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Spatial Distribution Patterns of the Antarctic Hair Grass *Deschampsia antarctica* in Relation to Environmental Variables on Barton Peninsula, King George Island

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Abstract

Understanding the patterns in species distribution and abundance along environmental gradients is a keystone in field ecological study. Because the Antarctic terrestrial communities are simple, they provide a suitable opportunity for studying species distribution patterns in relation to environmental gradients. We applied diverse geostatistic methods and classical statistic descriptors to analyze the spatial patterns of several variables, such as *Deschampsia antarctica* abundance, moss cover, topography, and soil physical and chemical properties. Directional semivariograms and kriged maps showed that strong anisotropy in a topographic variable was reflected in the soil variables. Especially, soil texture and moss cover were correlated with elevation, and electric conductivity and Na^+ were influenced by the distance from the shoreline. Furthermore, the heavy snowfall in 2009 evidently affected the survival of the grass. A short growing period and waterlogging induced by heavy snowfall may limit survival of *D. antarctica* and the amount of snowfall can be a important factor limiting the grass expansion.

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Introduction

It is important to understand the patterns in species distribution and abundance along environmental gradients (Rosenzweig, 1995; Dale, 1999). The Antarctic plant communities seem to offer particularly unique opportunities for such studies (Green et al., 1999; Smykla et al., 2007). This is because the Antarctic terrestrial communities consist of only a few species, and interspecies interactions are fewer than in more diverse and complex ecosystems (Block, 1994). This fact provides a suitable opportunity for studying species distributional patterns in relation to environmental gradients.

Although the Antarctic terrestrial environment is harsh for the survival of vascular plants because of cold temperatures, high UV-B radiation, and sea spray, several researchers have reported that the population of the native Antarctic hair-grass, *Deschampsia antarctica* Desv. (Poaceae), has increased on the west coast of the Antarctic Peninsula (Fowbert and Smith, 1994; Smith, 1994; Walther et al., 2002; Robinson et al., 2003). These monitoring studies suggested that the main reasons for this increase were an increasing mean summer temperature and concurrent lengthening of the growing season (Grobe et al., 1997; Day et al., 1999; Gerighausen et al., 2003; Kim et al., 2007). However, few studies have provided confident statistical results about the association between the abundance of *D. antarctica* and environmental variables. Furthermore, we investigated the effect of snowfall on the survival of *D. antarctica*.

This study was conducted to analyze the spatial characteristics of the distribution of *D. antarctica* in relation to diverse environmental factors by using geostatistic methods. Traditional statistical methods ignore data location and the spatial structure of data distributions (Kravchenko et al., 2003), whereas geostatistics provides a set of statistical tools for describing and modeling of spatial patterns, and which can be used for prediction of unsampled locations by interpolation (Goovaerts, 1999). Because many soil properties are spatially dependent within a certain range, classical experimental designs often violate independent sampling assumptions, rendering the analysis invalid (Jung et al., 2006). In recent studies, the importance of spatial autocorrelation in geographical ecology has been addressed (Lennon, 2000; Legendre et al., 2002; Lichstein et al., 2002; Hawkins et al., 2007).

The purposes of this study are as follows: (1) to understand the spatial patterns of *D. antarctica* in the cold Antarctic region; (2) to figure out the association between the abundance of *D. antarctica* and environmental variables; and (3) to evaluate the effect of heavy snowfall on the survival of *D. antarctica.*

Methods

STUDY LOCATIONS

The study was conducted on Barton Peninsula, King George Island (62°14′08″S, 58°43′3″W), in the area with largest local population of *D. antarctica* (Fig. 1, part A). Because King George Island is located at the northern part of maritime Antarctica, it has relatively high temperature and humidity and is characterized by strong oceanic influence. Only 10% of the island is ice free and able to provide favorable support for a relatively diverse terrestrial biota (Smykla et al., 2007). Because of relatively moderate climate, diverse terrestrial vegetation is found on Barton Peninsula, which is one of the richest botanical areas in all of the Antarctic. Vegetation around Barton Peninsula includes 62 lichens, 33 bryophytes, and two phanerogam species (Kim et al., 2006, 2007). The mean temperatures were 1.7 °C in January and −7.3 °C in July, and the mean annual precipitation was 487 mm, which were measured at nearby King Sejong Station from 2007 to 2011 (Ahn, 2013).

DATA COLLECTION

A grid sampling method, the most efficient method of sampling spatial variability (Olea, 1984), was applied to determine the

