Herbaceous Encroachment from Mountain Birch Forests to Alpine Tundra Plant Communities Through Above- and Belowground Competition

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Abstract: Alpine plant communities are highly sensitive to global warming. One of the consequences of the warming is encroachment by herbaceous plants from forests at low elevations into alpine ecosystems. In the Changbai Mountains, narrowleaf small reed (*Deyeuxia angustifolia* (Kom.) Y. L. Chang) from mountain birch forests encroached upward into alpine tundra, gradually replacing native tundra shrubs such as Rhododendron (*Rhododendron aureum* Georgi). How encroaching plants affect native plant communities is not fully understood. In this study, we analyzed above- and belowground biomass of alpine plant communities at five encroachment levels to investigate how biomass allocation changed at species and community scales. Our research showed that native plants are forced to change their morphology to cope with competition, at both above- and belowground levels, from encroaching plants. We found that (1) *R. aureum* increased the shoot height and leaf area in order to compete with *D. angustifolia*; (2) above- and belowground biomass of *D. angustifolia* increased while above- and belowground biomass of *R. aureum* decreased with increasing levels of encroachment; and (3) *D. angustifolia* encroachment reduced the total biomass of alpine tundra. Encroachment by herbaceous plants has a long-term negative impact on the ability of tundra plants to sequester carbon in the alpine tundra of the Changbai Mountains.

Keywords: herbaceous encroachment; alpine tundra; competition; biomass allocation

1. Introduction

Alpine tundra is a fragile ecosystem that is very sensitive to environmental change [1]. The main environmental stress for tundra is low temperature. Alpine tundra is typically covered by snow for most of the year and the period for plant growth is limited to the short summer season. The poor soil, strong winds, and high ultraviolet radiation make establishment and growth difficult for most native alpine tundra plant species.

Globally, rapid changes in plant communities in alpine and arctic tundra have been observed over the past few decades. Some plant species from low elevations have expanded to high elevations in accordance with climate warming in alpine ecosystems [2]. Among these plant species 24.6% of the non-native species were herbaceous [2]. In the central Andes, the diversity and cover of non-native plants including some herbs have been found increasing in high elevations in past decades [3–5]. Moreover, some non-native herbs have expanded quickly through corridors, such as road and trail, in the montane area of Drakensberg Mountains [6]. In a trend that is predicted to accelerate, herbaceous

species have expanded into the habitats of native species in the European Alps [7,8]. Such expansion would have significant influences on the structure and function of alpine plant communities.

Plants respond to different environmental conditions and levels of competition through changes of survival strategies [9]. In alpine tundra, encroaching herbaceous species elevated the competition for resources with tundra plants. Competition led to changes in survival strategies in all species (encroaching and tundra species) [10,11]. Encroaching plant species may have inhibitory effects on native plants, or even completely replace native plants in high-stress environments [12–14]. In order to compete for resources such as light and moisture, native plants can exhibit plasticity in morphological traits such as shoot height and leaf width [15] or adjust the carbon allocation to aboveground and belowground parts [15–18]. It has been suggested that plants may respond to environmental stress by increasing the distribution of the belowground parts to obtain more nutrients from soil [19]. Studies at a high arctic oasis on Ellesmere Island concluded that herbaceous species were more sensitive to nutrient availability than shrub species [20,21]. Encroaching plants in tundra may also make adjustments in survival strategies to compete for limited resources [22,23].

The alpine tundra of the Changbai Mountains is one of two tundra areas in China. This vegetative community has experienced rapid changes since the late 1990s [24]. Narrowleaf small reed (*Deyeuxia angustifolia* (Kom.) Y. L. Chang), a perennial herb that once existed in the understory of mountain birch forests at lower elevations, has now moved into the tundra plant communities. It is a small reed with narrow leaves, fast growth, clonal and sexual reproductive modes, high seed production, and anemochory. *D. angustifolia* has a short juvenile period and is generally distributed in moist habitats [25]. In the 1970s, *D. angustifolia* was absent in the tundra plant communities [26], while *D. angustifolia* was found in *R. aureum* communities with less than 10% at low elevation areas from the survey results of the 1990s [27]. Thus, we refer to *D. angustifolia* as an encroaching species [28]. *D. angustifolia* is now widespread with a patchy distribution in the alpine tundra. The expansion of *D. angustifolia* has altered the landscape and tundra plant community, greatly affecting the abundance of tundra plants such as *R. aureum*.

In this study, we intend to answer the following questions: What strategies do *D. angustifolia* use to gain a competitive advantage as an encroaching species? What strategies do tundra plants use in response to competition from *D. angustifolia*? How do changes in the composition of the tundra plant community affect carbon stock? We will answer these questions by testing the following predictions: (1) encroaching herbaceous plants gain advantages through both aboveground competition and belowground competition; (2) native tundra plants are forced to change their morphology to cope with competition from the encroaching species; and (3) herbaceous encroachment leads to an overall decrease in vegetation carbon stock of alpine tundra.

