The Importance of Conifers for Facilitation at Treeline: Comparing Biophysical Characteristics of Leeward Microsites in Whitebark Pine Communities

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The importance of conifers for facilitation at treeline: comparing biophysical characteristics of leeward microsites in whitebark pine communities

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ABSTRACT

In many of the alpine-treeline ecotones (ATE) of the Rocky Mountains, *Pinus albicaulis* (whitebark pine) is the most common conifer initiating tree islands through facilitation. We examined whether microsites leeward of *P. albicaulis* experience more moderate microclimate, less sky exposure, and more total soil carbon and nitrogen than other common types of leeward microsites. From July to September 2010, 2011, and 2012, in two study areas on the eastern Rocky Mountain Front, we compared microclimate, sky exposure, and total soil carbon and nitrogen leeward of four common microsites, *P. albicaulis*, *Picea engelmannii* (Engelmann spruce), rock, and unprotected (exposed). Microsites leeward of *P. albicaulis* did not consistently experience the most moderate microclimate, but both *P. albicaulis* and *P. engelmannii* leeward microsites had lower daily photosynthetically active radiation (PAR), lower average wind speeds, lower soil temperature maxima, and higher soil temperature minima. In general, conifer microsites had significantly lower values for sky exposure; but, the performance of each microsite type varied from micro to study-area scales. Our results highlight the importance of conifers as nurse objects for facilitating treeline community development in the ATE, and especially *P. albicaulis* because of its high abundance. High losses of *P. albicaulis* from infection by *Cronartium ribicola* may alter community dynamics and treeline response to climate warming.

INTRODUCTION

Recent studies have substantiated the importance of ecological facilitation in community processes (e.g., Callaway et al., 2002; Brooker et al., 2008). Facilitative interactions shape ecosystem structure at the population and community level in environments under high abiotic stress (Stachowicz, 2001; Bruno et al., 2003). "Nurse objects," such as rocks or tree stumps, may also facilitate seed germination and plant establishment (e.g., Angel Munguía-Ross and Sosa, 2008; Castro et al., 2011).

Facilitation often creates a microsite with conditions such as microclimate better suited to seed germination or seedling survival (Spittlehouse and Stathers, 1990; Maher et al., 2005; Resler, 2006). Microclimates are defined as "small-scale climates" influenced by light intensity, precipitation, humidity, wind, air temperature, soil temperature, and soil moisture, usually reflecting regional macroclimate (Spittlehouse and Stathers, 1990). Nurse objects and plants function as facilitators most often by moderating microclimate.

Interactions among species that are competitive in favorable environments often shift to facilitative

under adverse conditions, according to the stress gradient hypothesis (Callaway, 1998; Callaway et al., 2002; Sthultz et al., 2007). Plants in facilitative roles mitigate harsh environments by moderating soil temperatures (Breshears et al., 1998; Chambers, 2001), reducing solar radiation (Germino and Smith, 1999; Germino et al., 2002), increasing soil nutrients (Callaway et al., 1991), and reducing wind speeds (Baumeister and Callaway, 2006). For example, in the southwestern United States, a common shrub *Fallugia paradoxa* facilitates the establishment and survival of *Pinus edulis* at sites experiencing higher drought stress but not in sites of lower drought stress (Sthultz et al., 2007). At upper subalpine elevations in the Rocky Mountains of the United States, *Abies lasiocarpia* (subalpine fir) aggregate around mature *Pinus albicaulis* (whitebark pine), which provide protection in areas of high wind exposure (Callaway, 1998). In general, the plant species that are important facilitators are prevalent, tolerate prevailing conditions, and are able to provide shelter (e.g., Callaway et al., 2002; Baumeister and Callaway, 2006; Sthultz et al., 2007). Facilitative interactions, however, vary in outcome and effectiveness among and within nurse plant species, depending on recipient plant life history stage, extent of disturbance, and harshness of the abiotic environment (Lortie and Turkington, 2008; Soliveres et al., 2011; Michalet et al., 2015).

Facilitative interactions are particularly important in moderating harsh microclimate in treeline communities, where seedling establishment and growth may be limited by low soil temperatures, short growing seasons, winter injury, intense solar radiation, nighttime sky exposure, and leaf loss from extreme winds (Stevens and Fox, 1991; Sveinbjörnsson et al., 1996; Cairns and Malanson, 1997; Körner, 1998; Germino and Smith, 1999; Hoch et al., 2002; Maher et al., 2005). Low soil temperatures lead to photo-inhibition (Germino and Smith, 1999) and slow root growth (Landhäusser et al., 1996). Although photosynthesis rates generally increase as photosynthetically active radiation (PAR) increases, high ambient temperatures and full sunlight decrease survival (Germino et al., 2002; Moyes et al., 2013). Excess sky exposure also lowers soil moisture and results in colder nighttime temperatures from long-wave irradiance (Maher et al., 2005; Germino and Smith, 1999). High wind speeds and radiation reduce soil moisture as well (Holtmeier and Broll, 1992; Holtmeier, 2009). In the Rocky Mountains, soil moisture and the distribution of soil nutrients at treeline may differ among conifer species and with the proximity of trees or tree islands, resulting in differential soil fertility (Van Miegroet et al., 2000; Seastedt and Adams, 2001; Shiels and Sanford, 2001).

The alpine-treeline ecotone (ATE) in the Rocky Mountains represents the transition zone for conifers from upper subalpine forest communities to their upper elevational limits, where krummholz forms predominate (Holtmeier, 2009). Community structure and composition of the ATE are shaped by local processes, including seed dispersal, seed germination, and seedling establishment, which in turn are influenced by microclimate, snow accumulation, and timing of snowmelt (Moir et al., 1999; Alftine and Malanson, 2004; Maher and Germino, 2006; Malanson et al., 2007; Batllori et al., 2009). These processes encompass tree island initiation. This occurs when a solitary conifer facilitates the leeward establishment of another conifer (Bekker, 2005). Further conifer establishment builds a patch of closely associated trees, which we define as a tree island. Thus, seedling establishment may be aided by facilitation from conifers, other vegetation, nurse objects, or by topographic niches, which all moderate harsh conditions (Holtmeier and Broll, 1992; Germino et al., 2002; Maher et al., 2005; Resler et al., 2005; Resler, 2006; Batllori et al., 2009). Little is known, however, about the differences in leeward microclimate provided by different nurse objects or conifer species or how the quality of protection may vary relative to local climate or geographically.

In the ATE in the northern Rocky Mountains, *P. albicaulis*—a widely distributed subalpine conifer of the western United States and Canada—facilitates tree island development more often than associated krummholz conifers, with *Picea engelmannii* as the next most common initiator (Resler and Tomback, 2008; Tomback et al., 2014). *P. albicaulis* seeds are dispersed by Clark's nutcrackers (*Nucifraga columbiana*) throughout mountain terrain, including the ATE (Tomback, 1978, 1986, 2001; Hutchins and Lanner, 1982). Seeds cached by nutcrackers in the ATE near nurse objects and plants and in microtopography may be more protected than wind-dispersed seeds, providing germination and survival

advantage (Malanson et al., 2007; Tomback and Resler, 2007). However, *P. albicaulis* mortality from *Cronartium ribicola*, the non-native pathogen that causes white pine blister rust, is increasing in this region (Smith et al., 2008, 2013; Smith et al., 2011). Mortality of *P. albicaulis* reduces facilitative interactions at treeline (Tomback and Resler, 2007; Resler and Tomback, 2008; Smith-McKenna et al., 2013), which potentially alters community development and the response of treeline to climate warming (Tomback and Resler, 2007; Smith-McKenna et al., 2014).

