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Excessive Accumulation of Chinese Fir Litter Inhibits Its Own Seedling Emergence and Early Growth—A Greenhouse Perspective

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Abstract: Litter accumulation can strongly influence plants' natural regeneration via both physical and chemical mechanisms, but the relative influence of each mechanism on seedling establishment remains to be elucidated. Chinese fir (*Cunninghamia lanceolata*) is one of the most important commercial plantations in southern China, but its natural regeneration is poor, possibly due to its thick leaf litter accumulation. We used natural and plastic litter to study the effects of Chinese fir litter on its own seedling emergence and early growth, as well as to assess whether the effect is physical or chemical in nature. Results showed that high litter amount (800 g·m^{-2}) significantly reduced seedling emergence and the survival rate for both natural and plastic litter. Low litter amount (200 g·m^{-2}) exerted a slightly positive effect on root mass, leaf mass, and total mass, while high litter amount significantly inhibited root mass, leaf mass, and total mass for both natural and plastic litter. Root-mass ratio was significantly lower, and leaf-mass ratio was significantly greater under high litter cover than under control for both natural and plastic litter. Although the root/shoot ratio decreased with increasing litter amount, such effect was only significant for high litter treatment for both natural and plastic litter. Seedling robustness (aboveground biomass divided by seedling height) decreased with increasing litter amount, with high litter treatment generating the least robust seedlings. Because plastic and natural litter did not differ in their effects on seedling emergence and growth, the litter layer's short-term influence is primarily physical. These data indicated that as litter cover increased, the initial slightly positive effects on seedling emergence and early growth could shift to inhibitory effects. Furthermore, to penetrate the thick litter layer, Chinese fir seedlings allocated more resources towards stems and aboveground growth at the expense of their roots. This study provided experimental evidence of litter amount as a key ecological factor affecting seedling development and subsequent natural regeneration of Chinese fir.

Keywords: allelopathy; biomass allocation; forest regeneration; physical effects; plantation; plastic litter; robustness

1. Introduction

During the past decade, the focus of forest management has shifted from timber production to ecological functions [1–4]. Following this trend, one major aim of sustainable forest management is to convert forest plantations into naturally regenerating, and diverse ecosystems [5–8]. Natural regeneration is considered the backbone for sustainable forestry, and failure to establish natural regeneration hampers the efforts toward sustainable forest management [9,10]. Therefore, understanding the factors that control tree regeneration is a major research priority for forest managers worldwide [11,12].

The Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook.), an evergreen conifer, is one of the most important forest plantations in southern China, covering an area of over 12 million ha or about 6.5% of the world's plantation forests [13]. These forests are nutrient-poor, with shallow fertile soils [14]. Currently, the sustainability of Chinese fir plantations is threatened by biodiversity reduction, production loss, soil degradation, and a lack of self-regeneration, with the last being a particularly critical factor [14–20]. Although some Chinese fir plantations have reached reproductive maturity, very few fir seedlings or saplings are present beneath the understory, with only sparsely covered shrubs and herbs above a thick litter layer on the forest floor [14,19,20]. Thus, these plantations are ideal for, and would greatly benefit from, investigations on how to improve natural regeneration by influencing seedling emergence and growth. However, surprisingly few studies have addressed the ecological factors that influence tree regeneration in Chinese fir plantation.

In coniferous plantations, seedling emergence and early growth are the most vulnerable stages during natural regeneration [21]. Coniferous forests have low litter decomposition rates that make them prone to developing a thick needle layer below the canopy [22,23]. Thus, litter effects are especially important for seedling emergence and growth [14,24–26], given their ability to modify light, moisture, and microhabitat conditions (e.g., nutrient content, competition from established vegetation) [3,27–30]. Although litter can have both positive and negative effects on seedling emergence and growth [26,28,30–32], the extent highly depends on litter amount. Moderate litter cover may facilitate seedling emergence and early growth by attenuating extremes in moisture and temperature [26,33]. However, thick litter layers may inhibit seedlings emergence and growth through the reduction of light quantity and quality, leading to deep shade or total darkness [28,31]. Additionally, thick litter cover can produce more allelochemicals which hamper seedling growth or become an impenetrable physical barrier. This barrier prevents the cotyledon/radicle emergence and blocks seeds from reaching the soil [33–36]. By allocation of more energy toward hypocotyl growth and away from the radicle and cotyledons [36,37], plants' attempt to overcome this physical obstruction results in spindly, less sturdy seedlings with reduced ability to capture light, water, and nutrients [31].

Despite the presence of physical and chemical litter effects, only a few studies have attempted to separate the two [33,35,38–41]. For example, physical litter effects are generally stronger than chemical effects in grasslands [32,33,35,40,41]. The existing research also focuses on natural vegetation rather than plantations. Currently, studies examining litter effects on seedling emergence and growth have mainly focused on natural forests, old fields, grasslands, and riparian vegetation [24,34,41–44]. In Chinese fir plantations, few studies have examined the chemical effects on seedling emergence and growth [45,46] and to the best of our knowledge, no studies are available on the physical effects.

Thus, the objective of the present study is to determine how the chemical and physical properties of Chinese fir leaf litter separately affect the emergence and early growth of its own seedlings. Using a greenhouse experiment, we aimed to answer whether (1) the influence of physical effects is stronger than chemical effects; (2) seedling emergence and growth decline as leaf litter mass increases; and (3) increasing litter mass causes seedlings to allocate more resources toward stems and aboveground biomass than toward roots.