2. Materials and Methods

2.1. Study Area

The Changbai Mountain Nature Reserve is located in Jilin province, Northeast China (Figure 1). It has five unique vegetation zones arranged vertically from low altitude to high altitude: a deciduous broad-leaved forest zone below 500 m; a mixed deciduous broad-leaved/conifer forest zone between 500 and 1100 m; a coniferous forest zone between 1100 and 1700 m; a mountain birch forest zone between 1700 and 2000 m; and a tundra zone above 2000 m [29]. The alpine tundra of the Changbai Mountains has a short growing season between June and September every year. The tundra is covered by snow outside the growing season. The temperature during the growing season ranges from 7.3 to 10.6 °C (mean temperature is 8.9 °C). The mean growing-season temperature has increased by 0.239 °C per decade over the past several decades [30]. The annual precipitation ranges from 558.7 to 1553.7 mm (mean precipitation is 1056.27 mm) [31]. As a result of the harsh environment, the vegetation structure is relatively simple: typical tundra plants are dwarf shrubs. Our study area is located on the western aspect of the Changbai Mountain (41° 59′ N, 128° 01′ E; 2200 m). The dominant native

plant species in the tundra include evergreen dwarf shrubs such as Rhododendron (*Rhododendron aureum* Georgi)*,* blueberry (*Vaccinium uliginosum* Linn.), mountain avens (*Dryas octopetala* L.), azaleas (*Rhododendron confertissimum* Nakai), and Phyllodoce (*Phyllodoce caerulea* (L.) Bab.). Some perennial herbaceous species are widely distributed, such as Sanguisorba stipulata (*Sanguisorba sitchensis* C. A. Mey.), Sanguisorba parviflora (*Sanguisorba tenuifolia* Fisch. var. alba Trautv. et Mey.), hawkweed (*Hieracium coreanum* Nakai), *ligularia fischeri* (*Ligularia jamesii* (Hemsl.) Kom.), and monkshood (*Aconitum tschangbaischanense* S. H. Li & Y. H. Huan). During the past few decades, *D. angustifolia* from low elevations has been encroaching into the alpine tundra ecosystem, mainly threatening *R. aureum* communities [28]. We compared the data from Qian (1979) and Qian (1992) with ours to see whether the abundance of *D. angustifolia* increased gradually over time. Qian (1979) showed that the alpine tundra in Changbai Mountains was dominated by *R. aureum* and that *D. angustifolia* was absent in the tundra plant communities [26]. *D. angustifolia* was first reported by Qian in 1992 [27]. He found that *D. angustifolia* was found in *R. aureum* communities with less than 10% at low elevation areas. However, according to our recent survey in 2010, *D. angustifolia* became dominant at the same areas where *R. aureum* was found standing dead [30].
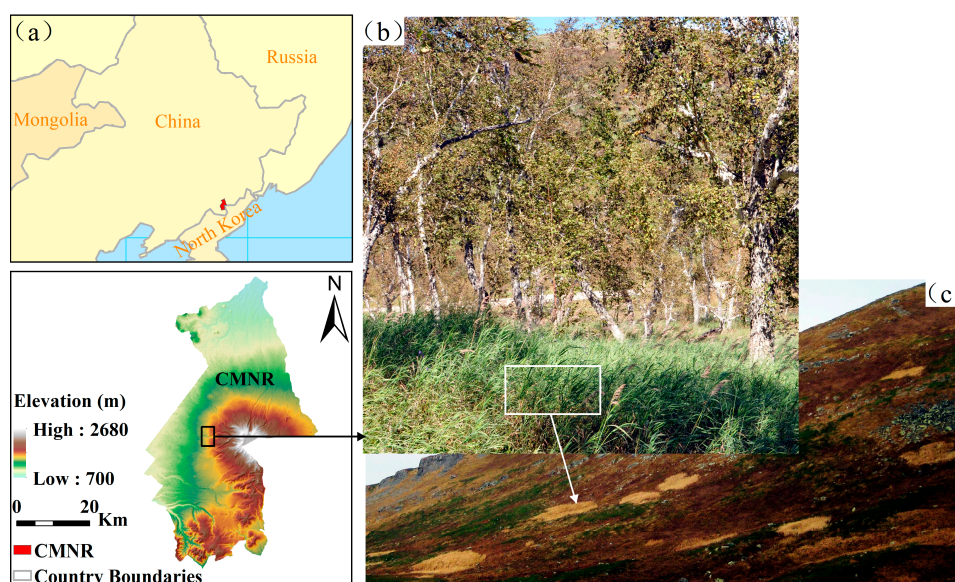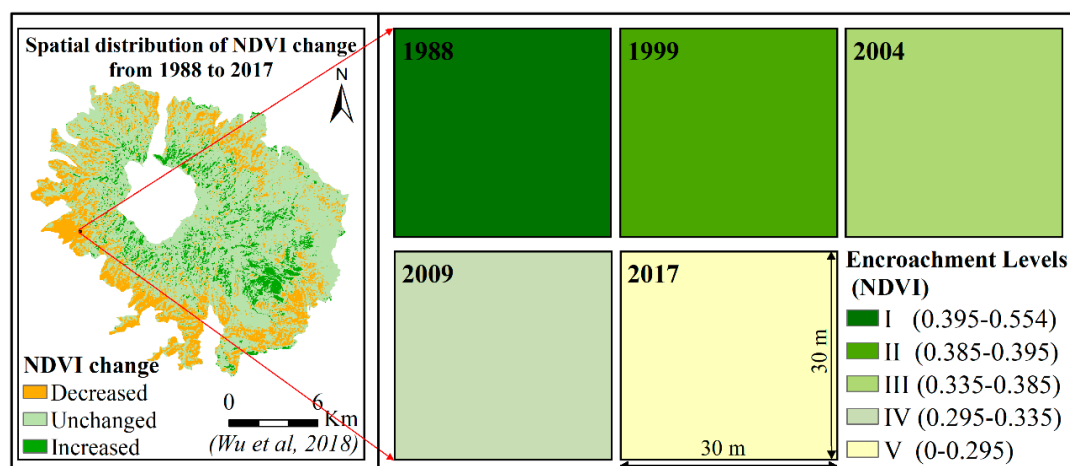

