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Effective Seed Distribution Pattern of an Upward Shift Species in Alpine Tundra of Changbai Mountains

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Abstract: The vegetation of alpine tundra in the Changbai Mountains has experienced great changes in recent decades. Narrowleaf small reed (*Deyeuxia angustifolia*), a perennial herb from the birch forest zone had crossed the tree line and invaded into the alpine tundra zone. To reveal the driven mechanism of *D. angustifolia* invasion, there is an urgent need to figure out the effective seed distribution pattern, which could tell us where the potential risk regions are and help us to interpret the invasion process. In this study, we focus on the locations of the seeds in the soil layer and mean to characterize the effective seed distribution pattern of *D. angustifolia*. The relationship between the environmental variables and the effective seed distribution pattern was also assessed by redundancy analysis. Results showed that seeds of *D. angustifolia* spread in the alpine tundra with a considerable number (mean value of 322 per m^2). They were mainly distributed in the low elevation areas with no significant differences in different slope positions. Effective seed number (ESN) occurrences of *D. angustifolia* were different in various plant communities. Plant communities with lower canopy cover tended to have more seeds of *D. angustifolia*. Our research indicated reliable quantitative information on the extent to which habitats are susceptible to invasion.

Keywords: plant invasion; effective seed number (ESN); alpine tundra; Changbai Mountains

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1 Introduction

Plant invasion consists of four spatio-temporal stages: transport, colonization, establishment, and landscape spread (Theoharides and Dukes, 2007). Among the stages, the movement of propagules of invasive species from the current range to a new area of habitat is a fundamental process (Wilson *et al.*, 2009), which strongly influences plant invasion success (Lockwood *et al.*, 2005; Colautti *et al.*, 2006). Once the propagules arrived, they may rapidly become potential threats to the local ecosystem. Therefore, distribution pattern of seeds of invasive plant species in the new environment determined which habitats were susceptible to invasion (DiVittorio *et al.*, 2007). It has been shown that habitat characteristics, associated with availability of resources and specific disturbance regimes, are crucial determinants of the outcome of invasions. And the critical step of management should focus on the analysis of the local ecosystem (Hejda *et al.*, 2009). However, after establishment, the invasion would quickly become unmanageable (Pauchard and Alaback, 2004; McDougall *et al.*, 2011). The prevention also became meaningless to some extent. To solve the problem, we need to know where

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the primarily potential threat range is. Seed distribution pattern of the invasive species can be used as a good predictor for the invasion risk assessment. With this knowledge, some effective precautionary approaches could be designed and conducted. In the previous researches, ecologists have paid much attention on the role of seed banks in the invasiveness (Krinke *et al.*, 2005). They emphasized the importance of seed distribution of invasive plant species in reinvading the cleared sites (Witkowski and Wilson, 2001) and the effects on the local soil seed bank (Vilà and Gimeno, 2007). However, little attention about this important issue has been paid on plant invasion in alpine ecosystem.

Alpine habitats are considered to be at low risk of plant invasions (Humphries *et al.*, 1991) because of the harsh environment such as strong winds, short growing seasons, high solar radiation, low temperatures and low nutrient availability (Körner, 2003). However, increasing researches have shown that plant invasions did occur and had led to serious consequences, such as species loss, replacement of the present native biota by invasive species (Halloy and Mark, 2003; Muñoz and Cavieres, 2008; Pauchard *et al.*, 2009). Alpine tundra of the Changbai Mountains is one of the two rare alpine tundra distributions in China, the other one located at the Altay Mountains. The vegetation has experienced great changes in recent decades. Narrowleaf small reed (*Deyeuxia angustifolia*) from the birch forest zone had crossed the tree line and invaded into the alpine tundra zone, which has had severe impacts on the alpine tundra ecosystem and cause the extinction of native plants. *D. angustifolia* is not an invasive plant. However, the consequences of its arrival in the alpine tundra are similar as an invasive plant did. Therefore, in this study, we conducted our research from the view of plant invasion. Using spectral and image analysis method, Zong *et al.* (2013b) found that *D. angustifolia* invasion begun in the 1980's. Nowadays, *D. angustifolia* has successfully invaded the alpine tundra landscape with a gradual trend along the altitudinal gradient. The range was extended from low elevations to high elevations. To reveal the mechanism, Zong *et al.* (2013c) carried out the experiments of transplant, temperature enhancement and seed germination. The results showed that seeds of *D. angustifolia* could not germinate if they did not meet the soil. Invasion of *D. angustifolia* was special in the stages of plant succession after the volcano eruption, which may represent the invasion of birch forest. *D. angustifolia* patches in the high elevations are scattered with distance. It can be confirmed that the formation of patches are primarily due to the seed dispersal. Therefore, to reveal the driven mechanism of *D. angustifolia* invasion, there is an urgent need to figure out the seed distribution pattern, which could tell us where the potential risk regions are and help us to interpret the invasion process, especially when the seeds primarily arrived at the alpine tundra. Furthermore, the seed distribution area was exactly the implication of potential threat range, which was useful for the manager to make effective countermeasure.