There are two nonexclusive explanations for the prevalence of *P. albicaulis* as a tree island initiator: (1) *P. albicaulis* may occur as a solitary krummholz tree more frequently than other conifer species in the ATE (Resler and Tomback, 2008; Blakeslee, 2012; Tomback et al., 2014) and thus has a higher probability of facilitating tree island development. However, higher abundance of solitary *P. albicaulis* does not always correspond to its dominance as a tree island initiator (Tomback et al., 2014; Resler et al., 2014). (2) *P. albicaulis* provides a more protective leeward microsite and moderate microclimate than other common conifers or nurse objects at treeline.

Here, we investigated the hypotheses that microsites leeward of *P. albicaulis* in the ATE experience less extreme microclimate, less sky exposure, and more total soil carbon and nitrogen than microsites

leeward of similarly sized krummholz *P. engelmannii* and rocks, or in open, unprotected microsites. To test these hypotheses, we compared values for nine biophysical variables among four common microsite types in two treeline study areas on the climatically harsh Rocky Mountain eastern front. In particular, we propose that *P. albicaulis* leeward microsites experience lower air and soil temperature maxima, higher air and soil temperature minima, moister soils, lower cumulative daily PAR, lower wind and gust speeds, but also lower sky exposure and greater percentages of soil carbon and nitrogen.

METHODS

Study Areas

Research was conducted at two ATE study areas separated by about 500 km and 3° latitude on the eastern Rocky Mountain Front, Montana, U.S.A., from 2010–2014 (Fig. 1). The Divide Mountain study area straddles the eastern boundary between Glacier National Park and Blackfeet Tribal Land (ca. 48°39′25″N, 113°23′45″W; elevation ca. 2200 m) and includes White Calf Mountain (White Calf), which lies directly south on the eastern edge of Glacier National Park, Montana (48°38′20.95″N, 113°24′08.72″W; elevation ca. 2270 m). The Line Creek Research Natural Area
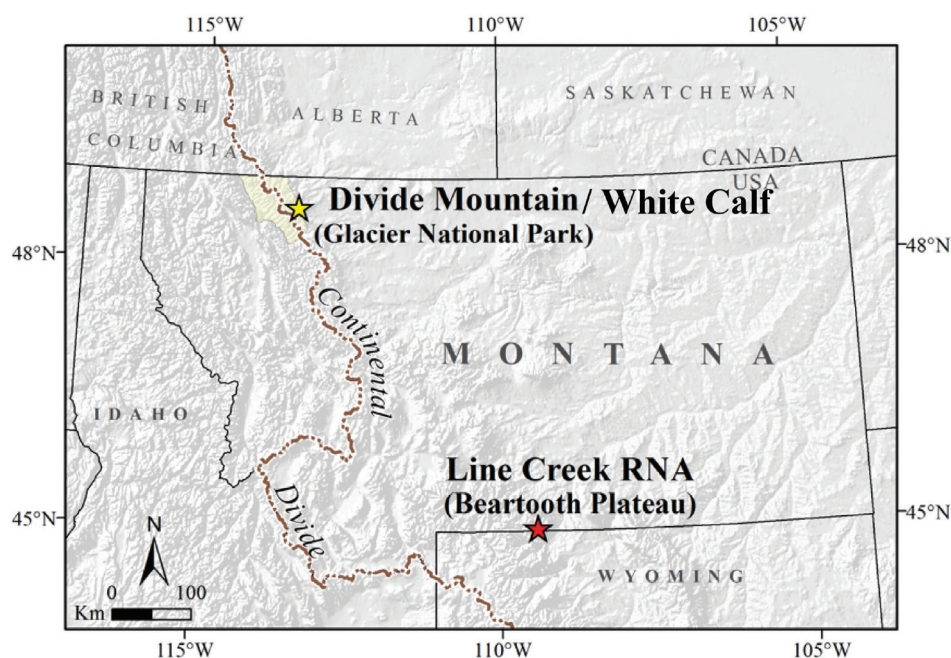
FIGURE 1. Study areas: Divide Mountain and White Calf Mountain on the Blackfeet Reservation and Glacier National Park, and Line Creek Research Natural Area in the Custer National Forest on the Beartooth Plateau in Montana. Map modified from Smith-McKenna et al. (2013). White Calf is adjacent to and 2.5 km south of Divide Mountain.

(Line Creek), Custer National Forest, lies on the east side of the Beartooth Plateau (ca. 45°01′47″N, 109°24′09″W; elevation ca. 2950 m). These study areas comprise ATE with conifers growing as solitary krummholz trees and in tree islands primarily composed of krummholz *P. albicaulis*, *P. engelmannii*, and *A. lasiocarpia*. Previous research in both study areas established that *P. albicaulis* is the majority tree island initiator, and *P. engelmannii* is the second most abundant conifer overall for both study areas (Resler and Tomback, 2008; Smith–McKenna et al., 2013; Tomback et al., 2014: Wyoming Creek = Line Creek Research Natural Area). Data from randomly placed sampling transects indicated that the proportions of solitary trees of *P. albicaulis* were significantly greater than *P. engelmannii* or *A. lasiocarpa* on 16 of 19 transects at Divide Mountain and on 12 of 15 transects at Line Creek (Blakeslee, 2012).

Study sites on Divide Mountain and White Calf are predominantly northeast-facing and on steep slopes (~20°). The bedrock in this region comprises white limestone of the Altyn Formation (Lesica, 2002). The Line Creek study area is also predominantly northeast–facing, but less steep (~11°), with a ridgeline providing west-facing topography. Soils are shallow, coarse, and relatively undeveloped (Nimlos et al., 1965). The local geology is characterized as an uplifted Precambrian granitic mass (Bevan, 1923).

Study Design

We defined a microsite as a circular space 20 cm in diameter and no taller than 15 cm directly leeward of a conifer or rock, or on open ground with no windward protection. Microclimate was recorded in microsites directly leeward of solitary, krummholz *P. albicaulis* and *P. engelmannii*, rocks—and in unprotected (exposed) microsites. Microsite types were grouped in blocks to reduce confounding variation in aspect and topography. Blocks consisted of a set of each microsite type occurring in close proximity (within 10 m). We sought nurse conifers of similar dimensions within a block, but the mean height of rocks (16–42 cm) and nurse trees (30–70 cm) depended on local availability (Appendix 1 [Table A1-1; note that appendices for this paper are available free with the online version of this paper]). In general, the mean tree heights for krummholz nurse conifers on Divide Mountain were nearly half the height of krummholz nurse conifers at Line Creek, reflecting environmental differences between the two study areas. In all cases, the heights were more than double the height of our defined microsite space.

Microsite position was determined by the direction of wind-flagging on branches of surrounding conifer tree islands. We defined the leeward microsite as directly opposite the source of wind causing the most prevalent branch flagging and tree sculpting at each study site. Selected microsites were not protected by nearby objects, trees, or tree islands. In 2010, we established two blocks at Divide Mountain and Line Creek, placing one on a northeast-facing slope and one on a west-facing slope (16 microsites total, 4 of each type). In 2011 and 2012, we focused on northeast-facing slopes, measuring the same three blocks at Divide Mountain and two blocks at Line Creek (20 microsites total, 5 of each type). Microsites at Divide Mountain typically supported a higher percent ground cover (75%–100%) and the understory plants *Arctostaphylos uva-ursi*, *Dryas octopetala,* and less commonly *Poa alpina*. Microsites at Line Creek supported less ground cover (50%–75%) and the plants *Carex* spp., *Aster alpigenus*, and *Geum rossii*. Conifer microsites differed from rock and unprotected microsites in that they often had a layer of conifer needle litter.

Microclimate Weather Station Setup

We measured the following microclimate characteristics at each microsite (Onset Computer HOBO sensors) from mid-July to mid-September, 2010 to 2012: PAR (μmol m^{-2} s^{-1}) 7 cm above ground (S-LIA-M003) (2010 only), air temperature (°C) 10 cm above ground (S-THB-M002), soil temperature (°C) 3 cm below the ground (S-TMB-M002), and soil moisture (m^3 m^{-3}) 6 cm below ground (S-SMC-M005). We measured wind and gust speeds (m s^{-1}) in 2011 and 2012 in each microsite with an anemometer (S-WSA-M003) 10 cm above ground level.

