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The Growth of Two Species of Subalpine Conifer Saplings in Response to Soil Warming and Inter-Competition in Mt. Gongga on the South-Eastern Fringe of the Qinghai-Tibetan Plateau, China

Hongtao Song[1*], Song Cheng[2], Yinsheng Zhang[1,3]

[1]Institute of Tibetan Plateau Research, Chinese Academy of Sciences (CAS), Beijing, China
[2]GeCheng Global Eco-Tech Inc., Columbus, OH, USA
[3]CAS Center for Excellence in Tibetan Plateau Earth Sciences, Beijing, China
Email: *songhongtao@itpcas.ac.cn

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Abstract

In conjunction with global climate change, soil temperatures have been recorded to be increasing more rapidly than air temperatures at Mt. Gongga, China. Plant density is also increasing, and a means of combining the effects of changes in soil temperature and competition on the growth and regeneration of the constructive coniferous species seedlings in the subalpine ecotones is needed. Thus, a split-plot design experiment was conducted with Sargent spruce (*Picea brachytyla*) and Purple cone spruce (*P. purpurea*) saplings, using four soil temperatures (control T_{soil} = 11.9˚C ± 0.3˚C, low T_{soil} = 13.4˚C ± 0.140˚C, intermediate T_{soil} = 15.4˚C ± 0.1˚C, high T_{soil} = 16.4˚C ± 0.2˚C) and three plant densities (one, two and three saplings per pot), in the subalpine ecotone. Soil temperatures were controlled through a cable heating system. After two growing seasons under the soil temperature treatments, 107 Sargent spruce saplings and 110 of the same-aged Purple cone spruce saplings were harvested. The results showed that Sargent spruce grew faster and with a greater biomass productivity than Purple cone spruce. Increased soil temperature significantly increased leaf biomass, branch biomass, above-ground biomass, and total plant biomass for developing crown architecture in Sargent spruce, whereas plant competition (*i.e.*, higher density) notably caused a decline in leaf biomass, branch biomass, and above-ground biomass. Purple cone spruce did not respond to either an increases in soil temperature or plant competition. Neither plant species was influenced by the interaction of soil temperature and plant competition. These

*Corresponding author.

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results suggest that Sargent spruce may expand the upper and lower limits of its distribution as global warming continues, but the expansion is likely to be restricted by plant competition in the future, including that from Purple cone spruce. Below-ground, fine root biomass does not change with soil warming although other sized roots do in both species. This signifies that light availability is more important in the acclimation of Sargent spruce to the changing environments than soil nutrient availability. Purple cone spruce is unaffected by the complex changing environment, suggesting that this spruce may stably grow and continue to thrive in the subalpine ecotone in future scenarios of climate change.

Keywords

Biomass Allocation, Soil Temperature, Plant Competition, Sargent Spruce, Purple Cone Spruce

1. Introduction

Increasing CO_2 and other greenhouse gases (CH_4 and N_2O) will lead to an increase of 1.5˚C - 4.5˚C in the mean global surface temperature by 2100 [1] [2]. Correspondingly, there will be an enhanced impact on soil temperatures, which are projected to increase by 1.9˚C - 3.38˚C by 2080, depending on the site location and horizon depth [2] [3]. High-elevation tree lines are expected to be particularly more sensitive to soil temperature [4]-[7].

Soil temperature is one of the key determinants of abiotic and biotic processes in the understanding of complex ecosystem dynamics under changing climate conditions in arctic-alpine regions [8] [9]. As one of the primary factors affecting plant growth and seedling establishment, soil temperature may be a better predictor of carbon assimilation than air temperature due to the small size and less daily and seasonal fluctuations compared with air temperature [10]-[13]. At the alpine/subalpine treeline, cold soil temperatures are one of the major factors that can limit seedling growth, which directly or indirectly influence the availability and absorption of nutrient and water uptake [14]-[16], root growth and respiration [17] [18], physiological activities [19]-[21], and eventually source-sink dynamics between roots and shoots [22], biomass production [2], and even carbon sequestration in future forest ecosystems [23] [24].

Tree recruitment and growth on alpine/subalpine ecotone have also been shown to be controlled by climate conditions [25] [26], and may be masked by interactions with other non-climatic biotic factors such as disturbance [27], plant-plant interactions [28] [29] or competition [18] [26] [30]-[32]. Seedling growth and survival are largely related to the competition conditions in forest and facilitation. Neighboring plants can limit seedling establishment through competition (commonly for light [33], space, or substrate [34]) to affect seedling regeneration and mortality across the alpine/subalpine ecotone [31] [35] [36]. Projected climate change is expected to result in modifications to tree density and natural disturbance regimes [37], and increasing in densities will result in higher competition among plants for resources such as light, increasing the difficulties of natural regeneration for all plant species [38]. However, competition among seedling individuals has been paid little attention [28] [39] [40], and the role of competition on seedlings under climate change condition would be decreased [41] or more pronounced [42] needs further investigation. On the other hand, no interactions between soil warming and competition are reported in these earlier studies on seedlings. It remains uncertain if and how these two environment factors changes will interact to influence different tree species in cold ecosystems in alpine and subalpine regions. Thus, region- and site-specific responses to the interaction of soil temperature and competition are needed to examine the growth and survival of seedlings as a result of global warming in forest ecosystems.

