

Effects of Nitrogen Deposition on Tundra Vegetation Undergoing Invasion by *Deyeuxia angustifolia* in Changbai Mountains

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Abstract: In recent years, herbaceous species such as *Deyeuxia angustifolia* (Kom.) Y. L. Chang has invaded alpine tundra regions of the western slope of the Changbai Mountains. Because atmospheric nitrogen deposition is predicted to increase under a warming climate and *D. angustifolia* is sensitive to nitrogen addition, field experiments were conducted from 2010 to 2013 to determine the effect of increased nitrogen deposition on the mechanisms of *D. angustifolia* invasion. The goal of this study is to evaluate the impact of increased nitrogen deposition on the changes in alpine tundra vegetation (consisting mostly of *Rhododendron chrysanthum* Pall. and *Vaccinium uliginosum* Linn.). The results showed that: 1) simulated nitrogen deposition affected overall characteristics and structure of *R. chrysanthum* and *V. uliginosum* communities and had a positive impact on the growth of tundra vegetation invaded by *D. angustifolia*; 2) *R. chrysanthum* was more resistant to invasion by *D. angustifolia* than *V. uliginosum*; 3) simulated nitrogen deposition could improve the growth and enhance the competitiveness of *D. angustifolia*, which was gradually replacing *R. chrysanthum* and *V. uliginosum* and might become the dominant species in the system in future, transforming alpine tundra into alpine meadow in the Changbai Mountains.

Keywords: nitrogen deposition; species invasion; *Deyeuxia angustifolia*; tundra vegetation; Changbai Mountains

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1 Introduction

Global nitrogen (N) deposition has increased over the past 100 years (Matson *et al.*, 2002; Galloway *et al.*, 2004; 2008). North America, Europe and East Asia are the three hotspots of N deposition around the world (MacDonald *et al.*, 2002; Dise *et al.*, 2009; Stevens *et al.*, 2010; van Dobben and de Vries, 2010; Zbieranowski and Aherne, 2012; McDonough and Watmough, 2015). The amount of atmospheric N deposited on the land surface has increased by nearly five times in China between 1901 and 2005 (Chen *et al.*, 2004; Cai

and Xie, 2007; Clark *et al.*, 2013; Liu *et al.*, 2013; Zhan *et al.*, 2014). N deposition has significantly increased in Northeast China (Jiang *et al.*, 2013; Du *et al.*, 2014).

The environmental impacts of N deposition on terrestrial systems have been recorded primarily for industrialized regions (Bobbink *et al.*, 1998; Driscoll *et al.*, 2001). However, symptoms of ecological changes owing to N deposition have been documented in more remote regions, including national parks and wilderness areas (Burns, 2003; Geiser and Neitlich, 2007). Bowman *et al.* (2006) confirmed that N deposition has increased because of human activities in the alpine tundra

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of Niwot Ridge, and N deposition at Niwot Ridge was already a driver of plant community change.

The rising levels of atmospheric nitrogen (N) deposition was found to affect the primary productivity and species composition of most terrestrial ecosystems (Lu *et al.*, 2008; Bobbink *et al.*, 2010; Liu *et al.*, 2011; Hurkuck, 2014). The responses of plants to increased N input are not consistent. Many studies found that the growth of many dominant species was not affected by increased N concentration, but some subdominant species, particularly herbs, showed increased growth and abundance with the increase in available N, thereby the structure of plant communities was changed (Bowman *et al.*, 1993; Gerdol *et al.*, 2002; Nordin *et al.*, 2005). European *Heather* shrubland was slowly converted into grassland because of increased competitiveness of the subdominant herb (*Brachypodium pinnatum*) under increased N deposition (Yoshida and Allen, 2001). In southern California, USA, an annual herb (*Brachypodium pinnatum*) is gradually replacing the coastal sagebrush shrubs. The majority view is that this change in vegetation was caused by grazing and fire, but an increasing number of scholars believe that atmospheric N deposition played an important role in recent years (Yoshida and Allen, 2001).

Atmospheric nitrogen (N) deposition could be a major driver of change in most natural and semi-natural terrestrial ecosystems. It particularly threatens species composition, diversity, and functioning of ecosystems that are nutrient poor (Hurkuck *et al.*, 2014). Smaller deposition rates can have a significant impact on those ecosystems where the ability to convert additional N inputs is weak. Alpine tundra is very sensitive to the biological effects of high N deposition because of the low primary production and weak soil microbial activity in this environment. Increased N deposition will cause changes in the composition of plant species in the tundra because of competition and substitution between species (Bowman and Steltzer, 1998; Johnson *et al.*, 2011).