2. Materials and Methods

2.1. Collection of Leaf Litter and Seeds

Chinese fir seeds were obtained from a Chinese fir plantation in Xinkou National forest Farm (26°10′ N, 117°27′ E), Sanming City, Fujian, China. Seeds were collected from at least 10 individual trees in late November 2015, then manually cleaned, air-dried, sterilized, and stored at 4 °C until needed for sowing. Sterilization involved soaking for 30 min in a 0.5% potassium permanganate (K_2MnO_4) solution. Floating seeds were discarded, while seeds that sank immediately were considered viable. Only viable seeds with similar size (length: 4.41 mm, width: 0.85 mm, height: 6.06 mm) and shape (flat oval) were used in this study.

Freshly senesced leaves of Chinese fir were obtained from the same plantation during spring 2016 as spring is the peak litter-fall season for Chinese fir [47]. Leaves were rinsed with distilled water to remove dust particles, air-dried at ambient temperature, and stored in paper bags until needed. We did not use oven-drying because the process could induce chemical changes in the litter [26,33].

2.2. Greenhouse Experiments

We used a completely randomized experimental design with five replications to study the effect of litter amount (control, 0 $g \cdot m^{-2}$; low, 200 $g \cdot m^{-2}$; medium, 400 $g \cdot m^{-2}$; high, 800 $g \cdot m^{-2}$) and litter type (natural and plastic litter) on seedling emergence and growth. Litter amounts were selected to reflect natural fluctuations in the annual litter production of Chinese fir forests [48,49]. The two litter types comprised naturally sourced Chinese fir litter and plastic fibers (3–4 mm wide, 30–40 cm long) cut from a light brown, synthetic cloth (plastic fiber) to simulate the size, consistency, and shape of natural litter. This plastic litter was designed to solely examine the physical effects of litter, without confounding chemical effects (e.g., nutrients, allelopathic compounds, or pathogenic spores) [33,35].

The selection of plastic litter was based on a preliminary study which evaluated a range of materials as artificial litter. These materials included plastic [33,35,50,51], shade cloth [34,52,53], brown paper towels [54], and toothpicks [55]. Plastic fiber emerged as the best option to avoid any possibility of leachate contamination. They also had similar properties to natural litter, including specific gravity and consistency.

Litter experiments were conducted in a greenhouse of the Fujian Agriculture and Forestry University (26°04′ N, 119°14′ E). In early April 2016, 35 experimental pots (including five control plots; diameter: 18 cm, height: 20 cm) were filled with commercial sterilized potting soil; each was sown with 50 pre-treated seeds. Pots were then randomly divided into seven groups, receiving 0 $g \cdot m^{-2}$ (control), 200, 400 and 800 $g \cdot m^{-2}$ (corresponding to 0, 5, 10 and 20 g of litter per pot) of natural litter or plastic litter per pot on top of the soil. Regular watering cycles maintained optimal water availability, and pots were rotated weekly in the greenhouse to ensure homogeneous conditions for all seeds.

Seeds were considered to have emerged once their shoots penetrated through the litter surface and were exposed to light [26]. The seedling emergence rate was calculated for each pot as the number of seedlings that penetrated the litter surface divided by the total number of seeds planted in each pot (i.e., 50). Similarly, the seedling survival rate was calculated as the number of living seedlings per pot at the end of the experiment (i.e., 3 months post-sowing), divided by the total number of seeds planted in each pot (i.e., 50).

At the end of the experiment, all seedlings were removed and carefully washed. Five seedlings per pot were randomly selected and separated into roots, stem, and leaves. Total seedling height (up to the apical meristem) and stem length (distance between the stem base and the first true leaf) were measured. All plant parts were placed in paper bags and oven-dried at 75 °C for 48 h. Subsequently, stems, leaves, and roots were weighed separately. Root biomass was divided by aboveground biomass (i.e., stem + leaves) to obtain the root/shoot ratio. Seedling robustness (mg/cm) (an indicator of seedling sturdiness) was calculated as the aboveground biomass divided by seedling height [31,37].

2.3. Statistical Analysis

All statistical analyses were performed in SPSS version 24.0 for Windows (SPSS Inc., Chicago, IL, USA). All the variables were examined for normally distributed (one-sample Kolmogorov–Smirnov test, $p > 0.05$). The samples were presented as mean and standard error (SE) for different treatments. A two-factor ANOVA was conducted to examine the differences in seedling emergence, survival, root length, stem length, seedling height, root mass, stem mass, leaf mass, total mass, root-mass ratio, stem-mass ratio, leaf-mass ratio, root/shoot, and robustness between treatments. The two factors for the ANOVA were litter mass (control, low, medium, high) and litter type (natural and plastic). Tukey's tests were used for multiple comparisons of means within significant explanatory variables under the ANOVA. Significance was set at $p = 0.05$.

3. Results

3.1. Effect of Litter on Seed Emergence and Survival

Litter amount significantly affected the emergence rate and survival rate for both natural and plastic litter (Table 1). As litter cover increased, the seedling emergence rate and survival rate both decreased. Under high natural and plastic litter cover, the emergence rate decreased by 28.5% and 32.8%, respectively, while the survival rate decreased by 38.4% and 40.8%, compared with control (Figure 1A,B). The seedling emergence rate and survival rate did not differ between natural and plastic litter (Table 1; Figure 1A,B).

Table 1. Results of two-factor ANOVA examining the effects of litter amount, litter type, and their interaction on seedling emergence, survival rate, root length, stem length, seedling height, root mass, stem mass, leaf mass, total mass, root-mass ratio, stem-mass ratio, leaf-mass ratio, root/shoot ratio, and robustness.