We constructed protective housing for data loggers and cables with vinyl gutter and PVC piping, to prevent damage from animals, weather, or wind-blown debris (Appendix 4 [Fig. A4-1]). We mounted the air temperature sensor within a temperature shield and PAR sensor by a specially designed bracket, both on a single wood block, 7.6

cm in height, secured in place by a metal stake. The anemometer was secured in the microsite by burying the stem. The data logger, placed 1 m away from the microsite, was mounted on plastic gutter pipe 30 cm above the ground for access and protection from run-off. The soil temperature and soil moisture sensors were positioned at least 4 cm from other sensors or anchoring points to avoid interference.

Using HOBOware Pro software (version 3.3.0), we set the Micro Station Data Loggers to record all microclimate variables every 15 minutes; the data loggers were launched from about mid-July to mid-September each year (dates differed by study area). Data loggers averaged wind speeds over each 15 minute interval from 1 minute observations. Gust speeds represented the highest wind speed over any 3 second period within each 15 minute logging interval. Because the data loggers had only four inputs, we eliminated PAR sensors in order to add wind anemometer sensors in 2011 and 2012.

Sky Exposure Measurements

We determined sky exposure for each leeward weather station microsite in 2010 and 2011 by positioning a Nikon D50 digital camera with 180° fisheye lens in each microsite and photographing the sky view. In 2014, we sampled sky exposure on the northeastern slope of White Calf, which has a greater expanse of ATE. We randomly selected 20 points in the ATE using Arc GIS (version 10.1). At each point, we found the nearest unsheltered solitary *P. albicaulis*, *A. lasiocarpa* (*P. engelmannii* was nearly absent on White Calf), rock, and exposed site. We determined the leeward microsite with respect to nearby tree flagging patterns and photographed sky exposure with the same digital camera and fisheye lens. Percent sky exposure was estimated digitally using Adobe Photoshop Elements 10 (2011) by selecting sky pixel counts and recording the percentage of sky pixels of total overhead pixels.

Soil Sampling

In the Divide Mountain and Line Creek study areas in 2011, we collected soil samples from 10 microsites leeward of *P. albicaulis*, *P. engelmannii*, rock, and from unprotected microsites, us-ing a 2.56-cm-diameter soil corer, following the procedures of Tan (2005). Each core was taken to below the O horizon (6 cm depth at Divide Mountain; 15 cm depth at Line Creek), the layer directly influencing seed and seedling growth (Bliss and Smith, 2006). In 2014, we sampled on White Calf, using the same 20 random points and 40 microsites selected for sky exposure photos to collect soil samples. Because of shallow soil layers and bedrock, we extracted soil using a steel spade to dig a V-shaped hole past the O-horizon (Tan, 2005). For all soil sampling, we transported soil samples in a cooler and refrigerated them until analysis.

In both years of soil sample collection, we dried, ground, and analyzed soil samples for percent total carbon and nitrogen using a LECO CN elemental analyzer at the EcoCore Analytical Services Lab at Colorado State University in Fort Collins, Colorado. Samples from both locations included high amounts of leaf litter, elevating the percentage of carbon beyond the limits of the elemental analyzer for soil determination; therefore, we designated these samples as vegetation for calibration.

Data Analysis

We used R statistical software, version 2.14.1 (R Development Core Team, 2011) for all data analysis. General ground-level climate patterns between the two study areas were compared using microclimate data from unprotected (exposed) microsites.

For 2010, 2011, and 2012 microclimate data, we performed a two-factor analysis for each climate variable to determine if data differed with block. Seasonal trends in temperature and PAR confounded analyses; thus, we fit our daily values (temperature maximums or minimums, and PAR sums over time) to both linear and quadratic models, and selected the model with the lowest Akaike Information Criterion (AIC) score (Appendix 2). Residuals, representing the difference between the observed value and the model value, were retained for comparative analysis among microsite types (Appendix 4 [Fig. A4-2]). This model was used to detrend data and removed time as a dependent variable. Thus, all reported comparisons among microsites for air and soil temperature variables and PAR are based on residual data sets.

To determine whether our replicates represented "true" replicates, we determined the interaction effect of blocks on microsite type by ranking the maximum, average, or minimum daily values for soil moisture, wind, and gust speed (or the data set residuals for PAR and temperature) and then compared the ranked values among microsites and blocks with two-way analysis of variance (ANOVA). Ranked rather than raw data were used because assumptions of normality and homoscedasticity were not met. Then, we compared daily values of microclimate variables with Kruskal–Wallis one-way ANOVA among microsites either separately among blocks or combined if no significant interaction effect was detected. We performed pairwise Wilcoxon rank sum tests for post hoc analysis among pairs of microsite types.

For comparisons of numbers of soil freeze-thaw events among microsites for each study area, we used a chi-square goodness-of-fit test. We used the Shapiro–Wilk normality test to examine sky exposure and soil carbon and nitrogen data. The sky exposure data were not normally distributed, so we used a Kruskal–Wallis one-way ANOVA and pairwise Wilcoxon rank sum tests with Bonferroni corrections for post hoc analysis to compare the differences in median percentages of sky exposure among all microsite types. For soil samples from 2011, carbon and nitrogen data did not depart significantly from normality, and percentages of total carbon and nitrogen in soil were compared among microsites and between study areas with parametric one-way ANOVA, followed by Tukey HSD tests for post hoc analysis. Soil data from 2014 departed from normality, and we used Kruskal–Wallis one-way ANOVA to compare the soil sample results.

Summary statistics for all microclimate variables are reported in Appendix 1; AIC scores fitting models to microclimate data, in Appendix 2; post hoc tests, in Appendix 3; and figures comparing residual values, in Appendix 4.
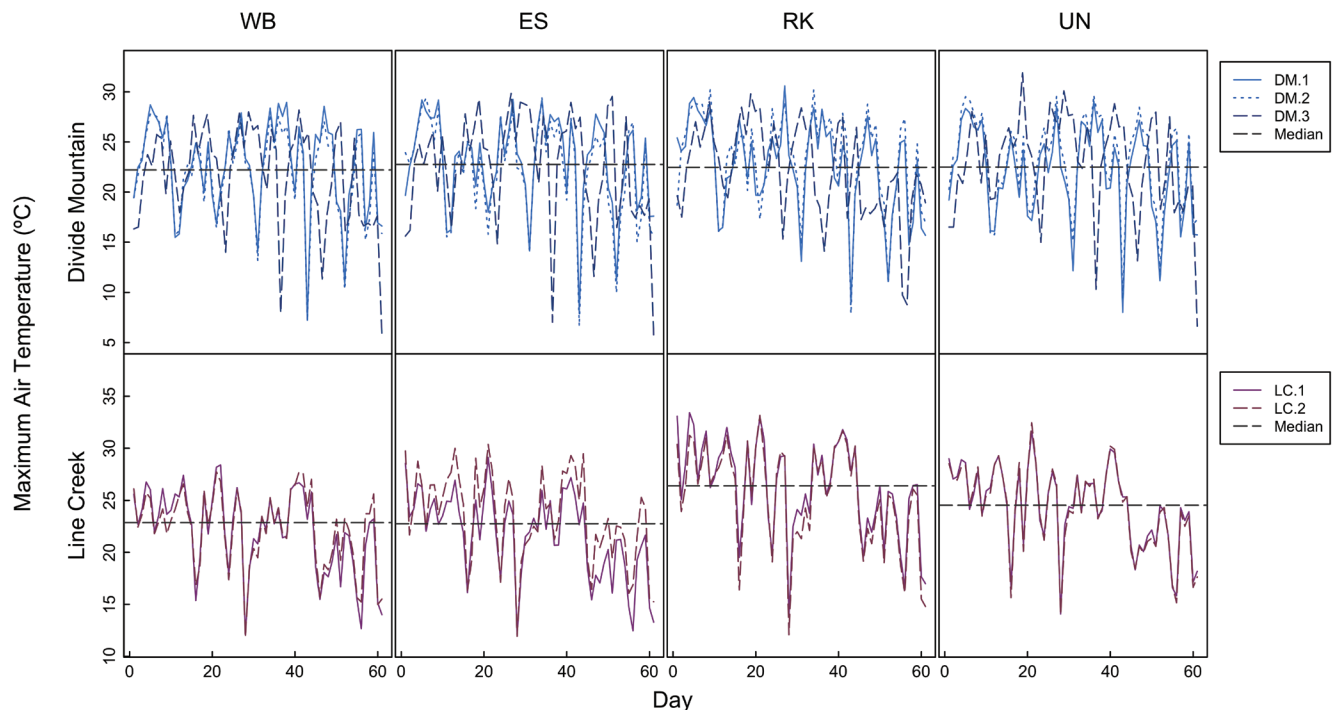
Results

