

Above-ground carbon storage in *Pinus pumila* along an alpine altitude in Khingan Mountains, Inner Mongolia of China

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Abstract

The carbon (C) cycle in alpine ecosystems is sensitive to climate change, but information about the C storage in its undergrowth is scarce. In October 2017, a total of 6231 *Pinus pumila* (Pall.) Regel trees were investigated for above-ground growth and density in 60 sub-plots (10×10 m) from 12 stands (50 × 50 m) along the altitudinal gradient (800-1500 m a.s.l.) in Great Khingan Mountains, Inner Mongolia, Northeast China. Sites were characterized by different crown densities (CDs) from 20% to 90%. Height and root-collar diameter (RCD) were higher in stands with CDs of 40-70% than CDs of 20-30%. Stem density (SD) and crown area (CA) had a positive correlation with altitude and CD. Equations from local shrub models were used to adapt the allometric growth models for estimation. There were variations in estimated above-ground C density depending on the model and the involvement of the canopy area. Above-ground C storage in *P. pumila* individuals ranged from 0.05-2.46 kg tree⁻¹, which corresponds to C storage density ranged from 0.17-37-ton ha⁻¹. The C density in *P. pumila* increased with crown density instead of stem density along increasing altitudinal gradients and increasing RCD. Hence, the crown density and diameter of a *P. pumila* plant can be used to predict the above-ground C density of its natural population.

Keywords: C sequestration; canopy tree; ecotone; global warming; treeline

Introduction

As an important carbon (C) reservoir, the alpine biomes are extremely sensitive to ongoing climate change (IPCC, 2014). Climate change has a negative impact on alpine, which affects C sequestration (Greenwood and Jump, 2014). There has been less attention given to the effect of climate change on alpine habitats compared to the arctic tundra and boreal ecosystems (Britton *et al.*, 2011). Although ambient C pools have been studied in degraded alpine grassland ecosystems that are experiencing anthropogenic pressures (Wen *et al.*, 2013), C pools in other types of alpine communities are still unclear. Forests contain more than 45% of terrestrial C (Bonnan, 2008; Wei and He, 2021). Projected future climate change will continue to alter C

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storage in forests (He *et al.*, 2020; Manusch *et al.*, 2014). There is a knowledge gap about forest C storage in sub-alpine regions (Wagner *et al.*, 2015).

Gross primary production (GPP) in terrestrial ecosystem is the largest CO₂ flux that supports ecosystem functions. Results from the biosphere model suggest a strong relationship between GPP and precipitation at the global scale (Beer *et al.*, 2010). At high-elevation mountain regions, global warming may have caused a depletion of stored C in alpine vegetation through species extinction and diversity decline (Grabherr *et al.*, 1994; IPCC, 2007). In contrast, in alpine tundra ecosystems, biomass, cover, and abundance in dwarf trees and shrubs were found to increase over the past century (Myers-Smith *et al.*, 2011). There is no way to determine the whole C pool in alpine tundra ecosystems because of a lack of species-specific response of C storage in alpine shrub plants.

Pinus pumila (Pall.) Regel is known as the alpine dwarf-pine (He *et al.*, 2021). They live mainly in the alpine zones of Japan, eastern Siberia, and mid-west Europe (Sano *et al.*, 1977). Current understanding of C storage in *P. pumila* mainly comes from relative comparison with other plant biomes (Okitsu, 1985; Makoto *et al.*, 2016). For example, biomass C storage in *P. pumila* was surmised to be 10 times larger compared to other alpine plants in the krummholz zone of Japan (Okitsu, 1985). In the northern Amur region of Far East Russia, above-ground productivity of *P. pumila* was found to be greater than that in local coniferous trees (Makoto *et al.*, 2016). Currently, there is limited information on the direct estimate of C storage in *P. pumila* populations. This is because its natural population has a very high density that makes field investigation nearly impossible. Recent reports revealed that *P. pumila* has expanded through local fellfield edges and snow-beds over the past three decades, increasing its distribution area by 14% (Amagai *et al.*, 2015). This invasion may not have affected local fine root biomass and soil C storage (Makoto *et al.*, 2016), but the effects on shoot C storage is still unclear. It is necessary to estimate the above-ground C storage in *P. pumila* to evaluate the impact of its expansion on C pools in endemic tundra plants at alpine regions.

Above-ground growth of *P. pumila* might be sensitive to elevation in alpine zones (Sano *et al.*, 1977; Takahashi, 2003; Amagai *et al.*, 2015) because annual shoot elongation was found to be driven by early summer temperature (from early June to late July) (Sano *et al.*, 1977; Takahashi, 2003; Amagai *et al.*, 2015). Temperature and other abiotic and biotic factors change as a gradient along mountain elevation (Guo *et al.*, 2019; Wei *et al.*, 2019, 2021b). *P. pumila* poorly tolerates even slight shading (Moskalyuk, 2008); hence its above-ground growth is depressed under tall tree canopies (Okuda *et al.*, 2008). Therefore, *P. pumila* populations showed two types of vegetative growth patterns. At high altitudes, like other alpine plants, the height of *P. pumila* was depressed (Takahashi and Yoshida, 2009); at low altitudes, they dominate the undergrowth stratum in the open space to avoid tall tree shade (Takahashi, 2003; Okuda *et al.*, 2008). Above-ground C storage in *P. pumila* is shaped by not only physical factors but also, more importantly, change along the altitudinal gradient.