Model	df	M.S.	F	*p*	Model	df	M.S.	F	*p*
Emergence					**Leaf mass**				
Amount	3	2252.37	49.99	0.000	Amount	3	1190.252	7.112	0.001
Type	1	84.100	1.870	0.181	Type	1	1.770	0.011	0.919
Amount × Type	3	12.100	0.270	0.848	Amount × Type	3	124.838	0.746	0.533
Survival					**Total mass**				
Amount	3	3470.53	76.69	0.000	Amount	3	2812.985	8.756	0.000
Type	1	67.60	1.490	0.231	Type	1	19.101	0.059	0.809
Amount × Type	3	15.60	0.350	0.793	Amount × Type	3	252.388	0.786	0.511
Root length					**Root-mass ratio**				
Amount	3	68.816	5.805	0.003	Amount	3	146.160	16.516	0.000
Type	1	2.973	0.251	0.620	Type	1	18.150	2.051	0.162
Amount × Type	3	1.434	0.121	0.947	Amount × Type	3	12.962	1.465	0.243
Stem length					**Stem-mass ratio**				
Amount	3	4.693	44.789	0.000	Amount	3	43.210	7.864	0.000
Type	1	0.021	0.201	0.657	Type	1	0.200	0.036	0.850
Amount × Type	3	0.056	0.535	0.662	Amount × Type	3	5.007	0.911	0.447
Seedling height					**Leaf-mass ratio**				
Amount	3	11.762	8.198	0.000	Amount	3	36.173	3.427	0.029
Type	1	0.065	0.046	0.832	Type	1	14.552	1.379	0.249
Amount ×Type	3	1.400	0.976	0.417	Amount ×Type	3	3.024	0.286	0.835
Root mass					**Root/shoot**				
Amount	3	317.197	12.928	0.000	Amount	3	0.039	16.697	0.000
Type	1	3.234	0.132	0.719	Type	1	0.004	1.608	0.214
Amount × Type	3	16.020	0.653	0.587	Amount × Type	3	0.002	1.034	0.391
Stem mass					**Robustness**				
Amount	3	4.833	2.301	0.097	Amount	3	22.473	24.392	0.000
Type	1	1.542	0.734	0.398	Type	1	0.521	0.565	0.458
Amount × Type	3	0.890	0.424	0.737	Amount × Type	3	0.438	0.476	0.702

Note: robustness (mg/cm) (an indicator of seedling sturdiness) was calculated as the aboveground biomass divided by seedling height.

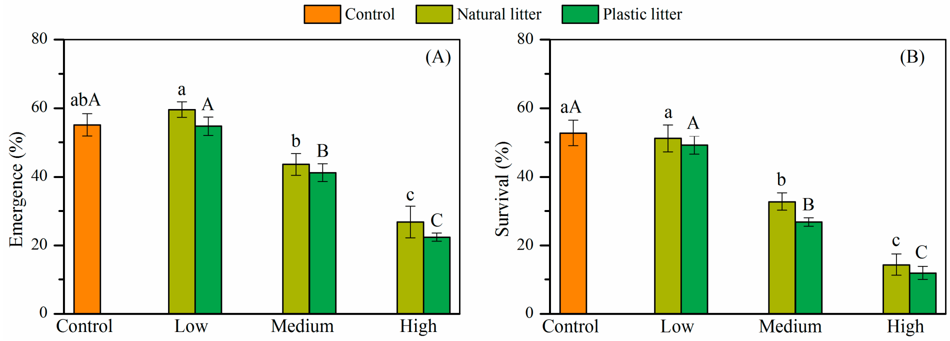

Figure 1. Effects of different litter treatments on the seedling emergence rate (**A**) and survival rate (**B**). Bars are means ± SE. Control (0 g·m^{-2}), low (200 g·m^{-2}), medium (400 g·m^{-2}) and high (800 g·m^{-2}) refer to litter amount. Bars with different lowercase letters represent significant differences across litter amount for natural litter (p < 0.05). Bars with different capital letters represent significant differences across litter amount for plastic litter (p < 0.05). Litter type and amount × type interaction did not significantly affect either variable.

3.2. Effect of Litter on Seedling Growth

Litter amount (for both natural and plastic litter) did not significantly alter root length compared with control (Figure 2A). However, seedlings under medium and high litter cover had significantly higher stem length than control (Figure 2B). Under high litter cover, stem length increases by 79.2% and 74.9% for natural and plastic litter, respectively, compared with control. Seedling height increased significantly only under high litter cover treatments for both natural and plastic litter (Figure 2C). In keeping with results for the seedling emergence survival rate, root length, stem length, and total seedling height did not differ between natural and plastic litter (Table 1; Figure 2A–C).

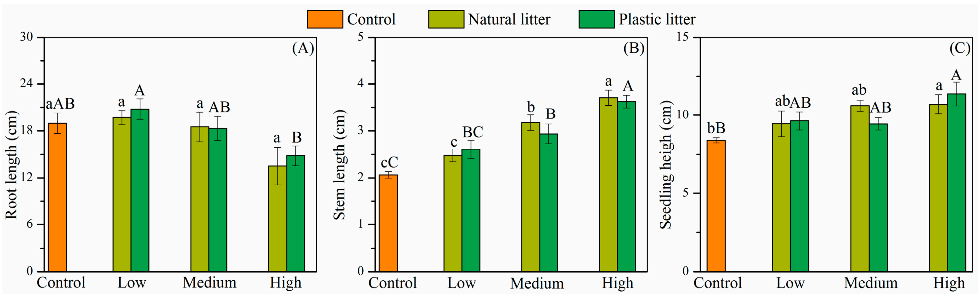

Figure 2. Effects of different litter treatments on root length (**A**), stem length (**B**), and seedling height (**C**). Control (0 g·m^{-2}), low (200 g·m^{-2}), medium (400 g·m^{-2}) and high (800 g·m^{-2}) refer to litter amount. Bars are means ± SE. Bars with different lowercase letters represent significant differences across litter amounts for natural litter (p < 0.05). Bars with different capital letters represent significant differences across litter amount for plastic litter (p < 0.05). Litter type and amount × type interaction did not significantly affect any variable.