The alpine tundra of the Changbai Mountains is the only tundra in the humid region of China. Dwarf species such as *Rhododendron chrysanthum* and *Vaccinium uliginosum* are the dominant species. In recent years, the community has been invaded by herb species such as *Deyeuxia angustifolia*, but the mechanisms are not well understood (Jin *et al.*, 2013; Zong *et al.*, 2013). Nitrogen deposition, climate warming, disturbances, and natural

succession of tundra vegetation are all suspected causes of *D. angustifolia* invasion.

Experiments with simulated N addition were conducted from 2010 to 2013 in the alpine tundra zone of the Changbai Mountains. The goals of this study are to evaluate the impact of increased N deposition on changes in alpine tundra community composition (specifically *R. chrysanthum* and *V. uliginosum* communities) and to examine the effects of N deposition on *D. angustifolia* invasion of the alpine tundra zone.

2 Materials and Methods

2.1 Study area

The study area was located in the alpine tundra zone on the western slope of the Changbai Mountains (41°59'31"N, 128°00'55"E) in the northeast China. Elevation of the experimental site was about 2218–2222 m above sea level and the plot size was 100 m × 50 m. Most of the ground surface of the study area is covered by residues of alkali trachyte of weathering with a small amount of volcanic ash. The landform is a typical slope of the volcanic cone area transformed by surface runoff water. The study site is characterized by thin alpine tundra soil and alpine tundra climate. The annual average temperature is about −6°C. Winter is cold and long, with an average temperature in January of −25°C and a minimum temperature of −40°C. The summer is cool and short, and the average temperature in July is below 10°C. The active accumulated temperature ($\geq 10^{\circ}\text{C}$) is 300°C–500°C. The number of frost-free days is between 80 and 100. The climate is humid with mean annual precipitation is ranging from 1100–1300 mm. Windy days occur perennially and the wind speed can exceed 40 m/s (Zong *et al.*, 2013).

Polar and alpine plants account for 80% of the species in the study area. Shrubs that are in low stature or close to the ground dominate the vegetation in the area. The belowground root system and biomass is greater than that above the ground. The plant form is xeromorphic and the leaves are leathery or villous in the back. The *R. chrysanthum* Pall. and *V. uliginosum* Linn. communities are the most representative communities in this tundra zone. There are two layers including the shrub and the moss-lichen synusium. There are few herb species; in particular, *D. angustifolia* has not yet formed into an herb layer.

Deyeuxia angustifolia is a perennial hygro-mesic rhizome grass and belongs to *Deyeuxia* in Gramineae. It occurs in open forest and low-lying wetland. It is commonly found under the *Betula ermanii* forest on the western slope of the Changbai Mountains near the timberline. *D. angustifolia* has invaded the tundra zone on the western slope of the Changbai Mountains since the late 1980s. *D. angustifolia* first appeared in the lower edge of the tundra, then increased in abundance and spread upward year by year. The invasion increased gradually and formed several different patches (Fig. 1), which continue to expand.

2.2 Experimental design and measurement

Experiments with increased N deposition were conducted from 2010 to 2013 on the alpine tundra of the Changbai Mountains. In early September 2009, we selected the experimental site, which displayed mild invasion (abundance of 25%) by *D. angustifolia* in the tundra zone. Simulated N deposition experiments were designed and divided into two groups: the *R. chrysanthum* group and the *V. uliginosum* group.

We defined the N medium/high addition based on previous gradient studies. Similar experiments were designed in studies of nitrogen saturation experiments project in Europe and Harvard forest in the United States (Wright and Rasmussen, 1998; Magill et al., 2004; Ren et al., 2013). Our experiments included three N deposition treatments: the control without N addition (CK, 0 g N/(m²·yr)), medium N deposition level (Medium N, 7.5 g N/(m²·yr)) and high N deposition level

(High N, 15 g N/(m²·yr)). The three treatments were arranged in a randomized block design, and included four replicates in the 2 m × 2 m plots (24 plots in total). Plots were established at flat area which was not affected by the micro topography and gully, and the distance between plots was more than 3 m. Fertilizer (NH₄NO₃) was dissolved in water and sprayed onto plots three times each year on June 1, July 1 and August 1. Every time, ammonium nitrate (NH₄NO₃) was used for 0 g/m², 7.2 g/m² and 14.3 g/m² for three treatments.