The objective of this study was to determine the effect of soil temperature and competition on the biomass allocation of Sargent spruce (*Piceabrachytyla*) and Purple cone spruce (*P. purpurea*), two dominant species in the subalpine coniferous forest in western Sichuan Province, China. Sargent spruce is a shade tolerant native *Picea* species in China, inhabiting altitudes ranging from 1500 - 3500 m. The purple cone spruce is rarer, and is distributed in China, Korea, and Siberia, at altitudes of 1500 - 2000 m [43]. The overlap in their altitudinal distribution shows that ecotone research with these two species could lead to insights into potential changes in community composition with climate change. The value of using ecotones for ecological research includes the following: identifying indicators of plant species responses to environmental gradients; understanding how species diversity is dependent on immigration (*i.e.*, sinks); identifying indicators of climatic change; and understanding the regulation of the spatial flux of species, matter and energy [44]. Even though it is known that the forests of subalpine ecotone regions will be sensitive to global climate change, relatively few studies have been conducted into the effect of increased soil temperature and how the two *Picea* species will grow and survive in the ecotone. Since 1988, *in situ* meteorological observations have shown that soil temperatures have increased at a higher rate (1.5˚C) than atmospheric temperatures (0.6˚C).

Given the importance of soil temperature and competition on forest dynamics, there is an obvious need to understand how changes in these two factors will affect future sapling regeneration. The present study attempted to address the following questions: (1) Is there an effect of species differences on biomass allocation and growth strategies in response to soil warming between seedlings of the two native coniferous species; (2) What are the combined effects of changes in soil temperature and competition on the two *Picea* species?

2. Material and Methods

2.1. Experimental Design

The experiment was performed at the Mt. Gongga Forest Ecology Research Station of the Institute of Mountain Hazards and Environment, Chinese Academy of Science. The station is located at an altitude of 3000 m in the Hailuogou scenic area of Mt. Gongga, Sichuan province (29˚34'40.89"N, 101˚55'23.91"E) (**Figure 1**). A soil temperature control system was installed in an experimental area beside the meteorological station, within which the natural soil temperature at 10 cm depth was automatically recorded every 10 minutes by a datalogger. The data were used to determine the controlled temperatures for the following experiment [45].

The experiment was a split-plot design with three soil temperature treatments (13.42, 15.45 and 16.42˚C for two growing seasons, respectively, with control of 11.97˚C), and three densities (1, 2 and 3 individual saplings per container). Soil temperature was regulated by a system consist of temperature control device, temperature sensors and heating cables (**Figure 2**) [45]. In the system, aboveground environment was natural, diurnal and monthly soil temperatures changed with changing air temperature (a more detailed description of the system is given by Cheng *et al*. [45]).

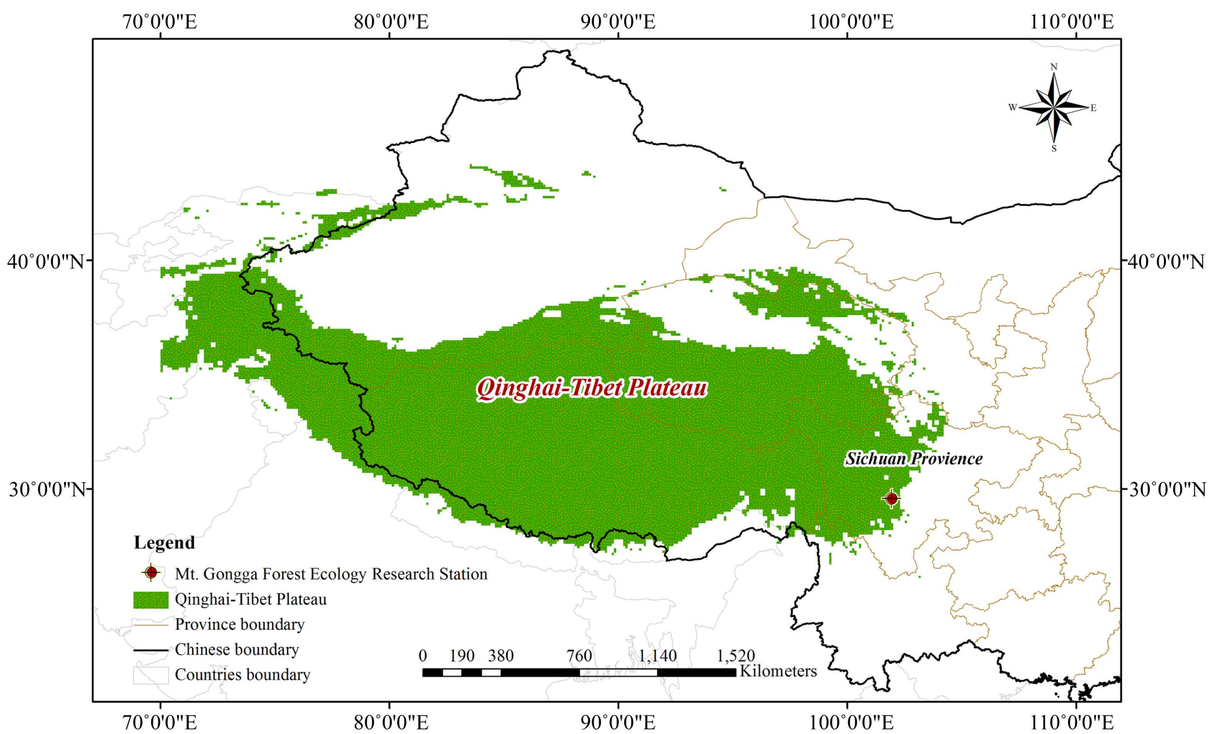

Figure 1. Location of the experiment site.

