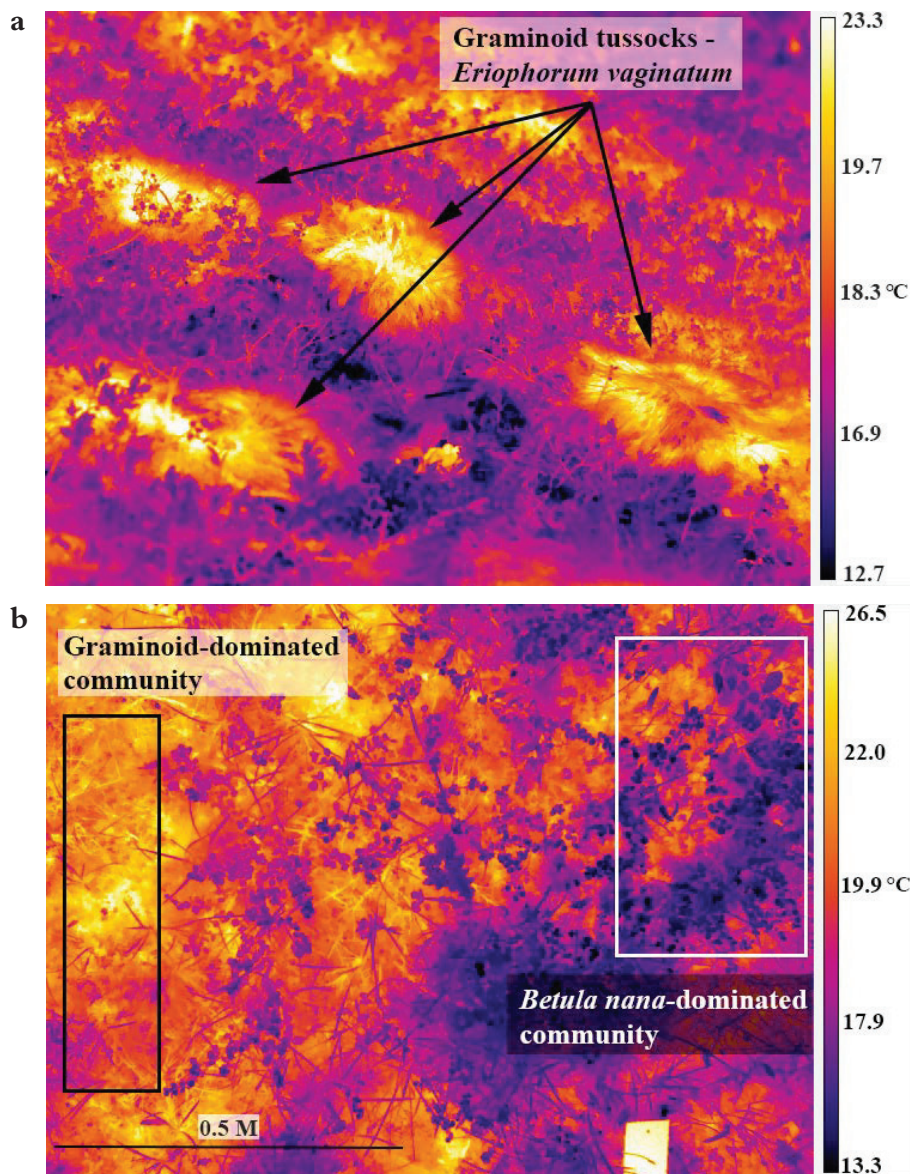
FIGURE 3. (A) Infrared image showing the warming effect of *Eriophorum vaginatum* tussocks relative to inter-tussock areas. (B) Infrared image showing the difference between *Betula nana* (shrub) communities and graminoid communities.

cepted solar radiation and causes snow melt to occur earlier relative to intertussock areas). A potential hypothesis for explaining this paradox between spatial scales is that *E. vaginatum* tends to grow in MTT, which typically has moist soil and a low stature canopy (Britton, 1966; Shaver and Chapin, 1991; water track tundra as described in Chapin et al., 1988). Therefore, even though the leaves of *E. vaginatum* are warmer than other species' leaves and intertussock space, the background environmental properties of the community type (evaporation from the moist soil) may be swamping that warming signal. Relatedly, because MTT typically has a shorter statured canopy, the back-

ground signal of the soil may be more prevalent even if in certain areas the soil is not significantly moister than other tundra types. We suggest that in order to gain a mechanistic understanding of thermographic patterns at the plot scale, further examination is needed of the thermal properties and contributions of underlying biotic and abiotic components that combine and interact in complex ways to affect plot-level temperatures.