Figure 1. Location of the Changbai Mountain Nature Reserve (CMNR) in Northeastern China (**a**), mountain birch and *Deyeuxia angustifolia* (inset) communities in mountain birch forests located between 1700 and 2000 m (**b**), and alpine tundra (above 2000 m) with patches of encroaching *D. angustifolia* located on the western aspect of the Changbai Mountains (**c**).

2.2. Sampling Design

According to our previous study, there was a gradual expansion process of *D. angustifolia* after it established in the *R. aureum* communities. From remote sensing which revealed long-term dynamics of *D. angustifolia* communities, Zong et al. (2013) analyzed changes in the NDVI of *D. angustifolia* patches from 1983 to 2008 and found that NDVI decreased gradually [30]. *R. aureum* showed greenness, while *D. angustifolia* showed yellowness at the end of the growing season. We concluded that *D. angustifolia* gradually replaced *R. aureum* during the past three decades. In addition, Zong et al. (2014) transplanted *D. angustifolia* patches (30 × 30 cm) into *R. aureum* patches to observe the expansion process of *D. angustifolia* and found that *D. angustifolia* expanded outside of the patches at rate of 9 shoots per year, indicating a low expansion rate [28]. Furthermore, Wu et al. (2018) processed time-series Landsat satellite images (from 1988 to 2017) of the sampling areas [32]. The resolution of the image was 30 × 30 m. Randomly taking single pixels from images, including those of our sampling area, Wu et al. (2018) showed that NDVI gradually decreased over time at the sampling areas, which indicated that
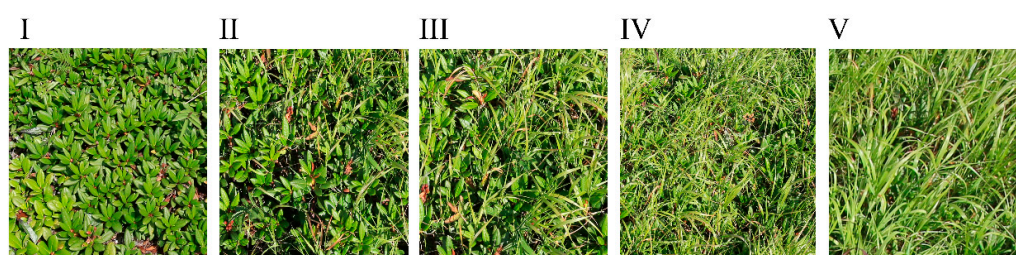
the encroachment levels of *D. angustifolia* gradually increased (Figure 2). Thus, we believe the method of "space-for-time substitution" can be used [33] to investigate the biomass reallocation process at the community level.

Figure 2. Location of our sampling area in alpine tundra (above 2000 m) of Changbai Mountains (on the left of figure [32]) and NDVI of the time-series satellite images of communities with different *D. angustifolia* encroachment levels in the sampling area (on the right of figure).

At each of our plots, we classified the *D. angustifolia* encroachment into one of five levels based on the percentage of cover of *D. angustifolia* and *R. aureum*: no encroachment (I) (cover of *D. angustifolia* 0%; *R. aureum* 100%), low encroachment (II) (0% < cover of *D. angustifolia* ≤ 30%; 70% ≤ cover of *R. aureum* < 100%), medium encroachment (III) (30% < cover of *D. angustifolia* ≤ 70%; 30% ≤ cover of *R. aureum* < 70%), high encroachment (IV) (70% < cover of *D. angustifolia* < 100%; 0% < cover of *R. aureum* < 30%), and complete encroachment (V) (cover of *D. angustifolia* 100%; *R. aureum* 0%) (Figure 3). Communities with no encroachment or complete encroachment were monoculture communities that included only *R. aureum* or *D. angustifolia*. Mixed communities at a low encroachment level, a medium encroachment level, and a high encroachment level with unitary structures included a mixture of the two. We did not consider other plants in these communities because of their low abundances.

Figure 3. Pictures of *Rhododendron aureum* communities under five *Deyeuxia angustifolia* encroachment levels: no encroachment (**I**) had a cover of *D. angustifolia* of 0%, low encroachment (**II**) had a cover of *D. angustifolia* between 0 and 30%, medium encroachment (**III**) had a cover of *D. angustifolia* between 30 and 70%, high encroachment (**IV**) had a cover of *D. angustifolia* between 70 and 100%, and complete encroachment (**V**) had a cover of *D. angustifolia* of 100%.