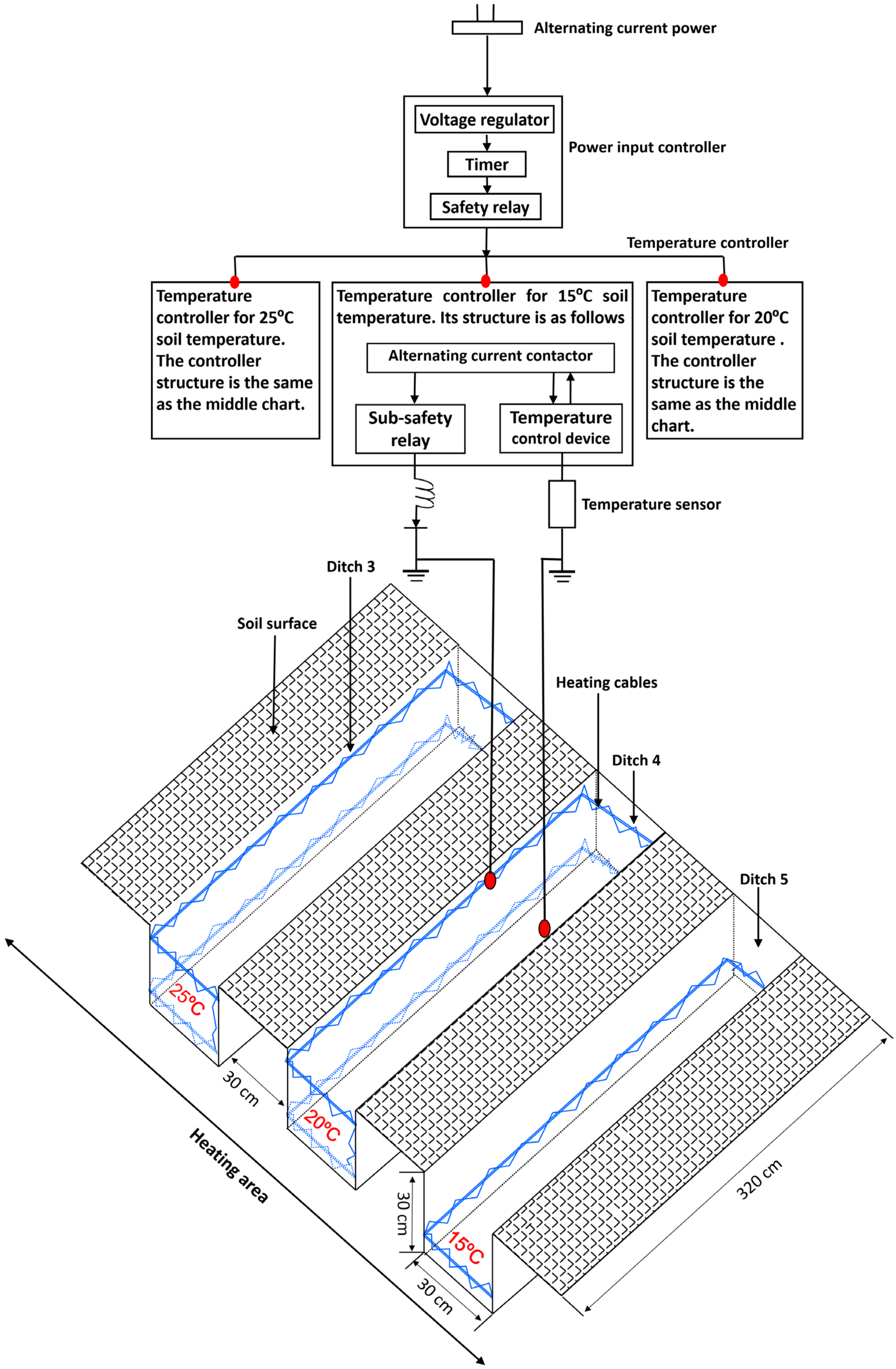

Figure 2. Structure of the soil temperature control system [45].

107 Sargent spruce and 110 purple cone spruce saplings of 4-years old, grown from seeds originating from a local orchard, were transplanted into each container(25 cm tall, 20 cm top diameter and 18 cm bottom diameter) with three densities (low = 1, intermediate = 2 and high = 3 individual saplings of the same species). The containers were filled with natural soil collected from the local coniferous forest and were made of heavy-duty plastic film, which enabled the efficient exchange of heat between the soil inside and outside of the container [45]. Each container had a hole in the bottom of it to facilitate the free drainage of irrigation water. Two containers of each of the three densities, of each species, were fixed to the bottom of each ditch randomly and uniformly and all of the ditches were filled with natural soil. The temperature control was automatically controlled by a time-control switch, which was turned on from seven am to seven pm every day during the growing season. Other saplings, with the same specifications, were placed near the nine experimental ditches as a control.

At the beginning of the experiment, the initial height and basal diameter of each sapling was measured. These growth traits were measured every month for two growing seasons. After this time, the sapling height and diameter had responded to the soil temperature, and the saplings were harvested. Daily and monthly soil temperature of control and three treatments were list in **Table 1**.

2.2. Plant Harvest and Measurements

Before harvest after two growing seasons, final heights and basal diameters were measured using a measuring tape and digital caliper. The saplings were then cut at the root collar, and the needles, branches and stems were separated. The roots were then split into small fine roots (≤2.0 mm in diameter), coarse-fine roots (2 mm < diameter ≤ 5 mm) and coarse roots (>5.0 mm in diameter) using a digital caliper. The fresh plant parts were weighed using a digital balance and the dry mass was also weighed after drying in an oven at 60˚C for at least 75 hours.

2.3. Data Analysis

All statistical tests were performed in SPSS 17.0 (SPSS Inc., Chicago, IL). One-way, two-way and three-way analyses of variance (ANOVA) were used to analyze the effects of species, soil temperature, plant competition and their interactions on sapling growth, with $p < 0.05$ being considered as significant. Test for normality and homogeneity of variance were verified to insure the data were parametric and ANOVA was an appropriate test. Initial height and initial basal diameter of saplings (as a continuous variable in the ANOVA) have previously been shown to significantly affect the growth of individual plant organs and whole plants [46]. Thus, both initial variables were used as covariates to remove their effects on the analyses.