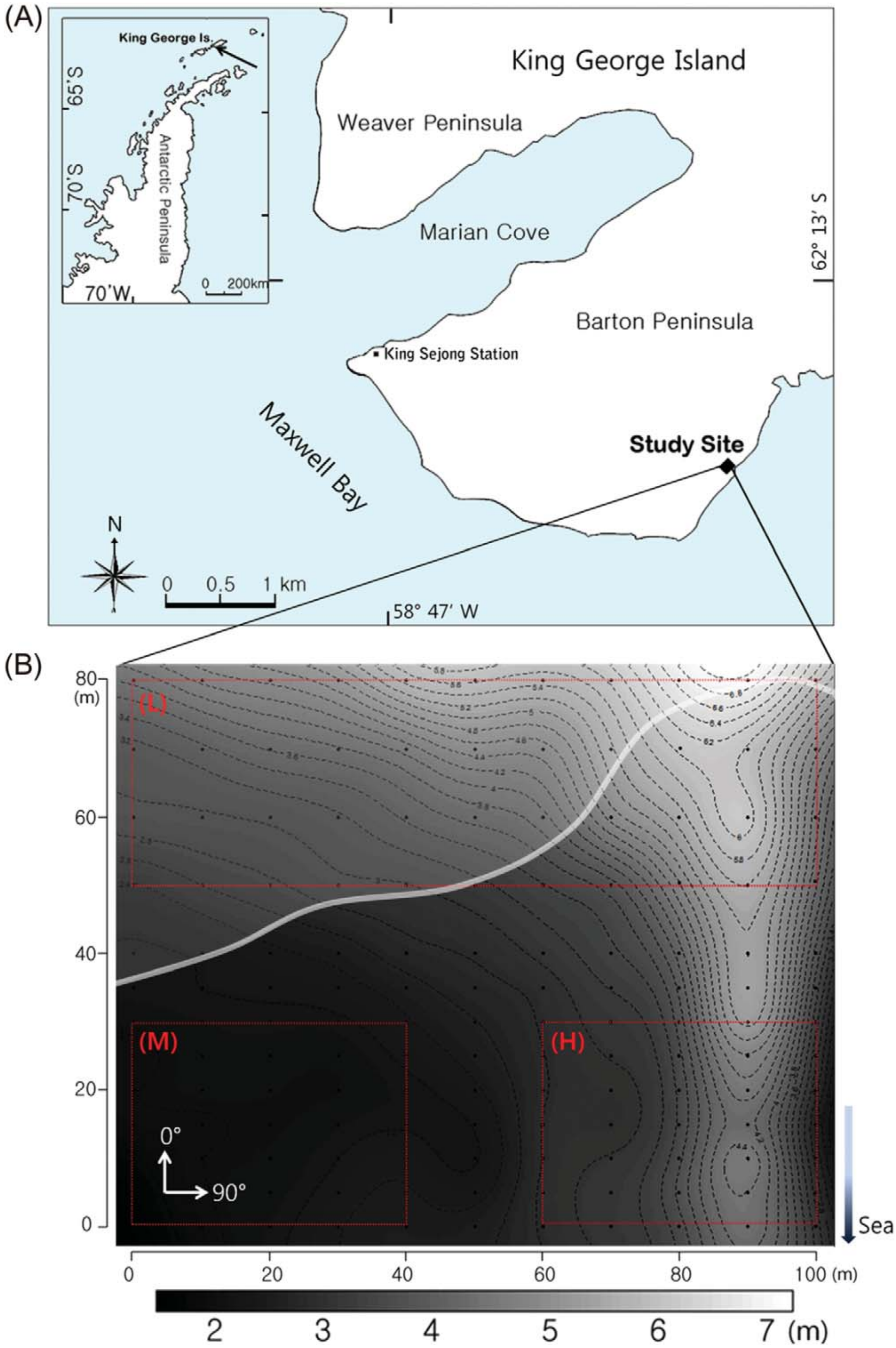

FIGURE 1. (A) Map showing the location of the study site on King George Island, and (B) elevation of the study site and sampling design. Black dots represent sampling spots, and white arrows are the directions of the variogram. White line and translucent area represent a snowpack in January 2010. The legend represents the elevation from the seawater level. Depending on the abundance of *D. antarctica*, the study site was subdivided into three plots (L, low; M, middle, and H, high).

spatial characteristics of *D. antarctica* abundance and environmental factors. The abundance of *D. antarctica* was measured as the number of visually distinguishable tufts within a square of area 1 m^2. We defined a tuft as more than five shoots of hair-grass that was held together at ground bottom; seedlings were excluded from the count of tufts in the quadrat. We distinguished each tuft based on the shape of the bunch in the carpet of grass. Moss abundance was calculated as the percentage of ground covered based on pictures analyzed in the laboratory using image analysis software (ImageJ 1.34 s; Wayne Rasban, National Institutes of Health, U.S.A.). In January 2010, 189 sampling squares were placed at the intersections of a 5 m by 5 m grid within a 100 × 40 m^2 plot; 99 squares were used to identify associations between the abundance of *D. antarctica* and environmental factors.

In January 2010, we also placed 99 squares at the intersections of a 10 m by 5 m grid within the 100 × 40 m^2 plot for soil sampling. Soil samples were taken from 3 of the square corners and mixed thoroughly to produce a composite sample for each sampling square. In 2011, we extended the plot to 100 × 80 m^2 and sampled 143 squares (Fig. 1, part B). To determine the *D. antarctica* seedling survival rate, we placed numbered tags near 50 seedlings in January 2009 and then checked seedling mortality in January 2010 and 2011. Grass survival was identified by shoot greenness and root vitality.

SOIL ANALYSIS

Soil electrical conductivity and pH (soil:distilled water, 1:5) were measured using an electrical conductivity meter (Orion model 150A, U.S.A.) and pH meter (Orion model 720A+, U.S.A.), respectively. Water content was determined by measuring the amount of weight lost after drying the samples in a 105 °C oven for 48 h. The organic matter content was calculated according to the weight loss after the samples were kept in a muffle furnace at 550 °C for 4 h (John, 2004). NO_3-N was extracted using 2 M KCl and measured using an automatic Kjeldahl protein/nitrogen analyzer (Kjeltec Auto 1,035/1,038 System; Tecator AB, Sweden). The total nitrogen content was determined in an element analyzer (EA1110, CE Instruments, U.K.) at the National Center for Inter-University Research Facilities, Seoul National University. Mehlich-3 extract solution (Ziadi and Sen Tran, 2008) was used to extract PO_4-P from air-dried soil, and the ascorbic acid reduction method (Solorzano, 1969) was used to determine the content of available phosphorus. The minerals Ca^{2+}, K^+, and Na^+ were extracted using Mehlich-3 extract solution and measured using ICP (Inductively Coupled Plasma) Optical Emission Spectrometer (ICP-730 ES, Varian, Australia). The soil texture was determined by the hydrometer analysis method (Day, 1965). Forty grams of air-dried soil (<2.0 mm) was mixed with 100 mL sodium hexametaphosphate solution. After shaking 16 h, the mixture was transferred into a 1000 mL mass cylinder, and distilled water was added to bring the volume to 1000 mL. After shaking for one minute, the percentage of sand (after 40 s), clay (after 7 h), and silt were determined by using equations given in Day (1965).

DATA ANALYSIS

Data sets were analyzed using classical statistical descriptors such as mean, standard deviation, coefficient of variation, skewness, kurtosis, and Pearson's correlation coefficient. The Shapiro-Wilk test revealed that most variables were not normally distributed except for distance from shoreline and clay content. Because semivariograms are sensitive to highly skewed distributions, diverse transformations (see Table 1) were performed to obtain a nearly normal distribution before the geostatistical analysis (Jongman et al., 1995). To identify major gradients in soil variables in terms of the abundance of *D. antarctica*, principal component analysis (PCA) was applied to correlations in soil variables. The study site was divided into three subplots (L, M, and H) based on the grass abundance, and 30% of the quadrats in each subplot were randomly selected to minimize the spatial autocorrelation. We excluded some variables that were strongly spatially autocorrelated (e.g. Shoreline, Snow) and did not produce any meaningful ecological explanations of the grass distribution (e.g. Silt, K^+, Ca^{2+}).

The correlogram is frequently employed to investigate patterns and the underlying spatial covariance in ecological data (Brown et al., 1995; Steen et al., 1996; Thomson et al., 1996). The cross-correlogram represents the correlation existing between the

TABLE 1

Descriptive statistics of *D. antarctica* density and soil variables that are transformed for normality. Elevation: elevation from sea water level; Shoreline: distance from shoreline; WC: water content; OM: organic matter; EC: electric conductivity; TN: total nitrogen; AP: available phosphorus; recip: reciprocal; exp: exponential; cube: cubic power; tenth: tenth power.

