

Article

Converting Larch Plantations to Larch-Walnut Mixed Stands: Effects of Spatial Distribution Pattern of Larch Plantations on the Rodent-Mediated Seed Dispersal of *Juglans mandshurica*

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Abstract: Larch (*Larix* spp.) is planted after a clear-cut of secondary forests (SFs) to meet the timber demand of Northeast China. However, the declination of soil fertility and the acidification of surface runoff in larch plantations (LPs) resulting from mono-species composition have threatened the sustainable development of LPs. Converting pure LPs into larch-walnut mixed forests can solve those problems, in which it is crucial to promote the seed regeneration of *Juglans mandshurica* in LPs. The success of walnut seed regeneration is dependent on rodent removing seed away from mother trees and the dispersal processes rely on the stand structure. The spatial distribution pattern between LPs and SFs is a type of stand structure that might affect seed dispersal. There are two typical spatial patterns in Northeast China due to different topographical conditions, that is, contour type (C-T, LPs and SFs located at the same slope position and aspect) and downslope type (D-T, LPs located at the down slope of the adjacent SF in the same aspect). The objectives of our study were to verify the effects of the spatial distribution pattern of LPs on rodent-mediated seed dispersal and to determine the optimal spatial distribution type for seed dispersal. The field trial was conducted by releasing tagged *J. mandshurica* seeds at three stages of seed rain during two continuous growing seasons in two types of spatial distribution patterns for LPs. We found that contour type had a substantial advantage in the rodent-mediated seed dispersal, that is, the dispersal rate and the proportion of scatter-hoarded seeds in LPs of C-T stands were much higher than in D-T stands, respectively. These differences may be caused by the variation in the topographic factor for these two types of spatial distribution pattern of LPs. In the C-T stands, it was a translational motion for rodents to remove walnuts from SFs to LPs, which would be an energy efficient and favorable method of seed dispersal. Fluctuation of seed abundance had an effect on rodent behaviors and seed fates, that is, there was a faster dispersal rate and lower proportion of seeds in situ in the non-masting year of 2015 than in the masting year of 2016 and proportion of scatter-hoarded seeds reached the highest during the early stage and lowest at the middle stage of seed rain. Thus, the contour type of LPs with a favorable terrain advantage is potentially conducive to dispersing walnut seeds by rodents during early stage of seed rain and converting larch plantations into larch-walnut mixed forests.

Keywords: plantation management; contour type; downslope type; seed dispersal rate; masting year

1. Introduction

In Northeast China, as much as 70% of primary forests (the mixed broadleaved Korean pine forests) have been destroyed by the destructive disturbances of human beings or extreme natural disasters since the 1950s [1] and have degraded into secondary forests (SFs) [2]. Compared with primary forests, SFs cannot provide enough timber production and water conservation or biodiversity maintenance [3]. Therefore, larch (*Larix* spp., mainly including *Larix olgensis* A.Henry, *Larix principis-rupprechtii* Mayr. and *Larix kaempferi* (Lamb.) Carr.) has been widely planted as a fast-growing commercial tree species and mosaic plantation/secondary forest landscapes have been formed [4]. However, the continuous problems in larch plantations (LPs) have seriously threatened the sustainable development of forest ecosystems. Related studies have indicated the problems in LPs as follows: (1) compared with SF, soil fertility (including soil total carbon and soil total nitrogen) has declined by 33.6% and 35%, soil has gradually acidulated ($\text{pH}_{\text{LP}} (5.4) < \text{pH}_{\text{SF}} (6.4)$) and nutrient leaching is increasingly serious in LPs [5,6]; and (2) biodiversity has decreased and forest development is unsustainable in LPs [7]. All of these issues are caused by single species composition and a mono stand structure in LPs [7,8]. It has been proven that improving the natural regeneration of broad-leaved tree species in the pure larch plantation (i.e., converting pure LPs into larch-broadleaf mixed forests) is the key to solving the above problems [4].

Natural regeneration (including seed regeneration and sprout regeneration) is considered to be a solid foundation for the sustainable development of forests, with lower investment costs and better adaptation to microhabitats, compared with artificial regeneration [9]. Seed dispersal, a significant stage of seed regeneration, can increase the chances that seeds will arrive at safe sites in sufficient numbers [10], allow for plants to reach specific habitats that are favorable for survival [11] and even allow for plants to colonize vacant habitats and new geographic regions [12]. It is the first and critical step in natural regeneration whereby seeds can successfully invade into larch plantation with the help of dispersal media [13]. Therefore, how to improve the seed dispersal of broad-leaved tree species into LPs is a great challenge for forest managers [4].

