

Article

Tree Height-Diameter Relationships in the Alpine Treeline Ecotone Compared with Those in Closed Forests on Changbai Mountain, Northeastern China

Xiaoyu Wang ^{1,2,3}, Dapao Yu ^{1,*}, Shoule Wang ^{1,2}, Bernard J. Lewis ¹, Wangming Zhou ¹, Li Zhou ¹, Limin Dai ¹, Jing-Pin Lei ⁴ and Mai-He Li ^{1,3}

¹ Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China; wangxiaoyu12@mails.ucas.ac.cn (X.W.); yudp2003@iae.ac.cn (D.Y.); wangshoule123321@sina.com (S.W.); lewisbern@gmail.com (B.J.L.); zhouwangming@126.com (W.Z.); zhoul930@iae.ac.cn (L.Z.); lmdai@iae.ac.cn (L.D.); maihe.li@wsl.ch (M.-H.L.)

² College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China

³ Tree Ecophysiology Group, Swiss Federal Research Institute WSL, Zuercherstrasse 111, CH-8903 Birmensdorf, Switzerland

⁴ Research Institute of Forestry, Chinese Academy of Forestry, Beijing 100091, China; lejiping@hotmail.com

* Correspondence: yudp2003@iae.ac.cn; Tel.: +86-248-397-0329

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Abstract: Height-diameter relationship is one of the most important stature characteristics of trees. It will change with climatic conditions because height and diameter growth displays different sensitivities to climatic factors such as temperature. Detecting and understanding changes in the stature of trees growing along altitudinal gradients up to their upper limits can help us to better understand the adaptation strategy of trees under global warming conditions. On Changbai Mountain in northeastern China, height-diameter datasets were collected for 2723 Erman's birch (*Betula ermanii* Cham.) in the alpine treeline ecotone in 2006 and 2013, and for 888 Erman's birch, spruce (*Picea jezoensis* Siebold & Zucc. Carr.), larch (*Larix olgensis* A. Henry), and fir (*Abies nephrolepis* Trautv. ex Maxim.) along an altitudinal gradient below the alpine treeline in 2006. These datasets were utilized to explore both changes in the stature of birch at the alpine treeline over time and variations in tree stature of different tree species across altitudes at a given time point (2006). Results showed that birch saplings (<140 cm in height) became stunted while birches with a height of >140 cm became more tapered in the alpine treeline ecotone. The stature of birch along the altitudinal gradient became more tapered from 1700 to 1900 m above sea level (a.s.l.) and then became more stunted from 1900 to 2050 m a.s.l., with 1900 m a.s.l. being the altitudinal inflection point in this pattern. The treeline birch, due to its great temperature magnitude of distribution, displayed higher stature-plasticity in terms of its height-diameter ratio than the lower elevation species studied. The stature of birch is strongly modulated by altitude-related temperature but also co-influenced by other environmental factors such as soil depth and available water, wind speed, and duration and depth of winter snow cover. The high stature-plasticity of birch makes it fare better than other species to resist and adapt to, as well as to survive and develop in the harsh alpine environment.

Keywords: allometric growth; *Betula ermanii*; Erman's birch; tree architecture; tree forms; tree stature; treeline

1. Introduction

The alpine treeline ecotone, constituting the transition zone from uppermost closed montane forest to treeless alpine vegetation, commonly represents the most obvious forest boundary [1,2]. It is widely acknowledged that low temperature at high altitudes inhibits tree growth above the treeline [3]. Although many studies have focused on how low temperature constrains tree growth and survival at the alpine treeline [4–6], the specific ways in which trees respond or adapt to the cold environment at high altitudes have received less attention.

In the alpine treeline ecotone, two tree forms—upright (single-stemmed) and shrubby tree (multi-stemmed)—are generally observed, distributed as patches and/or along an altitudinal gradient. This is considered as trees' direct response to low temperature in combination with wind, edaphic conditions, and seasonal snow cover patterns [7–9]. A multi-stemmed shrubby tree (either multi-stemmed shrubby tree or a group of single stems) has two main advantages relative to their upright counterparts under cold conditions. The first advantage is that the bulk of their mass is located closer to the ground, which helps to create their microclimate to decouple from the cold ambient air, and to achieve higher heat accumulation in their leaf canopy than taller individuals [2,10–12]. The best evidence for this comes from an infra-red thermal imagery study in which upright trees always represent “cold fingers” surrounded by warmer air [2]. The second advantage is that shrubby trees are more flexible in adjusting their xylogenetic processes under cold conditions than their upright counterparts [2]. These advantages explain why shrubby trees are more commonly found at higher altitudes in comparison to upright trees.

Given that low temperature is the leading factor determining tree form at the alpine treeline, once temperature condition becomes more favorable for plant growth, seedlings do not need to first grow in a creeping form but can directly form a single stem stature with upright growth [7,8,13]. Studies on the Ural Mountains have found that, with the climate warming over the past centuries, the dominant tree forms changed from multi-stemmed creeping to multi-stemmed upright stature, and further to a single-stemmed tree form [7,8]. This implies that, over a longer time span, trees' forms may adapt to the environment in which they are growing.