	2010 (n = 99)					2011 (n = 143)					
Variable	Transformation	Mean	CV	Skewness	Correlation	Transformation	Mean	CV	Skewness	Correlation	Unit
D. antarctica	recip	−0.62 (4.08)	−62.0 (126.8)	0.24	1	recip^2	−0.71 (2.39)	−59.1 (321.2)	0.79	1	No.
Moss	cube	0.57 (78)	54.1 (28.9)	−0.34	0.18	cube	0.51 (72)	63.7 (37.9)	−0.16	0.17*	%
Elevation	log	0.43 (2.78)	27.9 (30.2)	0.68	0.17	log	0.48 (3.22)	30.6 (36.7)	0.47	−0.08	m
Shoreline	none	72.03	30.5	0.19	0.04	none	84.9	34.9	0.35	−0.27**	m
Sand	arcsine	1.27 (91.2)	3.7 (2.97)	−0.46	−0.03	tenth	0.36 (89.3)	39.3 (5.94)	−0.37	0.15	%
Silt	none	4.94	48.4	0.17	0.11	log	0.77 (5.81)	31.1 (73.2)	−0.09	−0.04	%
Clay	none	3.86	35.6	−0.32	−0.14	none	4.88	42.9	0.38	−0.24**	%
WC	log	1.12 (12.9)	12.1 (35.2)	0.26	−0.12	recip	−0.13 (9.52)	−43.8 (62.7)	−0.46	−0.12	%
OM	recip	−0.32 (3.29)	−21.4 (26.6)	0.51	0.42***	recip	−0.41 (2.64)	−24.4 (32.5)	0.40	0.18*	%
pH	exp	533.5 (6.25)	21.1 (3.67)	−0.23	−0.27**	exp	443.7 (6.08)	17.9 (3.41)	−0.71	−0.24**	
EC	recip	−17.8 (66.8)	−35.3 (55.3)	−0.12	0.33***	recip	−19.7 (60.6)	−36.5 (57.3)	−0.41	0.30***	μS/cm
TN	recip	−3.71 (0.11)	−34.0 (88.3)	−0.75	0.28**						wt%
NO_3-N						log	1.83 (77.7)	12.8 (53.3)	−0.02	0.38***	mg/kg
AP	recip	−0.21 (7.54)	−49.0 (99.1)	0.00	0.22*	log	0.62 (5.36)	48.9 (81.7)	0.54	0.11	mg/kg
Na^+	recip	−8.63 (0.13)	−23.6 (38.1)	−0.06	0.10	recip	−12.8 (0.08)	−23.6 (36.3)	0.21	0.14	mg/g
K^+	recip	−15.5 (0.07)	−27.4 (37.9)	0.25	−0.11	recip	−20.2 (0.06)	−34.1 (43.5)	−0.25	0.04	mg/g
Ca^{2+}	log	2.74 (0.58)	4.7 (29.7)	−0.34	0.10	log	2.59 (0.41)	5.0 (30.6)	−0.05	0.16	mg/g

two variables (Kravchenko et al., 2003). We used the spline cross-correlogram, which is an adaptation of the nonparametric covariance function (Bjørnstad et al., 1999; Bjørnstad and Falck, 2001). This method provides a 95% confidence envelope for the function with a bootstrap algorithm. The nonparametric covariance function is calculated as follows:

$$\widetilde{p}(\delta)=\frac{\sum_{i=1}^{N}\sum_{j=1+1}^{N}G\left(\frac{\delta_{ij}}{h}\right)\delta_{ij}}{\sum_{i=1}^{N}\sum_{j=i+1}^{N}G\left(\frac{\delta_{ij}}{h}\right)}, \quad (1)$$

where G is a kernel function with kernel bandwidth h, and δ_{ij} is the geographic separation distance between the values of variable i and values of variable j by metric Euclidean distance.

The semivariogram $\gamma(h)$ is estimated by calculating half the average squared difference between all pairs of points that are separated by a given distance. The empirical semivariogram was calculated as follows (Isaaks and Srivastava, 1989):

$$\gamma(h)=\frac{1}{2n(h)}\sum_{i=1}^{n(h)}\left[z(s_i)-z(s_{i+h})\right], \quad (2)$$

where $n(h)$ is the number of lag pairs at distance intervals of h, and $z(s_i)$ and $z(s_{i+h})$ are values of the measured variable at spatial locations i and $i+h$, respectively. Although a number of variogram functions have been suggested, the Matérn function was fitted to the empirical semivariograms using ordinary least squares (Matérn, 1986; Marchant et al., 2011):

$$\gamma(h)=c_0+c_1\left\{1-\frac{1}{2^{v-1}}\Gamma(v)\left(\frac{h}{a}\right)^{v}K_v\left(\frac{h}{a}\right)\right\} \text{ for } h>0, \quad (3)$$

where c_0 is the nugget variance, c_1 is the partial sill variance, a is the distance parameter, v is a smoothness parameter fixed in 1, K_v is a modified Bessel function, and Γ is the gamma function. The best-fit models for the semivariograms are selected based on the R^2 between model predictions of variance for each lag distance and the measured values. The proportion of spatial structure $c_1/(c_i + c_0)$ is a measure of the proportion of sample variance (c_0 + c_0), which is explained by spatially structured variance (c_1). As the value approaches 1, the spatial autocorrelation becomes stronger (Cambardella et al., 1994).

To apply the kriging methods, each variable was checked for trend and anisotropy. If a variable had a geographic trend, then the mean was assumed as a first-order polynomial on the coordinates rather than constant mean over the region (Crawford and Hergert, 1997; Lark and Webster, 2006; Diggle et al., 2007). Interpolated maps were then computed using ordinary kriging with a trend based on the calculated parameters that assumed linear trend surface to evaluate the regional patterns of variation (Diggle et al., 2007). The geostatistical software, GeoR version 1.7-2 under R version 2.14.0, was used in the geostatistic analysis (Ribeiro and Diggle, 2001). For the interpolation of the *D. antarctica* density, Bayesian analysis for the Poisson–log normal model is implemented by the function pois.krige.bayes in the geoRglm package (version 0.9-2) of R, because applying ordinary kriging is not suitable for count data (Diggle et al., 2003).

A generalized random effect logistic regression model was applied to analyze the survival of *D. antarctica* by adding environmental covariates and random effect. We selected the 47 quadrats where the tuft number decreased or did not change, and excluded the quadrats in which the grass was not found in both years. Spatial autocorrelation was not found among the selected quadrats. The purpose of including a random effects term is to account for the influence of unobserved covariates. The random effect model has several strengths compared to fixed effect models. They can improve efficiency of estimation (Welham et al., 2004). In addition, random effects are no longer estimated independently, so it is possible to have more honest accounting for uncertainty (Kéry, 2010). Our model can be expressed as follows:

$$C_i \sim Binomial(p_i, n_i) \quad (4)$$

$$Logit(p_i) = \beta 0 + \beta 1 * X_{moss(i)} + \beta 2 * X_{clay(i)} + \beta 3 + X_{snow(i)} + \beta 4 * X_{shoreline(i)} + b_i \quad (5)$$

$$b_i = Normal(0, \tau) \quad (6)$$

where i is the index of the quadrat, C_i and n_i are the number of tufts in 2011 and the number of tufts in 2010 in the ith quadrat, respectively. The probability of survival of *D. antarctica* is p_i, and the link function is the logit, as is customary for a binomial distribution (Kéry, 2010). The random effect term b_i is used to account for unstructured over-dispersion (OD) and is typically taken to be independently identically distributed with variance σ^2, and follows a normal distribution. Explanatory variables have been centered by subtracting the mean values and standardized by dividing the standard deviation to improve the efficiency of the Markov Chain Monte Carlo (MCMC) algorithm (Elith, 2002).