Diplochory is a common means of seed dispersal in temperate and tropical communities, usually refers to a sequence of two seed dispersal steps or phases. Phase one is the initial seed movement with dispersal vectors (e.g., wind, ballistic), away from parent trees and density-dependent seed or seedling mortality and phase two is the subsequent seed dispersal, which is often carried out by animals, such as scatter hoarding rodents or ants [14,15]. Animal-mediated seed dispersal, especially the scatter-hoarding behavior of animals (e.g., chipmunks, squirrel), is the principal method for dispersing large edible seeds and determines the survival and placement of seedlings and recruits and regulates the reproductive success of maternal trees [16–18]. A large body of literature highlights that the process of animal-mediated seed dispersal is sensitive to both abiotic factors (e.g., habitat structure with varying micro-environments [19], climate change [20,21]) and biotic factors (e.g., seed and animal traits [22,23], indirect seed-seed interactions [24,25]). Stand structure regulation (including density regulation and spatial allocation), an anthropogenic interference in the management of planted forests, affects animal behavior and animal-mediated seed dispersal by influencing the micro-environments (e.g., light availability) in stands [26]. We have found that changing the stand canopy density by creating gaps with a larger size [26,27] or thinning (unpublished data) is potentially feasible to promote rodent-mediated seed dispersal of the Manchurian walnut by changing micro-environments in LPs.

In the mosaic plantation/secondary forest landscapes, the spatial allocation of LPs (i.e., the spatial distribution pattern between LPs and SFs) is a type of stand structure. Two common and typical spatial distribution types of LPs within the SFs have been formed in Northeast China due to different topographical conditions, that is, the Contour Type (C-T, LPs and SFs located at the same slope position and aspect) and the Downslope Type (D-T, LPs located at the down slope of the adjacent SFs in the same aspect) [13,28]. The previous studies have indicated that these two spatial patterns have an impact on wind-mediated seed dispersal and distribution patterns of soil seed bank for broadleaved tree species [13,28]. Animal-mediated seed dispersal is an important part of seed input in the seed

bank [29]. However, little is known about how the spatial patterns affect animal-mediated seed dispersal, which may limit the sustainable development of LPs. Animal behavior and the subsequent seed dispersal process may be affected by these two spatial patterns of LPs because of topographical conditions [30]. Thus, we hypothesized that the C-T stand was beneficial for rodents by saving energy to disperse more seeds from SFs into LPs.

Besides spatial distribution types of LPs within the SFs, fluctuated seed production (masting seed: the intermittent production of large seed crops by a plant population) and seed shedding (seed rain) have effects on animal-plant interactions [31,32]. Seed abundance and availability changing with masting year and seed rain are key factors likely to influence scatterhoarder's strategy [33,34]. In the secondary forest ecosystems of Northeast China, *Juglans mandshurica* Maxim., *Quercus mongolica* Fisch. and *Pinus koraiensis* Sieb. have large seeds who depend animals to disperse seeds [26,35,36] and their fruit-falling periods are in August–September, August–September and September–October, respectively [26]. Because of high economic value, harvest of Korean pine seeds by humans is very serious and rodents have lost the competition for the dispersal of Korean pine seeds [37]. Highly nutritious and palatable walnut and low nutritious and unpalatable acorn are alternative food for rodents [38,39] and the fates of alternative seeds handled by scatter-hoarding rodents may vary with forest disturbance and seasonal food availability [34].

In the present study, we used *J. mandshurica* as a study species due to the following reasons: (1) planting Manchurian walnut seedlings in LPs can promote mutual growth [40–42] and can also greatly improve soil fertility in LPs [43] and (2) the successful seed regeneration of *J. mandshurica* depends on rodent-mediated seed dispersal away from the mother trees to relieve the barriers of root exudates (i.e., juglone) [26,41,44,45]. Thus, promoting rodent-mediated seed dispersal and the potential natural regeneration of *J. mandshurica* in LPs is a crucial way to solve the problems in LPs. Thus, we released tagged *J. mandshurica* seeds at three stages of seed rain (early, middle and final stages) during two continuous growing seasons in two types of spatial distribution pattern for LPs (C-T and D-T). We tracked seed fates and distance dispersed by small rodents. The objectives of this study were (1) to determine whether these two typical spatial distribution types of larch plantations have a great effect on animal-mediated dispersal and (2) to determine the optimal spatial distribution type of larch plantations to raise the possibility of converting them into larch-walnut mixed forests by promoting animal-mediated dispersal of *J. mandshurica* in LPs.

2. Materials and Methods

2.1. Study Site

This research was conducted at the Qingyuan Forest CERN, Chinese Academy of Sciences, in a mountainous area of Liaoning Province in Northeast China (41°51' N, 124°54' E and 500–1100 m above sea level). This region has a continental monsoon climate with windy spring, humid and warm summer and cold and dry winter. The mean annual frost-free period is 130 days, with an early frost in October and late frost in April. The mean annual air temperature is between 3.9 °C and 5.4 °C; the minimum and maximum air temperatures are −37.6 °C in the coldest month, January and 36.5 °C in the warmest month, July. Annual precipitation varies from 700 to 850 mm, with 80 percent falling during the period of June–August [5].