Measurements were taken in early September each year. The number of species and the number of each species were counted and plant height and coverage were measured in a 1 m × 1 m quadrat for each plot. Leaf area index was measured using the LAI-2200 Plant Canopy Analyzer. Plots were harvested at the end of the growing season in 2013. For each plot, samples (10 cm depth intact cube of soil and its associated above- and below-ground vegetation) were destructively harvested from a 30 cm × 30 cm quadrat. The soil sampled to 10 cm depth was sufficient to capture the belowground biomass, including the vast majority of roots, because of the thin soil at the study site. We carefully dug out samples and left as much of the root systems intact as possible. Roots were washed. Samples were oven dried at 65°C to constant weight to determine the amount of above- and below-ground biomass.

2.3 Indices of species diversity

The community species diversity was measured by α diversity index: Shannon-Wiener index (H) (Equation (1)) and Pielou index (E) (Equation (2)):

$$H = -\sum_{i=1}^S (P_i \ln P_i) \quad (1)$$

$$E = H / \ln S \quad (2)$$

where S is the number of species; P_i is the proportion of the i th species individuals in all individuals in the sample.

2.4 Statistical analysis

Data were analyzed by SPSS 16.0 statistical software (version 16.0, SPSS Inc., Chicago, IL, USA). Analysis of variance (ANOVA) was used to detect the effects of different nitrogen deposition treatments. A least significant difference (LSD) multiple range test was used to identify significant differences ($P < 0.05$).



Fig. 1 Invasion of *D. angustifolia* in tundra zone (shown as yellow patches), and patches of *R. chrysanthum* (green) and *V. uliginosum* (brown). The photograph was taken on 16 September, 2010

3 Results

3.1 Change in overall characteristics of tundra communities

Changes in the overall characteristics of the community were described using vegetation coverage, leaf area index, biomass and α diversity index.

The experiments with three N deposition treatments were conducted on *R. chrysanthum* and *V. uliginosum* communities invaded by *D. angustifolia* over four years. The results showed that vegetation coverage, leaf area index, biomass and α diversity index all increased over time (Figs. 2–6). The rates of increase for vegetation coverage, leaf area index, biomass and α diversity index were lowest under the natural N deposition conditions (the control treatment without N addition). These rates increased with increasing N deposition.

Through continuous observation of simulated N deposition over four experimental years, we found that the changes in vegetation coverage and leaf area index for *R. chrysanthum* under the medium and high N deposition conditions were similar. The values for these indices under the medium and high N deposition conditions were significantly higher than that under the control without N addition from 2011 to 2013 ($P < 0.05$) (Figs. 2a and 3a). The changes in vegetation coverage

and leaf area index for *V. uliginosum* under the high N deposition treatment were the largest among three N deposition treatments from 2010 to 2013. The changes from 2012 to 2013 in vegetation coverage and leaf area index were significant for three N deposition treatments ($P < 0.05$) (Figs. 2b and 3b).

Biomass was also sensitive to N increases for both *R. chrysanthum* and *V. uliginosum* invaded by *D. angustifolia*. The increase in biomass for the high N deposition treatment was greater than those for the medium and control N deposition treatments from 2010 to 2013, but the increase was significant only from 2012 to 2013 ($P < 0.05$) (Fig. 4).

The Shannon-Wiener diversity index and Pielou index increased with increasing amounts of N over four years for both *R. chrysanthum* and *V. uliginosum* communities invaded by *D. angustifolia* (Fig. 5). The α diversity index for high and medium N were significantly higher compared with the control from 2012 to 2013 ($P < 0.05$) (Fig. 6).

3.2 Changes in community structure

Four indices were selected to describe changes in community structure, including comparison to abundance of *D. angustifolia*, layer height, aboveground and belowground biomass of dominant species in the *R. chrysanthum* and *V. uliginosum* communities.