The parameter estimation was based on a sample of 5000 values after a burn in 2500 iterations from 3 chains. The convergence was assessed using the CODA package (Plummer et al., 2006) for model selection using R. Model selection was performed using the deviance information criterion (DIC), where a lower DIC suggests a better trade-off between model fit and parsimony. We used WinBUGS version 1.4.3 (Spiegelhalter et al., 2003) via R2WinBUGS package (Sturtz et al., 2005) for R, which implements Markov Chain Monte Carlo (MCMC) methods using a Gibbs sampler.

Results

NON-SPATIAL ANALYSIS

The basic statistical summary data for the density of *D. antarctica,* moss cover, and soil chemical properties are shown in Table 1. The change of moss cover was imperceptible in the same quadrats. Soil water content in January 2011 dramatically decreased (36.5%) compared to that in 2009 because of the lower precipitation in 2010. Correlations between the density of *D. antarctica* and soil variables were tested using Pearson's correlation coefficient. We performed non-spatial analyses to screen for correlation among variables, but these results could have been overestimated because they were obtained by ignoring the spatial dependence. In other words, the samples may account for a greater weight than that if the samples had been spatially independent. Correlation results show that soil organic matter, electric conductivity, and nitrogen variables were positively correlated with grass abundance, and soil pH and distance from the shoreline were negatively correlated with grass abundance.

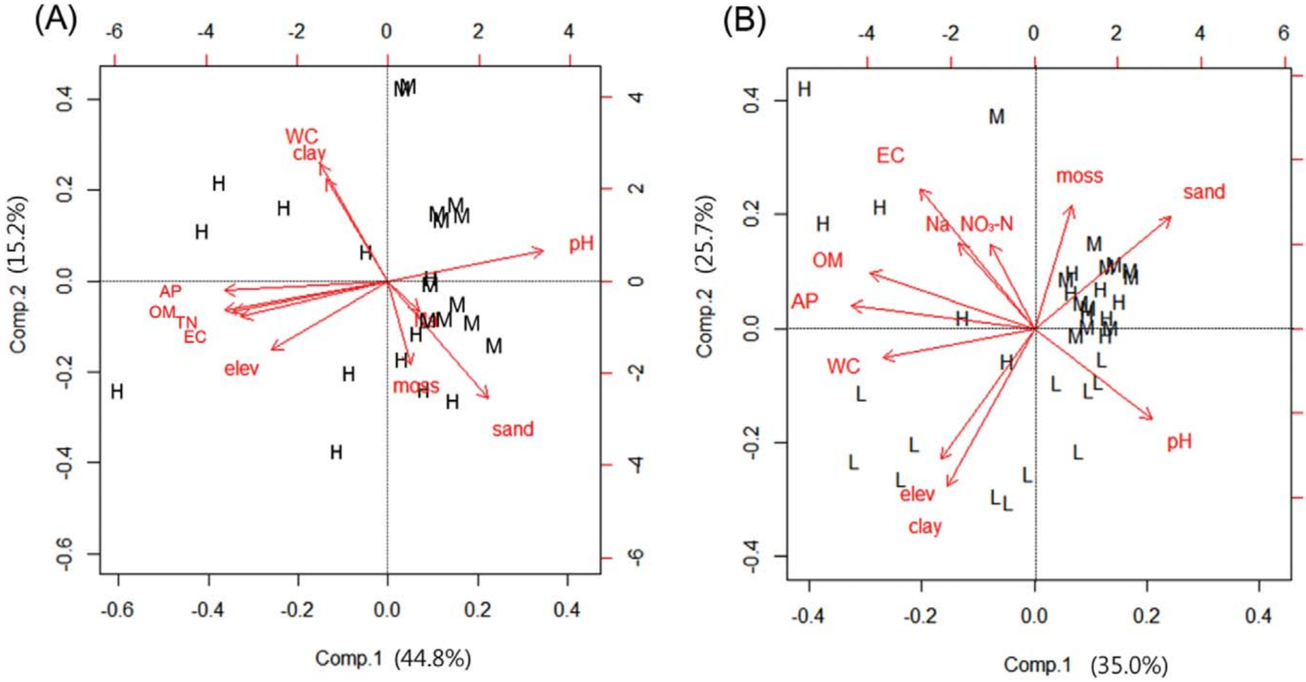

FIGURE 2. Biplot of soil variables and sampling quadrats depending on the *D. antarctica* abundance measured in (A) 2010 and (B) 2011. L, low density; M, middle density; H, high density; WC, water content; EC, electrical conductivity; TN, total nitrogen; OM, organic matter; and AP, available phosphorus.

We conducted PCA to condense the information from the 11 soil variables that were selected in the correlation analysis. The study site was subdivided into 3 plots based on the abundance of *D. antarctica* and was presented in the biplots (Fig. 2). Because the low-density plot (L) was covered with snow in 2010, we compared only sub-plots M and H in 2010. Two principal components explained 60% of the total variation (Fig. 2, part A). Component 1, with an eigenvalue of 5.68, had a highly negative load on organic matter (−0.383), total nitrogen (−0.382), and available phosphorus (−0.379). This biplot (A) shows that the high-density plot (H) had higher nutrient content than the low-density plot (L). Figure 2, part B, demonstrates that 2 principal components explained 60.8% of the total variation. Component 1, with an eigenvalue of 3.86, had a highly negative load on available phosphorus (−0.466), organic matter (−0.418), and water content (−0.386). Component 2, with an eigenvalue of 2.83, had a high negative load on clay (−0.464) and elevation (−0.384) and had a positive load on electric conductivity (0.409) and moss cover (0.36). Figure 2, part B, demonstrates that low-density plots (L) had higher clay content and elevation, and lower electric conductivity and moss cover, than the middle- and high-density plots.

