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Effects of logging on the trade-off between seed and sprout regeneration of dominant woody species in secondary forests of the Natural Forest Protection Project of China

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Abstract

Background: Promoting natural regeneration (including seed and sprout regeneration) of dominant woody species is essential for restoring secondary forests. However, such restoration processes have been decelerated by the enclosure under Natural Forest Protection Project of China (NFPP). It remains unclear how to implement appropriate management measures (e.g., whether to apply logging and the suitable intensity) to facilitate natural regeneration according to the responses of two regeneration modes to management measures. We monitored the early stages of seed regeneration (seed rain, soil seed bank, and 1–3-year-old seedlings) and sprout regeneration (stump sprout rate, stump survival rate, probability of sprouting, and number of sprouts per stump) over the first 3 years (2017–2019) after logging under three intensity regimes (control [0%], 25%, and 50% logging intensity) in secondary forests.

Results: The seed rain density decreased markedly, seedling density increased insignificantly after logging, and logging promoted seedling survival at an increasing conversion rate of 3-year-old seedlings (37.5% under 0%, 100% under 25%, and 80.95% under 50% logging) compared to those of the control. The proportion of 3-year-old seedlings increased with logging intensity and was the highest (16.2%) at 50% logging intensity. Sprout density was not affected by logging intensity, however, under 25% and 50% logging, it decreased by 27% and 6% in 2018, and by 37% and 33% in 2019, respectively. Seedling density was 41.65- and 15.31-fold higher than that of sprouts in the 50% and 25% logging treatments, respectively. Based on the relative contributions of the two regeneration modes after logging, three groups of natural regeneration patterns were classified for dominant woody species in temperate secondary forests, i.e., seed regeneration preference (*Betula dahurica*, *Carpinus cordata* and *Fraxinus mandshurica*), sprout regeneration preference (*Acer mono* and *Acer pseudosieboldianum*) and no preference (*Quercus mongolica*, *Fraxinus rhynchophylla*, and *Juglans mandshurica*).

Conclusion: In addition to enclosure, appropriate logging can be applied according to the responses of various natural regeneration patterns of dominant woody species to logging in temperate secondary forests under the NFPP.

Keywords: Secondary forest, Seed regeneration, Sprout regeneration, Seedling recruitment, Light availability

Introduction

Secondary forests or second-growth forests, derived from natural regeneration after destructive disturbances of primary forests, have become the predominant forest resource (accounting for 60% and 72% of the forest area worldwide and Northeast China, respectively)

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(Longworth and Williamson 2018; Zhu et al. 2019). However, compared with primary forests, secondary forests are associated with substantial challenges such as irrational stand structures, declining biodiversity, and lower productivity (Lu et al. 2018; Zhao et al. 2019), which mainly results from lacking natural regeneration of dominant tree species (Gu et al. 2005; Yan et al. 2019). Consequently, promoting their natural regeneration is imperative to improve ecosystem services and stability of secondary forests and to restore them to primary forests (van Kuijk et al. 2008; Zhang et al. 2018).

To restore the ecosystem services of natural forests (including primary and secondary forests), the Chinese government has fully implemented the Natural Forest Protection Project of China (NFPP) by enclosing and strictly protecting forests from human activities and prohibiting any management measures since 1998 (Yu et al. 2011). According to the current application effect, the NFPP policy effectively reduces deforestation and restores the primary forests, which show higher stability and self-regulating potential than secondary forests (Zhu 2002). However, this policy may extend the recovery period of secondary forests due to lacking natural regeneration of dominant tree species, increase their total area and consequently, vitiate the purpose of the NFPP policy (Zhu 2002; Liu et al. 2018). Selective logging, an effective method of sustainable forest management (Qi et al. 2016), considers both the harvest of forest resources and the promotion of secondary forest regeneration by regulating logging intensities (e.g., Knapp et al. 2017; Zhang et al. 2018; Sukhbaatar et al. 2019; Gagné et al. 2019). This is because after logging or creating a gap, environmental factors are modified, including soil temperature and nutrient availability, and particularly the incident light reaching the understory (Yan et al. 2010; Lochhead and Comeau 2012; Olson et al. 2014). Considering the potential effects of selective logging on natural regeneration, it is imperative to explore reasonable and moderate forest management methods of logging in the light of the NFPP to restore secondary forests in a timely manner.