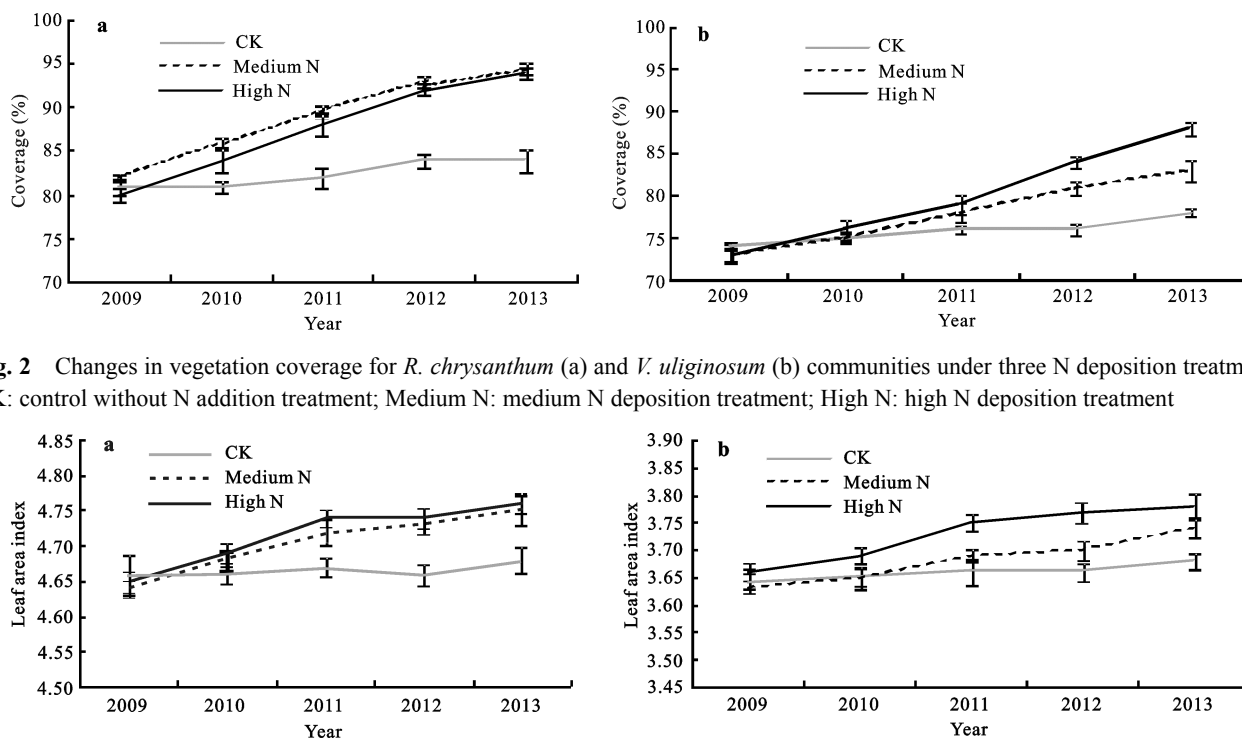


Fig. 3 Changes in leaf area index for *R. chrysanthum* (a) and *V. uliginosum* (b) communities under three N deposition treatments

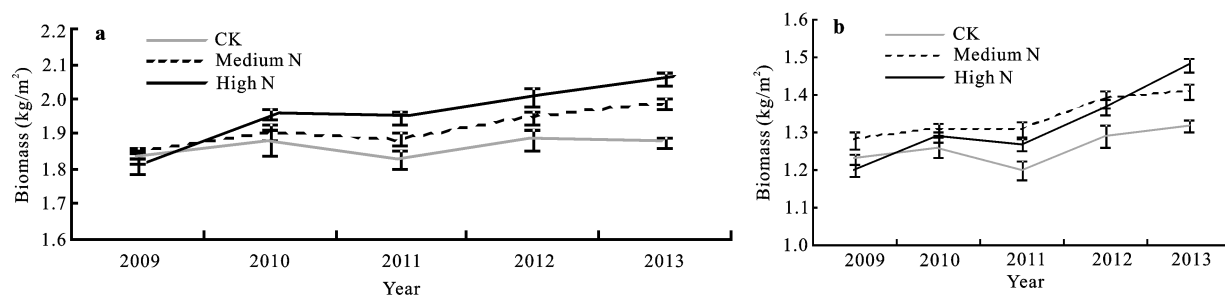


Fig. 4 Changes in biomass for *R. chrysanthum* (a) and *V. uliginosum* (b) communities under three N deposition treatments