SPATIAL ANALYSIS

All of the variables were checked for spatial trends and anisotropy in order to apply the geostatistical tests. Semivariance estimates for interesting variables were fitted using nonlinear ordinary least-squares regression analysis based on the Matérn function (Table 2). When we compared four directions (0°, 45°, 90°, and 135°) to figure out the anisotropy with a 22.5° tolerance angle, several variables showed strong spatial dependence at specific directions. The ranges of spatial dependence were diverse among variables, ranging from 30 to >300. Beyond the 300 m ranges, semivariance steadily increased without convergence. *D. antarctica* abundance had the highest semivariance in the 135° direction, meaning that this grass was distributed with the strongest spatial variability in the 135° direction compared to the other directions. The change of semivariance for each lag distance was similar between both years. Moss had the opposite directional spatial variability with *D. antarctica*. Moss showed the longest range in the 45° direction, but the range was shorter than that of *D. antarctica*. As shown in Figure 1, the elevation continually increased in the 45° direction, so its proportion of spatial dependence was stronger than that of other variables. Clay showed the same directional spatial dependence as elevation, which means that clay is correlated with elevation (simple Pearson's correlation: $R^2 = 0.57$, $p < 0.001$). Water content and NO_3-N showed isotropic distributions, and they had short ranges and moderate proportions of spatial dependence. Electrical conductivity and Na^+ content, which are governed by the distance from the shoreline, showed strong spatial dependence in the 0° direction.

Figure 3 shows an example of six kriged maps for moss cover, sand content, water content, organic matter, pH, and available phosphorus sampled in 2011. Moss cover was low at the high-elevation area and positively correlated with sand content ($R^2 = 0.35$, $p < 0.001$). We found that moss cover has negative spatial correlation with elevation according to the directional semivariogram and kriged map. Although the values of soil variables changed at the same quadrat between years, their spatial patterns remained remarkably constant. The water content was low in the high sand content quadrat ($R^2 = -0.684$, $p < 0.001$). The organic matter and available phosphorus were high in the high-elevation area, and they negatively correlated with sand and pH.

TABLE 2

Parameters of the anisotropic semivariogram model for variables sampled in 2011. The directions listed for each variable are the strongest and the weakest spatial-dependent direction among the four directions (0°, 45°, 90°, 135°).

Variables	Direction	Nugget (C_o)	Partial sill (C_1)	Range	$C_1/(C_o+C_1)$	R^2
D. antarctica	135°	0.11	0.26	166	0.691	0.97
	45°	0.10	0.06	45	0.353	0.61
Moss	45°	0.07	0.1	89	0.613	0.87
	135°	0.06	0.03	45	0.325	0.76
Elevation	45°	0	0.98	>300	1.000	0.99
	135°	0.001	0.01	90	0.883	0.59
Sand	45°	0.009	0.063	296	0.875	0.95
	90°	0.007	0.013	80	0.661	0.41
Clay	45°	1.36	177	>300	0.992	0.99
	135°	0.29	4.6	85	0.940	0.87
WC	—	0.002	0.002	48	0.514	0.62
OM	135	0.000	0.033	253	1.000	0.90
	0	0.003	0.005	60	0.597	0.68
pH	135°	3467	38960	>300	0.918	0.95
	45°	3563	3035	109	0.460	0.80
EC	0°	17.4	1604446	>300	1.000	0.86
	90°	18.3	19	37	0.504	0.99
NO_3-N	—	0.01	0.046	30	0.839	0.64
AP	135°	0.04	0.169	202	0.815	0.97
	0°	0.04	0.042	103	0.543	0.69
Na^+	0°	4.73	435022	>300	1.000	0.79
	90°	1.24	6.8	42	0.845	0.76

Figure 4 presents the specifics of the spatial patterns of the two variables and the strength of the spatial correlation between them in 2010 by using spline cross-correlograms. The cross-correlogram between the abundance of *D. antarctica* and 3 variables (snow, OM, EC) exhibit similar spatial correlation range or the distance over which the variables are correlated. They had positive spatial correlation from 0 to 40 m and were negatively correlated from 40 to 100 m. However, the shape of the correlogram was different. The cross-correlogram between *D. antarctica* and snow had the steepest slope among all other cross-correlograms, which means that two variables had strong spatial dependence and distance from the snowpack and is an important factor determining distribution of hair-grass. The spatial cross-correlation between *D. antarctica* and OM had the second steepest slope and the similar shape with snow because of strong correlation (0.681, $p < 0.001$) between snow and OM. The correlograms calculated with the data set for 2011 also had similar spatial correlation range and shape to those for in 2010. Sand content was significantly correlated with diverse soil properties (WC, OM, and AP). They had negative spatial correlation from 0 to 20 m, and WC had the strongest spatial correlation with sand among all other environmental factors. Spatial correlations between sand and soil chemical factors were more significant in 2011 than those in 2010.

THE EFFECT OF SNOWFALL ON SURVIVAL OF THE HAIR-GRASS

In 2009, precipitation was twice as high as the 10-year average (Fig. 5). Precipitation during winter months (May to November) was particularly high. We found that approximately half of our study area was covered with snow in January 2010, and most of the snow cover remained until in 21 February. Some *D. antarctica* tufts were covered with snow for the whole summer season.

Figure 6 shows the interpolated maps of hair-grass abundance. When we compared the number of tufts in 2010 and 2011, the total number of tufts of 2011 decreased by 27.8% compared to 2010. The tuft number decreased in 37 out of 99 sampling squares and increased in only 9. Figure 7 presents the grass seedling survival rate between years. We found that all remaining 30 tagged seedlings survived in January 2010. However, 9 out of 19 tagged seedlings were still survived in January 2011.

As shown in Figure 8, distance from shoreline, and distance from snow and clay content were significantly associated with survival of *D. antarctica* tufts, which indicates that the grass survival was higher in sampling squares located far from the snow and having high clay content. Moss cover was not associated with the survival of the grass tufts. Unstructured over-dispersion (OD) had a reasonable variance, and DIC score (107) also had the lowest value among several possible models.

Discussion

SPATIAL DISTRIBUTION PATTERNS

This study has applied a geostatistical approach to analyzing and interpreting the distribution of *D. antarctica* and related soil chemical and physical variables as well as topographic properties. Semivariograms and kriged maps revealed that all of the variables were spatially correlated; therefore, spatial estimation was valid (Ver Hoef et al., 2001; Dayani and Mohammadi, 2010). Especially, *D. antarctica* was strongly spatially autocorrelated in the 135° direction. Spatial autocorrelation provides important ecological infor-