P. pumila mainly dwells in deforested areas in the boreal subalpine belt, which is characterized by strong wind and heavy snow accumulation in winter and in spring (Okitsu and Ito, 1989). In cold seasons, *P. pumila* shoots are buried under snow which helps them to escape the desiccating and freezing impacts of winter winds (Moskalyuk, 2008). Therefore, dominancy of *P. pumila* diminished gradually from wind-exposed sites to snow-depositing sites (Okitsu and Ito, 1984). Given that *P. pumila* plants have dense and compact crowns carrying thick needles (Moskalyuk, 2008) that cover the forest floor (Takahashi, 2003), crown density can be an indicator of the distribution of *P. pumila* communities. Although the height of dwarf pines does not make it inconvenient to measure whole-tree C storage, the variance in the density of individuals at different altitudes still hinders the precision of C storage estimates on *P. pumila* in large populations.

In China, forests were estimated to have a biomass C sink of 1896 Tg during 1977-2008 with an annual C sink of 70.2 Tg year⁻¹ and was projected to sequester C at this annual rate until 2050 (Chen *et al.*, 2016). However, the estimate on C storage in alpine regions' tree community is still limited. In this study, *P. pumila* was investigated for above-ground growth along the altitude gradient to estimate their above-ground C storage

using empirical allometric growth models. The purpose is to fill the knowledge gap on above-ground C storage in *P. pumila*.

Materials and Methods

Study site

The study area is located in the Great Khingan Mountains (51°39'-51°54' N, 121°36'-122°07' E) 45-120 km to the north of Genhe, Hulun Buir, Inner Mongolia, Northeast China. Local terrain consists of alpine and sub-alpine ecosystems in altitudes between 800-1500 m a.s.l. Ambient investigation was conducted on *P. pumila* communities with different crown densities (CDs) (20-90%) at upper (1500 m above sea level [a.s.l.]) and lower altitudes (800 m a.s.l.). The site area is at a cold temperate climate zone, where average temperature is -5.3 °C, annual precipitation ranges between 50 mm and 80 mm, and the annual frost-free period is about 90 days. Lands are highly covered by forests (92%). Dominant trees include *Larix gmelinii* (Rupr.) Rupr., *Pinus sylvestris* L., *Betula platyphylla* Sukaczew, and *Populus davidiana*.

Data investigation

A pre-investigation was conducted before the study and all *P. pumila* communities were classified into four CDs (20-30%, 40-50%, 60-70%, and 80-90%) (Figure 1). A total of 12 research plots, 50 × 50 m in size, were created from 24 to 31 October, 2017 (Table 1). Each group of three plots were randomly placed as a replicate for one CD classification. Five sub-plots, spaced 10 × 10 m, were established at the four corners and the center of each plot. Every individual *P. pumila* plant in one sub-plot was investigated for height, root-collar diameter (RCD), crown area (CA), and stem number. Height was measured as the length between the tip of the main stem and the root-collar. RCD was measured as the basal diameter of the main stem. Crown area was calculated as the product of largest crown length and width. The height, RCD, and CA values of the five sub-plots were averaged to obtain their respective mean values for the overall plot. Similarly, the stems in the five sub-plots were summed to obtain the stem number of the plot. Stem density (SD) was then calculated by dividing 250 m² from the plot stem number. In total, 6231 *P. pumila* individuals were measured from all 60 sub-plots.

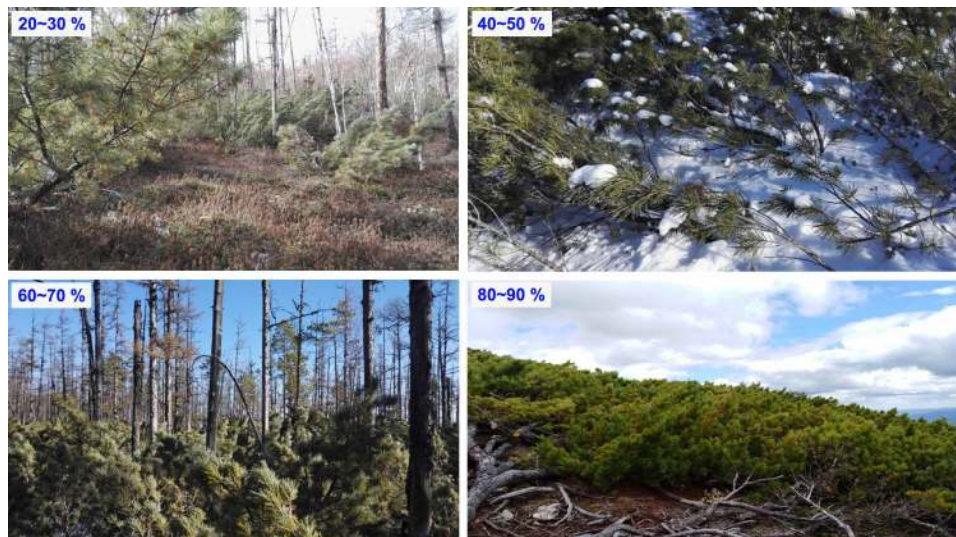


Figure 1. Stands of natural distributed *Pinus pumila* communities with different characteristics of crown densities