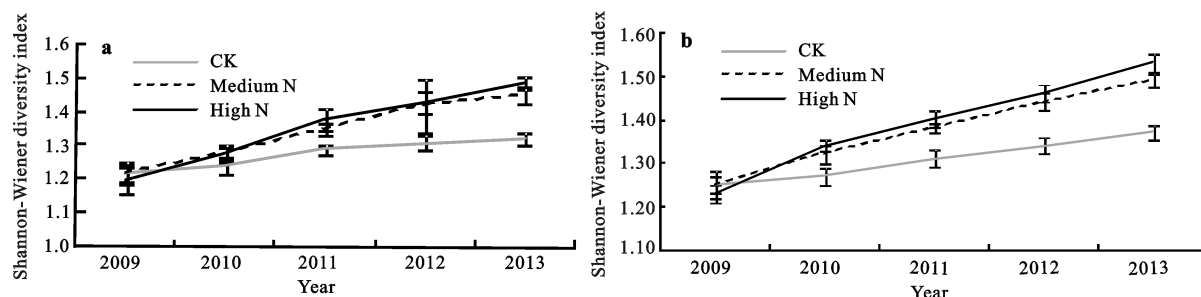


Fig. 5 Changes in Shannon-Wiener diversity index for *R. chrysanthum* (a) and *V. uliginosum* (b) communities under three N deposition treatments

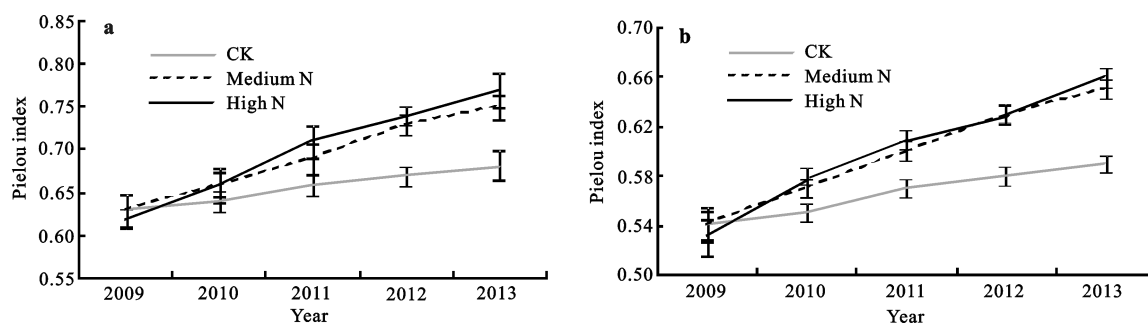


Fig. 6 Changes in Pielou index for *R. chrysanthum* (a) and *V. uliginosum* (b) communities under three N deposition treatments

3.2.1 Abundance of *Deyeuxia angustifolia*

Over four years' experimental N deposition to *R. chrysanthum* and *V. uliginosum* communities invaded by *D. angustifolia*, the numbers of *D. angustifolia* increased significantly, *D. angustifolia* became one of the dominant species. The rate of increase of *D. angustifolia* was lowest under natural N deposition and increased with increasing N deposition. Abundance of *D. angustifolia* in the *V. uliginosum* group was greater than that in the *R. chrysanthum* group in the medium and high N addition treatments. These results suggested the *V. uliginosum* communities were more vulnerable than *R. chrysanthum* communities to *D. angustifolia* under N increases (Fig. 7).

3.2.2 Height of shrub and herb layers

The herbaceous height of *D. angustifolia* was higher than that of the shrub in the mid and late growing season

in the *R. chrysanthum* Pall. and *V. uliginosum* Linn. communities invaded by *D. angustifolia*. With increasing N deposition, the shrub height of *R. chrysanthum* and *V. uliginosum* decreased and the herb height of *D. angustifolia* increased under the medium and high N deposition conditions from 2011 to 2013 (Fig. 8). The changes in height of *D. angustifolia* was not significant from 2010 to 2013 compared with 2009 under the controlled treatment without N addition ($P > 0.05$). The changes in height of *D. angustifolia* were significantly from 2012 to 2013 compared with 2009 under the high and medium N treatments ($P < 0.05$). Height difference of *D. angustifolia* in the *V. uliginosum* group from 2010 to 2013 compared with 2009 was larger than that in the *R. chrysanthum* group under the high and medium N treatments (Fig. 9).