Independent and paired stands of approximately 60-year-old SFs and 35 to 45-year-old adjacent LPs were chosen from separate watersheds over an area of 100 ha, with slopes <15° and altitudes ranging from 589 to 836 m a.s.l. (Table 1). There were three stands for Contour Type (C-T) and Downslope Type (D-T). In the SFs, the tree layer consisted of *Fraxinus rhynchophylla* Hance., *J. mandshurica*, *Phellodendron amurense* Rupr., *Quercus mongolica* Fisch. ex Ledeb. and *Acer mono* Maxim. The understory components include *Acer. mandshuricum* Maxim., *Acer triflorum* Kom, *Acer tegmentosum* Maxim. and *Syringa reticulata* Blume. The herb layer is composed of *Cardamine leucantha* Tausch., *Allium monanthum* Maxim., *Arisaema amurense* Maxim and *Polygonatum involucreatum* Maxim. The larch

plantations include *A. tegmentosum*, *Acer pseudo-sieboldianum* Komarov., *Schisandra chinensis* (Turcz.) Baill., *Syringa wolfii* Schneid. and *Acanthopanax senticosus* Maxim. in the shrub layer and *Cardamine leucantha* (Tausch) O. E. Schulz, *Rubia sylvatica* Maxim and *Spuriopimpinella brachycarpa* Kom in the herb layer [6]. All six plantation stands were in their first rotation. The basic information of six stands is shown in Table 1.

Table 1. Characteristics of study site.

Spatial Allocation Pattern of Larch Plantations	Center Coordinates	Altitude (m)	Area (ha)	Slope (°)	Gradien (°)	Mean DBH (cm)	Mean Height (m)	Stand Density (tree/ha)	Distance to Closest Site (km)
Downslope type	N 41°51'15", E 124°56'39"	625	0.25	186	<15	38.1	20	766 ± 115	Closest site
	N 41°50'43", E 124°56'48"	620	0.25	248	<15	37.2	25	1233 ± 450	1.8
	N 41°50'57", E 124°56'45"	613	0.25	213	<15	39.2	23	1160 ± 289	2.7
Contour type	N 41°50'81", E 124°56'57"	644	0.25	330	<15	38.1	19	1466 ± 231	1.6
	N 41°51'56", E 124°56'70"	603	0.25	340	<15	43.4	24	1033 ± 208	1.7
	N 41°50'57", E 124°55'55"	615	0.25	335	<15	40.5	24	1566 ± 289	2.3

2.2. Seed Collection and Marking

Seed collection: *J. mandshurica* seeds were collected from secondary forests in the same region in September 2015 (non-masting year) and 2016 (masting year) [26]. In total, we chose 6000 healthy and roughly equal weighty (10.51 ± 0.04 g) seeds as the study object. We placed 2400 seeds in four plots in 2015 and put 3600 seeds in six plots in 2016.

Seed marking: we labeled walnuts with plastic-tagged methods—a hole with 0.3 mm in diameter was drilled through each walnut far from the embryo and then a plastic tag (2.5×3.5 cm, <0.3 g) with a unique ID was tied through the hole using a 10-cm-long thin steel thread [46,47]. Small rodents can bury the tagged walnuts in the soil and leave the tags on the ground surface and the weight of the plastic tag and 10 cm steel thread was too small (0.36 g) to increase the gross weight of seeds. Meanwhile, it was easy to re-locate the seeds by using the plastic-tagged methods.

2.3. Seed Release and Seed Removal

Seed release: we set up four seed stations (1.5×0.5 m for each station) at the junction of SF and LP in each plot and each seed station was located at 12 m away from each other (Figure 1). We evenly placed 50 tagged walnut seeds at each seed station in the early (20 August–10 September), middle (10–30 September) and final (30 September–20 October) stages of seed rain in 2015 and 2016, respectively.

Seed removal and fates: we took the average amount of lost seeds from the station per day as seed removal rate. We recorded the seed fates every day in the first three days of seed release in both 2015 and 2016. Then, we tracked the seed fates every other day in the later period until all of the seeds were removed or consumed. Seed fates were classified into six categories: (1) intact in situ (IS), (2) moved and eaten leaving only plastic tags and seed fragments (EAR), (3) intact after removal to another location (IAR), (4) scatter-hoard in the larch plantation (SH-LP), (5) scatter-hoard in the secondary forest (SH-SF) and (6) missing where their true fates were unknown (MISS). The retrieved seeds included EAR, IAR, SH-LP and SH-SF. When a cache was discovered, we carefully recorded the seed code numbers and measured the distance and direction between the tagged walnuts and the corresponding seed stations.

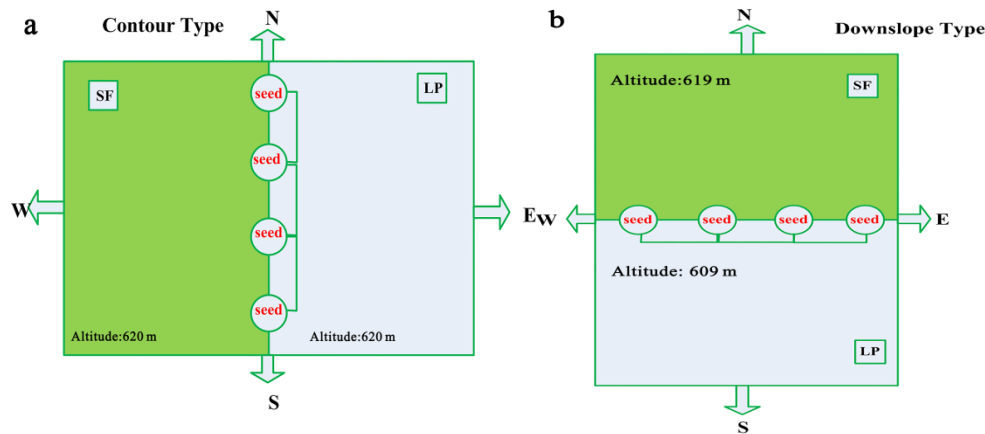


Figure 1. The sketch map of seed stations setting in two typical spatial distribution patterns of larch plantations (LPs) within a secondary forests (SFs). (a) Seed station setting in contour type stands. (b) Seed station setting in downslope type stands and the south is the download direction of LPs from SFs.