Table 1. The field condition of *Pinus pumila* sites

Site No.	Investing date	Latitude (N)	Longitude (E)	CD ¹ (%)	Altitude (m)	Slope aspect	Slope position
1	25 Oct. 2017	51°48'25"	122°04'19"	20	878	East	Medium-low
2	26 Oct. 2017	51°49'49"	122°02'54"	30	997	Southwest	Medium-low
3	31 Oct. 2017	51°39'06"	122°00'12"	20	872	North	Low
4	26 Oct. 2017	51°49'24"	122°03'48"	50	918	East	Medium-low
5	28 Oct. 2017	51°52'12"	121°41'25"	40	933	East	Medium-low
6	31 Oct. 2017	51°39'07"	122°00'04"	40	916	North	Medium-low
7	26 Oct. 2017	51°49'49"	122°04'24"	60	1115	-	Top
8	29 Oct. 2017	51°41'24"	122°07'01"	70	1125	Southwest	Up
9	30 Oct. 2017	51°46'01"	121°36'01"	70	923	Southwest	Valley
10	24 Oct. 2017	51°50'36"	122°02'12"	90	1505	Southwest	Up
11	27 Oct. 2017	51°54'36"	121°43'42"	80	1209	Southwest	Up
12	30 Oct. 2017	51°46'18"	121°35'43"	90	994	-	Top

¹ SC, crown density.

Above-ground C estimation

Above-ground C storage was estimated for each *P. pumila* using biomass allometric growth models summarized by Li *et al.* (2010). The models were empirically used for shrub species in Northeast China. The botanical nomenclature of these species and the empirical equations are listed in Table 2. Above-ground C storage in *P. pumila* was estimated ten times. The results therefrom allow for comparison and screening for the best fitted estimates.

Table 2. The estimation models for shoot carbon (C) stock in *P. pumila* using empirical allometric growth models

Applicative species	Allometric growth model	Height range (m)	Diameter range (cm)
<i>Euonymus verrucosoides</i> ¹	$C_{shoot} = 0.152 \times D^{2.505}$	0.67~4.09	0.5~4.8
<i>E. alatus</i> ¹	$C_{shoot} = 0.095 \times D^{2.655}$	0.33~3.21	0.4~5.1
<i>Corylus mandshurica</i> ¹	$C_{shoot} = 0.044 \times D^{2.957}$	0.34~3.95	0.3~3.8
<i>Viburnum burejaeticum</i> ¹	$C_{shoot} = 88.627 \times CAH^{0.646}$ ²	0.59~3.54	0.4~3.1
<i>Lonicera maackii</i> ¹	$C_{shoot} = 180.832 \times CA^{1.395}$	0.67~4.41	0.4~7.4
<i>Spiraea ussuriensis</i> ¹	$C_{shoot} = 93.014 \times CAH^{0.912}$	0.55~1.48	0.3~1.0
<i>Acanthopanax senticosus</i> ¹	$C_{shoot} = 132.269 \times CAH^{0.838}$	0.36~2.97	0.3~1.0
<i>Deutzia parviflora</i> var. <i>amurensis</i> ¹	$C_{shoot} = 99.779 \times CAH^{0.957}$	0.26~2.25	0.2~1.6
<i>Philadelphus schrenkii</i> ¹	$C_{shoot} = 34.54 \times H^{2.51}$	0.18~3.13	0.3~2.7
<i>Sorbaria sorbifolia</i> ¹	$C_{shoot} = 68.018 \times CAH^{1.021}$	0.55~1.48	0.5~1.9

¹ Adapted from Li *et al.* (2010); ² CA, crown area (m²).

Data analysis

All of the data calculation and analysis were performed using SAS software (SAS Institute Inc., Cary, NC, USA). The mean, above-ground C density for each plot (*ACD*) was calculated using the following equation (Zhang *et al.*, 2015):

$$ACD = \frac{\sum_{i=1}^n \sum_{j=1}^m \frac{C_{ij}}{PA}}{n} \quad (1)$$

where C_{ij} is the C density for the j th *P. pumila* unit (kg unit^{-1}) in the i th sub-plot; PA is the project area of the sub-plot ($PA=100 \text{ m}^2$); m is the total number of units in the sub-plot; n is the total number of sub-plots ($n=5$). With the goal of evaluating an accurate estimation, the six sets of data about C storage were analyzed for the principal components (PCs) using the ‘princomp’ procedure. Thereafter, datasets with the greatest similarity in distribution patterns were averaged to estimate the C storage.