In the birch forest zone, *D. angustifolia* is the main understory companion species of Mountain birch (*Betula. ermanii*) trees. *D. angustifolia* is characterized by fast growth, clonal and sexual reproduction, short juvenile period, high seed production and anemochory (Williamson and Fitter, 1996; Marco and Páez, 2000; Baret *et al.*, 2004). These traits ensure that they could overcome the stressful abiotic conditions and successfully survive in alpine tundra (Quiroz *et al.*, 2009). High seed production resulted in a large number of seeds capable of dispersing in the alpine tundra. However, only the seeds conserved in the soil layer could be the effective threats to the local ecosystem. Therefore, in this study, we treated such seeds as effective seeds and focus on its distribution pattern. The aims of this study are 1) to characterize the effective seed distribution pattern of *D. angustifolia* in alpine tundra, and 2) to assess the relationship between various environmental gradients, such as elevation and slope, and the effective seed distribution pattern.

2 Materials and Methods

2.1 Study area

The Changbai Mountains in Northeast China have unique vertical spectra with five vegetation zones: 1) deciduous broad leaved forest zone (below 500 m); 2) mixed deciduous broad-leaved/conifer forest zone (500–1100 m); 3) coniferous forest zone (1100–1700 m); 4) birch forest zone (1700–1950 m); and 5) tundra zone (> 1950 m) (Zheng *et al.*, 1997). The Changbai Mountains Nature Reserve was protected since 1960. There is no grazing and cutting history. The alpine tundra zone (41°53′–42°04′N, 127°57′–128°11′E) lies between 1950 m and 2761 m (Zheng *et al.*, 1997; He *et al.*, 2002; Wei *et al.*, 2007). The climate in the alpine tundra is characterized by low temperature, heavy precipitation and a short growing season. Mean annual temperature in the growing season (June–September) range from 3.37℃ to 8.82℃ (mean temperature is 5.87℃). Average annual precipitation ranges from 700 mm to 1400 mm (Zong *et al.*, 2013a). Weather data are from the Tianchi Meteorological Station which located at 2623 m and 6.2 km away from our study area. Corresponding to the tundra climate, common plants are low stature or prostrate shrub, graminoids forming tussocks, herbaceous perennials forming rosettes and cushion plants (Huang and Li, 1984). The growth rate of alpine plants is very slow due to low temperature and short growing season. Harsh environment of alpine tundra is not favorable to plant organism that limits photosynthesis capability and vegetative growth (Huang and Li, 1984; Körner, 2003). Grass communities on the west slope were very common whereas shrub communities were common on the north slope. In the study area investigated (Fig. 1), Rhododendron-Salixpurpurea (*Rhododendron chrysanthum-Salix rotundifolia*) community was the most common plant community (42 sites), which was also the community being invaded by *D. angustifolia*. There was also a large number of Sanguisorba sitchensis-Ligularia james (*Sanguisorba stipulata-Ligularia jamesii*) community (37 sites) and Blueberry-Mountain avens (*Vaccinium uliginosum-Dryas octopetala*) community (33 sites). *D. angustifolia* community accounted for about 10% of the total sites (198 sites). Mountain avens-Polygonaceae (*Dryas octopetala-Polygonum viviparum*) community was the scarcest (16 sites).

2.2 Study species

D. angustifolia is characterized as hygro-mescophytes, perennial herb, with erect culms, a stature slender to delicate and 90–150 cm in height. The favorite habitats of *D. angustifolia* are the moist places corresponding to its life-history characteristics. In the alpine tundra, the current distributions of *D. angustifolia* mainly spread in the low elevations. The seeds of *D. angustifolia* are mature in late August which is in brown color and in ovoid shape. The weight of one thousand seeds of *D. angustifolia* is 0.161 g (Li *et al.*, 2009). The spread of *D. angustifolia* is facilitated by the production of large numbers of wind-dispersed light weight seeds (pappus-bearing). The seed dispersal season was short (about one