Spatial coordinate system: besides releasing seeds and recording the seed removal and fate in both 2015 and 2016, we also took the coordinates of seed location to measure the seed dispersal distance and dispersal preference and accurately described the spatial pattern of scatter-hoarding seeds in the different distribution types of LPs in SFs only in 2016. In the spatial coordinate system, the center of the junctions of SFs and LPs was defined as a coordinate (0, 0); the east-west orientation of SF and LP was defined as the X axis and the north-south orientation was defined as the Y axis.

2.4. Identification of Seed Disperser

We placed an infrared camera trap in each seed station to monitor the rodent type, the residence time and the visitation of rodents at three different stages of seed rain in 2016. The rodent frequency of each species was calculated as the ratio of its visitation days to a standardized sampling period of 20 days.

2.5. Statistical Analysis

The difference in proportion of rodent captured by infrared cameras between C-T and D-T stands was analyzed by the chi-square test. The survival analysis of Cox Regression was used to examine the difference in seed survival at the seed station between C-T stands and D-T stands and inter-annual variation and three stages of seed rain as covariates and seed station nested within the site as random structure. Generalized linear mixed-effects models (GLMMs) with a binomial error distribution was used to analyze the proportion of seed fates (SH-LP, SF-SF, EAR, IS, IAR, MISS). GLMMs with Gaussian error distribution were used to test the effects of treatment (spatial allocation type of LPs and SFs, year and stage of seed rain) on dispersal distance (log-10-transformed) of the scatter-hoarded seeds. In GLMMs, spatial allocation of LPs and SFs, inter-annual variation and the three stages of seed rain were taken as fixed factors and seed station nested within the site was taken as a random factor. The best-fitting models were selected by the lowest AIC value (see Table A1). All data were shown with a mean \pm SE and the significant statistical level was set at $\alpha = 0.05$. SPSS for Windows (Version 20.0, IBM, Armonk, NY, USA) was used to conduct the statistical analysis.

3. Results

3.1. Identification of Seed Dispersers

A total of one type of rodent (i.e., *Sciurus vulgaris*) was captured by infrared cameras during the seed dispersal period (Table 2). According to the Chi-square test, there was insignificant difference in

the proportion of rodent captures between C-T and D-T stands ($\chi^2 = 0.75$, $df = 1$, $p = 0.39$, χ^2 : statistic parametric test the correlation of data; df : degree of freedom).

Table 2. Residence time and visitation frequency of rodents recorded by infrared cameras at three stages of seed rain in 2016 in contour type and downslope type stands.

Spatial Allocation Pattern of Larch Plantations	Rodent	Residence Time at Three Stages of Seed Rain (minutes)			Frequency at Three Stages of Seed Rain (time/10 days)		
		Early Stage	Middle Stage	Final Stage	Early Stage	Middle Stage	Final Stage
Contour type	<i>Sciurus vulgaris</i>	10	1	2	3	2	2
Downslope type	<i>Sciurus vulgaris</i>	1	2	2	1	1	1

3.2. Seed Dispersal Rate

Cox regression analysis identified that there was a significant difference in the seed removal rates between the Contour Type and Downslope Type ($df = 1$, $Wald = 15.72$, $p < 0.001$) (Table 3) and the removal rate in C-T was higher than that in D-T. The inter-annual variation of seed production had a significant effect on the seed removal rate ($df = 1$, $Wald = 120.4$, $p < 0.001$); that is, the removal rate in the non-masting year (2015) was four times higher than that in the masting year (2016). The seed removal rate at the early stage of seed rain reached the fastest but was the lowest at the middle stage ($df = 2$, $Wald = 27.9$, $p = 0.034$) (Figure 2).

Table 3. Effects of two spatial allocation patterns, different stages of seed rain and inter-annual variation of seed yield on seed dispersal. Significant effects ($p < 0.05$) are bolded. (All models and their AIC scores are presented in Table A1).

Response Variable	Spatial Allocation Model			Different Stage of Seed Rain			Inter-Annual Variation		
	df	F-Ratio	p-Value	df	F-Ratio	p-Value	df	F-Ratio	p-Value
Seed removal rate	1	15.72	<0.001	2	27.9	0.034	1	120.4	<0.001
IS proportion	1	0.41	0.53	2	0.95	0.39	1	22.21	0.001
EAR proportion	1	0.53	0.47	2	3.53	0.03	1	0.19	0.66
SH-SF proportion	1	8.37	0.62	2	0.47	0.004	1	0.69	0.69
SH-LP proportion	1	0.07	0.008	2	7.29	0.001	1	6.98	0.79
MISS proportion	1	0.11	0.75	2	8.71	<0.001	1	51.03	<0.001
Seed dispersal distance	1	0.41	0.52	2	0.54	0.59	1	0.37	0.99