The normal distribution of data was checked by the Shapiro-Wilk test using the ‘univariate’ procedure. Indices with normally distributed data were compared among CDs using analysis of variance (ANOVA). Unnormally distributed data were compared in pairs with Wilcoxon Signed-Rank test (Guan *et al.*, 2017). The significance was taken at the 0.05 level for ANOVA, and at the 0.0083 level due to the Bonferroni correction for six pairs of comparison. The Spearman correlations were analysed for all data using the ‘corr’ procedure.

Results

Screening of shoot biomass estimate models

According to the PC analysis on above-ground C estimates, the first two PCs accounted for 94.53% of the total data variation. In the first axis, all estimated C storage from the ten models showed the same trend of data variation (Figure 2). In the second axis, estimated data on C storage of *Euonymus verrucosoides*, *E. alatus*, *Philadelphus schrenkii*, and *Corylus mandshurica* showed different variation patterns with the other six species. Therefore, assessment of C storage can be classified into two groups according to the PC results.

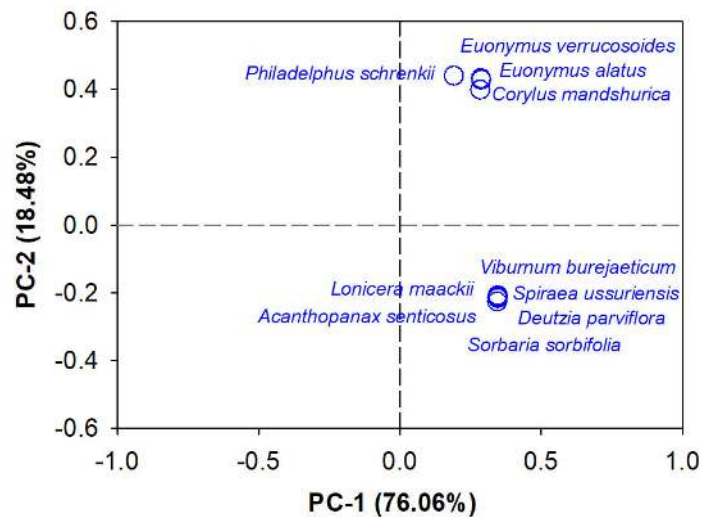


Figure 2. The principal component (PC) analysis on estimated above-ground C storage using empirical allometric growth models on ten local shrubs
Botanical nomenclature is supplied beside the scattered dots

Above-ground growth

Among above-ground indices, only data on height followed the normal distribution ($W=0.9689$; $P < W$, 0.1293). Above-ground height in CDs of 20-30% were about 210% greater than above-ground height in CDs of 40-50% and 60-70% (Figure 3A). RCD in denser CDs was 6.5-7 times higher than RCD in CDs of 20-30% (Signed-Rank $S=60$; $P \geq |S|$, <0.0001) (Figure 3B). CA was greatest in CDs of 80-90%, which was 17-23% higher than that in sparser CDs (Signed-Rank $S=60$; $P \geq |S|$, <0.0001) (Figure 3C). SD increased at a rate of 20-40% with the increase of CD (Figure 3D).

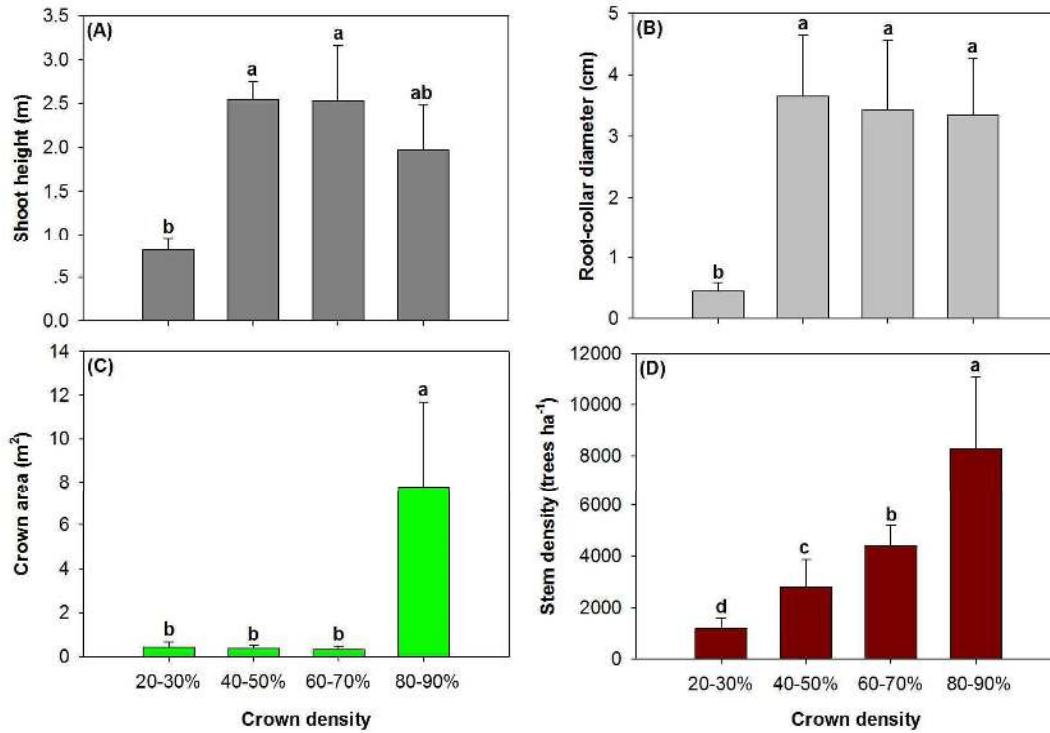


Figure 3. Above-ground growth parameters of *P. pumila* in response to different crown densities. Different letters indicate significant differences at 0.05 level for above-ground height (A) through analysis of variance (ANOVA), and at 0.0083 level for root-collar diameter (B), crown area (C), and stem density (D) through paired-comparison using the Wilcoxon Signed-Rank test.