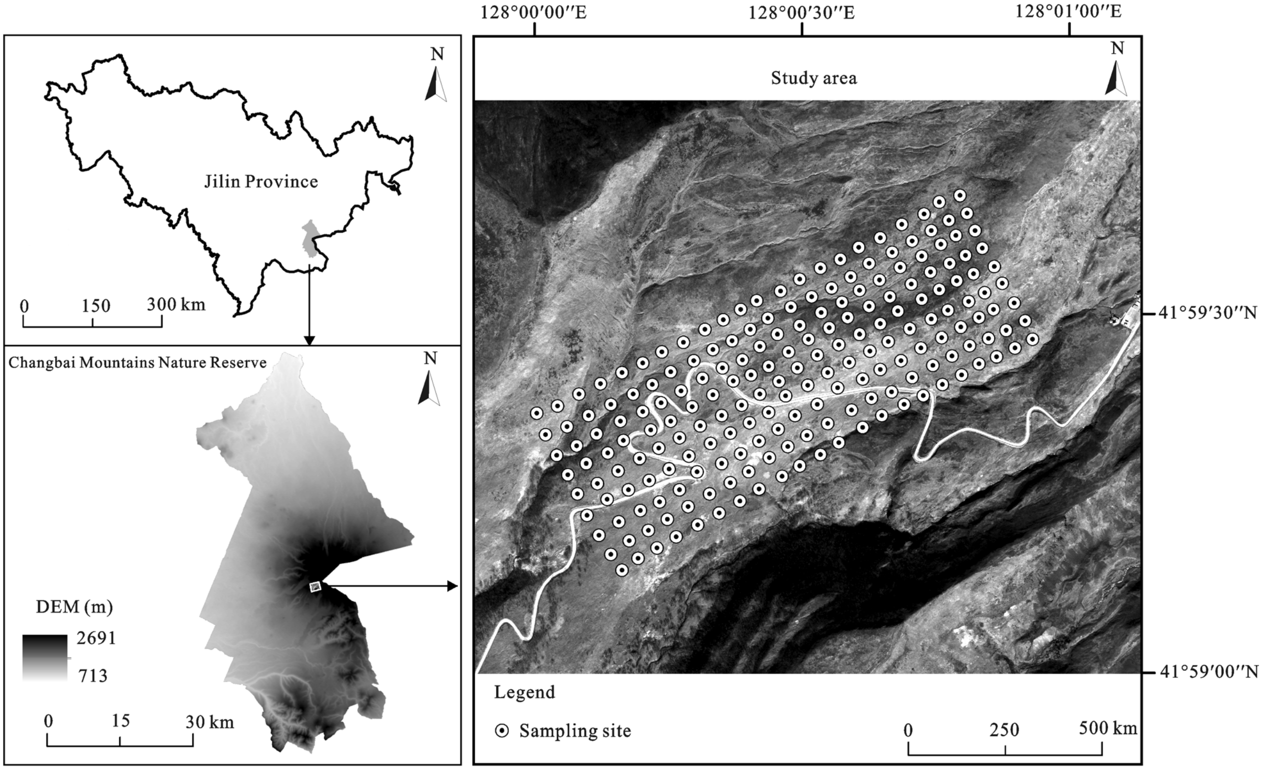

Fig. 1 Location of study area and sampling sites

week) and finished in early September. Seed germination begins in late July in the study area.

2.3 Sampling methods

Sampling was conducted during 10–20 June in 2011, 2012, and 2013 after snow melting. Nine parallel 1000 m transects with interval of 50 m were established. Along each transect, 22 sampling sites were established at 50 m intervals. Sample grid map was shown in Fig. 1. The total surveyed area ranged from the forest edge (1980 m) to the high alpine tundra (2450 m). Every sample site was treated as the permanent site to make it possible to achieve consecutive sampling in the same place in the next year. In each site, one plot (area of 1 m^2) separated by four subplots (area of 0.25 m^2) was established. In each subplot, after removal of the litter layer, three replicated soil cores were randomly taken using a soil hand bore, 5 cm in diameter in one of the subplots. Consider that burial depth of *D. angustifolia* seeds could not exceed 10 cm in the very thin covering of soil in the alpine tundra; sampling depth was set to 10 cm. In total, there were 198 sites × 3 core samples, giving the total of 594 estimates each year. Within each site, the micro-topography measurements included the altitude and slope was conducted using Global Positioning System (GPS) equipment and gradient ruler. Community investigation including plant height, vegetation composition, as well as the canopy cover of the community was conducted in the plot scale (area of 1 m^2). The slope measurement was conducted at a 2 m × 2 m scale.

2.4 Seed germination

Seeds of *D. angustifolia* could hardly be identified in the soil. Besides, only the seeds with the ability of germination could become the effective threats to the alpine tundra. Therefore, we conducted the seed germination experiment to check the effective seed number. Soil was passed through a fine sieve (mesh width 2 mm). The remainder was spread onto individual trays of 25 cm × 25 cm. According to Li *et al.* (2007), seeds of *D. angustifolia* are light-insensitive and the suitable temperature for germination is 30℃. Therefore, the trays were placed in the greenhouse maintained at day/night temperature of 30℃/22℃ with no artificial lighting and watered daily. The number of emerged seedlings was counted two weeks later when no new seedlings emerged. We defined the effective seed number (ESN) as the germinated seed in each sample site. To illustrate the pattern, ESN were expressed per 1 m^2, based on the data of the core samples.