IS: intact in situ; EAR: removed and eaten leaving only plastic tags and seed fragments; SH-SF: scatter-hoarding in the secondary forest; SH-LP: scatter-hoarding in the larch plantation; MISS: missing where their true fates were unknown. (F-Ratio: statistic parametric test the significant, df : degree of freedom)

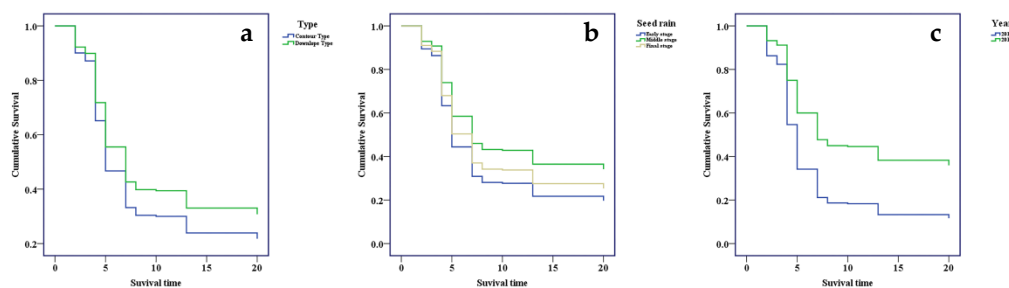


Figure 2. Seed removal rate in larch plantations with contour type and downslope type at three stages of seed rain in 2015 (non-masting year) and 2016 (masting year) by using the Cox Regression. (a) Seed removal rate for two types of larch plantations (i.e., contour type and downslope type). (b) Seed removal rate for three stages of seed rain (i.e., early, middle and final stages). (c) Seed removal rate for the year of 2015 and 2016.

3.3. Seed Fates

Seed fates (EAR and SH-LP) showed significant differences between C-T and D-T stands ($F = 7.29$, $df = 1$, $p = 0.008$) (Table 3). The proportion of SH-LP in the C-T stands (29.82%) was greater than that in D-T (19.88%); the proportion of EAR in the C-T stand (4.87%) was less than that in D-T (6.19%) (Figure 3E). Inter-annual variability of seed yield significantly influenced the proportions of MISS and IS ($F = 22.21$, $df = 1$, $p = 0.001$; $F = 51.04$, $df = 1$, $p < 0.001$) (Table 3). The proportion of IS in the non-masting year (2015) was less than that in the masting year of 2016 ($IS_{2015} = 4.94\% < IS_{2016} = 25.96\%$) but the proportion of MISS was opposite to IS ($MISS_{2016} = 38\% > MISS_{2015} = 26\%$). SH-LP, EAR, SH-SF and MISS showed significant differences among stages of seed rain ($F = 7.29$; $df = 2$, $p = 0.001$; $F = 3.53$, $df = 2$, $p = 0.03$; $F = 0.47$; $df = 2$, $p = 0.004$; $F = 8.71$; $df = 2$, $p < 0.001$) (Table 3). The proportion of seed fates among three stages of seed rain were $SH-LP_E = 34.08\% > SH-LP_F = 20.77\% > SH-LP_M = 19.70\%$ (Figure 3A); $EAR_F = 6.54\% > EAR_E = 3.46\%$ (Figure 3B); $SH-SF_E = 30.08\% > SH-SF_M = 28.22\% > SH-SF_F = 24.22\%$ (Figure 3C); $MISS_F = 34.48\% > MISS_M = 26.76\% > MISS_E = 13.26\%$ (Figure 3D).