The relationship between altitude and above-ground indices

A Pearson correlation was found between altitude and CD ($n=12$; $R=0.6920$; $P=0.0127$), while a Spearman correlation was found between altitude and SD ($n=12$; $R=0.7273$; $P=0.0074$) and between altitude and CA ($n=12$; $R=0.6294$; $P=0.0283$). Therefore, the relationship between altitude and CD can be described by a linear regression model (Figure 4); the relationship between altitude and log-transformed SD can be described by a type II 2-parameter logarithmic equation; the relationship between altitude and square root of CA can be described by a 2-parameter single-exponential-growth equation. In addition, height was found to be positively correlated with RCD ($n=12$; $R=0.9390$; $P<0.0001$).

The relationship between crown density and above-ground indices

A Pearson correlation was found between CD and the square root of RCD ($n=12$; $R=0.6421$; $P=0.0244$) and between CD and the square root of CA ($n=12$; $R=0.6624$; $P=0.0189$), while a Spearman correlation was found between CD and log-transformed SD ($n=12$; $R=0.9543$; $P<0.0001$). Therefore, the relationship between CD and the square root of RCD or the square root of CA can both be described by a linear regression model (Figure 5); the relationship between CD and log-transformed SD can be described by a 2-parameter exponential-growth equation (Figure 5).

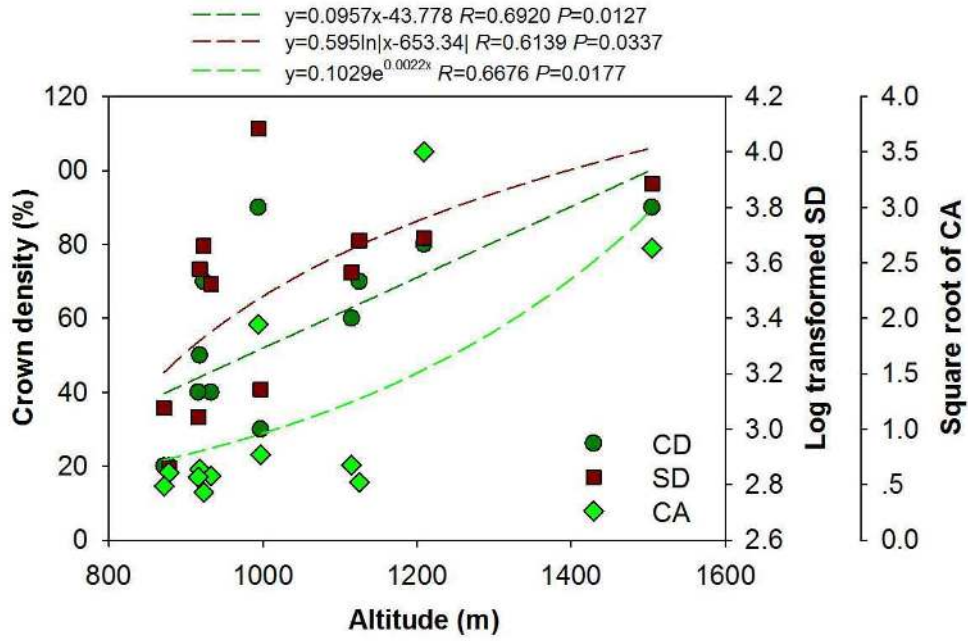


Figure 4. The best-fit curves for correlations of altitude with indices of canopy density, log-transformed stem density (SD), and the square-root of canopy area (CA) in *P. pumila* populations