2.5 Statistical analysis

All the data acquired were tested to determine if they met the normality assumption of analysis of variance (ANOVA). The data were converted to $\ln(X + 1)$ prior to ANOVA. Then, one-way ANOVA with Tukey post hoc tests was used to detect differences in ESNs of different years. Linear and polynomial regression analyses were used to check the relationship between ESN and environmental factors. All the statistical analyses were done using SPSS (version 16.0, SPSS Inc., Chicago, IL). The levels of significance were $P < 0.05$.

Multivariate analyses were performed to determine the relationship between ESN and environmental factors using the program canonical community ordination (CANOCO) (Jongman *et al.*, 1995). The ESN data were log-transformed and centered. According to Lepš and Šmilauer (2003), ordination analysis should be conducted based on the primary result by detrended correspondence analysis (DCA) on the data. The DCA results could supply the length of Gradient (LG) which was used to determine the ordination method. If LG was less than 3, then linear method, such as redundancy analysis (RDA) method, should be applied. If LG was more than 4, the unimodal method, such as canonical correspondence analysis (CCA) should be applied. In our DCA result, LG was 0.21, less than 3. Therefore, RDA method was applied. In RDA, the biplot yields information about correlations between ESN and environmental variables. Arrows pointing towards an environmental variable point indicate a high positive correlation, arrows pointing in an opposite direction indicate a high negative correlation, and arrows pointing at a right angle from a line connecting the environmental variable point with the center indicate a near-zero correlation. The significance of both, environmental variables and RDA axes, was tested by the Monte Carlo permutation (999 permutations) test with restricted permutations based on the *F*-statistic (Titus and del Moral, 1998; Chang *et al.*, 2001).

3 Results

3.1 Effective seed number (ESN) along altitudinal transects

The ESN showed a significant decreasing trend along the altitudinal transect with fluctuations (Fig. 2). The fluctuations may relate to the variations of micro-topographic conditions. The polynomial fitting lines indicated that seed-dispersal of *D. angustifolia* were in line with the normal pattern which was seed density declined with altitude increased ($R^2 = 0.8354$, $P < 0.05$) (Fig. 2). We separated the altitudinal range into six classes at the intervals of 50 m (Table 1). High ESN occurred at the altitudinal range of 2000–2100 m (about 548 per m^2). As elevation increased, the ESN gradually decreased. At the altitudinal range of 2300–2355 m, the ESN was only about 70 per m^2. The long distance and strong wind at high elevations may restrain the stay of the seeds. It can be inferred that elevation was the main limiting factor for the seed transportation of *D. angustifolia*.

3.2 Effective seed number (ESN) along slope transects

There was no significant decreasing trend of ESN along the slope transects (Fig. 3). The fluctuant change was obvious, which indicated that the differences of ESN at different slope were site dependent. Linear regression method was applied on the ESN and fitting results were not well ($R^2 = 0.4615$, $P < 0.05$) (Fig. 3). We separated the slope range into six classes at the intervals of 7° according to the data distribution of slope (Table 1). High ESN occurred at the slope range of 0°–7°, i.e., the flat areas (about 564 per m^2). As the slope increased, the ESN gradually decreased. At the slope range of 35°–42°, i.e., the steep areas, the ESN was only about 109 per m^2. However, it was notable that the standard deviation was large in each class (Table 1), which indicated that variability of ESN along the slope transect was large. It can be inferred that slope was not the dominant factor determining the seed distribution of *D. angustifolia*.

3.3 Effective seed number (ESN) along community transects

There were seven types of plant communities in the study area (Table 2). Community characteristics differed among these communities, especially at the height and

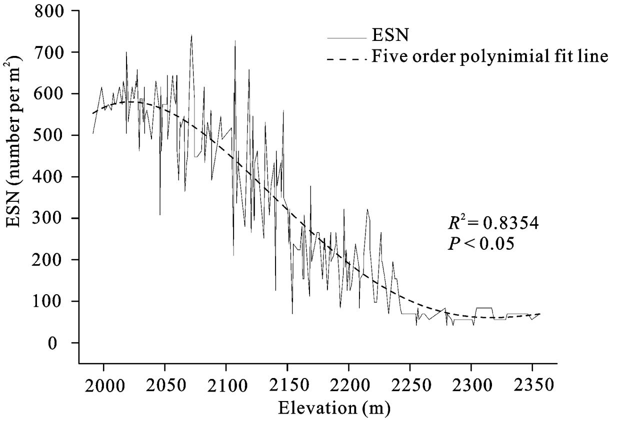

Fig. 2 Effective seed number (ESN) along altitudinal transects. Five-order polynomial fitting analysis was applied on the ESN