Because the arctic system has unique characteristics, such as underlying permafrost and short stature plant communities, and because this study was a snapshot in time of day and time of season, extrapolating the findings of this study to other systems and

to other times of year requires caution. Because the permafrost may be playing a role in dictating temperatures in this system, the scaling relationships may differ in systems without frozen soil. Also, because the model with PPT had more explanatory power in communities with less structural complexity, the findings of this study may have more relevance for similar short statured communities. Similarly, because leaf temperature is sensitive to environmental conditions, for scenarios with relatively greater intensity of turbulent mixing, due to increased canopy roughness and/or wind speed, these scaling relationships may be more complex. Additionally, in other systems where sunrise and sunset can lead to more dramatic changes in absorbed solar radiation, plant physiology, and environmental conditions, the relationship between leaf and canopy temperatures may differ more at various times of day. The findings of this study should therefore be understood as the relationship between leaf and canopy during midday. Also, because this study was a snapshot in time during peak growing season, it does not address these scaling relationships in the context of phenological shifts. Therefore, a next step in understanding these relationships between spatial scales would be to document the thermal phenology of both leaves and canopies for the area of interest.

CONCLUSION

This study has shown that in the Alaskan arctic tundra (1) dominant plant species significantly differ in leaf temperatures, (2) canopy composition plays an important role in dictating canopy temperature, and (3) leaf temperatures of the dominant plant species do not dictate plot temperature. These findings have important implications for the changing arctic tundra, as well as for our understanding of the relationships between the thermal properties of vegetation at various spatial resolutions.

ACKNOWLEDGMENTS

REFERENCES CITED

Allen, R. G., Tasumi, M., and Trezza, R., 2007: Satellite-based energy balance for mapping evapotranspiration with internalized calibration (METRIC)—model. *Journal of Irrigation and Drainage Engineering*, 133(4): 380–394.

Anderson, M. C., Allen, R. G., Morse, A., and Kustas, W. P., 2012: Use of Landsat thermal imagery in monitoring evapotranspiration and managing water resources. *Remote Sensing of Environment*, 122: 50–65.

Ansari, A. Q., and Loomis, W. E., 1959: Leaf temperatures. *American Journal of Botany*, 46(10): 713–717.

Asner, G. P., 1998: Biophysical and biochemical sources of variability in canopy reflectance. *Remote Sensing of Environment*, 64(3): 234–253.

Atkin O. K., Bloomfield K. J., Reich P. B., Tjoelker M. G, Asner G. P., Bonal D., Bönisch G., Bradford M., Cernusak L. A., Cosio E. G., Creek D., Crous K.Y., Domingues T., Dukes J. S., Egerton J. J. G., Evans J. R., Farquhar G. D., Fyllas N. M., Gauthier P. P. G., Gloor E., Gimeno T. E., Griffin K. L., Guerrieri R., Heskel M. A., Huntingford C., Ishida F. Y., Kattge J., Lambers H., Liddell M. J., Lush C. H., Martin R. E., Maximov T. C., Maksimov A. P., Mahli Y., Medlyn B. E., Meir P., Mercado L. M., Mirotchnick N., Ng D., Niinemets U., O`Sullivan O. S., Philips O. L., Poorter L., Poot P., Prentice I. C., Salinas N., Rowland L. M., Ryan M. G., Sitch S., Slot M., Smith N. G., Turnbull M. H., Vanderwel M. C., Valladares F., Veneklaas E. J., Weerasinghe L. K., Wirth C., Wright I. J., Wythers K., Xiang J., Xiang S., Zaragoza-Castells J. 2015: Global variability in leaf respiration among plant functional types in relation to climate and leaf traits. *New Phytologist*, 206(2): 614–636. doi http://dx.doi.org/10.1111/nph.13253.

Beard, J. S., 1978: The physiognomic approach. *In Classification of Plant Communities*. Springer Netherlands, 33–64.