Height (H)-diameter (D) relationship, as one of the most important stature characteristics [2], has been recognized as one manifestation of the many ways in which trees adapt to changes in environment, and this process of stature change may last over decades or centuries. Stature change of trees with increasing altitude has been attributed to both heat deficiency and plants' responses to cold environments [4]. Tree stature change along altitudinal gradients can be represented by the relationship between height and diameter growth because height and diameter growth have different temperature sensitivities [14,15]. Although results have been insufficient to show exactly how the stature of treeline trees responds to changing climate, it has been reported that more biomass appears to be allocated to radial growth under colder climatic conditions [14,15], showing a decreasing H/D ratio with increasing altitude [2]. A large-scale study in the cold Northeast China also found that a lower proportion of biomass is allocated to height growth than to radial growth under conditions of intensified winter cold [16]. Thus, it may be hypothesized that warmer climatic conditions may lead to a more tapered tree stature rather than a stunted growth form.

When taking into account the fact that the stature of different sized trees may exhibit different responses to climate [17], the above hypothesis deserves more consideration. Saplings with a height of less than 0.5 m in the alpine treeline ecotone can become taller, since their height growth is mainly influenced by the near ground surface temperature associated with microclimate, while height growth of those trees taller than 3 m tends to be constrained by low temperature associated with meso-climate at high altitude [14]. In other words, smaller trees invest more carbon to height growth and taller trees use more carbon for diameter growth in the alpine treeline ecotone [14,15]. This result also implies that the current rapid climate warming may modify or shift these breakpoints (i.e., 0.5 m and 3 m) to a higher level. However, considering that trees have their own adaptive responses to climate, and shrubby and/or upright growth forms of treeline trees may have many functional differences,

as noted earlier, there is still a need to precisely understand how the stature of treeline trees will change with a warming climate. A closer focus on height-diameter relationship dynamics can therefore help us to better understand the adaptive mechanisms of tree stature in response to climate and climate change.

Erman's birch (*Betula ermanii* Cham.) is widely distributed across Northeast Asia, including in China, Japan, and eastern Russia [18,19]. On Changbai Mountain in northeastern China, this species is distributed from low altitude to high altitude and forms the alpine treeline at ~2050 m above sea level (a.s.l.). It has been reported that radial growth of this species was sensitive to temperature [20,21]. However, no studies have focused on the responses of height growth or the allometric relationship of height-radial growth of Erman's birch to temperature. In this study, fixed monitoring sample plots were established and investigated in the alpine treeline ecotone on Changbai Mountain in 2006, and reinvestigated in 2013. Using these data, we aimed to explore the changes in stature of birch in the ecotone over the 8-year study period. As references, we compared stature of birch to those of three other dominant species including spruce (*Picea jezoensis* Siebold & Zucc. Carr.), larch (*Larix olgensis* A. Henry) and fir (*Abies nephrolepis* Trautv. ex Maxim.) at six altitudes below the treeline on Changbai Mountain, using data investigated in 2006. These comprehensive analyses allow us to better understand the adaptive strategy of treeline birch to harsh environmental conditions and provide insight into the formative mechanisms of the alpine treeline.

2. Methods

2.1. Study Area and Climate

Field work was conducted on the north slope of the Changbai Mountain (Figure 1) Natural Reserve (approx. 200,000 ha; 41°43'–42°26' N, 127°42'–128°17' E) established in the 1960s [19,20], Jilin Province, Northeast China. The north slope of Changbai Mountain is characterized by four distinct vegetation zones along an altitudinal gradient ranging from 740 to 2691 m a.s.l. These zones include: (1) Korean pine (*Pinus koraiensis* Siebold & Zucc.) and broad-leaved mixed forest ranging from 740 to 1100 m a.s.l.; (2) Spruce-fir forest from 1100 to 1700 m a.s.l.; (3) Erman's birch forest from 1700 to 2000 m a.s.l.; and (4) a tundra belt above 2050 m a.s.l. (*Juniperus sibirica* Burgsd.; *Rhododendron chrysanthum* Pall.; *Vacciniumum liginosum* L.). The Erman's birch-tundra ecotone occurs at an altitude ranging from 1950 to 2050 m a.s.l., with the upper treeline comprised exclusively of birch. Larch is not a dominant species for any of these forest types but is scattered throughout them up to the altitude of 2000 m a.s.l. The alpine birch treeline is a climatic treeline and the ecotone has rarely been affected by human disturbance [19,20].

At the upper limit of forest distribution, the climate is characterized as cold and windy in the winter and rainy in the summer. The average annual temperature varies from −2.3 to −3.8 °C. Annual precipitation ranges from 1000 to 1100 mm, about 80% of which occurs between June and September, with August being particularly wet (approx. 240 mm). The duration of the frost-free period is about 65–70 days. The average annual air temperature decreases from −2.2 °C at 1600 m a.s.l. to −3 °C at 1800–1900 m a.s.l. and −3.4 °C at 2000–2100 m a.s.l. [19] (see Table S1 in Supplementary Materials). Over the past eight decades, this region has experienced a distinctive warming trend, with an average increase in summer temperature of about 0.5 °C per decade [22].