3.3. Effect of Litter on Seedling Biomass and Biomass Allocation

Seedling root mass, leaf mass, and total mass were highest in low litter and lowest in high litter cover for both natural and plastic litter (Table 1; Figure 3A,C,D), but the differences in leaf mass and total mass across litter amounts were not significant with plastic litter cover. Litter amount did not significantly alter stem mass (Figure 3B). Litter type did not have a significant effect on any measured biomass variable (Table 1).

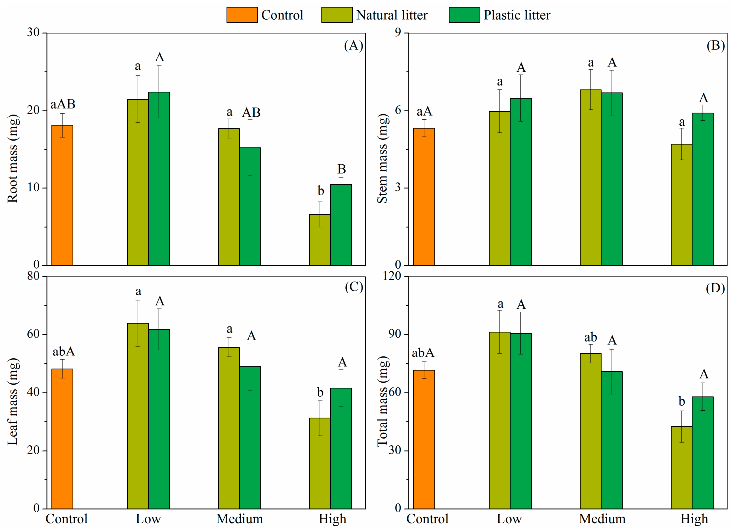

Figure 3. Effects of different litter treatments on root mass (**A**); stem mass (**B**); leaf mass (**C**); and total mass (**D**). Control (0 g·m^{-2}), low (200 g·m^{-2}), medium (400 g·m^{-2}) and high (800 g·m^{-2}) refer to litter amount. Bars are means ± SE. Bars with different lowercase letters represent significant difference across litter amount treatments for natural litter ($p < 0.05$). Bars with different capital letters represent significant difference across litter amount treatments for plastic litter ($p < 0.05$). Litter type and amount × type interaction did not significantly affect any variable.

Root mass ratio and root/shoot ratio were significantly lower under high litter cover, decreasing by 43.4% and 50.0% from control for natural litter, and by 26.9% and 32.4% for plastic litter, respectively, (Figure 4A,D). Stem-mass ratio and leaf-mass ratio increased significantly only under natural litter cover, but not in any plastic litter treatments (Figure 4B,C). Root-mass ratio, stem-mass ratio, leaf-mass ratio, and root/shoot ratio did not significantly differ between natural and plastic litter (Table 1).

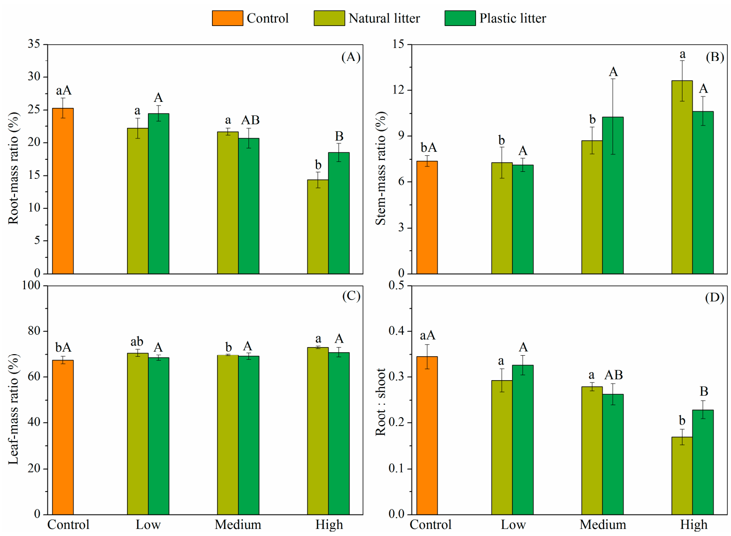

Figure 4. Effects of different litter treatments on root-mass ratio (**A**); stem-mass ratio (**B**); leaf-mass ratio (**C**); and root/shoot ratio (**D**). Control (0 g·m^{-2}), low (200 g·m^{-2}), medium (400 g·m^{-2}) and high (800 g·m^{-2}) refer to litter amount. Bars are means ± SE. Bars with different lowercase letters represent significant differences across litter amount for natural litter ($p < 0.05$). Bars with different capital letters represent significant differences across litter amount for plastic litter ($p < 0.05$). Litter type and amount × type interaction did not significantly affect any variable.

3.4. Effect of Litter on Robustness

Seedling robustness tended to decrease with increasing litter amount, but this decrease was only significant in high litter cover for both natural and plastic litter treatments (Figure 5). Seedling robustness, however, did not differ significantly between natural and plastic litter (Table 1).