3. Results

3.1. Effects of Soil Temperature on Biomass Allocation

As shown in **Figure 3**, the basal diameter and total plant, aboveground, leaf, branch and coarse root biomass of the seedlings were all significantly lower in the control than in the three temperature treatments, whereas there was no significant difference in the traits between the low, intermediate and high T_{soil} treatments (**Figures 3(B)-(E)**, **Figure 3(G)**, **Figure 3(K)**). The stem biomass of seedlings in the low and intermediate T_{soil} treatments was significantly higher than those in the control and high T_{soil} treatments (**Figure 3(F)**). The coarse-fine root biomass of plants in the high T_{soil} treatment was significantly higher than that in the plants of the control (**Figure 3(J)**). There was no significant difference between the total root biomass of the plants in the high T_{soil} treatment

Table 1. Ditch number and mean daily and monthly soil temperatures at 10 cm depth among the control, low, intermediate and high temperature treatments during the two growing seasons.

	Control ± S.E.	Low ± S.E.	Intermediate ± S.E.	High ± S.E.
Ditch number		2, 5, 8	1, 4, 7	3, 6, 9
Daily (˚C)	11.968 ± 0.254	13.425 ± 0.140	15.448 ± 0.140	16.422 ± 0.150
Monthly (˚C)	12.113 ± 1.038	13.480 ± 0.599	15.506 ± 0.599	16.513 ± 0.599

S.E. is the standard error. The definitions are the same as for other tables and figures.

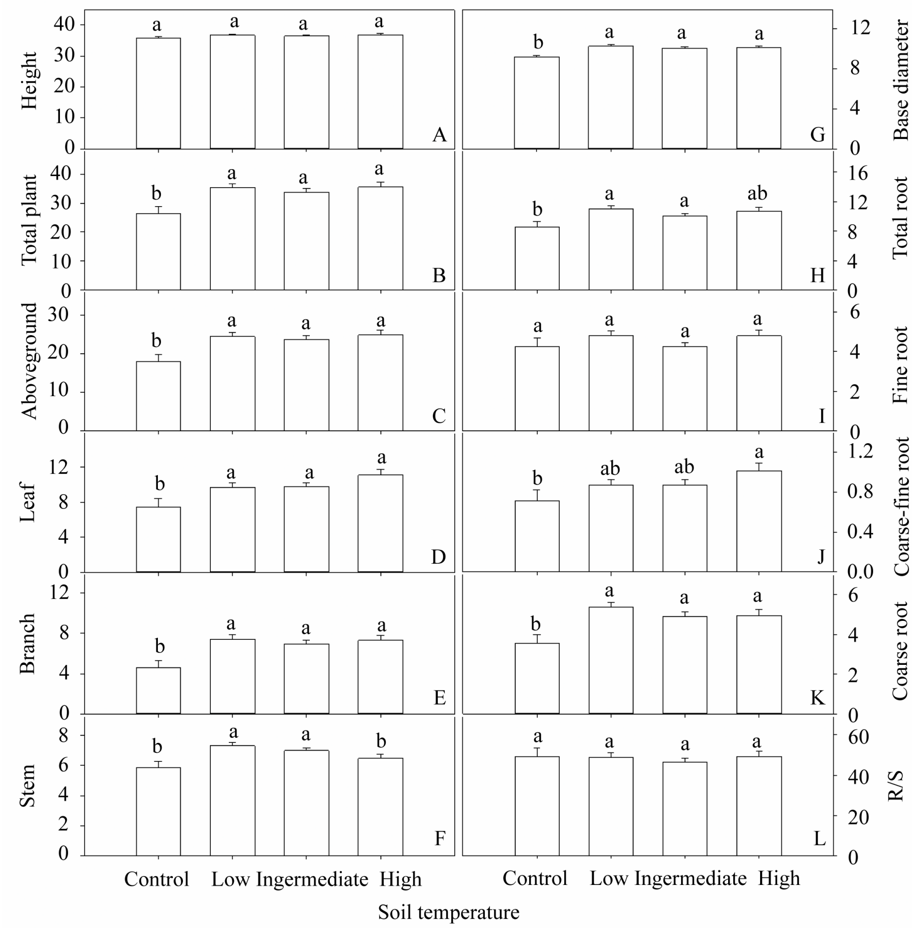

Figure 3. Single effect of soil temperature on the seedling biomass allocation in different parts.

and control, yet it was significantly lower in the aforementioned treatments compared with the low and intermediate T_{soil} treatments (**Figure 3(H)**). The seedling height (p = 0.217; **Figure 3(A)**), fine root biomass (p = 0.202; **Figure 3(I)**) and R/S ratio (p = 0.740; **Figure 3(L)**) in the plants among the four T_{soil} treatments were not significantly different.

3.2. Effects of Plant Competition on Biomass Allocation

In comparison to the two higher density treatments, as shown in **Figure 4**, the seedlings from the low density treatment had a significantly higher fine root biomass and almost all the aboveground variables, except stem biomass, were also significantly higher (**Figures 4(B)-(E)**, **Figure 4(H)**, **Figure 4(I)**). Stem biomass, coarse-fine root and coarse root biomass were not significantly different in plants within the high density treatment (three individuals) from those in the other two treatments; however, those traits in the low and intermediate density were significantly different from each other (**Figure 4(F)**, **Figure 4(J)**, **Figure 4(K)**). Sapling height (p = 0.248) and the R/S ratio (p = 0.926) did not differ between treatments (**Figure 4(A)**, **Figure 4(L)**).

3.3. Interactive Effects of Species and Temperature on Biomass Allocation

As shown in **Table 2**, the two-factor analysis of variance revealed that there were significant interactive effects of species and temperature on leaf biomass (p = 0.002), branch biomass (p = 0.026), aboveground biomass (p = 0.008), and total plant biomass (p = 0.009).