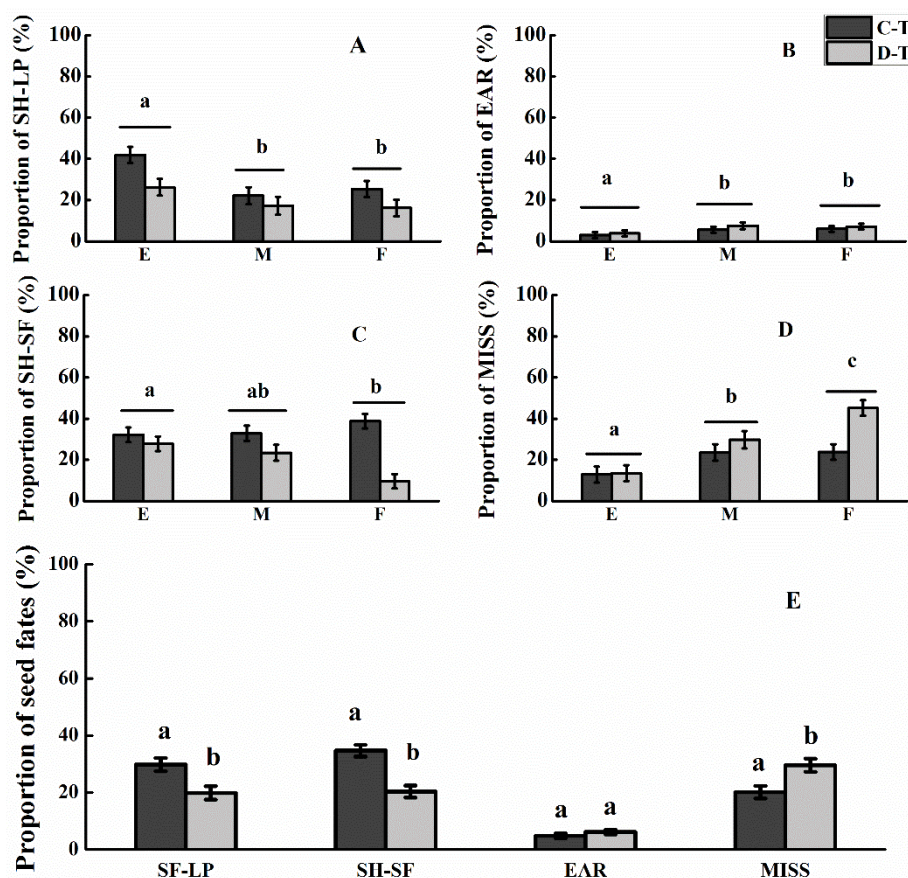


Figure 3. Seed fates of *Juglans mandshurica* in larch plantations with contour type (C-T) and downslope type (D-T) at three stages of seed rain. (A) The proportion of SH-LP at three stages of seed rain; (B) The proportion of EAR at three stages of seed rain; (C) The proportion of SH-SF at three stages of seed rain; (D) The proportion of SH-SF at three stages of seed rain; (E) Seed fates of *Juglans mandshurica* with contour type (C-T) and downslope type (D-T). SH-LP: scatter-hoarding in the larch plantation; SH-SF: scatter-hoarding in the second forest; EAR: removed and eaten leaving only plastic tags and seed fragments; MISS: missing where their true fates were unknown. E: early stage of seed rain; M: middle stage of seed rain; F: final stage of seed rain.

3.4. Seed Dispersal Distance

The spatial pattern of scatter-hoarding seeds in the different distribution types of LPs and SFs in 2016 is shown in Figure A1. The effects of inter-annual variability of seed production ($F = 0.34$, $df = 1$,

$p = 0.99$), the spatial distribution types ($F = 0.41$, $p = 0.52$, $df = 1$,) and the stages of seed rain ($F = 0.54$, $df = 2$, $p = 0.59$) on the seed dispersal distance were not significant (Table 3 and Figure 4).

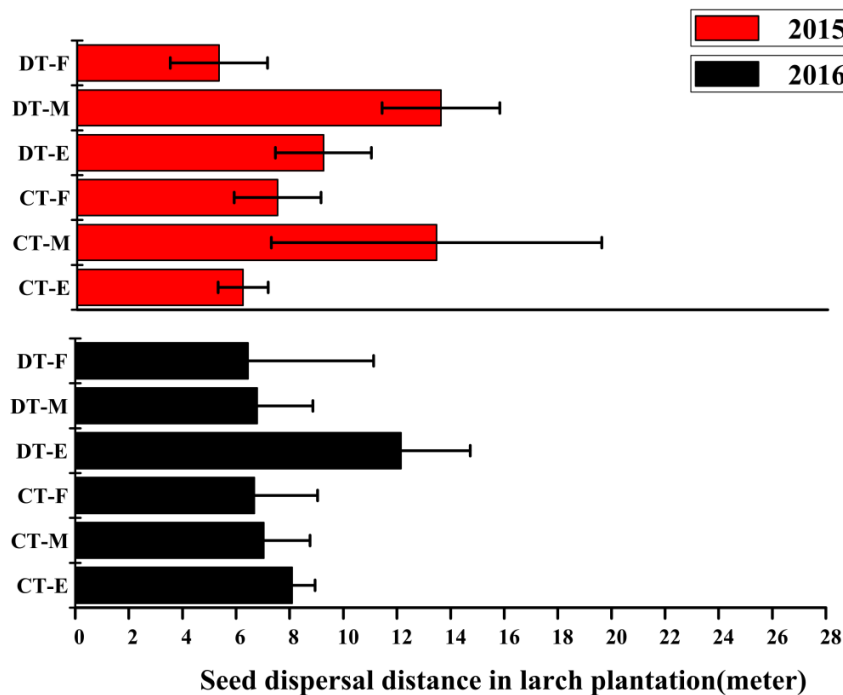


Figure 4. Seed dispersal distance in larch plantations with contour type and downslope type at three stages of seed rain in 2015 (non-masting year) and 2016 (masting year). CT-E: early stage of seed rain in the contour type of stands; CT-M: middle stage of seed rain in the contour type; CT-F: final stage of seed rain in the contour type; DT-E: early stage of seed rain in the downslope type; DT-M: middle stage of seed rain in the downslope type; DT-F: final stage of seed rain in the downslope type.

4. Discussions

We conclude from our study that, compared with the downslope type stands, a greater number of rodents (mainly *S. vulgaris*) was captured by infrared camera traps in the contour type stands and the contour type stands were more favorable for rodent-mediated seed dispersal (including seed dispersal rate, scatter-hoarded proportion and IS proportion). These results are largely in accordance with our hypothesis.