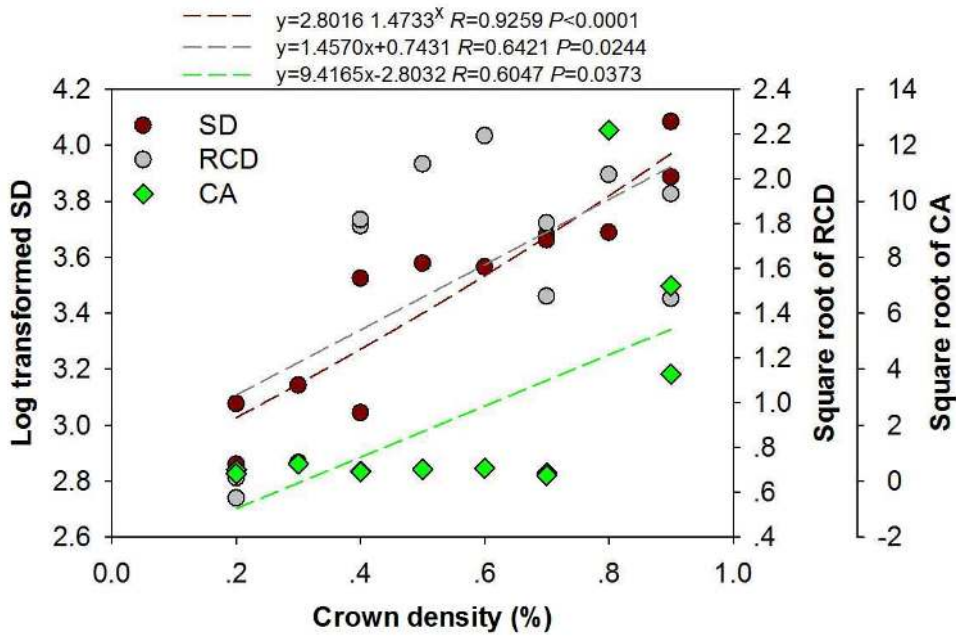


Figure 5. The best-fit curves for correlations of crown density with indices of log-transformed stem density (SD), the square-root of root-collar diameter (RCD), and the square-root of canopy area (CA) in *P. pumila* populations

The estimation of above-ground C storage

Using the models in Table 2, ten estimates of above-ground biomass were made (Table 3). These results can be used for PC analysis for classification (Figure 2).

The type-I group contained results from models on *E. verrucosoides*, *E. alatus*, *P. schrenkii*, and *C. mandshurica*, and the type-II group contained results from models on the other six species (Table 4). Above-ground C storage in *P. pumila* plants with CDs of 20-30% tended to have the lowest C storage, independent of the model used for estimation (Table 4). In sites with CDs denser than 30%, the C storage estimated by both Type-I and Type-II models was not statistically different for different CDs. C storages in other sites were all higher than the C storage of the site with a CD of 20-30% in both individual plant and site density. The mean value of above-ground C storage from the Type-I and Type-II models was higher in sites with CDs of 80-90 % than that in sites with CDs of 20-30%.

Table 3. The estimations for shoot carbon (C) stock in *P. pumila* using empirical allometric growth models

Percent of crown density	Ev ¹	Ea ²	Cm ³	Vb ⁴	Lm ⁵
20~30 %	0.08±0.18c ⁶	0.08±0.18b	0.07±0.18b	0.19±0.21b	0.26±0.25b
40~50 %	17.62±17.72b	21.00±22.33a	36.38±42.99ab	0.50±0.37b	0.40±0.31b
60~70 %	21.52±16.36ab	25.34±20.32a	42.79±39.18ab	0.68±0.43b	0.57±0.40b
80~90 %	33.46±22.96a	40.71±33.33a	77.35±87.61a	21.41±7.36a	63.48±25.62a
	Su ⁷	As ⁸	Dpa ⁹	Ps ¹⁰	Ss ¹¹
20~30 %	0.22±0.25b	0.28±0.29b	0.24±0.27b	0.24±0.36b	0.19±0.23b
40~50 %	0.74±0.59b	0.96±0.75b	0.84±0.68b	3.76±2.86a	0.62±0.51b
60~70 %	1.00±0.68b	1.29±0.86b	1.14±0.78b	5.59±3.26a	0.84±0.59b
80~90 %	29.52±12.01a	38.82±15.10a	33.23±13.89a	5.08±2.99a	24.29±10.55a

¹ Ev, *Euonymus verrucosoides*; ² Ea, *Euonymus alatus*; ³ Cm, *Corylus mandshurica*; ⁴ Vb, *Viburnum burejaeticum*; ⁵ Lm, *Lonicera maackii*; ⁶ Different letters indicate significant difference adjusted by Bonferroni correction; ⁷ Su, *Spiraea ussuriensis*; ⁸ As, *Acanthopanax senticosus*; ⁹ Dpa, *Deutzia parviflora* var. *amurensis*; ¹⁰ Ps, *Philadelphus schrenkii*; ¹¹ Ss, *Sorbaria sorbifolia*.

Table 4. The estimated C stock (mean ± S.E.) in *P. pumila* distributed in sites with different crown densities (n=12)

Percent of crown density	Type-I	Type-II	Mean
	Unit tree storage (kg tree ⁻¹)		
20~30 %	0.03±0.04b	0.07±0.05b	0.05±0.05b
40~50 %	2.52±2.16a	0.09±0.05b	1.31±1.10ab
60~70 %	2.18±1.62a	0.08±0.05b	1.13±0.83bc
80~90 %	2.74±3.43a	2.19±1.54a	2.46±2.42a
Fvalue	3.72	21.40	5.76
Pvalue	0.0164	<0.0001	0.0017
	C storage density (ton ha ⁻¹)		
20~30 %	0.12±0.19b	0.23±0.24b	0.17±0.21b
40~50 %	19.69±21.45a	0.68±0.53b	10.18±10.98b
60~70 %	23.81±19.72a	0.92±0.62b	12.36±10.14b
80~90 %	39.15±35.93a	35.13±13.90a	37.14±23.87a
Fvalue	5.52	70.31	14.23
Pvalue	0.0022	<0.0001	<0.0001

The relationship between estimated C storage and other indices

According to the Spearman correlation model, mean estimated C density is positively correlated with indices of altitude and CD according to the Spearman correlation model (Table 5). No correlation was found between above-ground C density and SD. For individual growth indices, both above-ground height and RCD

were found to have a positive relationship with mean values of estimated C storage. No relationship was detected between CA and estimated C storage.