Microsite Air and Soil Temperature

Air temperature varied with date at Divide Mountain and to greater extremes at Line Creek, trending seasonally from high values in July to lower values in September in both study areas in all three years (Fig. 2). At Divide Mountain, air temperature was not different in general at *P. albicaulis* microsites compared to other microsites. For northeast slope comparisons, from 2010 to 2012, median maximum air temperature did not differ among microsite types within more than half the block comparisons, and median minimum air temperature did not differ within any block comparisons (Table 1; Appendix 1 [Tables A1-2, A1-3, A1-4]; Appendix 3 [Tables A3-1, A3-5, A3-6]; Appendix 4 [Fig. A4-3]).

At Line Creek, maximum air temperatures differed across microsites within all blocks, but minimum air temperature differed within only one block (Table 1; Appendix 1 [Tables A1-2, A1-3, A1-4]; Appendix 3 [Tables A3-1, A3-5, A3-6]; Appendix 4 [Fig. A4-3]). *P. albicaulis* microsites at Line Creek, and especially *P. engelmannii* microsites, had lower maximum air temperature values than unprotected or rock microsites, and rock microsites had the highest maximum air temperatures (Table 1, Fig. 2). *P. engelmannii* microsites had the highest minimum air temperatures.

Soil temperatures similarly varied throughout the growing season for both study areas, with higher amplitude of variation at Line Creek; and, temperatures declined from higher to lower values by September (Fig. 3, parts A and B). At both study areas, microsites differed within nearly all blocks (Table 1). At Divide Mountain, *P. albicaulis* microsites did not have the lowest soil temperature maxima nor did they consistently have the highest soil temperature minima, but the conifer microsites together provided the lowest maximum and highest minimum soil temperatures (Table 1; Appendix 1 [Tables A1-5, A1-6, A1-7, A1-8]; Appendix 2 [Table A2-1]; Appendix 3 [Tables A3-1, A3-2, A3-3, A3-4]; Appendix 4 [Figs. A4-4, A4-5]).

At Line Creek, *P. albicaulis* did not consistently have the lowest soil temperature maxima or highest soil temperature minima, although the differences between the conifer microsites often were not significant (Table 1; Appendix 1 [Tables A1-5, A1-6, A1-7, A1-8]; Appendix 2 [Table A2-1]; Appendix 3 [Tables A3-1, A3-2, A3-3, A3-4]; Appendix 4 [Figs. A4-4, A4-5]). Both conifer microsites also had lower

FIGURE 2. Daily maximum air temperatures from the northeast slopes of Divide Mountain (DM) and Line Creek (LC) in 2012, which is representative of study results. Day 1 represents 4 July at Divide Mountain and 17 July at Line Creek. WB = Pinus albicaulis, ES = *Picea engelmannii*, RK = rock, and UN = unprotected (exposed) microsites.

daily soil temperature variance in the two study areas than rock or exposed microsites, but *P. engelmannii* had the lowest variance in the majority of comparisons (Table 1; Appendix 3 [Tables A3-1, A3-4]).

PAR and Soil Moisture

PAR, measured only in 2010 on both west and northeast aspects, declined from July to September, with variation introduced by intermittent periods of rain and overcast days (Fig. 4). PAR differed significantly among microsites within all blocks in both study areas (Table 1; Appendix 1 [Table A1-9]; Appendix 2 [Table A2-3]; Appendix 3 [Tables A3-1, A3-7]; Appendix 4 [Fig. A4-7]). On Divide Mountain, *P. engelmannii* microsites had the lowest PAR values, with *P. albicaulis* microsites the next lowest. At Line Creek, the trend was reversed, with *P. albicaulis* microsites on both the west and northeast aspects experiencing the lowest PAR values, followed by *P. engelmannii* microsites.

Median daily average soil moisture differed significantly and inconsistently among microsites for most but not all blocks at Divide Mountain and Line

Creek, although *P. albicaulis* had the highest median daily average overall for both study areas (Table 1; Appendix 1 [Table A1-10]; Appendix 3 [Tables A3-1, A3-10]; Appendix 4 [Fig. A4-6]). For some comparisons, neither conifer species had the highest average soil moisture, and they did not differ from each other in several post hoc tests (Appendix 3 [Table A3-10]).

Wind and Gust Speed

Median average daily wind speed in general was greater at Divide Mountain in 2011 but similar to that at Line Creek in 2012. Wind speed differed significantly across microsites within all blocks in both study areas (Table 1). Average wind speed was not consistently lowest in leeward *P. albicaulis* microsites within blocks (Fig. 5); however, on Divide Mountain the overall median average wind speed was lowest for *P. albicaulis* microsites (Table 1). At both study areas in 2011 and 2012, all protected microsites (conifer and rock microsites) experienced lower wind speeds than unprotected microsites, and the conifer microsites did not differ from one another in several

TABLE 1

Median and range (minimum, maximum) of values for microclimate variables measured during 2010–2012 for each microsite type. (Values measured in 2010 from the west-facing aspect not included.) % diff = percent of Kruskal–Wallis One-way ANOVA comparisons among microsite blocks that were statistically different (Divide Mountain, *n* = 7 comparisons; Line Creek, *n* = 5 comparisons). WB = *Pinus albicaulis*, ES = *Picea engelmannii*, RK = rock, UN = unprotected (exposed).