Elevation and topography gradients may create variable micro-environment (e.g., temperature and soil moisture), leading to changes in plant morphology [34,35]. To avoid this confounding factor, we used the stratified-random sample design. Stratified sampling was carried out in 6 random plots (equal size) with similar topographical conditions (a slope between 21 and 28° and soil moisture between 0.05 and 0.3 m^3/m^3) at an elevation of 2200 m, where plant communities with the five levels of *D. angustifolia* encroachment could be found. In each plot (10 × 10 m), we sampled the above- and

belowground biomass in three 10 × 10 cm quadrats randomly for each encroachment level (total = 15 quadrats per plot). Meanwhile, in each quadrat, we randomly selected three shoots that could reflect the average height of the species in the communities. We measured the height of *R. aureum* and *D. angustifolia* from three replicate plants, and the average height of the three plants was taken as the height of the two plant species in the communities. Leaf area was measured from the plants that were selected to represent the average status of growth using a leaf area meter (Yaxin-1241, Beijing Yaxinliyi Science and Technology Inc., Beijing, China). The aboveground vegetative parts in every quadrat was clipped at the soil surface and sorted into leaves and stems for *R. aureum* and *D. angustifolia*. To efficiently extract root form soil, we removed large stones first. Roots were separated from most of the soil through sieves of different mesh sizes as much as possible. We then placed roots into fine-mesh bags and washed the bags to remove soil. After the washing treatment, we extracted roots with different diameter using forceps [36]. The roots of *R. aureum* and *D. angustifolia* were identified after the above process. The soil sampling depth depended on how deep the roots of plants can reach. The root depth of *R. aureum* in monoculture community was about 16 cm, while the root depth of *D. angustifolia* in monoculture community was about 22 cm. The roots of the two focal species could be distinguished by color and texture: roots of *D. angustifolia* were white and smooth, while the roots of *R. aureum* were brownish or reddish with a woody texture [29]. We sorted roots to different fractions according to the root diameter: coarse roots (diameter > 3 mm), medium roots (1 mm < diameter ≤ 3 mm), and fine roots (diameter ≤ 1 mm) for *R. aureum*, and medium roots (1 mm < diameter ≤ 3 mm) and fine roots (diameter ≤ 1 mm) for *D. angustifolia*. All samples including above- and belowground parts were oven-dried at the temperature of 65 °C until the weight of dry mass no longer changed. We applied the mass density (kg/m^2) as a measure of all biomass parts.

2.3. Data Analysis

We calculated the aboveground biomass (e.g., stems and leaves), belowground biomass (roots of various diameters), and total biomass of *R. aureum*, *D. angustifolia*, and the entire plant community. In addition to weighing the absolute biomass, we also calculated root/shoot ratio and biomass fractions including the leaf biomass ratio, stem biomass ratio, fine root biomass ratio, medium root biomass ratio, and coarse root biomass ratio (Table 1) [37,38].

Table 1. Biomass variables used in analyses, together with formula and the descriptions.

Variables	Formula	Descriptions
Leaf biomass allocation (LBA)	Leaf biomass/total biomass × 100%	The percentage of leaf biomass of the total biomass of the plant
Stem biomass allocation (SBA)	Stem biomass/total biomass × 100%	The percentage of stem biomass of the total biomass of the plant
Fine root biomass allocation (FRBA)	Fine root biomass/total biomass × 100%	The percentage of fine root biomass of the total biomass of the plant
Medium root biomass allocation (MRBA)	Medium root biomass/total biomass × 100%	The percentage of medium root biomass of the total biomass of the plant
Coarse root biomass allocation (CRBA)	Coarse root biomass/total biomass × 100%	The percentage of coarse root biomass of the total biomass of the plant
Root/shoot ratio (R/S)	Belowground biomass /aboveground biomass	The relationship between aboveground and belowground biomass

In order to determine whether the data met assumptions of normality and homoscedasticity, all data were tested using Shapiro–Wilk and Levene tests in SPSS before using ANOVA to examine the difference in communities' biomass and biomass allocation among different encroachment levels. Results showed that most of the variables passed the test ($p > 0.05$). If data of any variable did not pass the test, we transformed the data to make it suitable for ANOVA analysis. We considered encroachment level and plot as two main factors in all statistical analyses by two-way ANOVA for analyzing above and belowground biomass. Subsequent Fisher's least significant difference (LSD) tests were used to examine the difference in communities' biomass and biomass allocation among different encroachment

levels. All statistical analyses were conducted using SPSS 22.0 (SPSS Inc., Chicago, IL, USA). For each of the statistical analyses, the levels of significance were $p < 0.05$.

3. Results

Results show that interactions between plots and encroachment levels were not significant ($p > 0.05$) (Tables S1 and S2). The main effects of plot and encroachment level were calculated (Tables 2 and 3). Table 2 shows the test results of the respective main effects of the plot and encroachment level of *R. aureum* biomass, height, and leaf area. Table 3 shows the test results of the respective main effect of the plot and encroachment level of *D. angustifolia* biomass, height, and leaf area. Results show that plot effects on most dependent variables, except for the leaf area (RAR) of *R. aureum*, were not significant. This might be because of the growth of plants at different habitats. Encroachment level effects on most dependent variables, except for medium root biomass (RMRB) and coarse root biomass (RCRB) of *R. aureum*, were significant, indicating that the allocation of plant biomass was affected by encroachment levels.

Table 2. The F tests the effect of the plot and of the encroachment level of *R. aureum* biomass, height, and leaf area.