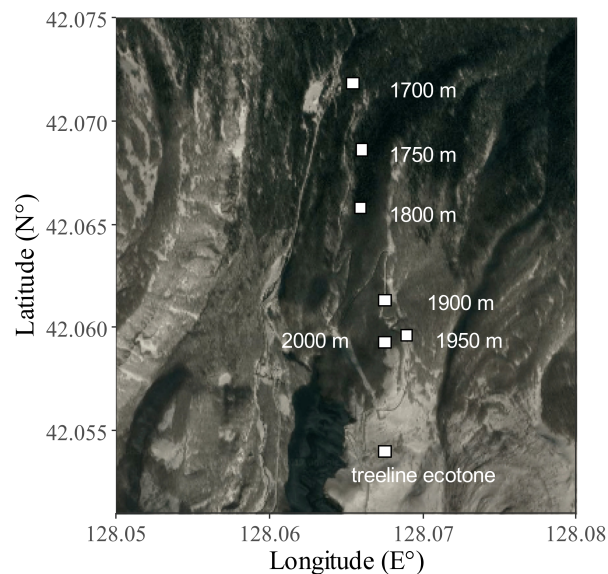


Figure 1. Study sites on the north-facing slope of Changbai Mountain, Northeast China. Data source: Google Earth.

2.2. Site Description and Field Investigation

Ten plots (each in 30 m × 30 m; 2000 ± 30 m a.s.l.) occupied exclusively by Erman's birch in the treeline ecotone on Changbai Mountain were identified for which data were available for the years 2006 and 2013. Three types of growth forms or tree architectures of birch trees were present in the plots. The criterion for classifying the three growth form types was tree height in combination with branching height. Saplings had a tree height of <1.4 m, irrespective of branching and branching height. Trees with a height of >1.4 m were divided into two groups depending on branching height: (1) an upright tree had a branching height of >1.3 m, and hence, was named as a single-stem tree, and (2) a shrubby tree (multi-stems) had a branching height of <1.3 m and then was named as multi-stems. A tree height of 1.4 m was defined so that the diameter at breast height (DBH) at 1.3 m could be measured. All trees in each plot were mapped and tagged in 2006. Tree height (H), DBH for upright and shrubby trees, or basal ground diameter (BD) for saplings were measured. DBH for a shrubby tree was recorded on a main stem or branch. A total of 2723 individual trees including 1038 upright trees, 886 shrubby trees, and 799 saplings in the 10 treeline plots were investigated in 2006 and reinvestigated in 2013 (Table 1).

Table 1. Number of trees, mean height, and diameter (±1 standard deviation) in 2006 and 2013 for Erman's birch with different tree forms, growing in the alpine treeline ecotone on Changbai Mountain, China.

| Attributes | Tree Form Class * | | | |
|---------------------|-------------------|--------------|--------------|-------------|
| | Upright Tree | Shrubby Tree | Sapling | Population |
| Number of trees | 1038 | 886 | 799 | 2723 |
| H ₂₀₀₆ | 2.10 (0.79) | 2.38 (1.05) | 0.97 (0.23) | 1.92 (0.99) |
| H ₂₀₁₃ | 2.44 (0.71) | 2.60 (0.81) | 1.64 (0.52) | 2.26 (0.80) |
| ΔH | 0.48 (0.44) | 0.56 (0.53) | 0.68 (0.52) | 0.56 (0.50) |
| DBH ₂₀₀₆ | 1.3 (1.5) | 2.0 (2.8) | - | 1.6 (2.3) |
| DBH ₂₀₁₃ | 2.4 (1.7) | 2.6 (1.8) | 1.0 (0.9) ** | 2.2 (1.7) |
| ΔDBH | 1.2 (0.8) | 1.3 (1.2) | - | 1.2 (1.0) |
| BD ₂₀₀₆ | - | - | 1.53 (0.57) | - |
| BD ₂₀₁₃ | - | - | 1.95 (0.64) | - |
| ΔBD | - | - | 0.59 (0.43) | - |

-: Not available or not measured. H: height (m); DBH: diameter at breast height (cm); BD: basal diameter (cm) for saplings. Δ: increment during the study period for the specific variable, H, DBH or BD. * Upright trees (branching height >1.3 m) and shrubby trees (branching height <1.3 m) had a tree height of >1.4 m, and saplings <1.4 m in height; ** Saplings that had reached the height of 1.4 m by 2013 were measured in terms of DBH instead of BD.

In addition to the dataset mentioned above, 18 plots (20 m × 20 m) containing birch, larch, fir, and spruce were investigated at six lower altitudes (1700, 1750, 1800, 1900, 1950, and 2000 m a.s.l.; three plots at each altitude) (Figure 1). For each plot, H, DBH, or BD of all trees were recorded in 2006 (see also Table 3). A total of 888 individuals were investigated (see Table 3). The field work was conducted in accordance with Forestry Standards “Observation Methodology for Long-Term Forest Ecosystem Research” of National Standards of the People’s Republic of China (GB/T 33027–2016).

2.3. Data Analysis

Data from 10 plots at the treeline and three plots at each lower altitude were utilized for analysis. Changes in measured attributes of Erman’s birch at the treeline from 2006 to 2013 were quantified by increment of H (m), DBH (cm), and BD (cm) (Table 1). Difference in tree height among the three growth forms was analyzed with one-way ANOVA, and difference in DBH between upright and shrubby trees was tested using t test (data not shown).

A power equation was utilized to model height-diameter relationships at the treeline for year 2006 and 2013. Data were fitted by $H = aD^b$ for each of the three growth form classes, and for the population excluding saplings in 2006 and 2013, respectively, where H = height, D = DBH or BD, and a and b are constants. The equation was transformed to $\log(H) = b\log(D) + \log(a)$. The change in the height-diameter relationship was analyzed by comparing the b values in 2013 and 2006. An increased b value in 2013 compared to 2006 indicates that the tree stature became more tapered over the 8-year study period, while a decrease in the b value from 2006 to 2013 indicates that the tree form became more stunted. The transformed equation was also utilized to analyze height-diameter relationships for each species ($n > 29$) along the altitudinal gradient in 2006. The b values were compared among species and the six altitudes.