Beringer, J., Chapin, F. S., Thompson, C. C., and McGuire, A. D., 2005: Surface energy exchanges along a tundra-forest transition and feedbacks to climate. *Agricultural and Forest Meteorology*, 131(3–4): 143–161.

Berry, J., and Bjorkman, O., 1980: Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology*, 31: 491–543.

Billings, W. D., and Mooney, H. A., 1968: The ecology of arctic and alpine plants. *Biology Review*, 43: 481–529.

Boelman, N. T., Gough, L., McLaren, J. R., and Greaves, H., 2011: Does NDVI reflect variation in the structural attributes associated with increasing shrub dominance in arctic tundra? *Environmental Research Letters*, 6(3): 035501. doi http://dx.doi.org/10.1088/1748-9326/6/3/035501.

Bret-Harte, M. S., Shaver, G. R., Zoerner, J. P., Johnstone, J. F., Wagner, J. L., Chavez, A. S., Gunkelman, R. F., IV, Lippert, S. C., and Laundre, J. A., 2001: Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. *Ecology* 82(1): 18–32.

Britton, M. E., 1966: *Vegetation of the Arctic Tundra*. Corvallis: Oregon State University Press.

Bunce, J. A., Chabot, B. F., and Miller, L. N., 1979: Role of annual leaf carbon balance in the distribution of plant

species along an elevational gradient. *Botanical Gazette*, 140: 288–294.

Chandler, W. H., 1913: *The Killing of Plant Tissue by Low Temperature*, Volume 6. Columbia: University of Missouri, College of Agriculture, Agricultural Experiment Station.

Chapin, F. S., Van Cleve, K., and Chapin, M. C., 1979: Soil temperature and nutrient cycling in the tussock growth form of *Eriophorum vaginatum*. *Journal of Ecology*, 67(1): 169–189.

Chapin, F. S., Fetcher, N., Kielland, K., Everett, K. R., and Linkins, A. E., 1988: Productivity and 451 nutrient cycling of Alaskan tundra: enhancement by flowing soil water. *Ecology*, 69: 693–702.

Chapin, F. S., Sturm, M., Serreze, M. C., McFadden, J. P., Key, J. R., Lloyd, A. H., McGuire, A. D., Rupp, T. S., Lynch, A. H., Schimel, J. P., and Beringer, J., 2005: Role of land-surface changes in arctic summer warming. *Science*, 310(5748): 657–660.

Cherry, J. E., and Cohen, L. R., 2014 and 2015: Meteorological monitoring program at Toolik, Alaska. Toolik Field Station, Institute of Arctic Biology, University of Alaska Fairbanks. http://toolik.alaska.edu/edc/abiotic_monitoring/data_query.php.

Doughty, C. E., Field, C. B., and McMillan, A. M., 2011: Can crop albedo be increased through the modification of leaf trichomes, and could this cool regional climate? *Climatic Change*, 104(2): 379–387.

Ehleringer, J. R., 1989: Temperature and energy budgets. *In* Pearcy, E. W., Ehleringer, J., Mooney, H. A., and Rundel, P. W. (eds.), *Plant Physiological Ecology.* Springer Netherlands, 117–135.

Elmendorf, S. C., Henry, G. H., Hollister, R. D., Björk, R. G., Boulanger-Lapointe, N., Cooper, E. J., Cornelissen, J. H., Day, T. A., Dorrepaal, E., Elumeeva, T. G., and Gill, M., 2012: Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change*, 2(6): 453–457.

Friedl, M. A., and Davis, F. W., 1994: Sources of variation in radiometric surface temperature over a tallgrass prairie. *Remote Sensing of Environment*, 48(1): 1–17.

Gillies, R. R., and Carlson, T. N., 1995: Thermal remote sensing of surface soil water content with partial vegetation cover for incorporation into climate models. *Journal of Applied Meteorology*, 34(4): 745–756.

Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Alonso, J. L. B., Coldea, G., Dick, J., Erschbamer, B., Kazakis, G., and Krajči, J., 2012: Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, 2(2): 111–115.

Gough, L., and Hobbie, S. E., 2003: Responses of moist non-acidic arctic tundra to altered environment: productivity, biomass, and species richness. *Oikos*, 103(1): 204–216.