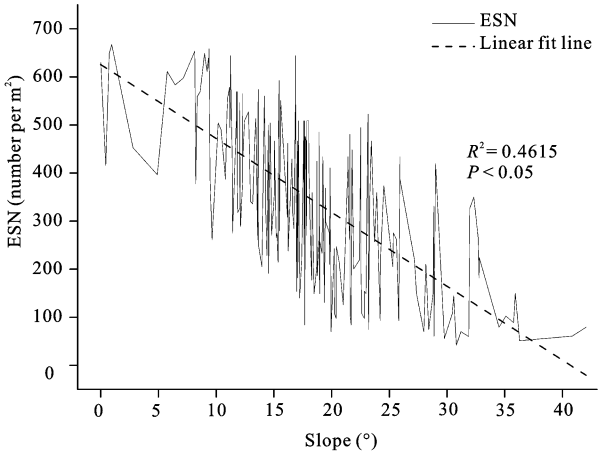

Fig. 3 Effective seed number (ESN) along slope transects. Linear regression analysis was applied on ESN

Table 1 Effective seed number (ESN) along altitudinal and slope transects set up into six classes

Elevation range (m)	ESN (number per m^2)			Slope (°)	ESN (number per m^2)		
	2011	2012	2013		2011	2012	2013
2300–2355	70.0±20.7a	66.5±21.6a	63.0±21.9a	35–42	109.2±87.1a	109.2±92.1a	84.0±29.8b
2250–2300	58.8±21.3a	61.6±21.7a	58.8±21.3a	28–35	187.6±113.1a	198.8±157.3b	238.0±196.2c
2200–2250	172.5±78.6a	165.0±69.5a	169.3±78.3a	21–28	299.3±184.5a	299.3±178.1a	291.4±198.1a
2150–2200	223.6±86.9a	192.9±80.1b	242.9±92.7a	14–21	306.3±187.4a	319.8±169.5a	317.5±152.9a
2100–2150	402.4±85.9a	425.4±79.9a	411.9±61.7a	7–14	443.0±196.8a	427.4±185.7a	423.4±194.7a
2000–2100	548.8±119.1a	556.1±114.3a	538.7±103.9a	0–7	564.7±205.8a	532.0±242.8b	560.0±147.1a

Notes: One-way ANOVA with Tukey post hoc tests was used to detect differences in ESN of different years. Different letters mean significantly different ($P < 0.05$)

canopy cover. It is obvious that ESN differed at different communities (Table 2). The *D. angustifolia* community had the highest ESN (about 536.7 per m^2) compared with other communities, which is because the community itself was the main seed source. It was notable that ESN showed an increasing trend during the three years ($P < 0.05$). *R. chrysanthum*-*S. rotundifolia* community and *V. uliginosum*-*D. octopetala* community also had a great deal of ESN, in which the interannual variability was not obvious ($P > 0.05$). The ESN of *Veratrum nigrum*-*Ligularia jamesii* community and *Aconitum monanthum*-*Saussurea manshurica* community was below 300 per m^2. As to *Sanguisorba stipulata*-*Ligularia jamesii* community and *D. octopetala*-*Polygonum viviparum* community, ESN highly reduced, especially at the latter one. It can be inferred that community height and canopy cover may play an important role in the capture of seeds. However, it was notable that *V. nigrum*-*Ligularia jamesii* community had the highest height and the lowest canopy cover among the plant communities did not have the highest ESN, which confirmed the effect of elevation and micro-topography.

3.4 Redundancy analysis (RDA) analyses

The first axis of RDA accounted for 85.2% of variance in the ESN data and 96.1% of the ESN-environment relationship (Table 3). The second axis accounted for 1.2% of variance in the ESN data and 55.3% of the ESN-environment relationship. The significance of all canonical axes was tested (Trace = 0.865, $P < 0.001$, data not given) after including five environmental variables which passed the forward selection. Therefore, the ordination was effective by using the first and second axis. The inflation factors of all the environmental variables were less than 20, which indicated that they could be used as the explanatory variables (Table 4). We separated the environmental variables into two categories (Table 4), the micro-topography type (elevation and slope) and the community type (community type, community height, and canopy cover). We did not focus on the interactions between the micro-topography type and the community type on explaining the marginal effect. However, in each type, we analyzed the variance explained by interactions (Table 4). Results showed that there existed an interaction between the environmental variables. The interaction between community type and community height could explain the variance of ESN change by 5.1%.