Dependent Variable		Plot			Encroachment Level		
		df	F	Sig.	df	F	Sig.
RLB	Contrast	5	0.095	0.993	3	52.642	0.000
	Error	63			63		
RSB	Contrast	5	0.219	0.953	3	44.168	0.000
	Error	63			63		
RFRB	Contrast	5	2.418	0.050	3	29.148	0.000
	Error	63			63		
RMRB	Contrast	5	0.408	0.841	3	2.552	0.076
	Error	63			63		
RCRB	Contrast	5	0.311	0.895	3	3.003	0.058
	Error	63			63		
RH	Contrast	5	0.408	0.841	3	199.027	0.000
	Error	63			63		
RAR	Contrast	5	2.698	0.028	3	71.157	0.000
	Error	63			63		

This test is based on the linearly independent pairwise comparisons among the estimated marginal means.

Table 3. The F tests the effect of the plot and of the encroachment level of *D. angustifolia* biomass, height, and leaf area

Dependent Variable		Plot			Encroachment Level		
		df	F	Sig.	df	F	Sig.
DLB	Contrast	5	0.789	0.561	3	120.950	0.000
	Error	63			63		
DSB	Contrast	5	0.970	0.443	3	97.236	0.000
	Error	63			63		
DFRB	Contrast	5	0.480	0.790	3	42.122	0.000
	Error	63			63		
DMRB	Contrast	5	0.886	0.496	3	89.355	0.000
	Error	63			63		
DAR	Contrast	5	1.276	0.286	3	40.698	0.000
	Error	63			63		
DH	Contrast	5	0.407	0.842	3	39.976	0.000
	Error	63			63		

This test is based on the linearly independent pairwise comparisons among the estimated marginal means.

3.1. Changes in Plant Morphology

Both *R. aureum* and *D. angustifolia* responded morphologically to inter-specific competition based on the level of encroachment (Figure 4). With increasing levels of encroachment, the height of *R. aureum* increased significantly (F = 199.027, $p < 0.05$) (Figure 3a), especially at the medium (III) and high (IV) encroachment levels. The height of *R. aureum* increased by 53% at the medium encroachment level and by 108% at the high encroachment level, compared with the low encroachment level. Similarly, the height of *D. angustifolia* also increased significantly (F = 39.976, $p < 0.05$), especially at the high (IV) encroachment level. It increased by 50% from the low encroachment levels, but the extent of the increase was not as high as *R. aureum*.
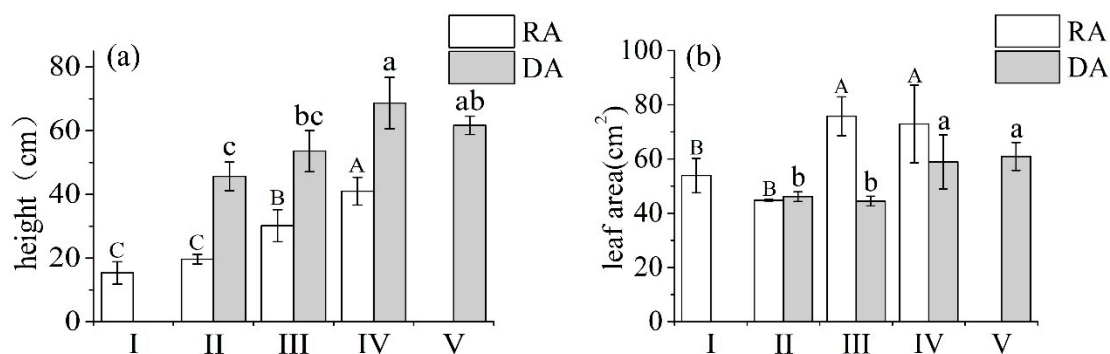
Figure 4. Plant height (**a**) and average leaf area (**b**) of *Deyeuxia angustifolia* (DA) and *Rhododendron aureum* (RA), in plant communities under five encroachment levels. Different capital and lower-case letters indicate significant differences among RA and DA, respectively, at the five encroachment levels ($p < 0.05$) according to two-way ANOVA with Fisher's least significant difference (LSD) test.

Increasing *D. angustifolia* encroachment resulted in the increase of average leaf area of both *R. aureum* (F = 71.157, $p < 0.05$) and *D. angustifolia* (F = 40.698, $p < 0.05$) (Figure 3b). In particular, compared with low encroachment levels (II), the average leaf area of *R. aureum* increased significantly by 79% at medium (III) and high (IV) encroachment levels. Average leaf area of *D. angustifolia* increased significantly by 35% at high (IV) encroachment levels.