Table 5. Spearman correlation analysis on the relationship between estimated C stock density and distribution parameters of *P. pumila* (n=12)

Independent	C density ¹	Independent	C density
Site characteristic		Individual growth	
Altitude	$R^2=0.3787$ $P=0.0332$	Height	$R^2=0.7887$ $P=0.0001$
CD ³	$R^2=0.3499$ $P=0.0428$	RCD	$R^2=0.9178$ $P<0.0001$
SD ⁴	$R^2=0.2678$ $P=0.0849$	CA	$R^2=0.2396$ $P=0.1063$

¹ unit, ton ha⁻¹; ² Bold numbers indicate significant correlation; ³ CD, crown density; ⁴ SD, stem density.

Discussion

Current knowledge on *P. pumila* communities is mainly derived from reports on natural distribution in Japan and Siberia. In central Japan (35° N), *P. pumila* distributes in mountain regions with altitudes from 2400 to 2850 m a.s.l. (Takahashi, 2003; Takahashi and Yoshida, 2009); in northern Japan (43° N), *P. pumila* distributes between altitudes of 1500 m and 2000 m a.s.l. (Okitsu and Ito, 1984, 1989; Amagai *et al.*, 2015). In Siberia (54° N), *P. pumila* distributes between altitudes of 250-500 m a.s.l. (Moskalyuk, 2008; Makoto *et al.*, 2016). These results suggest that the altitudinal distribution of *P. pumila* tends to decline with the increase of latitude. In this study, *P. pumila* distributes in altitudes of 800-1500 m a.s.l. in the Great Khingan Mountains (51° N). Fang *et al.* (2015) also found the distribution of undergrowth *P. pumila* in altitudes up to 1504 m a.s.l. in this region. Both the altitude and latitude of our *P. pumila* distribution fall between the altitude and latitude of *P. pumila* in Japan and Russia. Our *P. pumila* stands with CDs of 60-70 % that were located around treelines, but those in the 80-90% CD region locate near the alpine tundra and grassland (Figure 1).

Our C storage estimations had larger standard deviations than expected. This is because *P. pumila* has a high ontogeny among individuals on the basis of a high density in populations. In addition, our results were estimated in which errors may accumulate from the initial estimate to across-model averages. We found that estimated above-ground C storage had similar variation across Type-I models. These C estimation models all involved the height or diameter of a shrub, but the Type-II models employed the CA as a parameter. Therefore, using CA to estimate C storage created more variation in data compared to PC analysis without CA. Our sites were located along the altitude gradient, which had different relationship with RCD and CA, resulting in different responsive trends of estimated C storage by RCD and CA. Although the height of *P. pumila* did not correlate with other growth parameters, it was found to positively correlate with C storage which suggests that stem length positively contributes to above-ground C storage, independent of altitude gradient.

We did not find any relationship between altitudes and above-ground height for *P. pumila*. Our results disagree with those found in central Japan by Takahashi (2003) in spite no clear relationship was studied therein. Takahashi and Yoshida (2009) found that *P. pumila* were shorter in the upper distribution limit, but they did not study the relationship between height and altitude. Wang *et al.* (2017) measured 3500 dominant trees in Changbai Mountain, Northeast China, and found a very species-specific response regarding height along the altitude gradient. The height response of *P. pumila* to altitudinal gradient may be interrupted by either biotic factors (Takahashi and Yoshida, 2009) or canopy tree shading (Takahashi, 2003; Okuda *et al.*, 2008). Specifically, Kajimoto (1993) found that the length of current above-grounds and needles showed apparent decreasing trends with increasing altitude. We did not distinguish above-ground parts by ages; hence, no significant response was revealed. However, because altitude was found to be positively correlated with CD (Figure 4), height response to altitudinal gradient can be surmised according to the regression model and the

response to CD (Figure 3A). Height growth of *P. pumila* along the altitudinal gradient was positive from 800 m to 1200 m, but was negative around 1500 m.

We found a positive relationship between height and RCD in *P. pumila*. Similarly, Okitsu and Ito (1984) also found a positive relationship between height and annual increment index ($RCD^2 \times \text{Height}$). Wang *et al.* (2017) reported the linear relationship between height and diameter using data from 3500 dominant trees in Changbai Mountain, Northeast China. According to Sano *et al.* (1977), annual height and diameter growths of *P. pumila* were synchronized and both were driven by annual changes in climate. Like height, RCD did not respond to the latitudinal gradient (Figure 4), which corroborates Takahashi *et al.* (2012). Both height and RCD were lower in the site with CDs of 20-30% than in sites with denser CDs (Figure 3). This was the result of stress caused by tall trees (Moskalyuk, 2008; Okuda *et al.*, 2008; Takahashi *et al.*, 2012).