	Divide Mountain				
	WB	ES	RK	UN	% diff
Sum PAR (μmole m⁻² s⁻¹)	29,192.7 (575.2, 69,560.2)	21,630.2 (460.2, 66,515.2)	37,700.2 (2893.9, 68,115.2)	43,252.7 (6242.7, 70,880.2)	100
Maximum Air Temp (°C)	21.58 (1.83, 32.23)	22.18 (2.05, 31.89)	21.65 (3.67, 30.60)	21.75 (2.72, 31.97)	43
Minimum Air Temp (°C)	5.80 (−3.99, 14.15)	5.49 (−3.87, 13.59)	5.69 (−3.84, 14.31)	5.85 (−3.15, 14.51)	0
Maximum Soil Temp (°C)	15.22 (4.79, 24.53)	13.67 (4.43, 25.67)	15.65 (4.12, 23.45)	15.92 (4.19, 32.90)	100
Minimum Soil Temp (°C)	9.24 (0.41, 11.98)	9.53 (0.36, 13.62)	9.11 (0.74, 14.24)	9.14 (0.08, 14.36)	71
Variance in Soil Temp (°C)	4.75 (0.09, 16.75)	2.80 (0.04, 10.20)	5.01 (0.16, 16.51)	6.12 (0.26, 32.71)	100
Average Soil Moisture (m³ m⁻³)	0.08 (−0.16, 0.19)	0.06 (−0.17, 0.20)	0.02 (−0.07, 0.19)	0.06 (−0.16, 0.21)	86
Average Wind Speed (m s⁻¹)	0.08 (0.00, 1.31)	0.14 (0.00, 1.68)	0.80 (0.00, 2.22)	0.56 (0.00, 3.27)	100
Maximum Gust Speed (m s⁻¹)	10.62 (1.52, 16.37)	6.09 (0.00, 15.99)	6.47 (0.76, 17.13)	7.23 (2.66, 18.27)	83
	Line Creek RNA				
	WB	ES	RK	UN	% diff
Sum PAR (μmole m⁻² s⁻¹)	23,430.2 (6727.7, 39,267.7)	38,236.5 (8935.5, 51,255.2)	40,813.9 (9975.5, 59,255.2)	48,333.9 (10364, 66,805.2)	100
Maximum Air Temp (°C)	22.21 (9.14, 29.34)	21.23 (12.07, 30.37)	25.48 (10.98, 33.70)	23.09 (6.38, 32.46)	100
Minimum Air Temp (°C)	2.92 (−10.62, 10.61)	3.10 (−9.58, 10.66)	2.42 (−10.20, 10.22)	2.72 (−10.23, 10.69)	20
Maximum Soil Temp (°C)	18.70 (5.62, 28.12)	17.99 (6.26, 28.74)	23.73 (9.39, 33.37)	23.64 (10.05, 33.42)	100
Minimum Soil Temp (°C)	8.26 (1.13, 12.29)	8.18 (−0.20, 13.23)	6.72 (−2.36, 13.55)	6.31 (−3.36, 13.45)	100
Variance in Soil Temp (°C)	10.62 (0.79, 40.86)	10.13 (1.67, 41.34)	18.30 (3.10, 62.34)	18.60 (4.57, 102.91)	100
Average Soil Moisture (m³ m⁻³)	0.03 (−0.06, 0.17)	0.00 (−0.05, 0.14)	0.02 (−0.02, 0.17)	0.02 (−0.08, 0.14)	80
Average Wind Speed (m s⁻¹)	0.14 (0.00, 1.27)	0.07 (0.00, 0.89)	0.23 (0.00, 1.49)	0.42 (0.00, 2.16)	100
Maximum Gust Speed (m s⁻¹)	5.71 (2.28, 15.23)	4.19 (1.52, 10.28)	5.71 (1.90, 13.70)	5.52 (0.00, 12.94)	100

post hoc tests (Table 1; Fig. 5; Appendix 1 [Table A1-11]; Appendix 3 [Table A3-1, A3-8]; Appendix 4 [Fig. A4-8]).

Maximum wind gust speeds were not consistently lowest in *P. albicaulis* microsites. Although nearly all microsite comparisons within blocks differed sig-

nificantly, the majority of the post hoc comparisons between *P. albicaulis* and *P. engelmannii* did not differ (Appendix 3 [Tables A3-1, A3-9]). On Divide Mountain, *P. engelmannii* microsites had the lowest maximum wind gust speeds and *P. albicaulis* the highest (Table 1). At Line Creek, *P. engelmannii* microsites consistently had the lowest maximum gust speeds (Table 1; Fig. 5; Appendix 1 [Table A1-12]; Appendix 3 [Tables A3-1, A3-9]; Appendix 4 [Fig. A4-8]).

Sky Exposure and Soil Carbon and Nitrogen

Median sky exposure across the leeward weather station microsites differed significantly (χ^2 = 21.77, df = 3, P = 7.30e^{-05}), varying from a low of 50.59% in *P. albicaulis* leeward microsites to 94.22% in unprotected microsites (Table 2). Post hoc tests indicated that conifer microsites did not differ from each other, although they differed significantly from rock and exposed microsites (Appendix 3 [Table A3-11]). Sky exposure data collected from random points in 2014 ranged from a low of 60.08% at *P. albicaulis* microsites to 92.50% at unprotected microsites, differing significantly across microsites (χ^2 = 48.61, df = 3, P = < 2e^{-16}) (Table 2). Post hoc tests again indicated significant differences between conifer and nonconifer microsites (Z = 2.03, P = 0.0425), but no differences between *P. albicaulis* and *A. lasiocarpa* (Appendix 3 [Table A3-12]).

Percent total nitrogen and carbon were not consistently high in *P. albicaulis* leeward microsites or in conifer microsites for samples collected in 2012. At Divide Mountain, nitrogen ranged from a mean of 0.42% in *P. engelmannii* microsites to a mean of 0.48% in *P. albicaulis* microsites; at Line Creek, percent nitrogen ranged from a mean of 0.17% in *P. albicaulis* and rock microsites to 0.19% in *P. engelmannii* and unprotected microsites (Table 3). Carbon at Divide Mountain ranged from a mean of 8.58% in *P. engelmannii* microsites to 9.45% in unprotected microsites, and at Line Creek from 2.03% in rock microsites to 2.70% in *P. albicaulis* microsites (Table 3). Two-way ANOVA indicated that soil nitrogen (F = 0.84, df = 3, 74, P = 0.48) and carbon content (F = 0.27, df = 3, 74, P = 0.85) did not differ among the microsite types (Appendix 3 [Table A3-13]). For soils sampled on White Calf in 2014, however, *P. albicaulis* microsites had both the highest carbon and the highest nitrogen content, but the differences were not statistically significant (χ^2 =1.19, n = 20, P = 0.755, and χ^2 = 1.72, n = 20, P = 0.633, respectively) (Table 3).

Comparisons Between Study Areas

We characterized differences in general growing season microclimate between the two study areas based on data from the unprotected microsites on northeast-facing slopes (Table 4). Divide Mountain was on average warmer, wetter, and windier than Line Creek. Tree flagging and growth form sculpting indicated that prevailing winds were both strong and variable over short distances on Divide Mountain as a result of the complex topography. Tree growth forms were more strongly krummholz at Divide Mountain than at Line Creek.

Median daily average air temperatures were higher at Divide Mountain in 2011 and 2012, but median daily variance in temperature was greater at Line Creek in all three years. Line Creek experienced 15 soil freeze-thaw events in 2011 and 34 in 2012. Divide Mountain experienced significantly fewer soil freeze-thaw events—9 in 2011 (χ^2 = 9.55, df = 1, P = 0.002) and 13 in 2012 (χ^2 = 39.34, df = 1, P = 3.56e^{-10}). Divide Mountain daily average wind speeds reached higher maxima than Line Creek and had greater variance in both years (Fig. 5, Table 4).

Based on sampling in 2012, Divide Mountain soils had significantly higher mean percentages of total nitrogen and total carbon than Line Creek soils (Table 4, two-way ANOVA: Total nitrogen–microsite-study-area interaction effect, F = 0.7356, df = 7, 74, P = 0.5342; study area, F = 241.6890, df = 1, 74, P < 2e^{-16}; and total carbon–microsite-study-area interaction effect, F = 0.2666, df = 7, 74, P = 0.8492; study area, F = 253.7934, df = 1, 74, P < 2e^{-16}).