The ESNs of the three years showed inter-annual variations to some extent (Fig. 4). The angle between the ESN and the environmental variables indicated their

Table 2 Effective seed number (ESN) in different plant communities

Community	Height (cm)	Canopy cover (%)	2011	2012	2013
Deyeuxia angustifolia	60–90	85	536.7±98.08a	572.4±112.45a	675.8±84.72b
Rhododendron chrysanthum-Salix rotundifolia	6–20	75	508.0±135.32a	505.0±141.74a	548.0±149.04a
Vaccinium uliginosum-Dryas octopetala	10–15	75	491.3±93.77a	483.3±139.27a	473.5±132.13a
Veratrum nigrum-Ligularia jamesii	50–100	55	281.7±115.83a	264.2±111.79a	295.7±128.13a
Aconitum monanthum-Saussurea manshurica	20–40	80	245.6±114.61a	237.4±116.48a	204.5±129.16b
Sanguisorba stipulata-Ligularia jamesii	50–60	85	124.8±79.49a	127.1±87.62a	107.8±83.63b
Dryas octopetala-Polygonum viviparum	5	85	61.8±21.61a	64.2±22.51a	44.5±20.19b

Notes: One-way ANOVA with Tukey post hoc tests was used to detect differences in ESN of different years. Different letters mean significantly different ($P < 0.05$)

Table 3 Summary of results of redundancy analysis (RDA) ordination

	Axis 1	Axis 2	Axis 3	Axis 4	Total variance
Eigenvalue	0.852	0.012	0.001	0.085	–
ESN-environment relation	0.961	0.553	0.152	0.000	–
Cumulative percentage variance of ESN data	85.2	86.4	86.5	94.9	–
Cumulative percentage variance of ESN-environment relation	98.5	99.9	100.0	0.0	–
Sum of all eigenvalue	–	–	–	–	1.000
Sum canonical eigenvalue	–	–	–	–	0.865
Monte Carlo Test	$F = 42.026$, $P < 0.001$	–	–	–	$F = 9.532$, $P < 0.001$

Note: Significance tested by repeated measures Monte Carlo Test with 999 permutations

Table 4 Inflation factors and variance explained by interaction of environmental variables obtained by partial redundancy analysis (RDA)

	Elevation (E)	Slope (G)	Community type (CT)	Community height (CH)	Canopy cover (CC)
Inflation factor	3.5345	1.2571	3.8982	1.1227	1.0764
Interaction	E × G		CT × CH	CT × CC	CH × CC
Variance explained by interaction	3.6%		5.1%	4.7%	4.4%

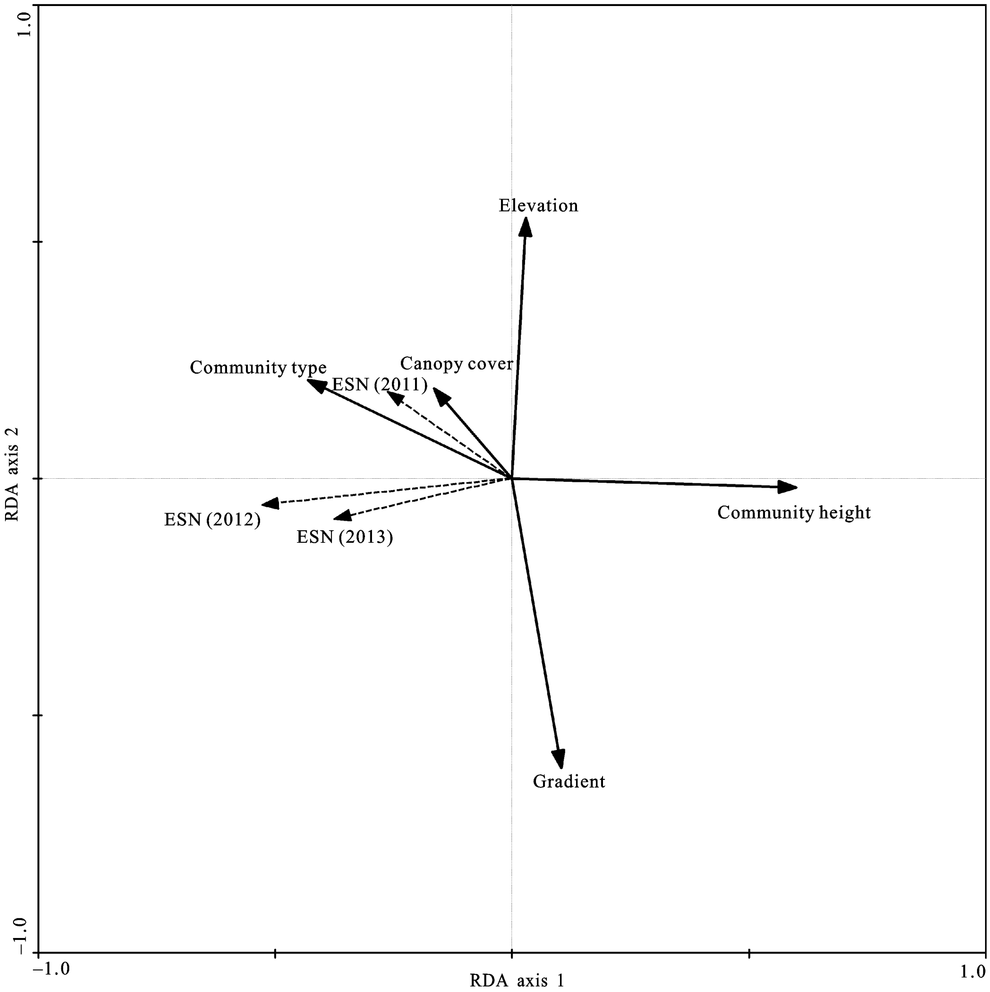

Fig. 4 Redundancy analysis (RDA) ordination of effective seed number (ESN) (dashed line with arrow) and environmental variables (solid line with arrow)