Both SD and CA were positively correlated with altitude and CD in *P. pumila*. SD was also found to positively correlate with altitude because of the increasing depression of tall tree competition (Takahashi *et al.*, 2012). The SD of *P. pumila* was mainly countered by the number of fascicle stems, which were sensitive to the low temperature and wind exposure (Kajimoto, 1993). Abundant needles contribute to the dense canopy (Uehara *et al.*, 2012) but needle longevity is also sensitive to the harsh condition in high altitudes (Kajimoto, 1993). However, in our study, the biotic condition in the high altitude was not limiting enough to negatively impact the density and crown of *P. pumila*.

Our results revealed that the above-ground C density in *P. pumila* increased with altitude and CD, while individual C storage positively correlated with height and RCD. Similar to our results, Takahashi *et al.* (2012) reported a positive relationship between altitude and absolute above-ground dry mass accumulation. Because our main model for the estimation of C storage used height and RCD as input variables, C increased with height and RCD growth. Correlation analysis for coefficient of determination showed interesting results, wherein the estimation on above-ground C density depended on altitude and canopy density only by less than 40%, but estimation on individual C storage depended on height and RCD by nearly 80-90%. These results suggest that the precision of C storage estimation is higher using data from the individual growth than data from the population characteristics. The coefficient of determination for the correlation between CD and C storage density for *P. pumila* in Northeast China was lower than for the correlation between observed C density and C storage density in the forests of Western China (Yue *et al.*, 2016). According to Beer *et al.* (2010), who summarized the data on C storage density in the terrestrial system, our C storage density may have been overestimated due to a low coefficient of determination (between 20-40%). However, our results were reasonable because some seed sources of *P. pumila* individuals in our study were mature trees whose annual growth are faster than seedlings with larger canopy area and subsequently greater C storage estimation (Okitsu and Ito, 1984).

The stem of *P. pumila* plants is not as tall as the other *Pinus spp.* trees. It is necessary to develop some model to estimate their C storage because their density was too high in natural populations. However, although estimating C storage through empirical models is an operational approach for large-scale C estimates, we still have several uncertainties in the estimation of C storage. Firstly, to estimate C storage through allometric models, only one to two growth parameters needs to be involved, but above-ground biomass should be responsive to multiple morphological indices. Despite the heavy workload to measure every individual growth in one time, more measurements are needed for greater precision. The limit of public data about shrub C estimation in the study also hindered the improvement of estimation precision. Finally, the estimation of C storage can be enhanced by referring to the empirical models and biomass of sampling individuals.

According to the allometric growth model, it was found that the above-ground C density in *P. pumila* at sites with CDs over 30% was estimated to range 10–37-ton ha⁻¹, which was much higher than that in CDs of 20-30% (Table 4). Our C storage density was much higher than that in alpine grassland (0.19-0.54-ton ha⁻¹) (Wen *et al.*, 2013) but close to that in alpine *Picea crassifolia* forest trees (43-ton ha⁻¹) (Wagner *et al.*, 2015) in Southwest China and sub-alpine broad-leaved trees in Switzerland (49-ton ha⁻¹) (Manusch *et al.*, 2014). However, our C storage density was much lower than that for above-ground live trees in temperate alpine

forests (81-ton ha⁻¹) (Bradford *et al.*, 2009). Therefore, the estimating precision can be acceptable but more accurate estimation still needs large-scale measurements for dry mass.

Conclusions

This study analysed the density and above-ground growth of 6231 *P. pumila* units from 60 sub-plots (10m × 10m), i.e. 12 plots (50m × 50m), from main populations in Great Khingan Mountains, Inner Mongolia, Northeast China in late October, 2017. The allometric growth models were adapted for estimation using equations from local shrubs' general models in the research area. The variation of data in estimated above-ground C density depended on the model and whether canopy area was involved. As a result, above-ground C storage in a *P. pumila* unit ranged 0.05-2.46 kg tree⁻¹, corresponding to C storage density ranged 0.17-37-ton ha⁻¹, respectively. The C density in *P. pumila* increased with crown density but not stem density along the increasing altitude gradient and increasing RCD. Hence, the crown density and diameter of a *P. pumila* plant can be grossly used to predict the above-ground C density of its natural population. Our data supplemented evidence to estimate the expansion of C pools in endemic tundra plants at alpine regions. Although our study is the first to estimate regional C storage in *P. pumila*, our data was limited to the study area. More studies are needed in the future on *P. pumila* communities in the Far East, Siberia, and the northern and central mountain regions of Japan to compare with our results because current studies are mainly conducted in these regions.

Authors' Contributions

Conceptualization: RC and FS; Data curation: RC, HY, and XP; Formal analysis: RC and FS; Funding acquisition: RC; Investigation: RC, HY, XP, and FS; Methodology: HY and FS; Project administration: RC; Resources: HY and XP; Software: XP and FS; Supervision: RC; Validation: HY and XP; Visualization: RC and FS; Writing - original draft: RC; Writing - review and editing: FS.

All authors read and approved the final manuscript.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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