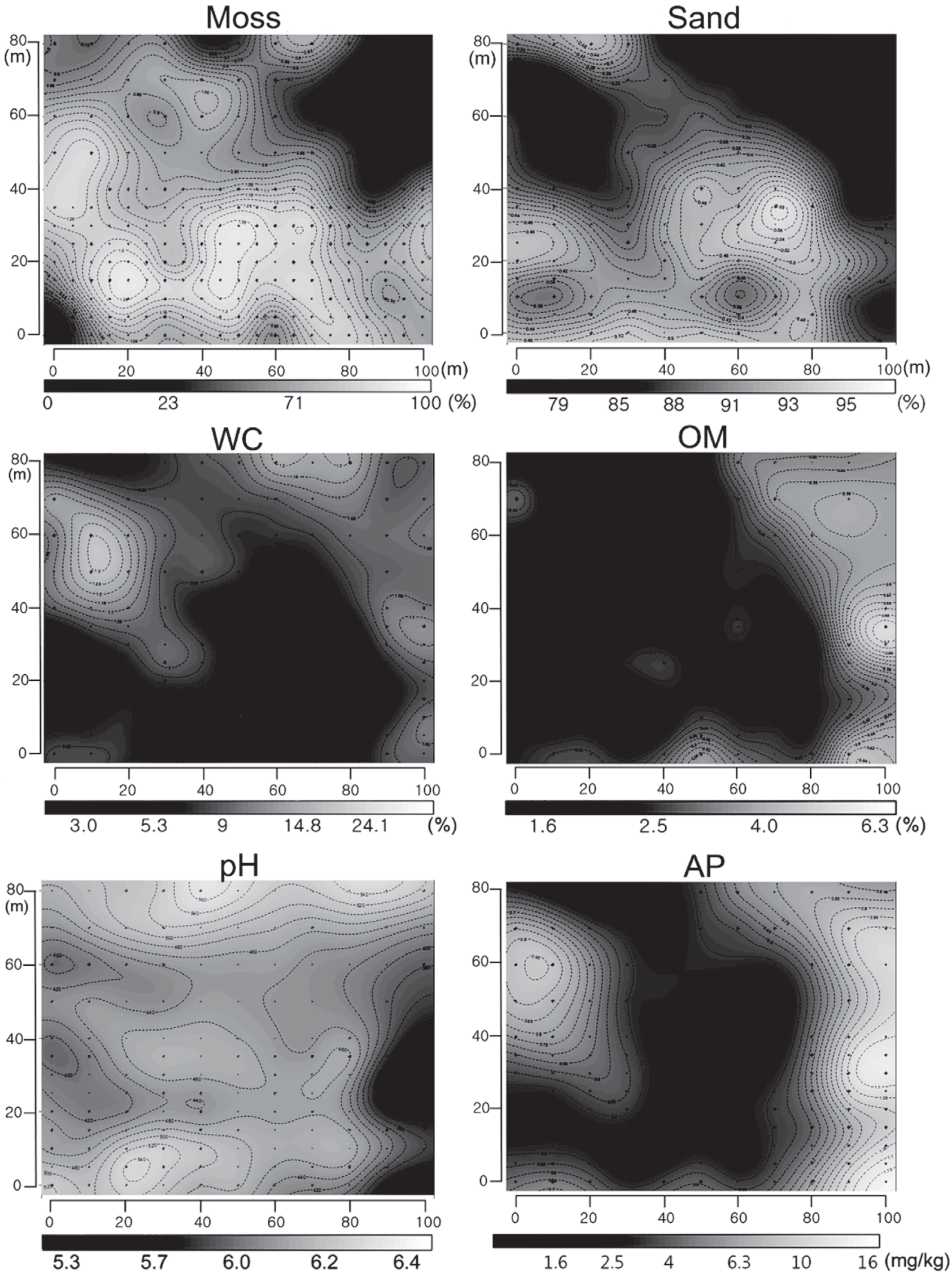

FIGURE 3. Interpolated maps of Moss (moss cover), Sand (sand content), WC (water content), OM (organic matter), pH, and AP (available phosphorus) from the data collected in 2011. The legends of each map are the back-transformed values.

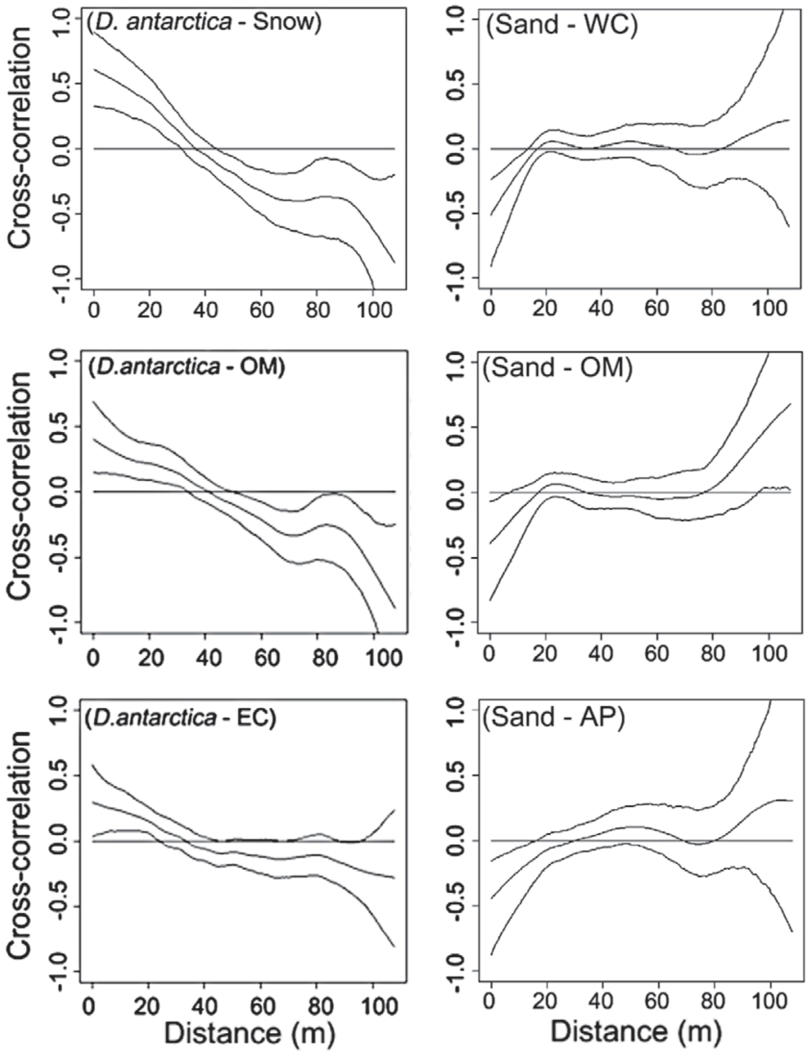

FIGURE 4. The nonparametric covariance function of the representative descriptors for *D. antarctica* and sand in 2010. The *x*-axes represent the geographic separation distance between the values of two variables, and the *y*-axes represent the cross-correlation. The middle line represents the estimated functions, and the upper and lower thin lines represent the 95% bootstrap confidence intervals as estimated using spline correlograms.