In addition to the above analysis, the height-diameter relationship for Erman’s birch at the treeline was investigated by piecewise-regression in order to identify the presence of one or more breakpoints where a noticeable shift in the progression (i.e., direction) of the relationship occurs. Data of H and DBH were fitted with a two-segment piecewise model to search for possible breakpoints, with the lowest residual mean squared error (MSE) serving as the criterion for the best model. The model [23,24] is represented as follows:

$$y = \beta_0 + [\beta_1 + \delta \times I(x - \varnothing)](x - \varnothing) + \epsilon \quad (1)$$

where y is height, x is diameter, and \varnothing is the breakpoint. $I(x < \varnothing)$ and $I(x > \varnothing)$ are essentially dummy variables. $I(x < \varnothing)$ is 1 if x is smaller than the breakpoint value, and $I(x < \varnothing)$ is 0 if x is larger than that value. $I(x > \varnothing)$ is 1 if x is larger the breakpoint value and $I(x > \varnothing)$ is 0 if x is smaller than that value. Thus, there are two sets of parameters being modeled, depending on the value of x . Data were analyzed and the figures were drawn in the software R (R Development Core Team, 2012) [25].

3. Results

3.1. Height and Diameter Growth of Treeline Birch

For 2723 birch in the treeline plots on Changbai Mountain, upright trees ($n = 1038$) accounted for the highest percentage (38.1%), while shrubby trees ($n = 886$) and saplings ($n = 799$) comprised 32.5% and 29.3%, respectively (Table 1). Treeline birch displayed dry mass accumulation for both height and diameter growth during the 2006–2013 period. From 2006 to 2013, the overall population of treeline birch displayed a mean ΔH of 0.56 m, mean ΔDBH of 1.2 cm, and mean ΔBD of 0.6 cm. There were significant differences in ΔH among tree form classes ($F = 37.85$, $p < 0.01$). ΔH for saplings (0.68 m) was significantly greater than that of shrubby and upright trees ($p < 0.001$), while ΔH of shrubby trees (0.56 m) was significantly greater than that of upright trees (0.48 m) ($p < 0.001$). With respect to ΔDBH , clear differences among tree form classes were detected, with the value for shrubby trees (1.3 cm) significantly greater than that of upright trees (1.2 cm) ($t = 3.87$, $p < 0.001$). For saplings, a significant increase in BD (+0.6 cm) was found from 2006 to 2013 ($t = -8.9$, $df = 326$, $p < 0.001$).

3.2. Stature Change in Treeline Birch from 2006 to 2013

For the population of birch in the treeline ecotone, the exponent b in the power equation increased slightly from 0.28 to 0.35 over the 8-year study period (Figure 2). The exponent increased for both upright and shrubby trees (Figure 3), while it decreased for saplings with BD. With respect to the overall population, the trend for saplings weakened the effect of the increase in b for the other two tree form classes. The b value for shrubby trees (0.31) exceeded that for upright trees (0.25) in 2006, while this trend disappeared in 2013 (0.34 for shrubby trees and 0.35 for upright trees). Meanwhile, saplings were the only class with a smaller b value in 2013 (0.18) than in 2006 (0.24). In addition, the breakpoints for the population level model in both 2006 and 2013 were located at $H = 2.25$ m (Figure 2).

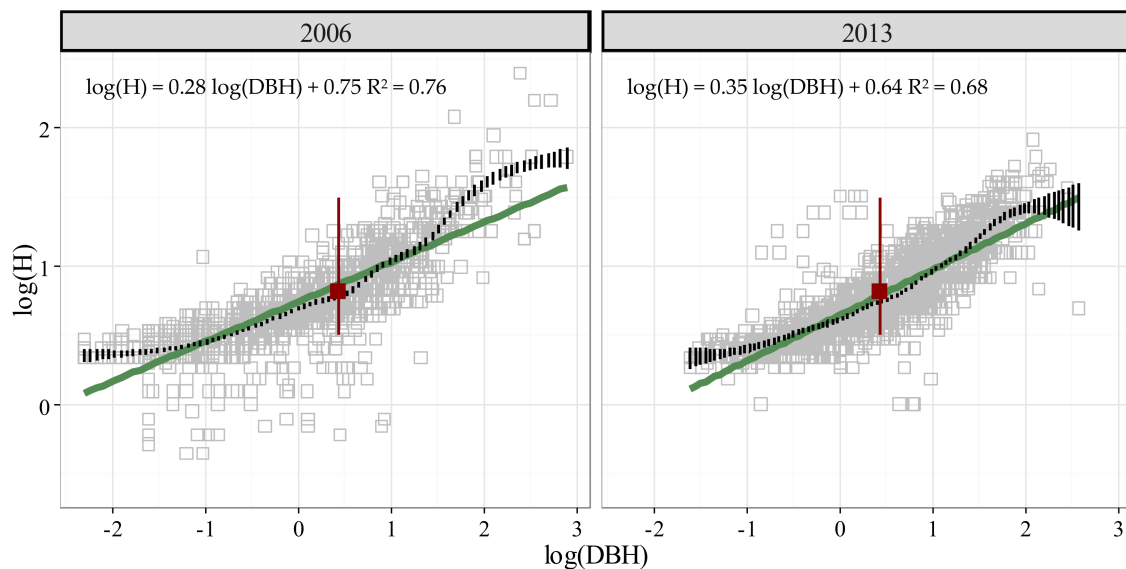


Figure 2. Stature change of treeline birch from 2006 to 2013. The value of b increased from 0.28 in 2006 to 0.35 in 2013, indicating that tree stature became more tapered. Green lines represent results fitted by the linear model; dotted black curves are smoothing splines. Breakpoints (dark red) were detected through the piece-wise regression method ($H = 2.25$ m for both years).