Gough, L., Shaver, G. R., Carroll, J., Royer, D. L., and Laundre, J. A., 2000: Vascular plant species richness in Alaskan arctic tundra: the importance of soil pH. *Journal of Ecology*, 88(1): 54–66.

Hobbie, S. E., and Chapin, F. S., 1998: The response of tundra plant biomass, aboveground production, nitrogen, and CO flux to experimental warming. *Ecology*, 79(5): 1526–1544.

Heskel, M., Bitterman, D., Atkin, O. K., Turnbull, M. H., and Griffin, K. L., 2013: Seasonality of foliar respiration in two dominant plant species from the arctic tundra: response to long-term warming and short-term temperature variability. *Functional Plant Biology*, 41(3): 287–300.

Heskel, M., Greaves, H. E., Turnbull, M., O'Sullivan, O. S., Shaver, G. R., Griffin, K. L., and Atkin, O. K., 2014: Thermal acclimation of shoot respiration in an arctic woody plant species subjected to 22 years of warming and altered nutrient supply. *Global Change Biology*, 20(8): 2618–2630.

Jarvis, P. G., and McNaughton, K. G., 1986: Stomatal control of transpiration: scaling up from leaf to region. *Advances in Ecological Research*, 15(1): 1–49.

Johnson, D. A., and Tieszen, L. L., 1976: Aboveground biomass allocation, leaf growth, and photosynthesis patterns in tundra plant forms in arctic Alaska. *Oecologia*, 24(2):159–173.

Jones, H. G., 1999: Use of infrared thermometry for estimation of stomatal conductance as a possible aid to irrigation scheduling. *Agricultural and Forest Meteorology*, 95(3): 139–149.

Jones, H. G., 2004: Application of thermal imaging and infrared sensing in plant physiology and ecophysiology. *Advances in Botanical Research*, 41: 107–163. doi http://doi.org/10.1016/S0065-2296(04)41003-9.

Lambers, H., Chapin, F. S., and Pons, S., 2008: *Plant Physiological Ecology*. New York: Springer.

Leuzinger, S., and Körner, C., 2007: Tree species diversity affects canopy leaf temperatures in a mature temperate forest. *Agricultural and Forest Meteorology*, 146(1–2): 29–37.

López, A., Molina-Aiz, F. D., Valera, D. L., and Peña, A., 2012: Determining the emissivity of the leaves of nine horticultural crops by means of infrared thermography. *Scientia Horticulturae*, 137: 49–58.

Loranty, M. M., and Goetz, S. J., 2012: Shrub expansion and climate feedbacks in arctic tundra. *Environmental Research Letters*, 7(1): 011005, doi http://dx.doi.org/10.1088/1748-9326/7/1/011005.

Loranty, M. M., Goetz, S. J., and Beck, P. S., 2011: Tundra vegetation effects on pan-arctic albedo. *Environmental Research Letters*, 6(2): 024014 doi http://dx.doi.org/10.1088/1748-9326/6/2/024014.

Martin, T. A., Hinckley, T. M., Meinzer, F. C., and Sprugel, D. G., 1999: Boundary layer conductance, leaf temperature and transpiration of *Abies amabilis* branches. *Tree Physiology*, 19(7): 435–443.

Matsushima, D., and Kondo, J., 2000: Estimating regional distribution of sensible heat flux over vegetation using satellite infrared temperature with viewing angle correction. *Journal of the Meteorological Society of Japan*, 78(6): 753–763.

McElwain, J. C., Beerling, D. J., and Woodward, F. I., 1999: Fossil plants and global warming at the Triassic-Jurassic boundary. *Science*, 285(5432): 1386–1390.

Mclaughlin, B. C., Xu, C.-Y., Rastetter, E. B., and Griffin, K. L., 2014: Predicting ecosystem carbon balance in a warming Arctic: the importance of long-term thermal acclimation potential and inhibitory effects of light on respiration. *Global Change Biology*, 20(6): 1901–1912. doi http://dx.doi.org/10.1111/gcb.12549.

McNaughton, K. G., and Jarvis, P. G., 1983: Predicting effects of vegetation changes on transpiration and evaporation. *Water Deficits and Plant Growth*, 7: 1–47.