The total plant and aboveground biomass of the Sargent spruce plants in the low, intermediate and high T_{soil} treatments were always significantly higher than those in the control, and all the Purple cone spruce plants in all

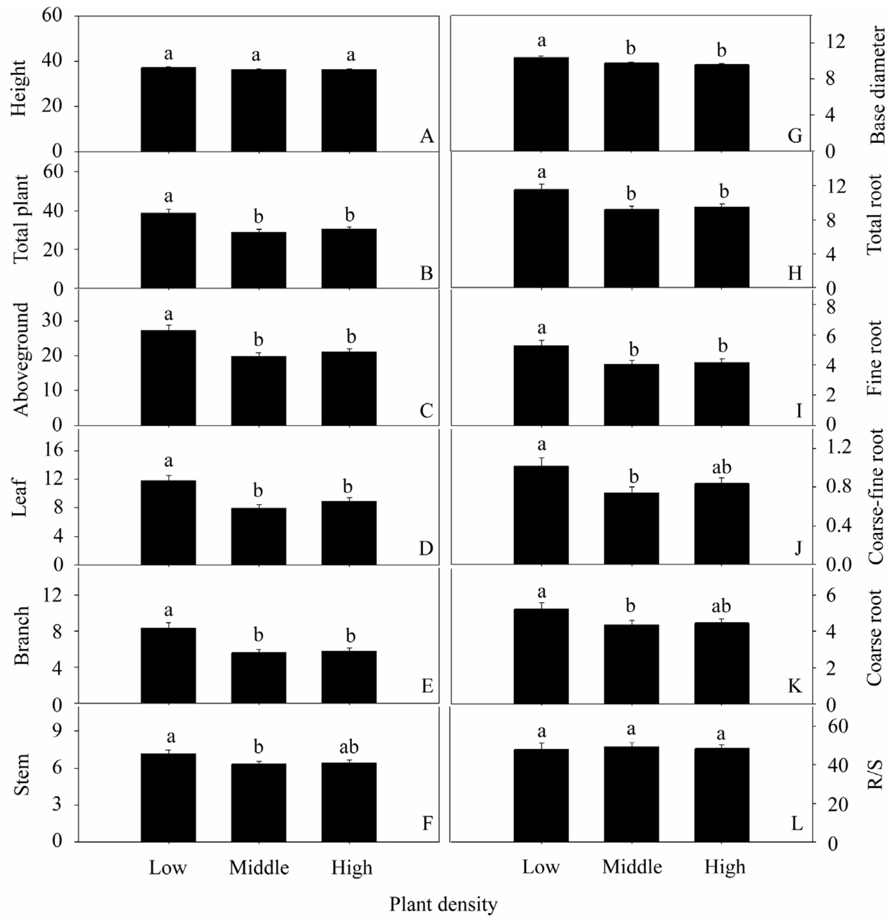

Figure 4. Single effect of competition on the seedling biomass allocation in different parts. Low, intermediate and high in density represent 1 or 2 or 3 saplings per pot.

Table 2. Analyses of covariance for the interactions of species (*S*), soil temperature (*T*) and Density (*D*) on height, basal diameter, total plant biomass, aboveground biomass, leaf biomass, branch biomass, stem biomass, total root biomass, fine root biomass, coarse-fine root biomass, coarse root biomass, and root to shoot ratios.

Source	*S* × *T*	*S* × *D*	*T* × *D*	*S* × *T* × *D*
	p	p	p	p
Height (cm)	0.282	0.308	0.692	0.453
Basel diameter(mm)	0.933	0.250	0.998	0.781
Total plant biomass(g)	**0.009****	**0.011***	0.793	0.458
Aboveground biomass (g)	**0.008****	**0.024***	0.751	0.386
Leaf biomass (g)	**0.002****	**0.032***	0.949	0.293
Branch biomass (g)	**0.026***	**0.001****	0.523	0.266
Stem biomass (g)	0.094	0.759	0.075	0.195
Total root biomass (g)	0.107	**0.008****	0.913	0.822
Fine root biomass (g)	0.088	**0.018***	0.759	0.409
Coarse-fine root biomass (g)	0.491	**0.039***	0.439	0.221
Coarse root biomass (g)	0.407	0.087	0.426	0.203
Root to shoot ratio (R/S) (%)	0.853	0.486	0.918	0.997

Initial height and initial basal diameter are as covariates to remove the effects of size on the data. p is the probability, the bold numbers with* and **indicate a significant difference at $p < 0.05$ and $p < 0.01$, respectively.

treatments. More specifically, the two traits did not significantly change in the Purple cone spruce plants in response to the increase in soil temperature (**Figure 5(A)**, **Figure 5(B)**).

In terms of leaf biomass, Sargent spruce seedlings in the low, intermediate and high T_{soil} treatments had significantly higher values (**Figure 5(C)**), with the increases in leaf biomass reaching 65.4, 82.1, and 109.2%, respectively, compared with the control. Furthermore, the leaf biomass of the Sargent spruce plants was significantly higher within the temperature treatments (except the control) than the leaf biomass of the Purple cone spruce plants. The leaf biomass of Purple cone spruce plants did not significantly change when the soil temperature increased from the control through to the highest T_{soil}.

The branch biomass of the Sargent spruce plants increased above that of the control and was the highest in the high T_{soil} treatment (**Figure 5(D)**); the increase in branch biomass of the Sargent spruce plants compared with the control temperature was 98.1, 100.5, and 108.6%, for the low, intermediate, and high T_{soil} treatments, respectively. The branch biomass of the Sargent spruce seedlings within the control was not significantly different from that of the Purple cone spruce plants in any treatment; further, there was no significant difference among temperature treatments for the Purple cone spruce plants.

In summary, for all the traits above, for the Sargent spruce, results for the control seedlings were always significantly below those for the three treatments with elevated temperatures (low, intermediate, and high). However, for the Purple cone spruce, temperature did not significantly affect the above traits.