DISCUSSION

Evaluating P. albicaulis Leeward Microsites

Given the prevalence of *P. albicaulis* as a tree island initiator in the northern Rocky Mountains, we hypothesized that microsites leeward of *P. albicaulis* experience less extreme microclimate, less sky exposure, and more total soil carbon and nitrogen than microsites leeward of *P. engelmannii*, rocks, or in unprotected
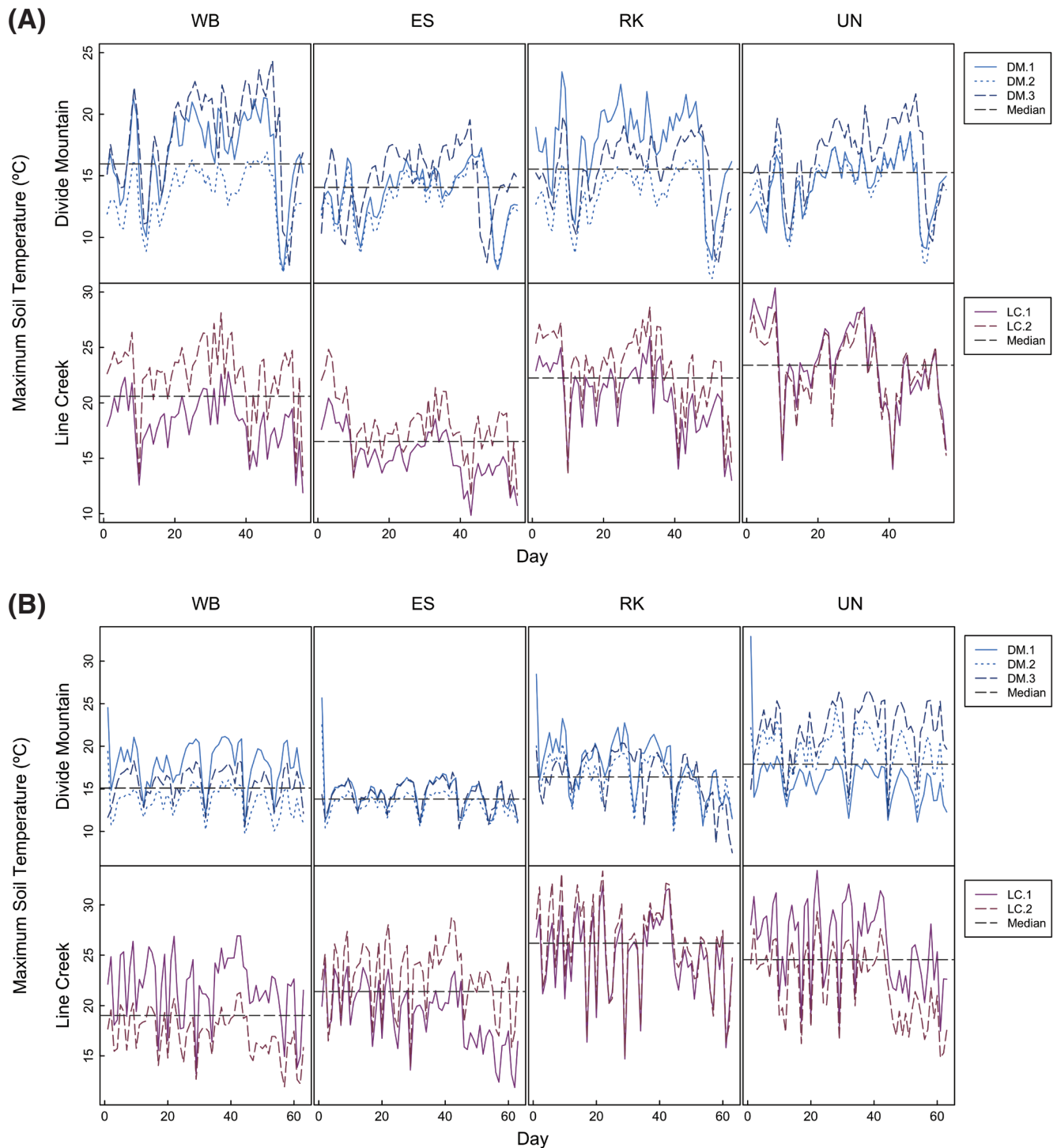
FIGURE 3. (A) Top, daily maximum soil temperatures from the northeast slopes of Divide Mountain (DM) and Line Creek (LC) in 2011. Day 1 represents 9 July at Divide Mountain and 22 July at Line Creek. (B) Bottom, daily maximum soil temperatures from the northeast slopes of Divide Mountain and Line Creek in 2012. Day 1 represents 4 July at Divide Mountain and 17 July at Line Creek. Abbreviations as in Figure 2.

microsites. We found that *P. albicaulis* leeward microsites did not consistently provide the most moderate microclimate and protective microsites, as defined by lower air and soil temperature maxima, higher air and soil temperature minima, moister soils, lower cumula-

tive daily PAR, and lower wind and gust speeds. In fact, *P. engelmannii* microsites may produce a somewhat more favorable leeward microclimate.

P. albicaulis microsites, however, were marginally advantageous for other biophysical measurements.
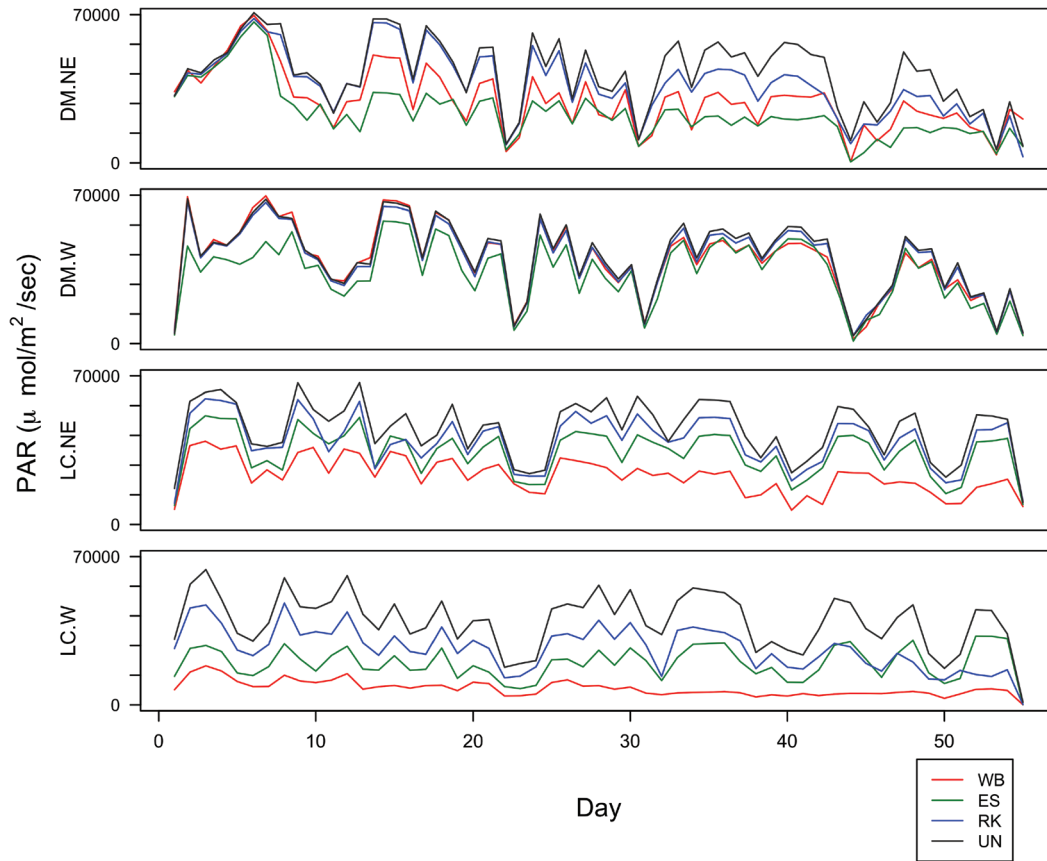
FIGURE 4. Daily photosynthetically active radiation (PAR), recorded only in 2010 on northeast- and west-facing slopes of Divide Mountain (DM) and Line Creek (LC). Day 1 represents 8 July at Divide Mountain and 22 July at Line Creek. Abbreviations as in Figure 2.