3.2. Changes in Biomass and Allocation

R. aureum's biomass differed significantly among the five encroachment levels (Figure 5a). With increasing levels of encroachment, the total (above- and belowground) biomass of *R. aureum* gradually reduced (F = 8.017, $p < 0.05$). The largest reduction occurred between the medium (III) and high (IV) encroachment levels. Both aboveground (F = 8.152, $p < 0.05$) and belowground (F = 10.759, $p < 0.05$) biomass allocations by *R. aureum* changed significantly (Table 4). From no encroachment (I) to medium encroachment (III), aboveground biomass allocations to leaves and stems increased, and belowground biomass allocations to roots decreased, but the changes were not significant ($p > 0.05$). However, at high encroachment levels (IV), *R. aureum* significantly reduced aboveground biomass allocations ($p < 0.05$) while significantly increasingly belowground biomass allocations ($p < 0.05$). Allocations to different parts of *R. aureum* changed differently across encroachment levels. From the no encroachment level (I) to the medium encroachment level (III), leaf biomass (kg/m^2) did not change significantly; however, leaf biomass was significantly reduced at the high encroachment level (IV) (F = 52.642, $p < 0.05$). Leaf biomass allocation had no significant changes ($p > 0.05$). Stem biomass (kg/m^2) (F = 44.168, $p < 0.05$) and stem biomass allocation (F = 11.230, $p < 0.05$) gradually reduced with increasing levels of encroachment. Fine root biomass (kg/m^2) (F = 29.148, $p < 0.05$) and fine root biomass allocation (F = 4.934, $p < 0.05$) also exhibited a gradual reduction as levels of encroachment increased. Medium root biomass and allocation did not change ($p > 0.05$). Coarse root biomass did not change ($p > 0.05$), but coarse root biomass allocation increased significantly (F = 12.348, $p < 0.05$). It was notable that,

at each encroachment level, belowground biomass was higher than aboveground biomass and the root/shoot ratio increased as encroachment level increased (F = 5.727, *p* < 0.05) (Figure 6).
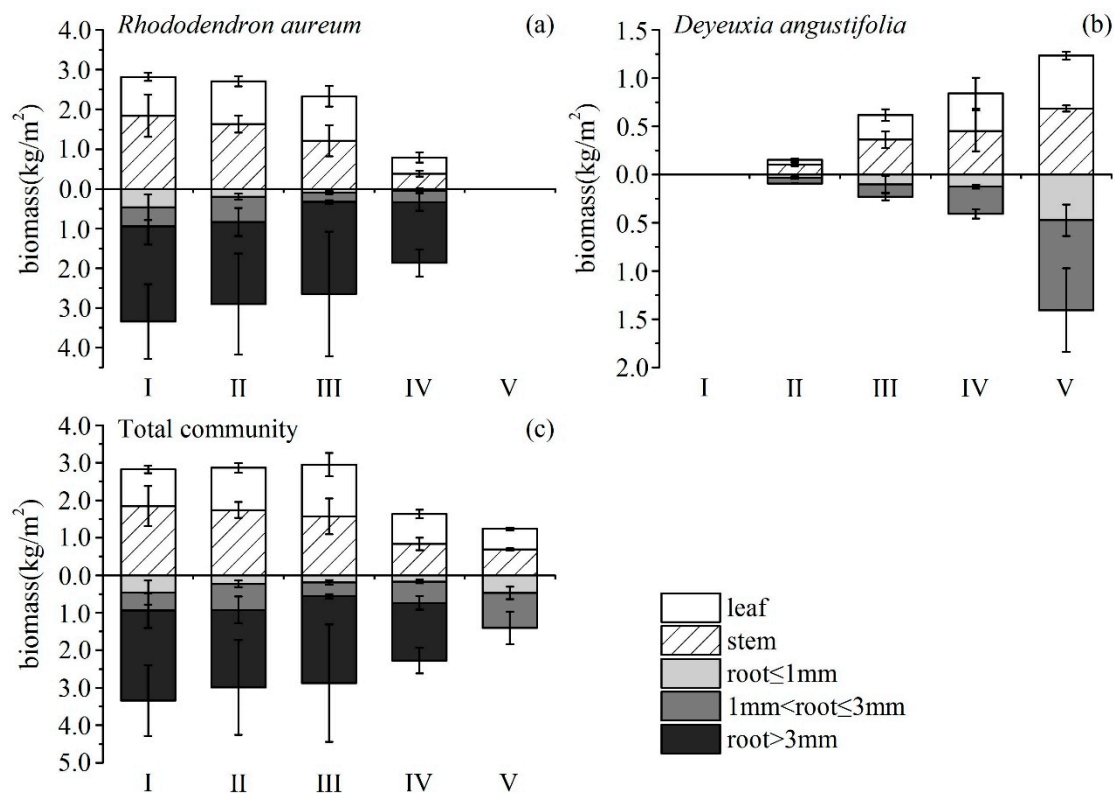
Figure 5. Biomass of different parts of *Rhododendron aureum* (**a**), *Deyeuxia angustifolia* (**b**), and the whole community (**c**), under five encroachment levels.

Table 4. Biomass allocation to different parts of *R. aureum* (RA) and *D. angustifolia* (DA) in plant communities under five encroachment levels.

Plant Type	Level of Encroachment	LBA	SBA	FRBA	MRBA	CRBA
RA	I	17.11 ± 0.06a	30.46 ± 0.03a	7.30 ± 0.04a	6.78 ± 0.05a	38.35±0.03ab
	II	19.52 ± 0.02a	29.64 ± 0.04a	3.49 ± 0.01ab	12.17 ± 0.07a	35.18 ± 0.14b
	III	27.70 ± 0.15a	29.19 ± 0.14a	2.19 ± 0.01b	5.84 ± 0.03a	52.01 ± 0.20ab
	IV	14.98 ± 0.02a	14.80 ± 0.04b	1.48 ± 0.02b	10.39 ± 0.08a	58.35 ± 0.12a
	V					
DA	I					
	II	19.64 ± 0.06b	43.12 ± 0.06a	13.38 ± 0.05ab	23.87 ± 0.02b	
	III	30.21 ± 0.05a	42.96 ± 0.07a	6.00 ± 0.01b	15.48 ± 0.03b	
	IV	30.79 ± 0.03a	35.32 ± 0.06ab	10.64 ± 0.04ab	23.25 ± 0.04b	
	V	21.21 ± 0.03b	26.65 ± 0.04b	17.94 ± 0.06a	34.20 ± 0.09a	

Different lower-case letters indicate a significant difference in results of RA and DA within five encroachment levels (*p* < 0.05) according to two-way ANOVA with Fisher's least significant difference (LSD) test.