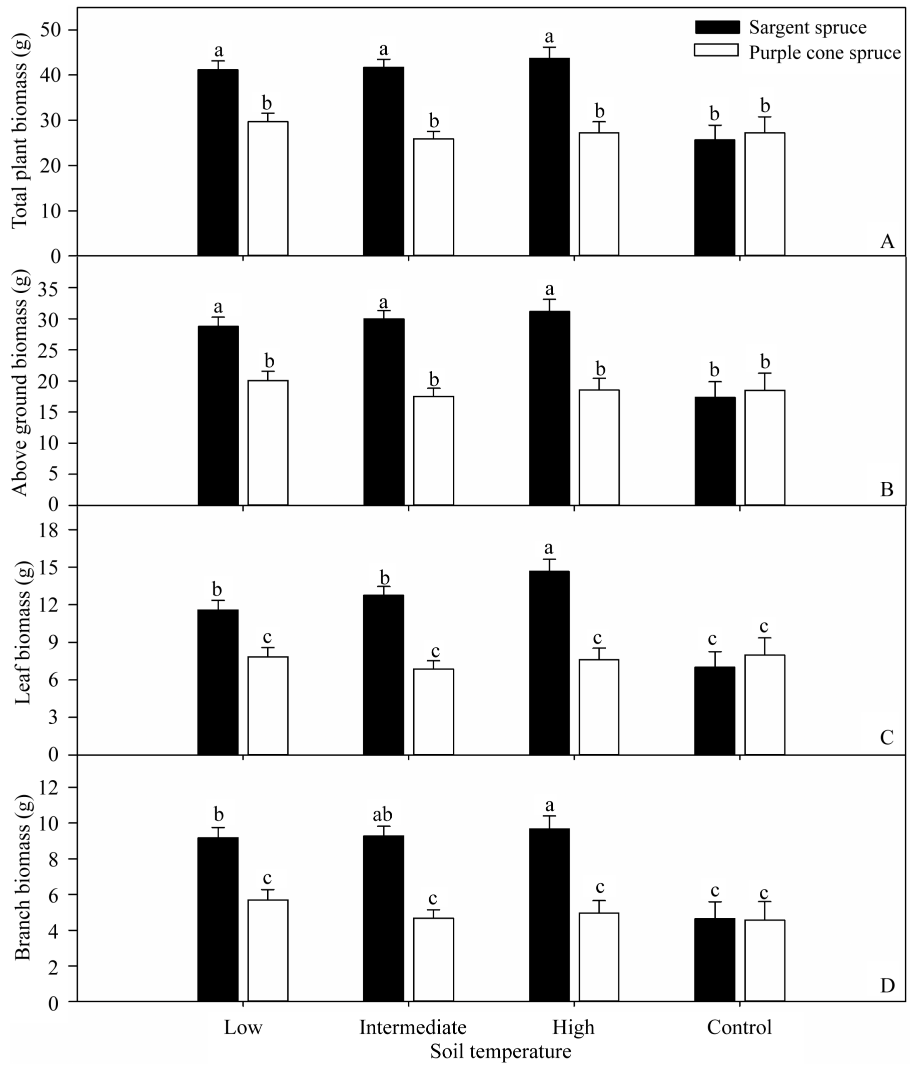

Figure 5. Interactive effects of species and temperature on total plant biomass (A), aboveground biomass (B) leaf biomass (C), and branch biomass (D). Different letters above the bars denote the significance level at $p < 0.05$.

3.4. Interactive Effects of Species and Competition on Biomass Allocation

As shown in **Table 2**, leaf, branch, aboveground, fine root, coarse-fine root, total root and total plant biomass all significantly changed because of the interactive effects of species and competition.

In terms of total plant biomass, Sargent spruce plants in the low density treatment had significantly higher total plant biomass, followed by the Sargent spruce high density group (by 35.3%) and then the Purple cone spruce plants in the intermediate and high density treatments (**Figure 6(A)**).

The Sargent spruce plants had the greatest leaf biomass in the low density treatment, which was significantly greater than both the high density treatment by 37.1% and intermediate density treatment by 69.8% (**Figure 6(C)**). The leaf biomass of the Sargent spruce plants in the intermediate density treatment was not significantly different from that of the Purple cone spruce plants at all density treatments. For the branch biomass and above-