Medina, E., Sobrado, M., and Herrera, R., 1978: Significance of leaf orientation for leaf temperature in an Amazonian sclerophyll vegetation. *Radiation and Environmental Biophysics*, 15(2): 131–140.

Miller, P. C., Stoner, W. A., and Tieszen, L. L., 1976: A model of stand photosynthesis for the wet meadow tundra at Barrow, Alaska. *Ecology*, 57(3): 411–430.

Miller, P. C., Miller, P. M., Blake-Jacobson, M., Chapin, F. S., Everett, K. R., Hilbert, D. W., Kummerow, J., Linkins, A. E., Marion, G. M., Oechel, W. C., and Roberts, S. W., 1984: Plant-soil processes in *Eriophorum vaginatum* tussock tundra in Alaska: a systems modeling approach. *Ecological Monographs*, 54(4): 362–405.

Monteith, J. L., and Unsworth, M. H., 1990: Radiation environment. *In Principles of Environmental Physics.* Second edition. London: Edward Arnold, 36–57.

Mooney, H. A., 1977: *Convergent Evolution in Chile and California: Mediterranean Climate Ecosystems.* Dowden, Hutchinson & Ross.

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K. D., Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E., and Boudreau, S., 2011: Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters*, 6(4): 045509, doi http://dx.doi.org/10.1088/1748-9326/6/4/045509.

Nobel, P. S., 1991: *Physicochemical and Environmental Plant Physiology*. San Diego: Academic Press.

Oberbauer, S. F., and Oechel, W. C., 1989: Maximum CO_2 assimilation rates of vascular plants on an Alaskan arctic tundra slope. *Holarctic Ecology*, 12(3): 312–316.

Oke, T. R., 1987: *Boundary Layer Climates.* New York: Routledge.

Orians, G. H., and Paine, R. T., 1983: Convergent evolution at the community level. *In Futuyma, D. J., and Slatkin, M. (eds.), Coevolution.* Sunderland, Massachusetts: Sinauer, 431-458.

Parmesan, C., and Yohe, G., 2003: A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918): 37–42.

Pincebourde, S., and Woods, H. A., 2012: Climate uncertainty on leaf surfaces: the biophysics of leaf microclimates and their consequences for leaf-dwelling organisms. *Functional Ecology*, 26(4): 844–853.

Rasband, W. S., 1997–2014. ImageJ. U.S. National Institutes of Health, Bethesda, Maryland. http://imagej.nih.gov/ij.

R Core Team, 2014: R: A language and environment for statistical computing. R Foundation for 641 Statistical Computing, Vienna, Austria. Version 3.1.1. http://www.R-project.org/.

Rich, M. E., Gough, L., and Boelman, N. T., 2013: Arctic arthropod assemblages in habitats of differing shrub dominance. *Ecography*, 36(9): 994–1003.

Schuepp, P. H., 1993: Tansley review no. 59: leaf boundary layers. *New Phytologist*, 125(3): 477–507.

Shaver, G. R., and Chapin, F. S., 1991: Production: biomass relationships and element cycling in contrasting arctic vegetation types. *Ecological Monographs*, 61(1): 1–31.

Sobrino, J. A., Jiménez-Muñoz, J. C., Balick, L., Gillespie, A. R., Sabol, D. A., and Gustafson, W. T., 2007: Accuracy of ASTER Level-2 thermal-infrared Standard Products of an agricultural area in Spain. *Remote Sensing of Environment*, 106(2): 146–153.

Stephenson, N. L., 1990: Climate control of vegetation distribution: the role of the water balance. *The American Naturalist*, 135(5): 649–670.

Stocker, T. F., 2014: *Climate Change 2013: The Physical Science Basis: Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge, U.K.: Cambridge University Press.

Stoner, W. A., and Miller, P. C., 1975: Water relations of plant species in the wet coastal tundra at Barrow, Alaska. *Arctic and Alpine Research*, 7(2): 109–124.

Stoner, W. A., Miller, P. C., and Miller, P. M., 1978: A test of a model of irradiance within vegetation canopies at northern latitudes. *Arctic and Alpine Research*, 10(4): 761–767.

Sturm, M., Racine, C., and Tape, K., 2001: Climate change: increasing shrub abundance in the Arctic. *Nature*, 411(6837): 546–547.