4.1. Effects of Spatial Allocation Type of LP and Adjacent SF on Rodent-Mediated Seed Dispersal

Topographic condition is an important abiotic factor that affects the secondary, animal-mediated dispersal of seeds [48]. In our study, the process of animal-mediated seed dispersal from SFs to LPs with the same slope position and aspect in the C-T stands is primarily a translational motion, while the process of seed dispersal from SFs to LPs in the D-T stands is mainly an up-and-down motion and will consume more energy of rodents. Therefore, rodents would remove seeds in greater speed and in larger number in the C-T stands at given physical conditions (Figure 3). Besides the direct effect of slope on rodents' activities, slope can also change herb coverage and indirectly affect the rodent population quantity. Generally, the greater the gradient of slope is, the more barren and drier the soil is [49]. Consequently, the abundance and coverage of herbaceous plants is reduced, which is disadvantageous for rodents' activities [50]. Therefore, the other reason for lower seed dispersal rate and scatter-hoarder proportion is the reduced rodent's population in the downslope type stands (Table 3).

A previous study elucidated that the primary dispersal stage of seeds (i.e., seed rain from the trees with gravity) for broad-leaved tree species (*J. mandshuricas*, *Q. mongolica*) did not show obvious

spatial differentiation in the C-T and D-T stands [27]. However, in the secondary dispersal stage of this study, we found that in the C-T stands, rodents prefer to carry more walnut seeds from SFs to LPs. Consequently, in the soil bank stage (the final results of seed primary and secondary dispersal), the *J. mandshuricas* seed quantity increases from the secondary forest to the larch plantation in the C-T stands [13]. Therefore, rodent-mediated seed dispersal changes the spatial allocation of seeds [50].

Contour type and downslope type are both common and typical spatial distribution types of LPs within the SFs [13,28]. The contour type shows an obvious advantage on rodent-mediated seed dispersal and the downslope type with an unfavorable topographic condition is adverse for rodents to remove and cache seeds. In the previous research, the contour type of LPs and SFs was chosen to regulate stand density (i.e., creating gaps or thinning) in larch plantation and it has been proven that this stand density regulation is favorable for rodent-mediated seed dispersal of walnuts in LPs and for forming larch-walnut mixed forests [26]. For example, rodent-mediated seed dispersal rate and distance in the contour type of LPs with middle gaps (130–206 m²) were 95% higher and 43% farther than in control stand [26]; the seed dispersal rate in the contour type of LPs with a 25% thinning intensity treatment (437–532 trees ha⁻¹) was 30% faster than in the control stand and the seed dispersal distance in LPs with 50% thinning intensity treatment (292–355 trees ha⁻¹) was 26% longer than in the control stand (unpublished data). Therefore, aiming to counteract the negative effects of the downslope spatial distribution types of LPs on rodent-mediated seed dispersal, stand density regulation (e.g., creating gaps or thinning with optimal intensity) in D-T stands may be a worthy of consideration for future research on converting LPs into larch-walnut mixed forests.

4.2. Effects of the Inter-Annual Variation of Seed Production and Different Stages of Seed Rain on Rodent-Mediated Seed Dispersal

The relative abundance of food strongly affects animal predatory behavior [51]. Both predator satiation hypothesis (mast seeding provide sufficient food for seed predators and more seeds escape from predation) and predator dispersal hypothesis (large seed crops increase seed removal rate and dispersal distance) are widely supported to explain this phenomenon [32,52]. Inter-annual variations of seed production had an effect on the seed dispersal rate and proportion of IS in the present study, that is, the seed removal rate in the non-masting year (2015) was four times faster than in the masting year (2016) but the proportion of IS in 2015 (4.94%) was less than that in 2016 (25.96%). Furthermore, the effects of different stages of seed rain on the seed dispersal rate were also dependent on seed abundance, that is, seed dispersal rate reached the slowest in the middle stage and the fastest in the early stage of seed rain. Besides that, less food resources offer signals and feedback to rodents to disperse more seeds, which results in largest proportion of walnuts being removed during early stage of seed rain and less during final stage of seed rain (Figure 3). The findings of this study are consistent with the previous studies in the LPs stands with thinning and gap formation treatment. In the gap and thinning treatment stands of LPs, rodents tended to remove more seeds with faster speeds and at shorter distances in 2015 and vice versa in 2016 and to remove most seeds at the early stage of seed rain and carry fewest seeds at the middle stage of seed rain [24], which is in accordance with the predator satiation hypothesis [24]. However, our results are inconsistent with Aliyu [34] who found that rodents would like to scatter hoard *Carapa oreophila* seeds in less disturbed forests, regardless of food abundance and availability. Seed traits may be the major reason causing this difference. In our study during the seed fall, Mongolian oak seeds with higher tannin content were always neglected and rodents preferred the higher nutritional and hard walnut seeds. Thus long-term monitoring of phenology for local large seed abundance and the interaction with animal seed dispersers needs to be emphasized in the future research.

5. Conclusions

Spatial distribution types of larch plantations strongly affected the residence time and visitation frequency of rodents and the rodent-mediated seed dispersal of walnuts in LPs. The contour type

of LPs and SFs provided a terrain advantage to promote rodents removing seeds more quickly and with higher proportion of scatter-hoard. Inter-annual variation of seed production just had effects on the seed dispersal rate and IS; that is, there was a faster removal rate with a lower proportion of IS in the non-masting year (2015) and vice versa in the masting year (2016). And seed fluctuations with different stage of seed rain have an effect on proportion of scatter-hoarded seeds. The proportion SF-LP reached the highest during the early stage and lowest at the middle stage of seed rain. For the sustainable management of larch plantations, we suggest creating the contour type distribution of larch plantations to promote rodent-mediated seed dispersal and improve the regeneration potential of *J. mandshurica*. Aiming to counteract the poor dispersal ability of rodents for *J. mandshurica* seeds, the regulation of the stand density (e.g., forming gaps or thinning) in the D-T stands with different silviculture objectives is suggested.