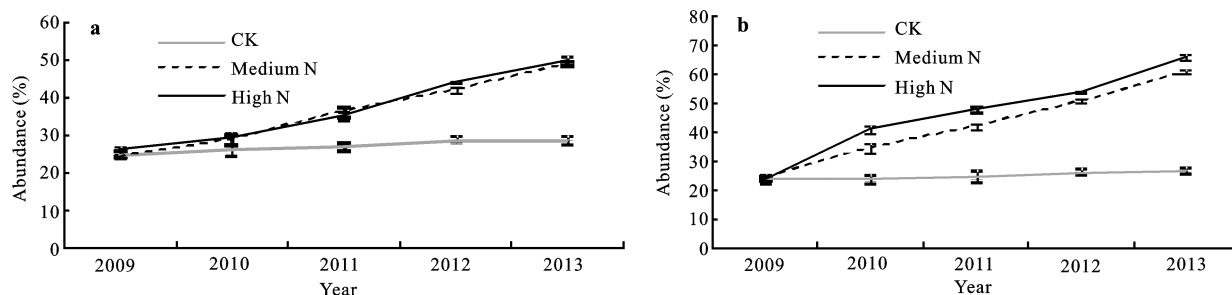


Fig. 7 Changes in abundance of *Deyeuxia angustifolia* in *R. chrysanthum* (a) and *V. uliginosum* (b) communities under three N deposition treatments

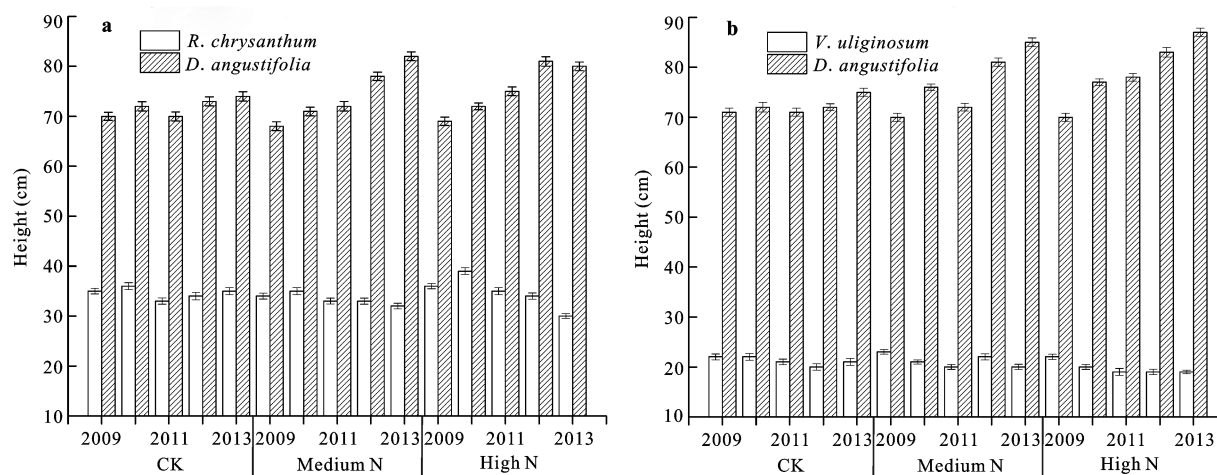


Fig. 8 Changes in height of shrub and herb layers for *R. chrysanthum* (a) and *V. uliginosum* (b) communities (cm) under three N deposition treatments

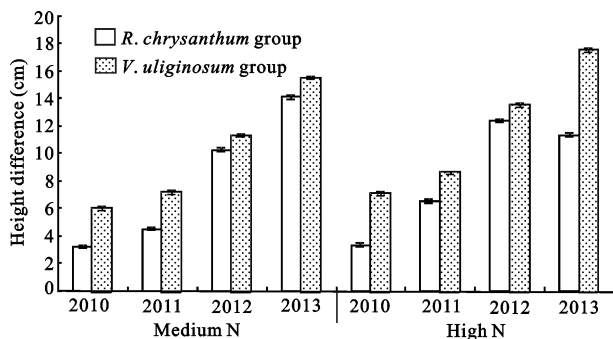


Fig. 9 Height difference of *D. angustifolia* from 2010 to 2013 compared with 2009 under medium and high N treatments in *R. chrysanthum* and *V. uliginosum* communities

3.2.3 Biomass of dominant species in alpine tundra

For the control N deposition treatment, the biomass of dominant species was not significantly different over the four years. With increased N deposition, the biomass of *D. angustifolia* increased, and the biomass of *R. chrysanthum* and *V. uliginosum* decreased. The aboveground biomass ratio and belowground biomass ratio of *R. chrysanthum* and *D. angustifolia*, *V. uliginosum* and *D.*

angustifolia dropped significantly for the high and medium N treatments, and was significantly different among the three N treatments ($P < 0.05$) (Figs. 10 and 11). The aboveground biomass decreased more than the belowground biomass, and in particular the change in ratio was larger for the *V. uliginosum* group (Figs. 10 and 11).