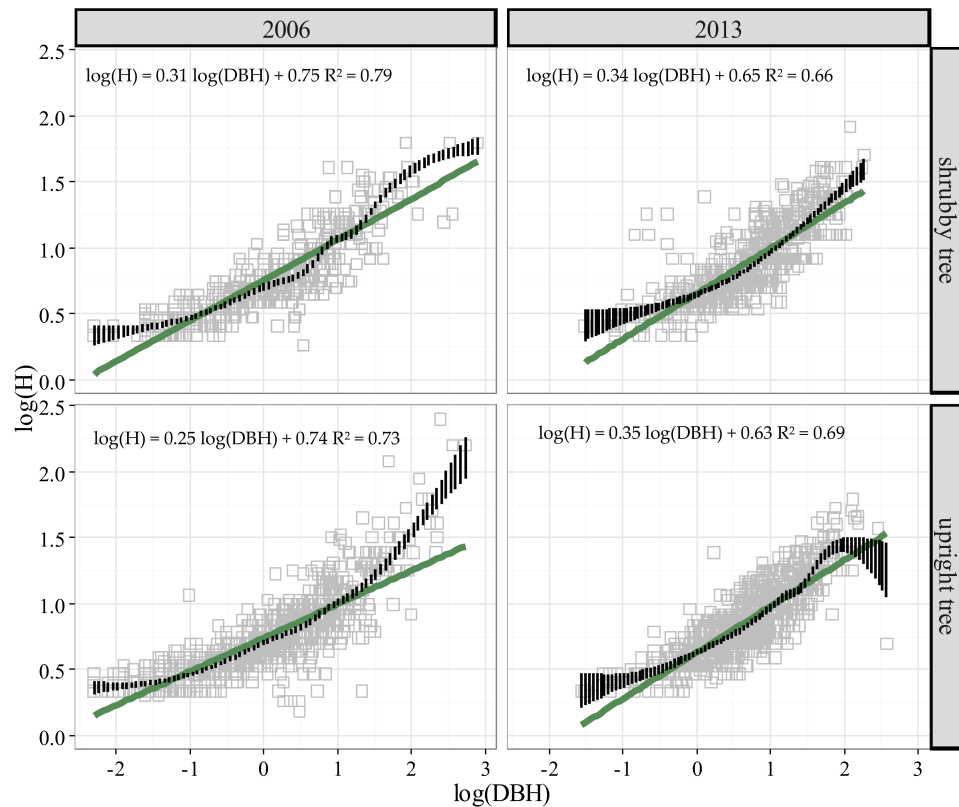


Figure 3. Stature change of upright and shrubby birch in the alpine treeline ecotone from 2006 to 2013. The value b of both shrubby (from 0.31 in 2006 to 0.34 in 2013) and upright birch (from 0.25 in 2006 to 0.35 in 2013) increased, indicating that tree stature of both growth forms became more tapered. Green lines represent results fitted by the linear model; dotted black curves are smoothing splines.

3.3. Change in Stature of Birch Along Altitudinal Gradients

Based on data collected in 2006, the exponent b in the power equation increased from 0.46 (1700 m a.s.l.), to 0.65 (1900 m a.s.l.) and 0.6 (1950 m a.s.l.), then dropped to 0.43 (2000 m a.s.l.), and ultimately to 0.31 at the treeline (Table 2).

Table 2. Tree stature parameters modelled by $\log(H) = b \log(D) + \log(a)$ for each species ($n \geq 29$) at each altitude *.

| Dataset | Altitude (m a.s.l.) | Species | n | Model Parameters | | R^2 |
|----------------|---------------------|---------------|-----|------------------|------|-------|
| | | | | $\log(a)$ | b | |
| Below treeline | 1700 | birch | 36 | 0.94 | 0.46 | 0.52 |
| | | fir | 165 | 0.08 | 0.81 | 0.89 |
| | 1750 | birch | 97 | 0.65 | 0.53 | 0.63 |
| | | spruce | 121 | 0.19 | 0.75 | 0.88 |
| | | larch | 29 | 0.62 | 0.57 | 0.85 |
| | | fir | 72 | 0.13 | 0.78 | 0.76 |
| | 1800 | birch | 80 | 0.75 | 0.53 | 0.69 |
| | 1900 | birch | 85 | 0.38 | 0.65 | 0.64 |
| | | larch | 47 | 0.33 | 0.67 | 0.58 |
| | 1950 | birch | 56 | 0.60 | 0.60 | 0.43 |
| Treeline ** | 2000 | birch | 39 | 0.89 | 0.43 | 0.48 |
| | >2000 | upright birch | 117 | 0.84 | 0.36 | 0.52 |
| | | shrubby birch | 248 | 0.93 | 0.30 | 0.63 |

* fir: *Abie sphenopholis*; larch: *Larix gmelinii*; birch: *Betula ermanii*; spruce: *Picea jezoensis*. ** To make treeline data comparable to the dataset for altitudes below the treeline, a subset of treeline data for trees taller than 3 m was utilized for calculations.