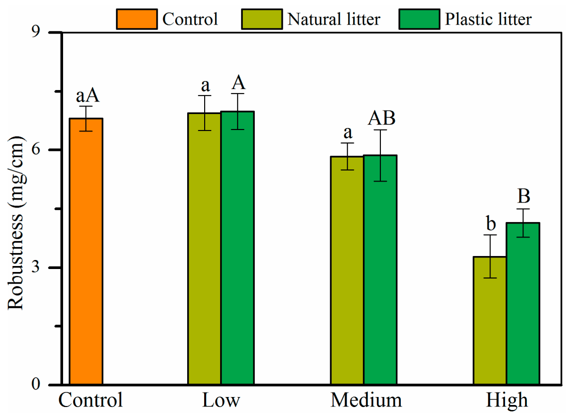

Figure 5. Effects of different litter treatments on seedling robustness. Control (0 g·m^{-2}), low (200 g·m^{-2}), medium (400 g·m^{-2}) and high (800 g·m^{-2}) refer to litter amount. Bars are means ± SE. Bars with different lowercase letters represent significant differences across litter amounts for natural litter ($p < 0.05$). Bars with different capital letters represent significant difference across litter amount for plastic litter ($p < 0.05$). Robustness (mg/cm) (an indicator of seedling sturdiness) was calculated as the aboveground biomass divided by seedling height. Litter type and amount × type interaction did not significantly affect seedling robustness.

4. Discussion

4.1. Physical versus Chemical Effects

Comparing the effects of artificial litter versus natural litter on seedling emergence and early growth allows us to separate the physical from chemical effects [33,35,50,51]. As plastic litter used in our study releases neither nutrients nor allelopathic compounds, its effect on seedlings should be entirely physical. In contrast, chemical (e.g., nutrient release) and biological (e.g., pathogens) effects only exist with natural litter [33,35]. We found that plastic and natural litters did not differ in their influence on Chinese fir seedling emergence and early growth, suggesting that the observed litter effects were primarily physical. These results are consistent with several previous studies showing that the short-term effects of litter tend to be physical rather than biological or chemical [32–35]. Thus, our findings suggest that the lack of Chinese fir seedlings under its own canopies in plantations may be partially explained by the inhibitory physical effects of its litter on seedling establishment. Such effects should be considered when designing restoration and management schemes for plantation systems.

4.2. Effects of Litter Amount on Seedling Emergence and Survival

Our experiment showed that while low litter cover (200 g·m^{-2}) slightly improved seedling emergence and survival rate, they were significantly inhibited by high litter cover (Figure 1). Our results are consistent with previous studies demonstrating that increasing litter depth reduces seedling emergence and survival rate [35,50]. Several possible explanations exist for this observation. First, the physical barrier under heavy litter cover may exhaust seed energy reserves before seedlings can break through to the litter's surface, leading to seedling death. Second, the horizontal orientation of seedling cotyledons may impede seedling ability to push upwards through the dense litter.

Third, light quantity and quality are reduced under high litter cover, resulting in a failure of photosynthesis to match the seedlings' respiration demand [33,34].

4.3. Effects of Litter Amount on Seedling Biomass Allocation and Robustness

As litter cover increased, root length tended to decrease (Figure 2A), while stem length and total seedling height increased (Figure 2B,C). This result suggests that stem elongation occurs at the expense of root development [36,37]. Several previous studies have also demonstrated that stem length is noticeably longer in seedlings emerging from greater depths [34,36]. Seedlings likely promote upward stem growth under increased litter cover to intercept light, as litter obstruction lowers near-surface light availability [37,56,57]. Our data on Chinese fir's resource allocation toward the stem instead of the root are similar to the documented behavior of *Rhus typhina* [37]. Although this morphological change allows seedlings to penetrate thick litter, some potential costs are associated with the shift in resource allocation, including reduced initial photosynthetic area and greater susceptibility to physical damage.

Resource allocation and use are essential plant activities that support growth and development [58,59]. In response to fluctuations in litter cover depth, seedlings face a trade-off between aboveground growth (for light interception) and root growth (for nutrient and water acquisition) [31,34]. Aboveground mass allocation is hypothesized to increase with increasing litter cover, so that vertical seedling growth can keep up with rising litter levels [31,34]. In our study, we found that as litter cover increased, root/shoot ratio and root-mass ratio decreased, in conjunction with an increase in the stem-mass ratio. Our results indicated that seedlings under high litter cover allocated a larger portion of their biomass to aboveground structures than seedlings under low litter cover. Likewise, shoot development is thought to be an efficient and adaptive strategy for seedlings under poor light conditions in deep litter [31,36,37], especially as root growth is hampered by poor photosynthetic conditions which limit photosynthate availability. Taken together, these survival strategies of Chinese fir are similar to those of *Celastrus orbiculatus* seedlings subjected to heavy litter cover [36]. The latter allocates more resources and energy aboveground, favoring rapid emergence from the litter cover and reinstatement of photosynthetic activity [36].

We also found that thick litter cover increased etiolation (elongation of stem and leaves under low light conditions) and therefore reduced seedling robustness (i.e., seedlings had weaker stems). The seedling height increase from etiolation was reflected in the greater allocation of biomass aboveground (Figure 4D). This morphological shift suggests a trade-off between longer, weaker stems that could reach a light source and shorter, stronger stems that may be more resistant to physical damage [31,36,37] (although the specific advantages of robust seedlings have not been demonstrated). Thus, our findings may have implications for population survival and recruitment in Chinese fir plantation forests.

5. Conclusions

Overall, we conclude that Chinese fir litter exerts a strong physical effect on its own seedling emergence and early growth. While litter cover was mildly beneficial to seedling emergence and survival at low levels, it became detrimental at high levels. In response to high litter cover, Chinese fir seedlings allocated more resources to aboveground biomass than belowground biomass. This shift in resources may help to spur subsequent growth from beneath a dense forest floor.