As the most rapid and economic regeneration method, natural regeneration is the basic approach for forest restoration, and it is more compatible with modern sustainable forest management and biodiversity conservation than artificial regeneration (e.g., planting seedlings) (Chazdon 2008; Löf et al. 2021). Many woody plants have two natural regeneration modes after disturbances (i.e., seed regeneration and sprout regeneration), and both regeneration modes are essential for the development and continuation of forest tree populations. Seed regeneration requires adequate seed production, effective dispersal and a suitable environment to facilitate germination and establishment of seedlings and saplings

establishment (Gang et al. 2015; Vergarechea et al. 2019). As a different common reproductive strategy, populations of many species have successfully recovered through sprouts, for instance, *Quercus liaotungensis* relies more heavily on stump sprout regeneration, because its seeds are vulnerable to predation and rot, and root suckers are rare (Li et al. 2013). However, sprouting recruitment cannot expand the original distribution of tree species as could be achieved through seed dispersal (Warner and Chesson 1985). The early processes of natural regeneration (i.e., the transformation from seed germination to seedling survival, and the sprouting probability from stumps) is a bottleneck with high mortality of young plants (frequently >90%), compared with that of adults, owing to considerable effects of biotic and abiotic factors (Reinhardt et al. 2015; Yan et al. 2016a).

In general, there is a trade-off between seed and sprout regeneration (i.e., the relative contributions of two natural regeneration recruitment modes) of woody plants in forests with various biotic and abiotic factors resulting from different disturbance regimes (e.g., logging intensities; see Winkler and Fischer 2001; Ky-Dembele et al. 2007; Escandón et al. 2013, 2020). Except for change in the forest environment after thinning, changes in seed rain and soil seed banks of dominant tree species vary between stand structure managements and logging intensities. Moderate intensity of selective logging promotes seed production, whereas heavy selective logging causes a lack of mother trees, and consequently, results in failure of seed regeneration (Gavin et al. 2015; Gagné et al. 2019). The response of sprouts to selective logging is significantly or insignificantly affected by logging severity. For example, *Acer saccharinum* and *Ulmus americana* show higher probabilities of sprout presence under conditions in which the residual basal area is $2.0 \text{ m}^2 \text{ ha}^{-1}$, compared to $8.0 \text{ m}^2 \text{ ha}^{-1}$ conditions (Knapp et al. 2017), whereas in *Quercus pagoda*, few differences between logging severity treatments were observed regarding sprouting success, survival and number of sprouts per stump (Lockhart and Chambers 2007). In African savannas, compared to root suckers (4%), coppices (5%), water sprouts (2%) and layering (less than 1%), sexual reproduction is the dominant regeneration mode after selective cutting, indicating that seedlings are predominant (88%) (Ky-Dembele et al. 2007). Thus, examining the relative contribution of these two regeneration modes may help determine promotion modes of the natural regeneration of dominant tree species and predict the development directions of secondary forests. However, little is known about the trade-off between seed and sprout regeneration in secondary forests after logging.

In this study, we investigated the early stages of seed regeneration (including seed rain, soil seed bank and

1–3-year-old seedlings) and sprout regeneration (stump sprouts of 1–3-year-old seedlings), examined the relative importance of these two natural regeneration modes (by comparing densities of seedlings and sprouts), and predicted future development patterns in secondary forest stands subjected to two logging regimes (25% and 50% logging intensity) and in a control area over three continuous growing seasons immediately after logging. We hypothesized that regarding the early stage (i.e., first 3 years after logging), higher logging intensity (i.e., 50% logging treatment) would contribute to promoting both seed regeneration and sprout regeneration, as more suitable environmental conditions (e.g., increased light availability) should promote seed germination and seedling survival and simultaneously promote sprouts survival and increase stump sprout rates. Our study provides a novel understanding of the tending measures used in secondary forest management to sustain forest development in the context of NFPP.

Materials and methods

Site description

This study was carried out in the Changbai Mountain Range, located near the Qingyuan Forest CERN, National Observation and Research Station in Northeast China (41° 51' N, 124° 47' E; 600–800 m a.s.l.), with typical temperate broadleaved secondary forests. The study area experiences a temperate continental monsoon climate with warm, humid summers and dry, cold winters. The mean annual temperature is 4.7 °C, with a mean maximum temperature of 21.0 °C in July and a mean minimum temperature of −12.1 °C in January. The average annual rainfall is between 700 and 850 mm, 80% of which falls from June to August. The frost-free period lasts approximately 130 days, and the growing season is from early April to late October. The study area was historically covered by primary forests (i.e., mixed broadleaved and Korean pine forests) until the 1930s. However, the primary forests were degraded to secondary forests after decades of destructive timber exploitation and a large fire in the early 1950s (Lu et al. 2021). Secondary forests have become the major forest resource (accounting for more than 70%) in the Changbai Mountain Range. A mixture of broadleaved tree species dominated by *Acer mono* (AM), *Acer pseudosieboldianum* (AP), *Cornus controversa* (CC), *Fraxinus mandshurica* (FM), *Fraxinus rhynchophylla* (FR), *Juglans mandshurica* (JM), and *Quercus mongolica* (QM), and mosaic stands of *Pinus koraiensis* and *Larix* spp. occurred at the selected secondary forest stands at Qingyuan Forest CERN; no invasive tree species were present in this area (Mao et al. 2007; Zhu et al. 2010, 2019; Wang et al. 2017). This type of secondary forest is representative of the Changbai Mountain Range. Tree species in the study area are listed in Table 1.