3.4. Allometric Height-Diameter Growth for Species at Different Altitudes

The four species reached their highest height and largest diameter at 1750–1800 m a.s.l. (Table 3, Figure 4). In addition, H/DBH differed between altitudes ($F = 29.8$, $p < 0.001$) and species ($F = 4.57$, $p = 0.03$). At 1700 m a.s.l., fir became the dominant species; the exponent b for birch was significantly smaller than that for fir ($0.46 < 0.81$). Above 1750 m a.s.l., birch and larch had similar b exponents (0.53 and 0.57, respectively), which were smaller than those of spruce and fir (0.75 and 0.78, respectively). Beyond 1900 m a.s.l., b values for larch (0.67) and birch (0.65) were similar (Table 2).

Table 3. Height and diameter of Erman's birch (*Betula ermanii*), fir (*Abies nephrolepis*), larch (*Larix gmelinii*), and spruce (*Picea jezoensis*) in 18 plots along an altitudinal gradient on the north slope of Changbai Mountain. a.s.l.: Above sea level.

| Altitude a.s.l. (m) | Species | Range of H (m) | Average H (m) | Average DBH (cm) | DBH/H | Number of Trees |
|---------------------|---------|----------------|---------------|------------------|-------|-----------------|
| 1700 | birch | 3–16 | 15.3 | 8.9 | 0.73 | 36 |
| | spruce | 3–15 | 14.1 | 8.1 | 0.66 | 9 |
| | fir | 2–18 | 11.1 | 7.5 | 0.75 | 165 |
| 1750 | larch | 4–17 | 35.8 | 14.1 | 0.45 | 29 |
| | birch | 3–23 | 19.9 | 9.6 | 0.59 | 97 |
| | spruce | 2–29 | 27.8 | 14.2 | 0.61 | 121 |
| | fir | 2–22 | 13.3 | 8.8 | 0.70 | 72 |
| 1800 | larch | 13–18 | 30.1 | 15.6 | 0.44 | 5 |
| | birch | 3–16 | 18.1 | 9.6 | 0.63 | 80 |
| | fir | 2.5–17 | 15.5 | 8.7 | 0.62 | 32 |
| 1900 | larch | 2–17 | 20.8 | 10.7 | 0.56 | 47 |
| | birch | 3–17 | 17.1 | 9.2 | 0.57 | 85 |
| 1950 | birch | 3–14 | 19.8 | 11.2 | 0.58 | 56 |
| 2000 | larch | 3–16 | 29.4 | 12.9 | 0.56 | 15 |
| | birch | 3–13 | 16.8 | 8.2 | 0.60 | 39 |

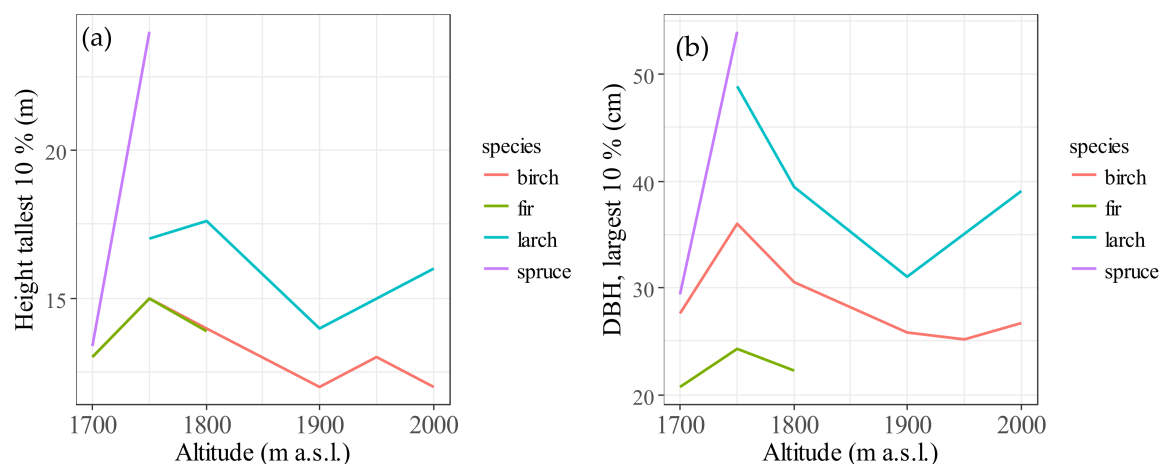


Figure 4. Height and DBH of the largest 10% of *Betula ermanii*, *Abies nephrolepis*, *Larix gmelinii*, and *Picea jezoensis* trees growing along an altitude gradient on Changbai Mountain: (a) height of the tallest 10% of trees for each species at each altitude; and (b) DBH of the 10% largest DBH-trees for each species at each altitude.

4. Discussion

4.1. Stature of Birch Growing Along an Altitudinal Gradient

In this study, the stature of birch on Changbai Mountain became more tapered as altitude increased from 1700 to 1900 m a.s.l., and then became severely stunted from 1900 to 2050 m a.s.l. (Table 2).