Sweet, S. K., Asmus, A., Rich, M. E., Wingfield, J., Gough, L., and Boelman, N. T., 2015: NDVI as a predictor of canopy arthropod biomass in the Alaskan arctic tundra. *Ecological Applications*.

Tape, K., Sturm, M., and Racine, C., 2006: The evidence for shrub expansion in northern Alaska and the Pan-Arctic. *Global Change Biology*, 12(4): 686–702.

Thompson, C., Beringer, J., Chapin, F. S., and McGuire, A. D., 2004: Structural complexity and land-surface energy exchange along a gradient from arctic tundra to boreal forest. *Journal of Vegetation Science*, 15(3): 397-406.

Van Wijk, M. T., Williams, M., and Shaver, G. R., 2005: Tight coupling between leaf area index and foliage N content in arctic plant communities. *Oecologia*, 142(3): 421–427.

Walker, D. A., Raynolds, M. K., Daniëls, F. J., Einarsson, E., Elvebakk, A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Melnikov, E. S., and Moskalenko, N. G., 2005: The circumpolar arctic vegetation map. *Journal of Vegetation Science*, 16(3): 267–282.

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T., Fromentin, J., Hoegh-Guldberg, O., and Bairlein, F., 2002: Ecological responses to recent climate change. *Nature*, 416(6879): 389–395.

Wilson, J. W., 1957: Observations on the temperatures of arctic plants and their environment. *The Journal of Ecology*, 499–531.

Whitehead, D., Jarvis, P. G., and Waring, R. H., 1984: Stomatal conductance, transpiration, and resistance to water uptake in a *Pinus sylvestris* spacing experiment. *Canadian Journal of Forest Research*, 14(5): 692–700.

Zhao, C., and Liu, Q., 2009: Growth and photosynthetic responses of two coniferous species to experimental warming and nitrogen fertilization. *Canadian Journal of Forest Research*, 39(1): 1–11.

Zhou, X., Liu, X., Wallace, L. L., and Luo, Y., 2007: Photosynthetic and respiratory acclimation to experimental warming for four species in a tallgrass prairie ecosystem. *Journal of Integrative Plant Biology*, 49(3): 270–281.

LEAF ENERGY BUDGET MODEL

To better understand the influence of various biotic and abiotic factors on leaf temperature, we used a version of the leaf energy budget equation (Miller, 1972; Ehleringer et al., 1989; Monson and Baldocchi, 2014) to calculate the predicted leaf temperature (explanation of variables in Appendix Table A1):

$$T_l = \frac{Q^n - 2\varepsilon\sigma T_a^4 - \dfrac{0.622\lambda\rho_a g_w (e_s(T_a) - e_a)}{P}}{2\rho_a C_p g_a - 8\varepsilon\sigma T_a^3 + \dfrac{0.622\lambda\rho_a g_w (de_s / dT_a)}{P}} + T_a$$

The environmental inputs were averaged measurements over the 30-minute interval in which leaf level measurements were made (Table A1). Toolik Field Station provided the meteorological data (Cherry and Cohen, 2014 and 2015). Stomatal conductances were maximum stomatal conductances for growth form that were taken from the literature (Oberbauer and Oechel, 1989; Oberbauer and Dawson, 1992). Leaf areas were found by averaging various online botanical library descriptions (Table A2). The species we looked at with this leaf energy budget model were *Betula nana, Salix pulchra*, and *Eriophorum vaginatum*. This leaf temperature model gave us leaf temperatures that were within 0.2 °C of each other (Table A2). *E. vaginatum* was 22.6 °C, *B. nana* was 22.7 °C, and *S. pulchra* was 22.5 °C. These modeled temperatures are not consistent with our observed leaf temperatures. Here we discuss reasons for this discrepancy.

One may predict that *E. vaginatum* would be more closely tied to atmospheric conditions due to its long and narrow leaf shape, and subsequent potential for relatively large convective heat loss. However, this model is not capable of capturing this effect because it takes only "leaf area" into consid-

TABLE A1

Leaf energy budget variables.