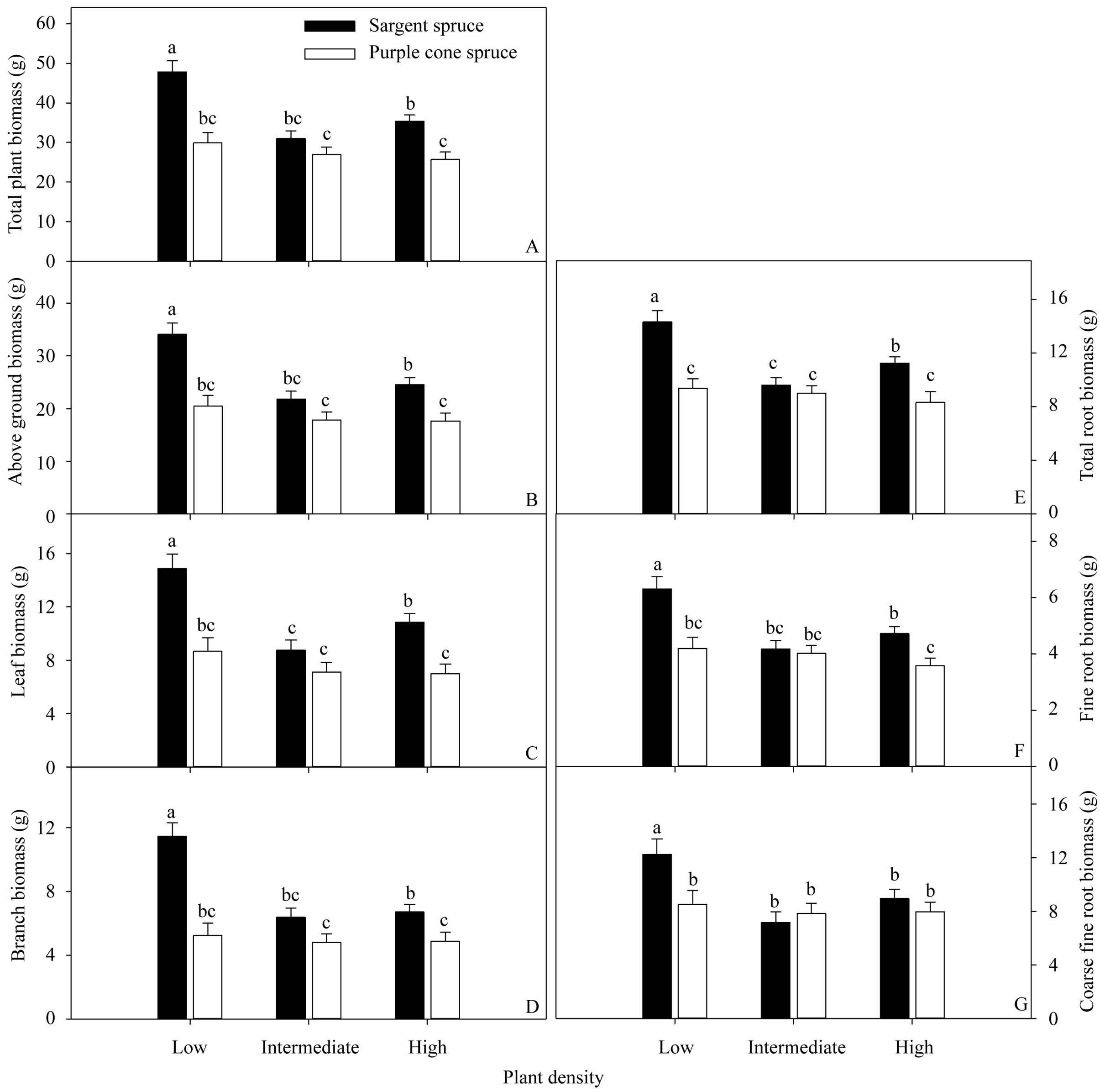

Figure 6. Interactive effect of species and competition on total plant biomass (A), aboveground biomass (B), leaf biomass (C), branch biomass (D), total root biomass (E), fine root (F), and coarse-fine root (G). Low, intermediate and high in densityre present 1 or 2 or 3 saplings per pot. The biomass values in different densities are averaged biomass of the saplings in each of the pots. Different letters above the bars denote the significance level at $p < 0.05$.

ground biomass traits, Sargent spruce plants in the low density treatment were significantly higher, followed by Sargent spruce plants in the high density treatment and then Purple cone spruce plants in the intermediate and high density treatments (**Figure 6(B)**, **Figure 6(D)**).

Sargent spruce in the low density treatment had the greatest total root biomass, followed by the Sargent spruce plants in the high density treatment by 27.2%, and then all the other groups (**Figure 6(E)**). Sargent spruce plants in the low density treatment had the highest fine root biomass, significantly higher than the species' plants in the high density treatment, which were in turn higher than the purple cone spruce plants in the high density treatment (**Figure 6(F)**). Sargent spruce plants in the low density treatment had the greatest coarse-fine root biomass; however, it was not significantly different in the other treatments of Sargent spruce plants and Purple cone spruce plants (**Figure 6(G)**).

In summary, for all the traits above, Sargent spruce plants in the low density treatment, *i.e.*, planted as one individual within one plot, had the highest growth results and were always significantly higher than any of the other interactive groups; whereas with the Purple cone spruce plants,there was no significant effect of competition.

3.5. Interactive Effects of Species, Temperature and Competition on Biomass Allocation

As shown in **Table 2**, no significant patterns were found with the three-way interaction between species, temperature, and competition, nor were there any significant interactions between temperature and competition alone.

4. Discussion

4.1. Enhanced Seedling Biomass after Two Growing Seasons of Soil Warming

Trees growing in treeline areas are indeed very sensitive to soil temperature [47]. Our results from a subarctic ecotone in northeastern Qinghai-Tibetan additionally demonstrate that such sensitivity has already been detected at the seedling stage. When analyzing the single temperature effect in detail within seedling species there was an increasing trend in both aboveground and belowground biomass allocation at increased soil temperatures compared with the natural cold temperature, which is in accordance with the theoretical pattern and earlier findings [20] [48]-[51]. Our single-factor results demonstrated that, net carbon assimilation strongly increased with soil temperature in the seedlings-soil system in this area under warming conditions, which suggests higher net rates of photosynthesis.

Our tree species-specific interaction results showed that the warming soil condition stimulated the total biomass production of Sargent spruce seedlings in this ecotone, and the increase in aboveground biomass was the primary contributing factor. For example, the increased soil temperature increased the leaf and branch biomass of Sargent spruce but had no significant effect on root biomass in any diameter class; this indicates that an increase in soil temperature stimulated above-ground growth to a relatively greater extent than root growth in Sargent spruce. This response agrees with the theoretical pattern proposed by McMicheal and Burke [52] and the response observed in other coniferous species, including: *Pseudotsuga menziesii*, *Abies amabilis*, *A. procera*, *P. contorta* and *P. ponderosa* [53]. In contrast to our studies, Domisch *et al*. [48] reported larger belowground biomass allocation under soil warming in *P. sylvestris* L. seedlings, whereas Pumpanen *et al*. [54] found 40% - 41% higher root growth responses in Norway spruce compared with the cold treatment. Weih and Karlsson [55] and Beckman [56] also suggested that a higher soil temperature may increase root growth of sub-arctic seedling more than the aboveground. Virjamo *et al*. [57] similarly found increased root to shoot biomass ratios in *P. abies* seedlings after warming. The extremely high temperatures of summer and the induced drier soil might explain the increased root to shoot ratio biomass in the above mentioned studies, and they suggest that increased soil respiration and rhizosphere respiration caused by high soil temperature also leads to increased root biomass [58] [59]. Increased root growth is related to strong a capability for water uptake in plants [60]; the high annual precipitation (range 1000 - 1900 mm) in our research area maintains the high soil humidity, which may explain the stable allocation of below-ground biomass under soil warming. Furthermore, the differences in the differential responses of above- and below-ground biomass to warming among different tree species, local spatial variability, and horizon depth should also be emphasized [61] [62]. Moreover, warming treatment differences, including warming amplitudes, time of duration, and underground warming depth should also be considered in evaluating the biomass allocation strategies under climate warming conditions.