Thus, 1900 m a.s.l. could be regarded as an inflection point for stature change of Erman's birch growing along the altitudinal gradient on that slope of Changbai Mountain. Most trees were tapered around 1900 m a.s.l., which might suggest that this altitude is an extreme point for tapered growth. Beyond 1900 m a.s.l., trees become more stunted to create a more suitable microclimate in order to survive. The stature of multiple tree species in several prominent mountain ranges was also found to become dramatically stunted across a relatively small altitudinal range of only 50 to 100 m below the treeline [26,27]. These results suggest that tree stature change is much faster or even abrupt in the alpine treeline ecotone or close to the alpine treeline.

To better understand this pattern of tree stature change in the alpine ecotone, both local and global environmental factors should be considered. Each individual treeline possesses particular local environmental characteristics which may modify the overall trend for the vertical temperature lapse rate. The growing season (May–September) soil temperature at 10 cm depth is 10.2 °C at 1800 m a.s.l. and is 8.5 °C at 1900 m a.s.l. on Changbai Mountain (see Table S2 in Supplementary Materials). It has been reported that when soil temperature is lower than 5 °C, a very small reduction in soil temperature may lead to a dramatic increase in the time required for mitotic division of plant cells and a doubling in the time needed for cell reproduction [27]. Moreover, resource allocation from storage tissues to a tree's apical meristems (height growth) yields a relatively lower reward relative to xylem (radial growth) due to the longer transport pathway [28]. Therefore, an abrupt change in tree stature at a temperature threshold seems to be possible.

In addition to temperature, soil (depth, texture, and available water) may also play an important role in determining tree stature. Beyond 1900 m a.s.l. on the study slope, soil is 20–30 cm in depth with high content of volcanic float stone [29], and this kind of soil type has a low water-holding capacity [20], which may lead to periodic water shortage, especially in the top soil layer. For example, soil moisture was much lower at 10 cm soil depth than at 20 cm soil depth in the present study (see Figures S1 and S2 in Supplementary Materials). Thus, trees can be found to grow at micro-sites with deeper and more humid soil beyond the alpine treeline. Yu et al. [19,20] found that soil moisture combined with temperature significantly affected radial and shoot growth of Erman's birch in the same study sites. Influence of water supply on height-diameter relationships has also been reported previously [30–34]. Wind may also be an important factor affecting tree stature at high altitude on Changbai Mountain. Strong wind was found to severely influence the height-diameter trend along altitude [13,35,36] and to make trees more multi-stemmed and stunted at higher altitudes [37]. We do not have detailed wind data for our study sites, but the presence of flag-shaped and supine birches above 1800 m a.s.l. indicates strong wind at high altitude (see pictures in Figure S3 in Supplementary Materials). Moreover, wind-induced snow redistribution is an additional main driver of tree stature [8,38].

The stature of birch along altitudinal gradients of Changbai Mountain is modulated by temperature, soil depth and available water, wind speed, and snow depth. There is a high correlation between presence of birch saplings and winter snow depth associated with micro-topography (see pictures in Figures S4 and S5 in Supplementary Materials). Micro-topography creates not only temperature differences comparable to those between altitudes [4], but also differences in soil quality, snow cover, wind, etc. The effects of these entire environmental variables on tree stature are also reflected in the spatial distribution patterns of upright or shrubby tree forms. At the treeline on Changbai Mountain, shrubby birch trees are distributed more randomly and the upright trees occur more on protected micro-sites, suggesting that the shrubby birch trees have a stronger adaptive capability than the upright trees [9]. On the other hand, trees with a shrubby form may, in turn, create a microclimate to protect themselves from the harsh environment.

Our results show that Erman's birch might possess adaptive mechanisms for coping with adverse conditions as altitude increases. The plasticity of tree stature and variation in the stature of trees growing along a climatic gradient imply convergence of growth and survival strategies of trees in unfavorable environments [39–41]. In support of this notion, an experimental plantation study examining how conifer saplings of equal age and origin adapt to climatic gradients with increasing

altitude found that tree height declines as altitude increases toward the treeline, while stem diameter changes much less [2,14,42].

4.2. Species-Specific Height-Diameter Relationship

Compared to other dominant tree species growing at high altitudes on Changbai Mountain, the high plasticity and variation in stature of Erman's birch may be one of the main reasons why it is the only tree species found at the treeline. At 1750 m a.s.l. on Changbai Mountain, spruce and fir were found to have a higher b exponent (0.75 and 0.78, respectively) in the power equation than that of birch (0.53). At the same time, the b exponent of larch (0.57) was close to that of birch, meaning that larch maintained a stature status similar to that of birch (Table 2). With respect to H/D, values of larch ranged from 0.44 to 0.56, while those of the other species were higher: 0.57 to 0.73 for birch, 0.62 to 0.75 for fir, and 0.61 to 0.66 for spruce (Table 3). This result indicates that larch tends to maintain a more stunted tree stature than the other species, while birch displays high plasticity, as reflected in its wider H/D range.

As a widely distributed treeline family, Betulaceae species are predominant throughout cool regions of the Northern Hemisphere. Species with high stature plasticity are expected to adapt better to severe climate conditions [43]. Birch dominates mountain ecosystems limited by severe cold, partly because of its high plasticity of tree stature. In previous studies, *Betula nana* L., and other birch species (*Betula populifolia* Marsh., *Betula papyrifera* Marsh., *Betula alleghaniensis* Britt.) have been found to show a higher degree of plasticity than other species found at higher altitudes [44,45]. While larch with an upright tree form grew faster than birch, larch with a 'cushion' or more stunted form grew more slowly than birch [46]. In this way, at higher altitudes where both species have adapted by assuming a more stunted architecture, birch outcompeted larch because of the slightly inferior growth rate of the latter species. This can be explained by a difference in their woody anatomy—fast-growing species are recognized as having greater plasticity of stature. Larch is distributed over a wider altitudinal range than spruce and fir, and its saplings are able to survive at the treeline. Based on plasticity of tree stature in larch, which is similar to but relatively less than birch, larch may be expected to survive and develop at higher altitudes on the north slope of Changbai Mountain with global warming.