Because our experiment was conducted under controlled conditions, we cannot fully extrapolate our results to the field. Heat, water, and light are likely to fluctuate more under field conditions than in the greenhouse experiment, raising the possibility that litter may play a more beneficial role in facilitating seedling emergence and growth. At the same time, other negative effects of litter on seedling emergence (e.g., harboring pathogens and predators) are also likely to be more prevalent under field conditions. Therefore, longer-term field studies are necessary to fully understand the complex environmental interactions that may affect the survival threshold of plants experiencing heavy litter cover in forest plantation ecosystems. Nonetheless, our findings suggest that physical litter effects at least partially explain the low numbers of Chinese fir seedlings under their own canopies. Given the importance of litter effects, restoration and management schemes in plantations should consider the effects of litter on natural regeneration, especially when litter reduction is an objective.

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Author Contributions: Bo Liu and Zhengning Wang designed the experiments, analyzed the data and drafted the manuscript. Yanjuan Li, Qingqing Liu and Chong Zhao assisted with data collection. Stefani Daryanto and Lixin Wang edited the English version of the manuscript. All the authors contributed to the writing of the manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Aubin, I.; Messier, C.; Bouchard, A. Can plantation develop understory biological and physical attributes of naturally regenerated forests? *Biol. Conserv.* **2008**, *141*, 2461–2476. [CrossRef]
2. Manson, D.G.; Schmidt, S.; Bristow, M.; Erskine, P.D.; Vanclay, J.K. Species-site matching in mixed species plantations of native trees in tropical Australia. *Agrofor. Syst.* **2013**, *87*, 233–250. [CrossRef]
3. Chazdon, R.L.; Guarlguata, M.R. Natural regeneration as a tool for large-scale forest restoration in the tropics: Prospects and challenges. *Biotropica* **2016**, *48*, 716–730. [CrossRef]
4. Zhang, C.L.; Li, X.W.; Chen, Y.Q.; Zhao, J.; Wan, S.Z.; Lin, Y.B.; Fu, S.L. Effects of Eucalyptus litter and roots on the establishment of native tree species in Eucalyptus plantations in South China. *For. Ecol. Manag.* **2016**, *375*, 76–83. [CrossRef]
5. Li, W.H. Degradation and restoration of forests ecosystems in China. *For. Ecol. Manag.* **2004**, *201*, 33–41. [CrossRef]
6. Rodriguez-Loinaz, G.; Amezaga, I.; Onaindia, M. Use of native species to improve carbon sequestration and contribute towards solving the environmental problems of the timberlands in Biscay, Northern Spain. *J. Environ. Manag.* **2013**, *120*, 18–26. [CrossRef] [PubMed]
7. Robert, H. Conservation through intensification? The effects of plantations on natural forests. *Ecol. Econ.* **2014**, *105*, 204–210. [CrossRef]
8. Pirard, R.; Secco, L.D.; Warman, R. Do timber plantations contribute to forest conservation? *Environ. Sci. Policy* **2016**, *57*, 122–130. [CrossRef]
9. Wang, J.; Ren, H.; Yang, L.; Li, D.; Guo, Q. Soil seed banks in four 22-year-old plantations in South China: Implications for restoration. *For. Ecol. Manag.* **2009**, *258*, 2000–2006. [CrossRef]
10. Bertacchi, M.I.F.; Amazonas, N.T.; Brancalion, P.H.S.; Brondani, G.E.; de Oliveira, A.C.S.; de Pascoa, M.A.R.; Rodrigues, R.R. Establishment of tree seedlings in the understory of restoration plantations: Natural regeneration and enrichment plantings. *Restor. Ecol.* **2016**, *24*, 100–108. [CrossRef]
11. Carnevale, N.J.; Montagnini, F. Facilitating regeneration of secondary forests with the use of mixed and pure plantations of indigenous tree species. *For. Ecol. Manag.* **2002**, *163*, 217–227. [CrossRef]
12. Dupuy, J.M.; Chazdon, R.L. Interacting effects of canopy gap, understory vegetation and leaf litter on tree seedling recruitment and composition in tropical secondary forests. *For. Ecol. Manag.* **2008**, *255*, 3716–3725. [CrossRef]
13. Hu, Z.H.; He, Z.M.; Huang, Z.Q.; Fan, S.H.; Yu, Z.P.; Wang, M.H.; Zhou, X.H.; Fang, C.M. Effects of harvest residue management on soil carbon and nitrogen processes in a Chinese fir plantation. *For. Ecol. Manag.* **2014**, *326*, 163–170. [CrossRef]
14. Chen, C.Y.; Liao, L.P.; Wang, S.L. *Ecology of Chinese Fir Plantation Forest*; China Science Publishing House: Beijing, China, 2000.
15. Yang, Y.S.; Guo, J.F.; Chen, G.S.; Lin, P. Litterfall, nutrient return, and leaf-litter decomposition in four plantations compared with a natural forest in subtropical China. *Ann. For. Sci.* **2004**, *61*, 465–476. [CrossRef]