D. angustifolia's biomass differed significantly across the five encroachment levels, (Figure 5b, Table 4). From low encroachment (II) to complete encroachment (V), aboveground biomass allocation reduced significantly, while belowground biomass allocation increased significantly (F = 50.565, *p* < 0.05; F = 21.424, *p* < 0.05, respectively). Leaf biomass (F = 120.950, *p* < 0.05) and leaf biomass allocation (F = 37.373, *p* < 0.05) increased significantly as encroachment level increased. Stem biomass increased significantly (F = 97.236, *p* < 0.05). Stem biomass allocation had no significant changes from low encroachment (II) to high encroachment (IV), but was significantly reduced at the complete

encroachment level (V) (F = 36.419, $p < 0.05$). Fine roots biomass, medium roots biomass, and their respective allocations showed no significant changes ($p > 0.05$) from low (II) to high (IV) encroachment levels. However, fine roots biomass and allocation (F = 42.122, $p < 0.05$, F = 4.260, $p < 0.05$, respectively), as well as medium roots biomass and allocation (F = 89.355, $p < 0.05$, F = 21.600, $p < 0.05$ respectively), increased significantly at the complete encroachment level (V). It was notable that, until complete encroachment, aboveground biomass was higher than belowground biomass, and the root/shoot ratio increased as encroachment level increased (F = 11.237, $p < 0.05$) (Figure 6).
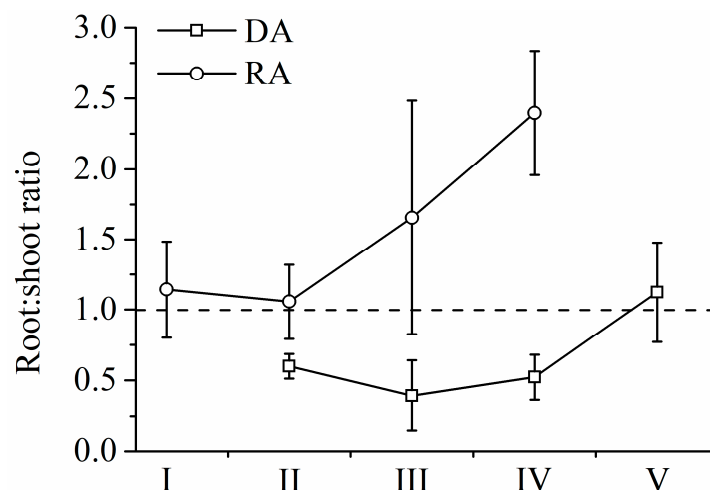
Figure 6. Root/shoot ratio of *R. aureum* and *D. angustifolia* under five encroachment levels.

Aboveground and belowground biomass of the community exhibited a gradual reduction as the encroachment level increased (F = 8.311, $p < 0.05$; F = 1.008, $p > 0.05$, respectively). The total biomass of the community showed a similar pattern (F = 3.190, $p < 0.1$) (Figure 5c), probably as a result of the significant decline in leaf (F = 10.747, $p < 0.05$) and stem (F = 7.325, $p < 0.05$) biomass throughout the community, especially at the high encroachment level. At the community level, fine root biomass and medium root biomass exhibited no significant changes as a result of encroachment ($p > 0.05$). It was notable that the patterns of allocation did not always show consistent differences with level of encroachment or no differences at all (Table 4). This may reflect that biomass was allocated to different plant tissues with different competition mechanisms.

4. Discussion

The alpine tundra ecosystem is under stressful environmental conditions in which plants compete for limited resources [39]. Competition intensifies as exotic species encroach under changing climate conditions [7,40]. Our results showed that, as encroachment levels increased in the alpine tundra of the Changbai Mountains, the biomass of *D. angustifolia* gradually increased while the biomass of *R. aureum* declined. This competitive relationship favored the expansion of *D. angustifolia* at the expense of native plants. Some studies have shown that plant interactions shift from competition to facilitation as levels of environmental stress increase in alpine ecosystems [41]. The main mechanism underlying facilitation is the amelioration of extreme thermal conditions and protection from the strong desiccating winds by neighboring plants [8]. Since growth is not temperature-dependent in either focal species [29], neither plant species may benefit from this sort of thermal facilitation. Instead, we found that both plant species prefer low-lying areas with high soil moisture, indicating similar habitat requirements [25,42]. Numerous studies have found that encroaching plant species generally become established within a specific site or plant community, which suggested foreseeable competition with native plants after this initial encroachment stage [8,43–45]. Therefore, we emphasize that competition plays as an important role in controlling community dynamics in the context of alpine plant movements.