correlations. The lower the angle was, the higher the correlation was. It can be seen that community type had positive correlation with ESN of the three years. Canopy cover had close relationship with ESN of 2011. On the contrary, elevation, slope, and community height had negative effect on the changes of ESN. From the sample-environment ordination plot (Fig. 5), it can be seen that sample distributions could be classified by the micro-topography conditions and community characteristics. The occurrences of ESN in different plant communities could be explained by the environmental variables, especially by community height, elevation, and slope. Therefore, it can be inferred that ESN distribution pattern was highly related to the plant community distribution. Moreover, the occurrences of ESN in different plant communities were subject to different environmental variables. For example, the lowest occurrences of ESN in the *Dryas octopetala-Polygonum viviparum* community at the second quadrant could be effectively explained by the canopy cover.

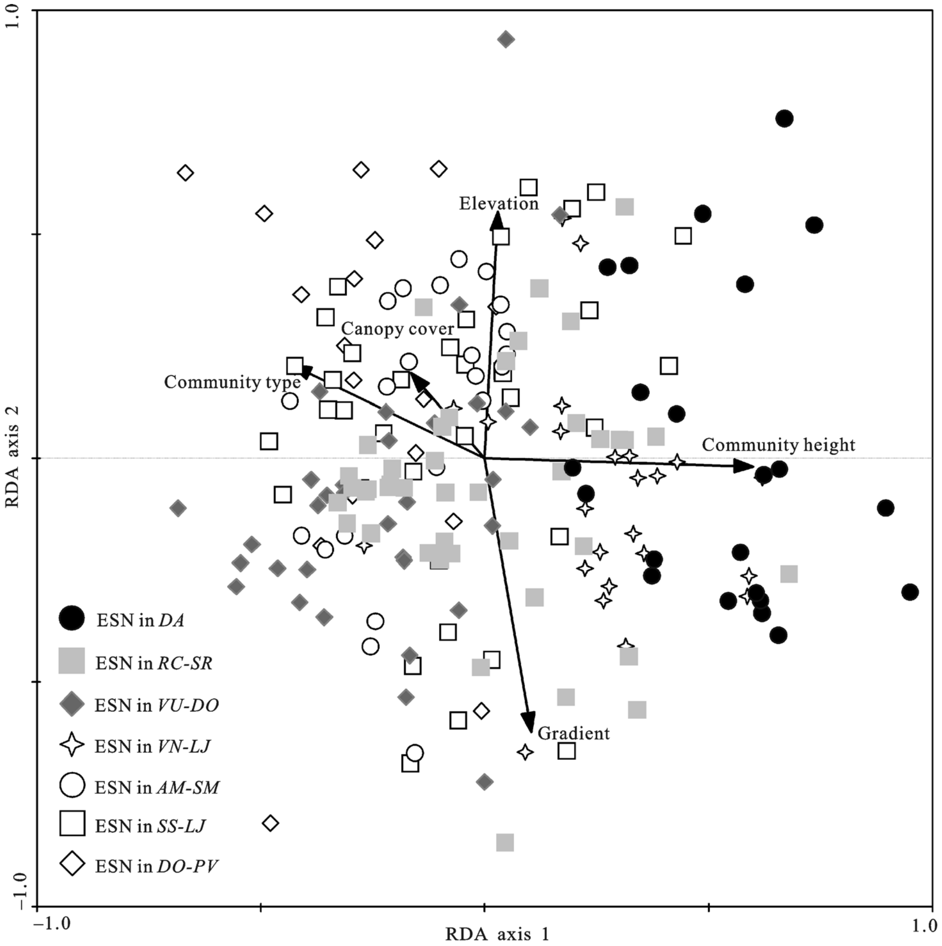

Fig. 5 Redundancy analysis (RDA) ordination of samples (symbols) and environmental variables (solid line with arrow). ESN means effective seed number. *DA* represents the *Deyeuxia angustifolia* community; *RC-SR* represents the Rhododendron chrysanthum-*Salix rotundifolia* community; *VU-DO* represents the *Vaccinium uliginosum-Dryas octopetala* community; *VN-LJ* represents the *Veratrum nigrum-Ligularia jamesii* community; *AM-SM* represents the *Aconitum monanthum-Saussurea manshurica* community; *SS-LJ* represents the *Sanguisorba stipulate-Ligularia jamesii* community; *DO-PV* represents the *Dryas octopetala-Polygonum viviparum* community