16. Bi, J.; Blanco, J.A.; Seely, B.; Kimmins, J.P.; Ding, Y.; Welham, C. Yield decline in Chinese fir plantations: A simulation investigation with implications for model complexity. Can. *J. For. Res.* **2007**, *37*, 1615–1630. [CrossRef]
17. Ma, X.Q.; Heal, K.V.; Liu, A.Q.; Jarvis, P.G. Nutrient cycling and distribution in different-aged plantations of Chinese fir in southern China. *For. Ecol. Manag.* **2007**, *243*, 61–74. [CrossRef]
18. Chen, L.C.; Wang, S.L.; Wang, P.; Kong, C.H. Autoinhibition and soil allelochemical (cyclic dipeptide) levels in replanted Chinese fir (*Cunninghamia lanceolata*) plantations. *Plant Soil* **2014**, *374*, 793–801. [CrossRef]
19. Zhu, N.H.; Yao, J.Y.; Zhou, G.Y.; Li, J.X.; Li, C.; Jing, M.Q.; Zhao, S.M. Study on natural vegetation regeneration from over maturity plantation of Chinese fir. *J. Cent. South Univ. For. Technol.* **2011**, *31*, 106–110. [CrossRef]
20. Luo, J.; Tian, Y.X.; Zhou, X.L.; Chen, J.H.; Zeng, Z.Q.; Li, X.Q.; Yao, M. Studies on the characteristics of soil seed banks under main forest types of close-to-nature forest management in Hunan. *J. Cent. South Univ. For. Technol.* **2014**, *34*, 56–61. [CrossRef]
21. Walck, J.L.; Hidayati, S.N.; Dixon, K.W.; Thompson, K.; Poschlod, P. Climate change and plant regeneration from seed. *Glob. Chang. Biol.* **2011**, *17*, 2145–2161. [CrossRef]
22. Wang, Q.K.; Wang, S.L.; Fan, B.; Yu, X.J. Litter production, leaf litter decomposition and nutrient return in *Cunninghamia lanceolata* plantations in south China: Effect of planting conifers with broadleaved species. *Plant Soil* **2007**, *297*, 201–211. [CrossRef]
23. Wang, Q.K.; Wang, S.L.; Xu, G.B.; Fan, B. Conversion of secondary broadleaved forest into Chinese fir plantation alters litter production and potential nutrient returns. *Plant Ecol.* **2010**, *209*, 269–278. [CrossRef]
24. Facelli, J.M. Multiple indirect effects of plant litter affect the establishment of woody seedlings in old fields. *Ecology* **1994**, *75*, 1727–1735. [CrossRef]
25. Nakamura, T. Ecological relationship between seedling emergence and litter cover in the earliest stage of plant succession on sandy soil. *Ecol. Res.* **1996**, *11*, 105–110. [CrossRef]
26. Eckstein, R.L.; Donath, T.W. Interactions between litter and water availability affect seedling emergence in four familial pairs of floodplain species. *J. Ecol.* **2005**, *93*, 807–816. [CrossRef]
27. Puhlick, J.J.; Laughlin, D.C.; Moore, M.M. Factors influencing ponderosa pine regeneration in the southwestern USA. *For. Ecol. Manag.* **2012**, *264*, 10–19. [CrossRef]
28. Loydi, A.; Donath, T.W.; Otte, A.; Eckstein, R.L. Negative and positive interactions among plants: Effects of competitors and litter on seedling emergence and growth of forest and grassland species. *Plant Soil* **2015**, *17*, 667–675. [CrossRef] [PubMed]
29. Fernandes, P.; Antunes, C.; Pinho, P.; Máguas, C.; Correia, O. Natural regeneration of *Pinus pinaster*, and *Eucalyptus globulus*, from plantation into adjacent natural habitats. *For. Ecol. Manag.* **2016**, *378*, 91–102. [CrossRef]
30. Zhang, R.; Hu, X.; Baskin, J.M.; Baskin, C.C.; Wang, Y. Effects of litter on seedling emergence and seed persistence of three common species on the Loess Plateau in Northwestern China. Front. *Plant Sci.* **2017**, *8*, 103. [CrossRef] [PubMed]
31. Kostel-Hughes, F.; Young, T.P.; Wehr, J.D. Effects of leaf litter depth on the emergence and seedling growth of deciduous forest tree species in relation to seed size. *J. Torrey Bot. Soc.* **2005**, *132*, 50–61. [CrossRef]
32. Quddus, M.S.; Bellairs, S.M.; Wurm, P.A.S. *Acacia holosericea* (Fabaceae) litter has allelopathic and physical effects on mission grass (*Cenchrus pedicellatus* and *C. polystachios*) (Poaceae) seedling establishment. *Aust. J. Bot.* **2014**, *62*, 189–195. [CrossRef]
33. Rotundo, J.L.; Aguiar, M.R. Litter effects on plant regeneration in arid lands: A complex balance between seed retention, seed longevity and soil–seed contact. *J. Ecol.* **2005**, *93*, 829–838. [CrossRef]
34. Donath, T.W.; Eckstein, R.L. Grass and oak litter exert different effects on seedling emergence of herbaceous perennials from grasslands and woodlands. *J. Ecol.* **2008**, *96*, 272–280. [CrossRef]
35. Ruprecht, E.; Józsa, J.; Ölvedi, T.B.; Simon, J. Differential effects of several "litter" types on the germination of dry grassland species. *J. Veg. Sci.* **2010**, *21*, 1069–1081. [CrossRef]
36. Ellsworth, J.W.; Harrington, R.A.; Fownes, J.H. Seedling emergence, growth, and allocation of Oriental bittersweet: Effects of seed input, seed bank, and forest floor litter. *For. Ecol. Manag.* **2004**, *190*, 255–264. [CrossRef]
37. Peterson, C.J.; Facelli, J.M. Contrasting germination and seedling growth of *Betula alleghaniensis* and *Rhus typhina* subjected to various amounts and types of plant litter. *Am. J. Bot.* **1992**, *79*, 1209–1216. [CrossRef]