The temperature × tree species interaction also showed that the biomass production of Sargent spruce was much more sensitive to soil temperature than that of Purple cone spruce. With the increase in soil temperature, there was no increase of biomass in any part of Purple cone spruce, compared with Sargent spruce. This means Sargent spruce, which is currently a faster growing and pioneer species that is characterized by rapid growth and a more shade-tolerant climax phase species after germination, can adapt to the warming subalpine growing conditions better than Purple cone spruce and may further increase the current differences in growth and biomass productivity or even continuously expand its altitudinal distribution in this ecotone under projected climate change scenarios. However, the actual effects of climate change on the growth and biomass of the two species may be more complex than those resulting from changes in soil temperature alone, because soil temperature may interact with other environmental variables to influence seedling growth [2]. Thus, field experiments *in vivo* are needed to verify the potential biomass changes under projected climate change scenarios.

4.2. Significant Reduction of Biomass Allocation Responses to High Interspecific Competition

In contrast to seedling response to soil warming, both above- and below-ground biomass showed a greater difference to elevated competition. Sargent spruce was much more sensitive to increasing density, and therefore competition, than Purple cone spruce. Low competition leads to relative high biomass allocation both in above- and below-round parts. The greater biomass allocation in leaf and branch in low competition suggests the importance of light acquisition for Sargent spruce seedling growth. Meanwhile, the increases in fine and coarse-fine root biomass were the primary contributing factors to the underground biomass increase in Sargent spruce seedlings, and not the coarse root for nutrients and water storage. This suggests that the strong competition may result in the underground limitation of resource absorption [63], and Sargent spruce saplings may exhibit growth limitation under competitive pressure; however, the effects differed depending on the part of the plant. This contrasted with hypothesis that as an intolerant species, the most serious limitations on the growth of Sargent spruce would occur under the high density treatment; this may be explained by an increase in the number of roots in association with a decrease in soil resource availability, because of a proportional increase in root competition experienced by the individual plants [64]. In summary, strong interspecific competition across this subalpine ecotone for resources and light among understory Sargent spruce may be important influences inhibiting seedling establishment and tree regeneration. All the above-mentioned differences were not observed in Purple cone spruce; this is in accordance with the known shade tolerance of this species [65]. In undergrowth with heavy shading, Sargent spruce tended to decrease its biomass allocation whereas Purple cone spruce showed no significant changes; a fact that might offset the dominant position of Sargent spruce and increase the regeneration opportunity of purple cone spruce, as an associated tree species under competition in the undergrowth community.

4.3. Neutralizing Effect of Interaction between Soil Warming and Interspecific Competition

The answer to our second question that we primarily attempted to address was quite surprising. The interaction of soil temperature and competition appeared to neutralize the factors' of individual effects on biomass allocation and productivity because no response of any part was found under this interaction. Changes in soil temperature and competition have significantly independent effects on seedlings biomass allocation; however, our results suggest that increased soil temperatures equalize these inter-specific growth differences and that the direct inter-specific competition limitations on growth processes do not control biomass responses to soil warming. Thus, under future climate conditions, increased soil temperature may, to a certain extent, compensate for the effects of competition in nutrients, water or light acquisition and decrease the effect of inter- and intra-specific differences in biomass productivity and the allocation of these two dominant subalpine species in this ecotone. Previous research results suggest that seedlings grow in treelinee cotones responded in a complicated and different fashion to the interactive environmental and biological effects [66] [67], and the lack of a positive soil warming interactive effect on seedling growth in our experiment was not simply because air was not simultaneously warmed; it remains uncertain whether such an interaction could have occurred if the entire system temperature had been increased. Furthermore, potential interactive effects maybe variable over longer timescales, such as altered nutrient availability, may not necessarily have been captured in our study. Understanding longer-term dynamics between inter-specific competition and soil warming remains as an important goal for global change research in different ecosystems.

Of course, soil temperature and competitive interactions among species do not represent a simple dichotomy but must be considered within a matrix of biological and physical interactions that are temporally dynamic. Although derived from one experimental site, the results point to a growth-density-controlled response to environmental change, with climate (soil warming) as an accompanying driver. This non-climatic drivers masking of an expected climate-driven seedling regeneration emphasizes the need to consider changes in alpine/subalpine ecotones along with climate change to avoid misleading interpretations of climate-driven treeline expansion.

5. Conclusion

Our research has important implications for understanding and managing the drivers of shifts in the treeline ecotones of Qinghai-Tibetan Plateau. Globally, treeline advance has been linked to recent global warming. However, changing competition condition may also play an important role in treeline advances. This study has shown that both the biomass productivity and growth of Sargent spruce saplings are significantly influenced by soil temperature and competition in northeastern Qinghai-Tibetan Plateau. Sargent's spruce tends to adapt to be a more dominant tree species in this ecotone under natural conditions and disturbances to density. The findings of this study emphasize that Sargent's spruce is likely to respond more positively to warming soil temperatures than Purple cone spruce as global warming continues, particularly above-ground for developing crown architecture; however, the former is more limited by competition than the latter, with increasing plant densities. It is expected that under future climate change, the differences in biomass productivity between these two species will be neutralized due to increases in grow densities and that the dominant position and the forest structure may change in the ecotone. Below-ground, fine root biomass does not change with soil warming; however, the other sized roots do in both species. This signified light availability is more important in the acclimation of Sargent spruce to changing environments than soil nutrient availability. The current research is based on the saplings of the tree species that do not represent the whole life history and growth of a species; therefore, further research should be performed to increase our understanding of these two species within the ecotone.

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