Since micro-topography played a role in mediating alpine vegetation [34,35], the patterns of biomass at the different levels of encroachment may be affected by different microsites at local scales. However, we did not pursue this line of research because the graduate encroachment process was more predominant than microsite effects in alpine tundra of the Changbai Mountains as verified by both time-series satellite images and field observations [26,27,32]. We expect that the levels of encroachment as a result microsite differences would lead to the similar results to those of graduate encroachment in terms of above and belowground biomass patterns.

4.1. Aboveground Competition

Our findings support the first hypothesis that native alpine tundra plants are forced to change their morphology in response to competition from an encroaching species from lower altitudes of the Changbai Mountains. Small size and slow growth rate is a survival strategy for alpine plants that experience strong winds, low temperatures, and low resources [42]. The native *R. aureum*, a dwarf alpine shrub, increased its height and average leaf area in response to competition from *D. angustifolia*. Previous studies have shown that plants may change morphology (e.g., increasing height for light) because of competition [13,46]. At our site, *D. angustifolia* grows into dense populations, creating a shaded environment, when it becomes dominant in the community. In such a community, *R. aureum* needs to increase the height and leaf area to ensure adequate levels of photosynthesis. However, increases in height may have negative impacts on plant growth [47]; tall shrubs may not be fully covered by snow, resulting in exposure to freezing damage. Damage from freezing temperatures may be particularly severe with reduced snow cover under warming climate conditions [48]. *R. aureum* is known to have a narrow thermal tolerance, especially for low temperatures [42]. By contrast, *D. angustifolia* keeps all living tissue underground during the winter, and is free of freezing damage. Therefore, *R. aureum* may suffer disproportionately from the consequences of increased plant height [49, 50], giving *D. angustifolia* a competitive edge over *R. aureum*.

4.2. Belowground Competition

Native alpine plants allocated about 70% of biomass to belowground tissues [49]. Hence, we conclude that belowground competition was important for the expansion of *D. angustifolia* compared with aboveground competition [29,51,52]. The root/shoot ratio of *R. aureum* increased as encroachment level increased, indicating that competition gradually shifted from aboveground to belowground [53]. *D. angustifolia* encroachment led to a significant reduction of fine root biomass of *R. aureum*, which may restrict the growth of *R. aureum*. Fine roots are an important part of belowground biomass, which determines the nutrient and water absorption of plants from the soil [54]. By contrast, fine root biomass of *D. angustifolia* increased significantly at higher levels of encroachment, which allowed *D. angustifolia* to gain a competitive advantage.

In alpine ecosystems where resources were limited, herbaceous species generally have a stronger ability to absorb nitrogen and a higher resource utilization efficiency (e.g., carbon assimilation per unit of resource) than shrubs [55]. In this study area, other analyses have indicated that the nitrogen fixation and absorption ability of *D. angustifolia* was stronger than that of *R. aureum* [56]. Thus, species-specific differences in the ability to absorb nitrogen may have played an important role in plant competition in this setting [57,58]. As a fast-growing plant species, *D. angustifolia* requires a large amount of nitrogen to complete its life cycle [29]. Other studies have shown that the organic compounds exuded from roots of encroaching plants influence the growth of microorganisms around the rhizosphere, which themselves alter the soil environment [59,60]. Encroaching plants can effectively replace native plants by establishing plant–soil feedbacks beneficial to encroaching plants [61,62]. Li et al. (2016) have suggested that *D. angustifolia* changes the soils' nutrient and microbial structure to form an environment suitable for its own growth [63] and establishment. Therefore, *D. angustifolia* may take advantage of its ability in nutrient absorption and alteration on plant–soil feedback through belowground competition.

4.3. Implications for Vegetation Carbon Stock in Alpine Tundra

Tundra vegetation dominated by native shrubs sequesters a significant amount of atmospheric carbon [64]. Previous studies have shown that climate warming causes changes of carbon stocks in the vegetation of alpine tundra [11,65–68]. A previous study of this system found that there were no significant changes in vegetative structure [29], indicating that climate warming would have limited impacts on the carbon stocks in the alpine tundra of Changbai Mountains. However, results of this study showed that *D. angustifolia* encroachment led to decreases in vegetative carbon stocks. Hence, the indirect effects of climate change on plant community structure, via plant encroachment, may play an important role in changing vegetation carbon storage in this alpine tundra ecosystem. With the herbaceous species continuing to expand and replace native plant species, the alpine tundra of the Changbai Mountains may become a carbon source.

5. Conclusions

Our study revealed that herbaceous encroachment in alpine tundra altered biomass allocation of native plant communities through above- and belowground competition. With the increasing level of encroachment, growth of native *R. aureum* was suppressed by encroaching *D. angustifolia*. Hence, competition played an important role in controlling community dynamics. We found that biomass allocation changed with the increasing levels of encroachment at species (*R. aureum* and *D. angustifolia*) and community scales. *D. angustifolia* increased both above- and belowground biomass while above- and belowground biomass of *R. aureum* decreased with the increasing level of encroachment. Thus, *D. angustifolia* gained advantages through both above- and belowground competition. To compete with *D. angustifolia*, *R. aureum* exhibited phenotypic plasticity in two morphological features (increased height and leaf area) to ensure adequate photosynthesis. *D. angustifolia* encroachment reduced the total biomass of communities. Our research highlights the fact that continued expansion by *D. angustifolia* should decrease the vegetative carbon stock of alpine tundra in the future.

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