4 Discussion

4.1 Changes of alpine tundra community

Atmospheric N deposition can be a major driver of change in most natural terrestrial ecosystems and particularly threatens species composition, diversity, and functioning of ecosystems adapted to nutrient poor conditions (Hurkuck *et al.*, 2014).

Generally, enhanced nutrient levels in plant communities lead to increased plant productivity (Bowman *et al.*, 1993; Gough *et al.*, 2000; Nordin *et al.*, 2005; Stevens *et al.*, 2010). Our results showed that the increased amount of N deposition had a significant impact on the

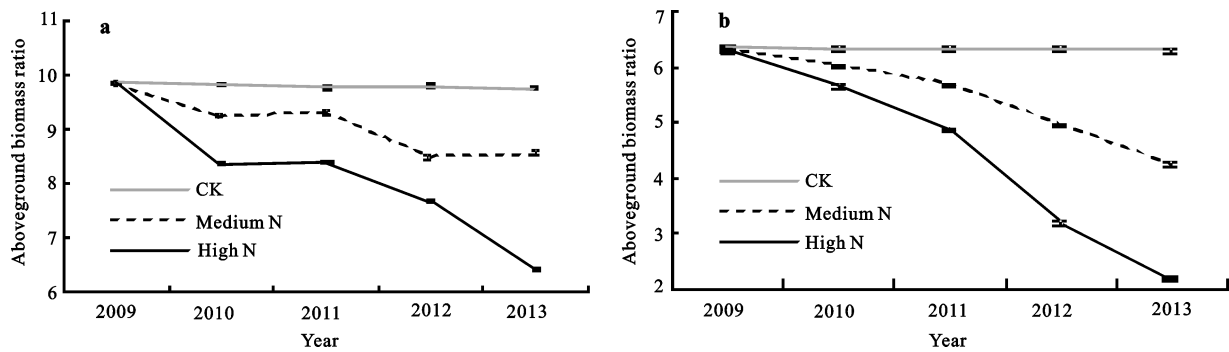


Fig. 10 Changes in aboveground biomass ratio of *R. chrysanthum* and *D. angustifolia* (a), *V. uliginosum* and *D. angustifolia* (b) under three N deposition treatments

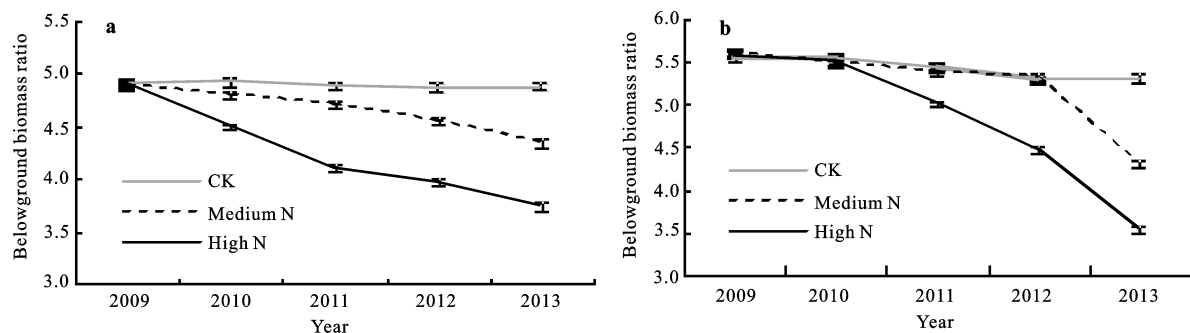


Fig. 11 Changes in belowground biomass ratio of *R. chrysanthum* and *D. angustifolia* (a), *V. uliginosum* and *D. angustifolia* (b) under three N deposition treatments

growth and biomass of the tundra vegetation invaded by *D. angustifolia*, e.g., vegetation coverage, leaf area index and biomass of the communities were increased. In *R. chrysanthum* and *V. uliginosum* communities invaded by *D. angustifolia*, the biomass of *D. angustifolia* is significantly increased, and the biomass of *R. chrysanthum* and *V. uliginosum* is not significantly decreased. It was possible that plants with a high potential growth rate (graminoids) will have advantages over plants with lower potential growth rate (dwarf shrubs) (Berendse, 1994) in environments with sufficient nutrients, enhanced nitrogen deposition can lead to increased the growth of often weedy species in nutrient-poor ecosystems (Clark *et al.*, 2013).