4 Discussion

4.1 Seed distribution pattern

If plant invasion occurred in locations with intense competition or harsh abiotic conditions, high propagule pressure may be necessary (Foster *et al.*, 2004). High seed production of *D. angustifolia* is a prerequisite to its success of invasion in alpine tundra. However, germination is another necessary condition for successful invasion (Forcella *et al.*, 1986). Thus, the seeds in the suitable habitats are truly the potential threats to the local ecosystem. We found that seeds of *D. angustifolia* do have a distribution pattern in the alpine tundra of the Changbai Mountains. They were mainly distributed in the low elevation areas. It seemed altitude was the main barrier to its dispersal. This result was consistent with the study of Molau and Larsson (2000). But, seeds of *D. angustifolia* had not clustered in the low slope areas. Commonly, wind-dispersed seeds may primarily fall on the rough surfaces by the wind followed the gravity, and then the secondary transportation by the wind or water may drive them to the low slope areas (Nathan and Muller-Landau, 2000). However, our results were opposite to this point. It seemed that effects of micro-topography on the seed distribution of *D. angustifolia* were not obvious. The ESN occurrences of *D. angustifolia* were different in the different plant communities in the alpine tundra. We consider that such variation of seed distribution may mainly due to the various capabilities of the different plant communities for trapping seeds. Certainly, germinate rate in alpine tundra was different with that in the artificial greenhouse where light, nutrients, and space are not limiting factors. The harsh environment in alpine tundra may lead to a large portion of seedlings death soon after the germination. However, our research, at least, offered types of habitats where potential threat ranges were (Alpert *et al.*, 2000).

4.2 Determining factors

The seed source of *D. angustifolia* consisted of two parts. One was from the *D. angustifolia* community in the birch forest zone at lower elevation areas. The other was from *D. angustifolia* community already established in alpine tundra. Wind dispersal is the main long distance dispersal mechanism for *D. angustifolia*. Mature seeds were primarily transported by wind to the alpine tundra in late August. In this processes, altitude was the limiting factor because many seeds were trapped by all kinds of surfaces during their long travel. Another determining factor for the seed distribution pattern was the surface characteristics of plant community. In our research, plant communities with lower canopy cover tended to catch more seeds of *D. angustifolia*. In this study, we did not measure the seed movement after snowmelt whereas some studies indicated dispersal can move seeds to new and even more favorable habitats with appropriate conditions (Gadgil, 1971). However, Scherff *et al.* (1994) showed that the seeds transported, on average, an additional 10 cm during snowmelt in the alpine snowbed habitats. We argue that water from snowmelt may move the seeds from the litter layer to the soil. But it may not be the determining factor affecting seed distribution in the large area in alpine tundra.

4.3 Implication for management

For invasive plants, dispersal or habitat choice is usually confined to the seed stage (Bazzaz, 1991; Chou *et al.*, 1992). Seeds of *D. angustifolia* spread in the alpine tundra with a considerable number (mean value of 322 per m^2). Spreading germination over time to await favorable conditions may be an efficient mechanism to reduce the hazardous effect of severe environmental conditions (Kalamees and Zobel, 2002). Therefore, to find out the effective seed distribution pattern could help the environmental managers to set up effective planning for control (Chytrý *et al.*, 2008b). Our study suggests that effective seed distribution pattern of *D. angustifolia* makes habitats the promising predictor of plant invasions. According to Richardson and Kluge (2008), preventing the accumulation of seed banks by limiting seed production through biological control is by far the most effective means, and in almost all cases the only practical means, of reducing seed numbers. After removing the effect of propagule pressure, some habitats actually invaded would have very low proportions of invasive plants (Chytrý *et al.*, 2008a). The feasibility of these measures should be deeply investigated combined with the current situation of *D. angustifolia* invasion in alpine tundra of the Changbai Mountains.

5 Conclusions

This study analyzed the effective seed distribution pattern of an upward shift plant, *D. angustifolia*, in alpine tundra of the Changbai Mountains. Environmental variables such as elevation, slope, and plant community characteristics were considered. Besides, the relationship between the environmental variables and the effective seed distribution pattern was also assessed. Sample survey results showed that there was a high spread density of seeds of *D. angustifolia* in alpine tundra and the seeds do have a distribution pattern that they mainly distributed in the low elevations and plant communities with low canopy cover. The effects of micro-topography such as slope on the distribution were not obvious. However, germination data was acquired from the lab experiment, which may be different from the actual data of field germination. In alpine tundra, harsh environments may suppress the germination of *D. angustifolia*, which showed the resistance of invasion. Therefore, we would conduct field germination experiment in the future to check the response of *D. angustifolia* survive to alpine environment.

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