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Appendix A

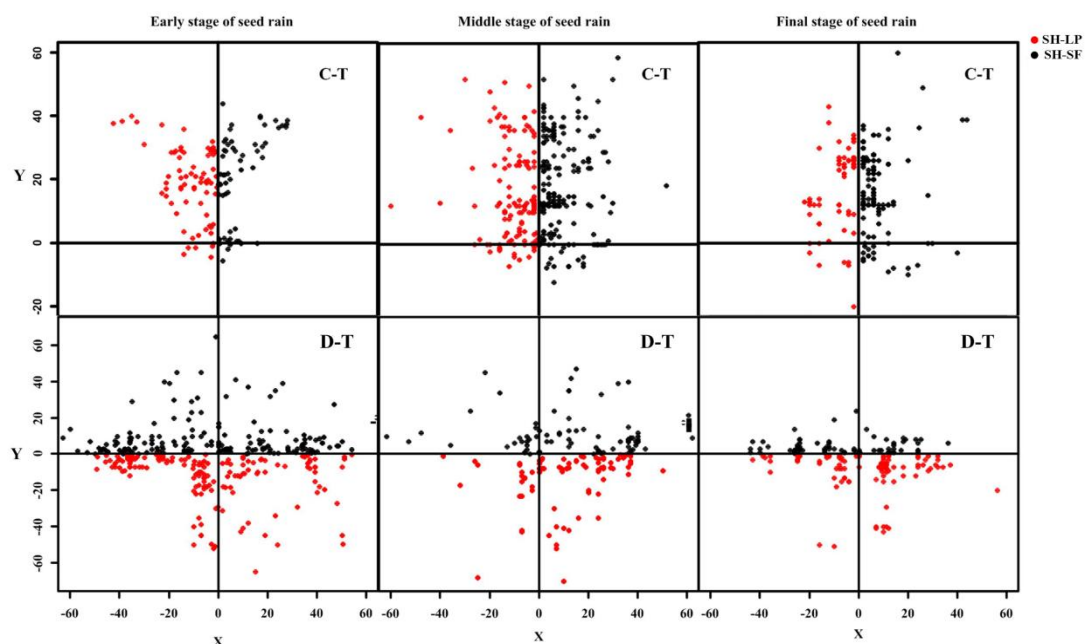


Figure A1. Spatial pattern of scatter-hoarding seeds in 2016. Red points represent the seeds cached in the larch plantations (SH-LP). Black points represent the seeds cached in the secondary forests (SH-SF). C-T: contour type; D-T: down slope type.

Table A1. Summary of GLMMs analyzed in seed fates and seed dispersal distance.

Response Variable	Explanatory Variables Used in Model	Likehoods	AIC	ΔAIC
SH-LP	Null model	−45.7	−47.70	8.55
SH-LP	allocation	−52.7	−50.70	5.55
SH-LP	allocation + year	−48.63	−46.63	9.62
SH-LP	allocation + year + seed rain + nests (station/site)	−58.25	−54.25	6.55
SH-LP	allocation + year + seed rain	−58.25	−56.25	0
SH-SF	Null model	74.04	72.04	155.77
SH-SF	allocation + year	−78.37	−78.37	160.1
SH-SF	allocation + year + seed rain	−72.86	−70.86	154.53
SH-SF	allocation + year + seed rain + nests (station/site)	−72.86	−68.86	154.59
SH-SF	allocation	−81.73	−83.73	0
MISS	Null model	77.13	79.13	106.62
MISS	allocation	12.99	14.99	42.48
MISS	allocation + year	−24.82	−22.82	4.67
MISS	allocation + year + seed rain + nests (station/site)	−31.49	−29.49	2
MISS	allocation + year + seed rain	−34.49	−27.49	0
IS	Null model	43.11	45.11	51.3
IS	allocation	4.12	6.12	12.31
IS	allocation + year + seed rain	−0.79	3.21	9.4
IS	allocation + year + seed rain + nests (station/site)	−0.79	1.2	7.40
IS	allocation + year	−8.19	−6.19	0
EAR	Null model	−265.63	−263.63	47.44
EAR	allocation + year	−302.73	−298.73	12.34
EAR	allocation + year + seed rain	−309.62	−307.59	7.66
EAR	allocation + year + seed rain + nests (station/site)	−302.73	−300.73	10.34
EAR	allocation	−313.07	−311.07	0
Distance	Null model	311.98	311.02	215.29
Distance	allocation	91.09	97.23	1.5
Distance	allocation + year	90.79	99.15	3.42
Distance	allocation + year + seed rain + nests (station/site)	102.11	108.32	12.59
Distance	allocation + year + seed rain	82.98	95.73	0

Significant explanatory variables are in bold.

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