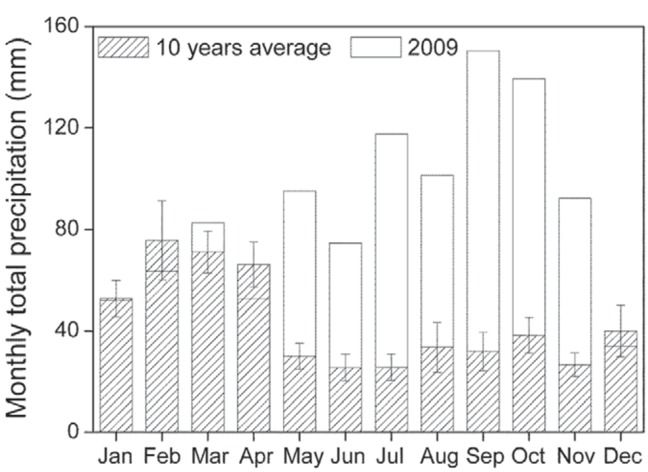

FIGURE 5. Monthly total precipitation in 2009 and 10 years average (± SE) from 2000 to 2010 except for 2009.

mation such as limits on the mobility of organisms, organism-specific dispersal mechanisms, and spatial aggregation of populations in the landscape (Dormann et al., 2007). Strong spatial autocorrelation of *D. antarctica* may be derived from its grass dispersal mechanisms at the study site. Vera (2011) suggested that birds may play an important role in long-distance dispersal of this species, while at short distances, *D. antarctica* may be dispersed by seeds or produced ramets (Edwards, 1972; Convey, 1996).

We also infer that strong anisotropy in geographic variables was reflected in the soil variables through directional semivariograms and kriged maps. For example, elevation and clay content had nearly the same range values and directional dependence, indicating the presence of possible co-regionalization. The spline cross-correlogram between soil texture and soil properties showed that soil texture significantly correlated with water content, organic matter, and available phosphorus (Fig. 4). It is well known that soil texture is one of the important factors governing the physical and chemical properties of soil (Warrick and Gardner, 1983; Tanji, 1990; Crave and Gascuel-Odoux, 1997). Several researchers have reported that soil formation and chemical weathering in the coastal regions of Antarctica occur more than we expected (Blume et al., 1997; Beyer et al., 2000). Further, Bölter et al. (1997) suggested that elevated clay and organic matter contents resulted in a high

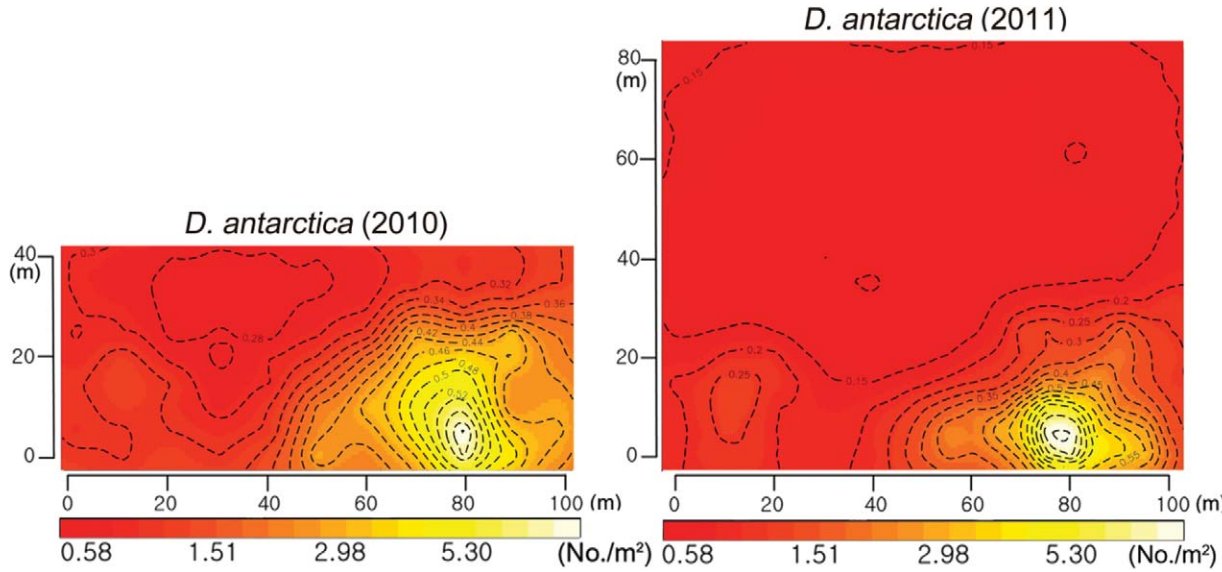

FIGURE 6. Interpolated maps of *D. antarctica* in 2010 and 2011. The legends of each map are the back-transformed values.

water and nutrient binding capacity that favors plant growth in maritime Antarctica. In our results, the *D. antarctica* abundance was positively associated with soil nutrient levels such as NO_3-N and available phosphorus. However, the clay content had a negative relationship with the grass abundance and a positive relationship with the sand content. These results indicated that *D. antarctica* favors well-drained soil. Furthermore, a high clay content area (L-subplot in Fig. 1) within the study area was covered with snowpack over a substantial portion of the growing season in 2010. It is well known that topographic characteristics and wind play important roles in the distribution of snowpack (Scott and Rouse, 1995). Strong winds may remove snow from exposed ridges (i.e. sub-plot H) and deposit it in areas protected by hillsides (i.e. sub-plot L). Therefore, the snow may melt early on sub-plot H due to its relatively thin layer. The results of this study and a random sampling study (Park et al., 2012) showed a significant association between the abundance of *D. antarctica* and distance from the snowpack. This is consistent with previous observation (Edwards, 1972; Vera, 2011) suggesting that early snowmelt may be an important factor in the distribution of *D. antarctica*.

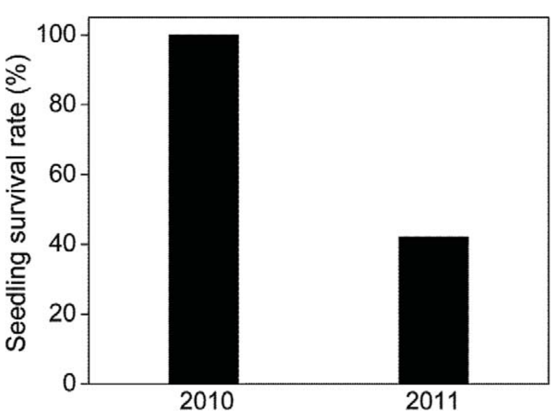

FIGURE 7. *D. antarctica* seedling survival rate on Barton Peninsula. The survived seedlings were counted in January 2010 and 2011.

In addition, moss cover was also spatially correlated with elevation and sand content. We found that *Sanionia* spp., the dominant genus of moss in the wet coastal region of King George Island (Ochyra, 1998), inhabits sandy soils and low elevation areas. This moss may either share the environmental preferences of *D. antarctica* or has a positive influence on growth of the grass (Kim et al., 2007; Park et al., 2012).