TABLE 2

Descriptive statistics for percent sky exposure for each microsite type associated with microclimate weather stations at Divide Mountain and Line Creek, and at randomly selected locations at White Calf. WB = *Pinus albicaulis***, ES =** *Picea engelmannii***, SF =** *Abies lasiocarpa***.**

Microsite	Year	N	Median	Minimum	Maximum
Divide Mountain and Line Creek					
WB	2012	8	50.59	16.97	78.23
ES			66.36	36.90	93.07
Rock			92.37	67.75	97.39
Exposed			94.22	86.11	99.73
White Calf					
WB	2014	20	60.08	42.35	84.47
SF			70.10	40.46	94.49
Rock			91.81	64.07	97.75
Exposed			92.50	62.90	98.82

TABLE 3

Descriptive statistics for percent total nitrogen and carbon in soils sampled at Divide Mountain and Line Creek in 2011 and at randomly selected locations at White Calf in 2014. WB = *Pinus albicaulis*, ES = *Picea engelmannii*, SF = *Abies lasiocarpa,* Exposed = open.

Divide Mountain			Percent Nitrogen			Percent Carbon		
Microsite	Year	*N*	Mean	Min	Max	Mean	Min	Max
WB	2011	10	0.48	0.38	0.61	9.28	7.60	11.43
ES			0.42	0.27	0.70	8.58	4.75	13.70
Rock			0.47	0.35	0.64	8.98	5.88	14.25
Exposed			0.45	0.30	0.65	9.45	4.71	14.69

Line Creek			Percent Nitrogen			Percent Carbon		
Microsite	Year	*N*	Mean	Min	Max	Mean	Min	Max
WB	2011	10	0.17	0.16	0.28	2.70	1.67	3.72
ES			0.19	0.16	0.23	2.38	1.80	2.88
Rock			0.17	0.09	0.22	2.03	0.90	2.66
Exposed			0.19	0.10	0.25	2.25	1.06	3.20

White Calf			Percent Nitrogen			Percent Carbon		
Microsite	Year	*N*	Median	Min	Max	Median	Min	Max
WB	2014	20	0.44	0.17	1.38	6.87	1.50	32.94
SF			0.35	0.03	1.55	4.29	0.18	31.55
Rock			0.31	0.15	1.40	4.54	1.36	31.93
Exposed			0.35	0.10	1.55	5.91	0.93	39.16

For the 2014 soil samples on White Calf, *P. albicaulis* microsites had greater percentages of soil carbon and nitrogen, which may indicate higher fertility in *P. albicaulis* microsites under some conditions across study areas. *P. albicaulis* leeward microsites also had slightly higher median average daily soil moisture than other microsite types. *P. albicaulis* microsites in the two sampling efforts experienced the lowest median percent sky exposure of all microsites—~15% lower than *P. engelmannii* microsites on Divide Mountain and ~10% lower than *A. lasiocarpa* microsites on White Calf. Although these differences were not significant in post hoc tests, they may be attributed to the longer needles and branches and more irregular, overhanging canopies of krummholz *P. albicaulis*. *P. albicaulis* shoots and needles, measured at our ATE study areas, are significantly longer than those of *P. engelmannii* and *A. lasiocarpa* (Blakeslee, 2012). A small reduction in sky exposure, a slight increase in soil moisture, or additional soil carbon or nitrogen provided by *P. albicaulis* microsites could improve leeward seedling survival.

If the microclimate protection offered by *P. albicaulis* leeward microsites is no greater than that offered by associated conifers, why is it the most frequent tree island initiator? First of all, the preceding information suggests that there may be some advantageous qualities to *P. albicaulis* leeward microsites beyond microclimate. However, the prevalence of *P. albicaulis* as a tree island initiator is generally predicted by its high relative abundance as a solitary tree, which may result from seed dispersal by Clark's nutcrackers to protective microsites at treeline and greater seedling hardiness. In fact, Tomback et al. (2016) found that the proportional abundance of *P. albicaulis* among solitary trees in the ATE across 10 study areas predicted its proportional abundance as a tree island initiator.

With respect to hardiness, Bansal et al. (2011) compared *P. albicaulis* and *P. engelmannii* seedlings grown at treeline and demonstrated that *P. albicaulis* had greater carbon gain, greater carbon use efficiency, and greater water-use efficiency in exposed microsites as well as greater resistance to low-temperature

TABLE 4

Comparisons of northeastern slope microclimate and overall average percent soil carbon and nitrogen between the Divide Mountain study area and Line Creek study area. These comparisons are based on data from unprotected (exposed) microsites. Microclimate data were collected from about mid-July though about mid-September in both study areas.

Variable	Year	Study Area	Median	Variance	Maximum	Minimum
Average Air Temperature (°C)	2010	Divide Mtn	11.41	22.70	19.73	0.77
		Line Creek	10.93	16.65	16.55	0.51
	2011	Divide Mtn	14.01	13.17	21.09	3.66
		Line Creek	11.35	7.98	17.14	2.40
	2012	Divide Mtn	14.24	16.71	19.97	2.27
		Line Creek	12.62	12.90	18.05	2.33
Variance in Air Temperature (°C)	2010	Divide Mtn	14.34	124.16	54.15	0.53
		Line Creek	33.02	277.49	71.80	4.41
	2011	Divide Mtn	23.64	653.31	128.10	−15.50
		Line Creek	56.59	849.79	137.97	−13.85
	2012	Divide Mtn	23.57	261.30	83.05	1.91
		Line Creek	47.47	441.03	96.56	10.59
Average Soil Moisture (m^3m^{-3})	2010	Divide Mtn	0.10	0.00	0.16	−0.12
		Line Creek	0.07	0.00	0.14	−0.02
	2011	Divide Mtn	0.01	0.00	0.15	−0.06
		Line Creek	0.04	0.00	0.11	0.00
	2012	Divide Mtn	0.09	0.00	0.21	−0.16
		Line Creek	−0.02	0.00	0.09	−0.08
Average Wind Speed ($m\ s^{-1}$)	2011	Divide Mtn	0.82	0.43	2.86	0.02
		Line Creek	0.42	0.12	1.70	0.00
	2012	Divide Mtn	0.42	0.48	3.27	0.00
		Line Creek	0.42	0.18	2.16	0.00

Variable	Year	Study Area	Mean	SD	Maximum	Minimum
Total % C	2011	Divide Mtn	9.07	2.50	14.69	4.71
		Line Creek	2.35	0.57	3.72	0.90
Total % N	2011	Divide Mtn	0.45	0.10	0.70	0.27
		Line Creek	0.19	0.04	0.28	0.09

photo inhibition. Blakeslee (2012) demonstrated that *P. albicaulis* were associated with less protective microsites for establishment and had higher vigor than other solitary krummholz trees. These factors may contribute both to higher relative abundance of *P. albicaulis* and more dependable protection.