38. Bosy, J.T.; Reader, R.J. Mechanisms underlying the suppression of forb seedling emergence by grass (*Poa pratensis*) litter. *Funct. Ecol.* **1995**, *9*, 635–639. [CrossRef]
39. Olson, B.E.; Wallander, R.T. Effects of invasive forb litter on seed germination, seedling growth and survival. *Basic Appl. Ecol.* **2002**, *3*, 309–317. [CrossRef]
40. Muturi, G.M.; Poorter, L.; Bala, P.; Mohren, G.M.J. Unleached *Prosopis* litter inhibits germination but leached stimulates seedling growth of dry woodland species. *J. Arid Environ.* **2017**, *138*, 44–50. [CrossRef]
41. Hovstad, K.A.; Ohlson, M. Physical and chemical effects of litter on plant establishment in semi-natural grasslands. *Plant Ecol.* **2008**, *196*, 251–260. [CrossRef]
42. Myster, R.W. Contrasting litter effects on old field tree germination and emergence. *Plant Ecol.* **1994**, *114*, 169–174. [CrossRef]
43. Stinchcombe, J.R.; Schmitt, J. Ecosystem engineers as selective agents: The effects of leaf litter on emergence time and early growth in *Impatiens capensis*. *Ecol. Lett.* **2006**, *9*, 258–270. [CrossRef] [PubMed]
44. Loydi, A.; Eckstein, R.L.; Otte, A.; Donath, T.W. Effects of litter on seedling establishment in natural and semi-natural grasslands: A meta-analysis. *J. Ecol.* **2013**, *101*, 454–464. [CrossRef]
45. Zhuang, Z.; Li, Y.J.; Liu, Q.Q.; Yang, Z.; Liu, B.; Liu, A.Q. Effects of Chinese fir litter extracts on the seed germination and seedlings. *J. For. Environ.* **2017**, *37*, 29–33. [CrossRef]
46. Xia, Z.C.; Kong, C.H.; Chen, L.C.; Wang, S.L. Allelochemical-mediated soil microbial community in long-term monospecific Chinese fir forest plantations. *Appl. Soil Ecol.* **2015**, *96*, 52–59. [CrossRef]
47. Yang, Y.S.; Xie, J.S.; Chen, Y.X.; He, Z.M.; Yu, B.N. Amount, composition and seasonal dynamics of litterfall in mixed forest of *Cunninghamia Lanceolata* and *Tsoongiodenaron odorum*. *Sci. Silvae Sin.* **2001**, *37*, 30–34. [CrossRef]
48. Wen, Y.G.; Wei, S.Z.; Qing, W.M. Analysis on the litter-fall dynamics of Chinese fir plantation and its correlation to climatic factors in North Guangxi. *Acta Ecol. Sin.* **1990**, *10*, 367–372. [CrossRef]
49. Gao, S.L.; He, Z.M.; Huang, Z.Q.; Lin, S.Z.; Liu, Z.M.; Zheng, L.J. Amount, composition and seasonal dynamics of litterfall in different ages of *Cunninghamia lanceolata* plantations. *Aata Agric. Univ. Jiangxiensis* **2015**, *37*, 638–644. [CrossRef]
50. Barritt, A.R.; Facelli, J.M. Effects of Casuarina pauper litter and grove soil on emergence and growth of understorey species in arid lands of South Australia. *J. Arid Environ.* **2001**, *49*, 569–579. [CrossRef]
51. Liu, G.X.; Wan, L.Q.; He, F.; Tong, Z.Y.; Liu, Z.K.; Li, X.L. Effects of litter, seed position, and water availability on establishment of seedling for two semiarid grass species. *Plant Ecol.* **2016**, *217*, 277–287. [CrossRef]
52. Harris, M.R.; Lamb, D.; Erskine, P.D. An investigation into the possible inhibitory effects of white cypress pine (*Callitris glaucophylla*) litter on the germination and growth of associated ground cover species. *Aust. J. Bot.* **2003**, *51*, 93–102. [CrossRef]
53. Amatangelo, K.L.; Dukes, J.S.; Field, C.B. Responses of a California annual grassland to litter manipulation. *J. Veg. Sci.* **2008**, *19*, 605–612. [CrossRef]
54. Yanes, C.V.; Segovia, A.O. Effects of litter from a tropical rainforest on tree seed germination and establishment under controlled conditions. *Tree Physiol.* **1992**, *11*, 391–400. [CrossRef]
55. Burgos, J.V.; Barradas, M.C.D.; Zunzunegui, M. Effects of *Pinus pinea* litter on seed germination and seedling performance of three Mediterranean shrub species. *Plant Growth Regul.* **2012**, *66*, 285–292. [CrossRef]
56. Facelli, J.M.; Pickett, S.T.A. Plant litter: Light interception and effects on an old-field plant community. *Ecology* **1991**, *72*, 1024–1031. [CrossRef]
57. Qi, S.S.; Dai, Z.C.; Miao, S.L.; Zhai, D.L.; Si, C.C.; Huang, P.; Wang, R.P.; Du, D.L. Light limitation and litter of an invasive clonal plant, *Wedelia trilobata*, inhibit its seedling recruitment. *Ann. Bot.* **2014**, *114*, 425–433. [CrossRef] [PubMed]
58. Enquist, B.J.; Niklas, K.J. Global allocation rules for patterns of biomass partitioning in seed plants. *Science* **2006**, *295*, 1517–1520. [CrossRef] [PubMed]
59. Liu, B.; Liu, Z.M.; Wang, L.X.; Wang, Z.N. Responses of rhizomatous grass *Phragmites communis* to wind erosion: Effects on biomass allocation. *Plant Soil* **2014**, *380*, 389–398. [CrossRef]