	Variable	Units	Input
T_l	Leaf temperature	K	Output
T_a	Atmospheric temperature	K	296.05
Q_n	Net radiation	w m^{-2}	570.57
ε	Emissivity	NA	0.97
σ	Stefan–Boltzmann constant	W m^{-2} K^{-4}	0.00000006
λ	Latent energy exchange (constant)	KJ mol^{-1}	44.1
ρ_a	Density of air	kg m^{-3}	1.225
g_w	Sum of boundary and stomatal conductance ($[0.5^*g_s^*g_a]/[g_s+g_a]$)	mol m^{-2} s^{-1}	Species specific
e_s	Saturated vapor pressure	kPa	2.808
e_a	Actual vapor pressure	kPa	0.924
C_p	Heat capacity	J mol^{-1} K^{-1}	29.3
g_a	Boundary layer conductance ($1.4^*0.147^*[\sqrt{u/d}]$)	mol m^{-2} s^{-1}	Species specific
de_s/dT_a	Slope of the saturation vapor function ($2508.3/[T_a+237.3]^2$)	kpa c^{-1}	0.009
P	Pressure	kpa	93.5
u	Wind speed	m s^{-1}	1.2
d	Leaf area	m^2	Species specific
g_s	Stomatal conductance	mol m^{-2} s^{-1}	Species specific

TABLE A2

Species–specific leaf energy budget inputs and outputs.

Species	Stomatal conductance (mol m^{-2} s^{-1})	Leaf area (m^2)	Source for leaf area	Leaf temperature output (°C)
Betula nana	0.27	0.00008	U.S. Forest Service	22.7
Eriophorum vaginatum	0.26	0.0003	E–Flora BC[a]	22.6
Salix pulchra	0.27	0.0006	CYSIP Botany[b]	22.5

[a]Electronic Atlas of the Flora of British Columbia.
[b]Central Yukon Species Inventory Project: Botany.

eration, not "leaf shape." For example, the input for leaf area of *B. nana* and *E. vaginatum* were 0.00008 and 0.0003 m^2, respectively. Thus, the prediction that *E. vaginatum* should be closely related to air temperature due to its long, narrow shape is not consistent with the output of this model due to the fact that *E. vaginatum* is considered to be larger than *B. nana* when the parameter for leaf size is "area". This area dimension complication then influences the output, which shows that *E. vaginatum* is cooler than *B. nana* and further away from air temperature, which is in contrast to our findings (which shows that *E. vaginatum* is further away from air temperature when compared to *B. nana*, but in the opposite direction [i.e., warmer]). Other potential reasons for the differences in modeled versus observed leaf temperature are leaf orientation, plant height, leaf albedo, and trichome characteristics (Ehleringer et al., 1989). These leaf traits are not included in the model's parameters. Therefore, we suggest that the discrepancy between modeled and observed leaf temperature is due to the complexity of interactions between leaf traits and leaf temperature.

References Cited

Cherry, J. E., and Cohen, L. R., 2014 and 2015: Meteorological monitoring program at Toolik, Alaska. Fairbanks, Alaska: Toolik Field Station, Institute of Arctic Biology, University of Alaska Fairbanks. http://toolik.alaska.edu/edc/abiotic_monitoring/data_query.php.

Ehleringer, J. R., 1989: Temperature and energy budgets. *In* Pearcy, E. W., Ehleringer, J., Mooney, H. A., and Rundel, P. W. (eds.), *Plant Physiological Ecology.* Dordrecht, Netherlands: Springer, 117–135.

Miller, P. C., 1972: Bioclimate, leaf temperature, and primary production in red mangrove canopies in south Florida. *Ecology*, 53(1): 22–45.

Monson, R., and Baldocchi, D., 2014: *Terrestrial Biosphere-Atmosphere Fluxes*. Cambridge and New York: Cambridge University Press.

Oberbauer, S. F., and Dawson, T. E., 1992: Water relations of arctic vascular plants. *In* Chapin, F. S., Jefferies, R. L., Reynolds, J. F., Shaver, G. R., and Svoboda, J. (eds.), *Arctic Ecosystems in a Changing Climate—An Ecophysiological Perspective*. San Diego: Academic Press, 259–279.

Oberbauer, S. F., and Oechel, W. C., 1989: Maximum CO$_2$ assimilation rates of vascular plants on an Alaskan arctic tundra slope. *Holarctic Ecology*, 12(3): 312–316.