Importance of Protected Microsites

Previous studies at Rocky Mountain alpine treelines have suggested that conifers offer microclimatic protection, aiding in subsequent conifer establishment and ultimately the formation of tree islands (e.g., Marr, 1977; Resler et al., 2005). Our results support this contention. Although species-specific differences in protection are not strongly evident, conifer microsites experienced measurably more moderated microclimate than rock and unprotected microsites. Unprotected microsites had higher daily average wind speeds, which can desiccate foliage and increase transpiration and soil evaporation rates, resulting in drought stress (Holtmeier, 2009). Too much solar radiation, which heats soils to high temperatures and harms foliage, has been shown to
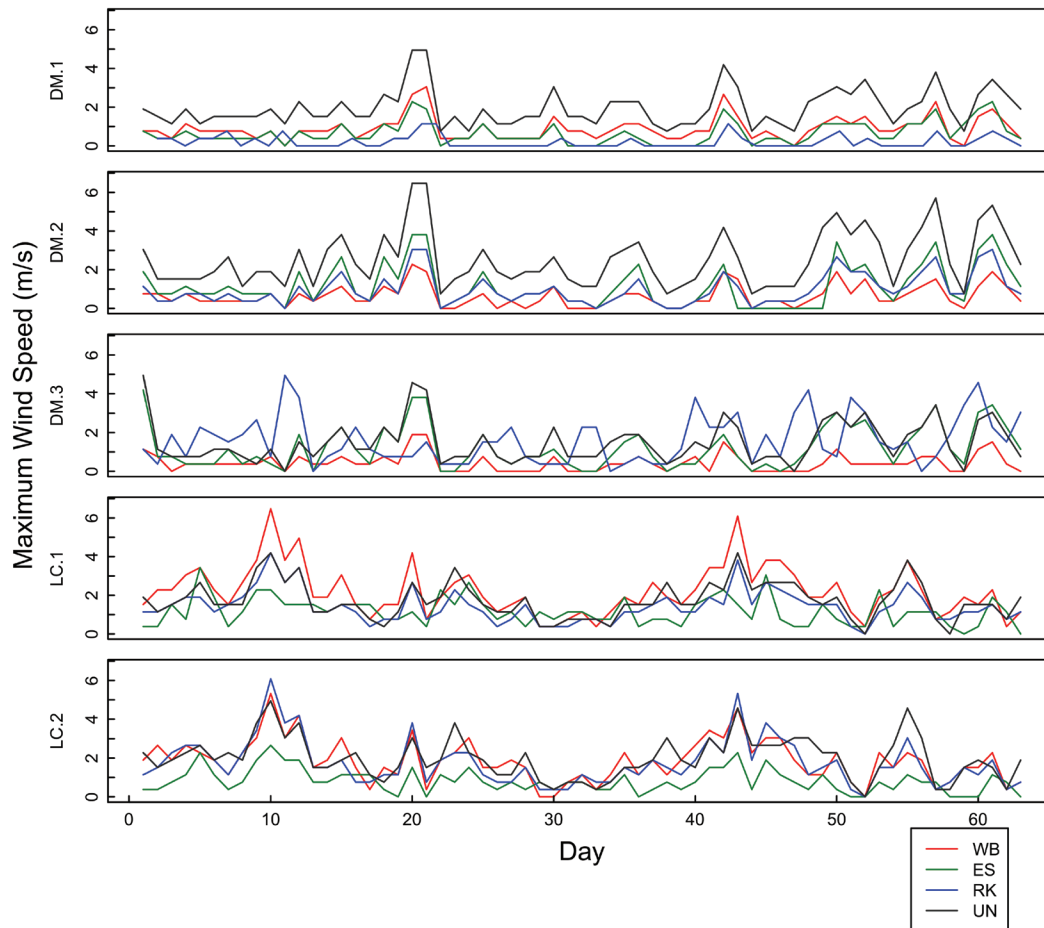
FIGURE 5. Wind speeds 10 cm above the ground from microsites on the northeast slope of Divide Mountain (DM) and Line Creek (LC) for the 2012 growing season. Abbreviations as in Figure 2.

kill young *P. engelmannii* and *A. lasiocarpa* seedlings (Cui and Smith, 1991; Germino et al., 2002). Furthermore, we found that conifer microsites reduced sky exposure. For seedlings, more sky exposure may lead to excess solar radiation including PAR, but also lower soil moisture and colder nighttime temperatures from long-wave irradiance (e.g., Maher et al., 2005; Germino and Smith, 1999). Conifer microsites did not always have the highest soil moisture. This effect may result from reduced sky exposure: overhanging canopies could intercept precipitation and reduce infiltration in leeward microsites. A better determinant of local soil moisture might be microtopographic "concavities" and "convexities," which influence moisture distribution regardless of type of nurse object (e.g., Smith-McKenna et al., 2013).

Conceivably, the quality of facilitation provided by different microsite types could vary with conifer life history stage. In a companion study, Blakeslee (2012) compared the protective quality of the same four treeline leeward microsites in the ATE on Divide Mountain (krummholz *P. albicaulis* and *P. engelmannii*, rock, and exposed site) by examining the germination and survival rates of sown seeds. Five *P. engelmannii* seeds from the appropriate seed transfer zone were sown in 20 replicates of each type of leeward microsite. Higher than expected germination occurred in rock microsites and fewer than expected in *P. albicaulis* microsites. However, the odds of cotyledon seedling survival during summer months in *P. albicaulis* microsites were about 7 times higher than for *P. engelmannii* microsites, 10 times higher than for rock, and 14 times higher than for exposed microsites.

Seedling survival in the ATE is generally low, especially for the first-year (Cui and Smith, 1991). Our microclimate results support previous findings that facilitative "nurse" objects, and especially conifers, potentially provide protection from extreme climate at treeline, enabling

seedling establishment (Callaway, 1998; Hätten-schwiler and Smith, 1999; Germino et al., 2002). *P. albicaulis* is the most prevalent solitary tree at both study areas, and thus potentially important for seedling establishment and community development (Blakeslee, 2012).

Differences in Facilitation Requirements by Study Area

The two treeline study areas were characterized by different climate extremes that could impact conifer growth and survival. The ATE at Divide Mountain was moister, warmer, but windier than the ATE at Line Creek. Higher wind speeds and maximum gust speeds would explain more krummholz growth and severe windward needle kill at Divide Mountain than at Line Creek. However, Line Creek experienced greater air and soil temperature variance, more freeze-thaw events, and less moisture.

Amelioration of extreme temperatures and PAR may be more important for survival at Line Creek than at Divide Mountain. Cold soil temperatures limit seedling growth at treeline (Landhäusser et al., 1996; Germino and Smith, 1999). Although conifers tolerate low temperatures throughout the winter (Sakai and Okada, 1971), cold hardiness is reduced during the growing season (Kalberer et al., 2006). Frequent summer freezes may lead to cold injury (Christersson and Fircks, 1988). Divide Mountain experienced higher median average wind speeds in 2011, and all nurse objects, but especially conifers, offered protection.

Variation in Facilitation by Microsite

We found that microclimate varied among similar microsite types between study areas, between slopes in the same study area, on the same slope aspect, and from year to year. This variation may result from numerous factors interacting, such as differences in regional climate and synoptic weather patterns between the two sites, topographically unique wind patterns (especially on Divide Mountain), slight variations in slope aspect and slope steepness, and differences in morphology and dimensions among nurse objects. All microclimate variables are affected, but particularly maximum soil temperature, daily average soil moisture, and wind speed and maximum gust speed. These results illustrate that the benefits of facilitation attributed to specific plants or nurse objects vary with specific environmental conditions, and we must be cautious about generalizations.

Conclusions

Our studies did not support the hypothesis that *P. albicaulis* leeward microsites experience the most moderate microclimate and suggest that other factors, such as additional protective microsite qualities and availability as a solitary tree, are responsible for the prevalence of *P. albicaulis* as the dominant tree island initiator in the ATE. Our results, however, underscore the ecological importance of conifers as nurse objects for facilitating treeline community development in the ATE, and especially *P. albicaulis*, given its high abundance in many harsh treeline communities. Previous studies in the ATE on the eastern slope of Glacier National Park documented infection rates of *P. albicaulis* by *C. ribicola* at ~35% (Resler and Tomback, 2008), and within the park at an overall 47% (Smith et al., 2011). *P. albicaulis* is a candidate species under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service, 2011) and listed as endangered in Canada (Government of Canada, 2012). As *P. albicaulis* declines from *C. ribicola*, the establishment rate of tree islands may also decline, resulting in changes in ATE community structure and composition. In turn, these changes are likely to cause lags in expected upslope treeline migration in response to climate warming (Tomback and Resler, 2007; Smith-McKenna et al., 2014).

Acknowledgments

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