4.3. Stature Change of Birch at the Treeline over Time

Over the eight-year study period (2006–2013), the stature of both upright and shrubby trees became more tapered (upright trees displayed a larger exponent b than shrubby trees). Saplings, however, became stunted over time, as reflected in a smaller b value for the scaling exponent in the power equation (Figures 2 and 3). This indicates that stature change of treeline birch is size-specific. Previous research has shown that the susceptibility of the apical meristem to cold conditions is the underlying cause of height limitation [28]; however, once the low temperature limit is broken (i.e., climate conditions become warmer), shrubby forms with multiple meristems are expected to display more hysteresis than upright forms. Saplings may also be less sensitive to warmer air temperature, because they are constrained more by ground temperature.

Breakpoints in the height-diameter pattern detected in this study indicate the boundary for the interaction of the tree crown with ambient atmosphere, which may also explain why stature change differs among birch trees of different sizes associated with coupling or decoupling with the mesoclimate [14,42]. Three meters has conventionally been adopted as the height distinguishing shrub and tree growth forms (irrespective of branching pattern) [27]; this height ensures that a 'tree' has its crown closely coupled to prevailing atmospheric conditions. In this study, we found that a tree height of 2.25 m serves as the inflection point for the trend in the height-diameter relationship (Figure 2). Saplings smaller than 1.4 m allocate more biomass to diameter, while trees taller than 2.25 m allocate more biomass to height. Thus, the tipping point for the trajectory of the H/D relationship occurs in the range of 1.4 to 2.25 m. Li, Yang, and Kräuchi [14] proposed that altitude, along with micro-topography, began to significantly affect the growth of trees within the subalpine zone of Tyrol

(for species other than birch) only when trees exceeded a certain height (0.5 m), while trees taller than 3 m grow irrespective of micro-topography. Regardless of the exact values of tree height, the finding is that the effect of meso- or micro-climate on growth is tree size-dependent. Therefore, a changing climate (warmer or colder) will certainly lead to different degrees of stature change for different tree forms or tree sizes in the alpine treeline ecotone, with saplings allocating more carbon to radial growth, but trees allocating more carbon to height growth. This may be the case of trees growing in the alpine ecotone where individuals are often isolated from each other. On the other hand, however, plant (or tree) individuals growing in a community with dense neighbors would invest more carbon to height growth so that they can reach the canopy level to capture more light [2,13]. Hence, it is still needed to understand how trees at the alpine treeline ecotone adjust the trade-off or balance of carbon investment between height and diameter growth.

5. Conclusions

Tree stature reflects both environmental factors (temperature, soil depth, wind speed, and snow cover) and trees' adaptation to those factors. The stature of trees growing along an altitudinal gradient is, therefore, modulated by both altitude-related changes in temperature and other environmental factors. In the cold alpine treeline ecotone, birch stature changed with an inflection point at a tree height of ~2.25 m, beyond which trees invest more carbon or resource to height growth relative to radial growth, leading to tree stature with higher H/D. On the other hand, saplings and small trees up to ~1.4 m in height invest more carbon to diameter growth than to height growth, resulting in small H/D stature. These height data are comparable with results from the Alps, i.e., 2–3 m for trees proposed by Körner et al. (2012) [1] and 0.5 m for saplings proposed by Li et al. (2003) [14], although the exact tree height of the inflection point seemed to vary with species and regions. The higher stature plasticity of the treeline species birch than the other non-treeline species studied may be a mechanism that makes the treeline species resist and adapt to cold conditions, as well as survive and develop in the harsh alpine environment. These findings can help us to better understand the alpine treeline formation and dynamics in a changing world.

Supplementary Materials: The following are available online at www.mdpi.com/1999-4907/8/4/132/s1, Table S1: Monthly and annual mean canopy temperature (°C) for Erman's birch growing along an altitudinal gradient on the north-facing slope of Changbai Mountain. Table S2: Annual average soil temperature (10 cm-depth) and length of growing season. Figure S1: Soil volumetric water content (VWC %) in ten plots in the treeline ecotone ($n = 170$ samples) on the north slope of Changbai Mountain. Figure S2: Micro-site effects on soil volumetric water content (VWC %) in 10 cm and 20 cm depth along an altitudinal gradient on the north-facing slope of Changbai Mountain. Figure S3: Presence of flag-shaped and supine Erman's birches at 1800 m (a.s.l.) indicates high wind speed at this altitude. Figure S4: Distribution patterns of Erman's birch associated with snow cover in mid-winter (a) and micro-topography (b). Figure S5: Abundance of Erman's birch with different tree form classes in relation to soil properties (C—total carbon, N—total nitrogen, P—total phosphorus, C:N—the ratio of C to N, and N:P—the ratio of N to P) and snow depth, assessed with Redundancy Analysis (RDA). Abundance of saplings displayed a high correlation with snow depth.

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