This study indicates that abundance of *D. angustifolia* was increased in *R. chrysanthum* and *V. uliginosum* communities by elevated N, resulted in the change of degree of invasion by *D. angustifolia* from mild to medium (Zong *et al.*, 2013). Other studies showed large responses to fertilizer applications in graminoids. In a tundra ecosystem in northern Sweden, Graglia *et al.* (2001) showed in a 10-year fertilization experiment that grasses increased in abundance in response to fertilizer

application. Similarly, Bret-Harte *et al.* (2004) reported that graminoids responded more strongly than other growth forms to fertilizers in an Alaskan tussock tundra.

Many studies have noted that high levels of N deposition can affect the primary production resulting in increases of nitrophilic species and decreases in plant diversity in nutrient-poor ecosystems (Verhoeven *et al.*, 2011). However, the increased biodiversity reported in this work differs from many previous researches. Since our experiments are four years, with *D. angustifolia* invasion, more herbaceous species invaded into the alpine tundra zone where dominant species were dwarf shrubs. Whereas continuous N deposition will favor nitrophilic species, which may ultimately reduce species richness.

Our results showed that increased N deposition improved the growth and enhanced the competitiveness of *D. angustifolia*. *D. angustifolia* have formed into a herb layer, and the herbaceous height of *D. angustifolia* was more higher than that of the shrub under N addition. The higher height of *D. angustifolia* can enhance aboveground competitiveness for light under N addition. Meanwhile, the roots of *Deyeuxia angustifolia* can occupy more belowground space because of more below-

ground biomass ratio under N addition, so the competitiveness of below ground plant parts was enhanced for nutrient. Those would give *D. angustifolia* a competitive advantage over *R. chrysanthum* and *V. uliginosum*. *Deyeuxia angustifolia* could gradually replace *R. chrysanthum* and *V. uliginosum* to become the dominant species in the system (Yoshida and Allen, 2001; Nordin *et al.*, 2005).

In alpine tundra ecosystems, a shift in dominance from one plant functional group toward another might have a great impact, transforming alpine tundra into alpine meadow in the Changbai Mountains (Dorrepaal *et al.*, 2005; Kool and Heijmans, 2009; Wardle *et al.*, 2013).

4.2 Causes of *D. angustifolia* invasion

On the western slope of the Changbai Mountains, *D. angustifolia* invaded the tundra zone in the late 1980s. In the 21st century, *D. angustifolia* gradually formed a stable community and became the dominant species. This change in community structure could be the result of multiple factors. Zong *et al.* (2013) showed climate warming was not the cause of *D. angustifolia* invasion. In our study, the change of plant community was not significant for the control without N addition treatment over four experimental years. This may suggest that natural succession may not be an obvious factor contributing to the herbaceous species invasion. In our other study (Jin *et al.*, 2014) have noted that the increase of nitrogen deposition is not the direct reason of invasion of *D. angustifolia* to tundra communities, since the structure of *R. chrysanthum* and *V. uliginosum* community with no *D. angustifolia* invasion did not change. Once *Deyeuxia angustifolia* invades into the tundra through some kind of mechanisms, elevated nitrogen deposition could accelerate the invasion of *D. angustifolia*. Disturbances are also the suspected causes of *D. angustifolia* invasion. The effect of wind-damage on the *Betula ermanii* forest might allow increased number of *D. angustifolia* seeds to reach the ground. Erosion and degradation of tundra make implantation of *D. angustifolia* seeds easier (Jin *et al.*, 2013; Zong *et al.*, 2013). Interaction of the above-mentioned factors with the effects of increased N deposition requires further study.

5 Conclusions

The results of our experiment suggest that the increased

amount of N deposition had a significant impact on the growth of the tundra vegetation invaded by *D. angustifolia*. The increased amount of N deposition had a weaker effect on overall community characteristics compared within-community structure that specifically measure species competitiveness of the tundra vegetation invaded by *D. angustifolia*. Under conditions of increased N deposition, *R. chrysanthum* community is less vulnerable to invasion by *D. angustifolia* than *V. uliginosum* community. Increased N deposition improved the growth and enhanced the competitiveness of *D. angustifolia*, which could gradually replace *R. chrysanthum* and *V. uliginosum* to become the dominant species in the system. From this research, it can be concluded that under increased nutrient deposition, alpine tundra is more likely to turn into alpine meadow in the Changbai Mountains.

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