Another interesting topographic variable was the distance from the shoreline. Electrical conductivity and Na^+ had strong spatial autocorrelations in the 0° direction (distance from the shoreline), and weak spatial dependences in the 90° direction, which mean that seawater spray affected the soil salinity. Cross correlation between the abundance of *D. antarctica* and EC was positively correlated from 0 to 35 m, suggesting that seawater spray was not a critical limiting factor for the distribution of hair-grass. Several researchers also reported that *D. antarctica* has high tolerance for salinity (Ochyra, 1998; Smykla et al., 2007; Ruhland and Krna, 2010).

THE EFFECT OF SNOWFALL

There have been several reports that the distribution of *D. antarctica* is expanding with increases in temperature and lengthening of the growing season (Grobe et al., 1997; Day et al., 1999; Gerighausen et al., 2003; Kim et al., 2007). Kim and Chung (2004) and Kim et al. (2007) reported that populations of *D. antarctica* had rapidly increased around Barton Peninsula. However, in 2011, the abundance of *D. antarctica* decreased sharply in this area. In particular, the seedling survival rate decreased by more than 50% compared to the previous year. We suggest that these results may be due to critical weather effects such as low temperatures or heavy snowfall. Air temperatures in 2009 and 2010 (mean: −2.0 °C, minimum: −8.2, maximum: 2.4 °C) were not significantly different from the 10-year average (mean: −1.6 °C; minimum: −11.4 °C; maximum: 2.8 °C), and the temperatures during the grass growing

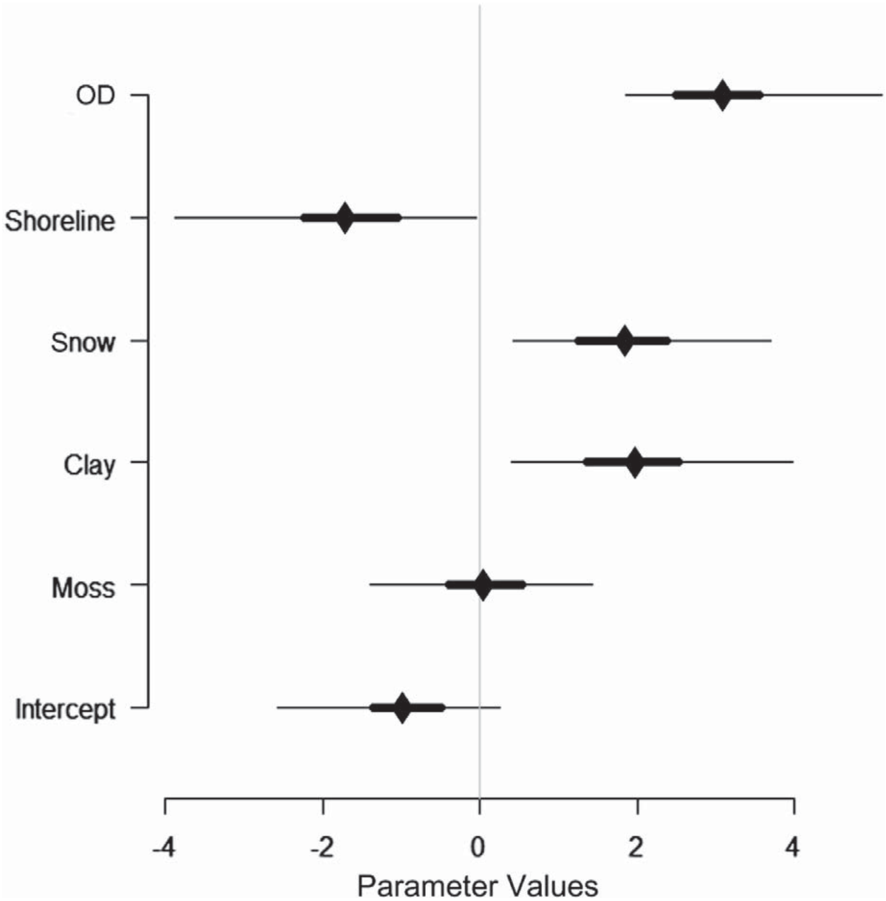

FIGURE 8. Predictors of the survival of *D. antarctica* tufts. Diamonds are the estimated posterior mean values, short thick lines are the 50% credible intervals, and long thin lines are the 95% credible intervals. Those intervals not overlapping the zero line are considered significantly different from zero.

season (December–March) were also similar to the 10-year monthly values. On the other hand, high precipitation (1055.3 mm), mostly in the form of snow, was observed in 2009. The amount of precipitation was about twice the annual average for years between 2000 and 2010 (516.8 mm). Thus, *D. antarctica* was likely strongly affected by snowpack during the growing season in 2010.

Many studies of snow-vegetation interactions have been carried out in alpine and arctic areas (Billings and Bliss, 1959; Rouse, 1984; Scott and Rouse, 1995). Snow cover greatly influences the distribution of vegetation, and plant growth is affected by climate factors controlled by the timing of the snow season in alpine ecosystem (Jones, 1999; Jonas et al., 2008). Although plants in cold regions can survive under deep snow cover due to the insulating capacity of snow (Jones et al., 2001), snow cover reduces the amount of light available for photosynthesis, and gas permeability of the snowpack is strongly decreased by the formation of ice layers (Jones, 1999). There is a possibility that the oxygen concentration can be decreased because of the respiration of soil microorganisms, which makes plants more vulnerable to a cold injury (Rixen et al., 2003). Furthermore, snowmelt results in wetter summer conditions (Rouse, 1984). In our study, soil water content in January 2010 was 36.5% higher than in 2011 in the same quadrats. Scott and Rouse (1995) observed that the abundance of moisture-intolerant plants declined sharply at the snow fence region, and suggested a strong association between moisture conditions and changes in plant species due to an increase in the volume of winter snow. *D. antarctica* is not a water-tolerant species and inhabits well-drained soils (Edwards, 1972; Kim and Chung, 2004; Park et al., 2012). Although the grass could be damaged by low temperatures in the spring and autumn, a short growing period and waterlogging induced by heavy snowfall may be more critical factors limiting survival of *D. antarctica* in the maritime Antarctic region.

In summary, topographic characteristics might more directly influence the soil chemical and physical attributes in maritime Antarctica than in the temperate zone, because the Antarctic area has fewer interference factors such as dense vegetation and thick topsoil. These topographic and soil properties have multiple influences on the distribution of *D. antarctica*. We also found that *D. antarctica* is severely vulnerable to heavy snowfall. Assuming that temperature increases and lengthening of the growing season are occurring in King George Island, *D. antarctica* may be expanding rapidly due to an increase in suitable habitats for its growth. However, in some regions, the amount of snowfall and/or accumulation of drift snow may be a limiting factor in the expansion of *D. antarctica*.

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