Logging intensity

Special approval of selective logging was obtained from the local forestry administration agency, but the experiment was still limited and can only be carried out in contiguous forest stands. The selective logging trial was executed in March 2017 in natural secondary forests with homogenous topography (north slope and slope gradient of 12–42%), which was relatively similar in terms of tree species and age of stands (Table 2). We investigated diameter at breast height (DBH), and residual tree species composition again after logging. The total logging area of the experimental site was 9.1 ha, which included 4.8 ha of high-intensity treatment with 50% of the basal area removal and residual stand density of 305 individuals ha⁻¹ (50% logging intensity) and 4.3 ha of moderate-intensity treatment with 25% of the basal area removal and residual stand density of 473 individuals ha⁻¹ (25% logging intensity). The control area of 9.1 ha was not logged, and the stand density was 608 individuals ha⁻¹. Defective, over-mature, and infected trees were eliminated first, and other mature trees were considered for logging to achieve adequate distribution of the remaining trees. We confirmed logging type by the ratio of logging intensity calculated by the number of trees removed and the basal area removed (NG ratio):

$$\text{NGratio} = \frac{N_{\text{removed}}/N_{\text{total}}}{G_{\text{removed}}/G_{\text{total}}} \quad (1)$$

where N_{removed} and N_{total} represent the number of trees removed and the number of trees before the removal. G_{removed} and G_{total} represent the basal area (m² ha⁻¹) removed and total basal area (m² ha⁻¹) before the removal. NG values > 1: selective logging is from below; NG values < 1: selective logging is from above (Gadow et al. 2012; Sukhbaatar et al. 2019). Besides, we used chainsaws rather than large machinery and only removed logged trees to avoid potential adverse effects on the soil, shrub, and herb layers during logging.

Investigation of the early stages of seed regeneration

Seed rain and soil seed bank investigation

In the first 3 years after logging (i.e., 2017–2019), the early stages of seed regeneration for dominant woody species were investigated. In each treatment plot, three parallel sampling line transects (10 m apart and 150 m long) were established. Thirty seed traps were installed 5 m apart along each line transect in early August 2017 to investigate seed rain (Fig. 1). Each trap (1 × 1 m) was supported by four PVC tubes 1 m above the ground and consisted of a 1 mm nylon mesh draped to form a deep pouch. This method has been widely used because the seeds collected in the trap can represent the seed state after primary dispersal, and the trap can prevent seeds

Table 1 Tree species information of selected stands in secondary forests

Species	Abbreviation	Type of value	Importance values in study area (%)	Existence form in the sample plots			
				Residual trees	Seeds	Seedlings	Sprouts
<i>Acer barbinerve</i> Maxim	AB	3	3.0	✓	✓	✓	✓
<i>Acer mono</i> Maxim	AM	1,3	14.2	✓	✓	✓	✓
<i>Acer pseudosieboldianum</i> (Pax) Komarov	AP	1,3	18.6	✓	✓	✓	✓
<i>Acer tegmentosum</i> Maxim	ATe	1,3	3.9	✓	✓		
<i>Acer triflorum</i> Komarov	ATr	1,3	–	✓	✓		
<i>Betula dahurica</i> Pall	BD	1	–	✓	✓	✓	✓
<i>Betula yphylla</i> Suk	BY	1	–	✓			✓
<i>Carpinus cordata</i> Bl	CCo	3	4.2	✓		✓	✓
<i>Cornus controversa</i> Hemsley	CC	3	*	✓	✓	✓	✓
<i>Corylus mandshurica</i> Maxim	CM	1	–	✓		✓	
<i>Cerasus serrulate</i> (Lindl.) G. Don ex London	CS	3	–	✓		✓	
<i>Fraxinus mandshurica</i> Rupr	FM	1,2	3.1	✓	✓	✓	✓
<i>Fraxinus rhynchophylla</i> (Hance) E. Murray	FR	1,3	3.2	✓	✓	✓	✓
<i>Juglans mandshurica</i> Maxim	JM	1,2	6.4	✓	✓	✓	✓
<i>Phellodendron amurense</i> Rupr	PA	1,2	–	✓		✓	
<i>Padus avium</i> Miller	PAv	3	–	✓		✓	
<i>Populus davidiana</i> Dode	PD	1	–	✓		✓	✓
<i>Pinus koraiensis</i> Siebold et Zuccarini	PK	1,2,3	–	✓		✓	
<i>Quercus mongolica</i> Fischer ex Ledebour	QM	1,2,3	12.1	✓	✓	✓	✓
<i>Ribes mandshuricum</i> (Maxim.) Kom	RM	1	–	✓		✓	
<i>Sorbus alnifolia</i> (Sieb. et Zucc.) K. Koch	SA	1,3	–	✓	✓	✓	
<i>Syringa reticulata</i> subsp. <i>amurensis</i> (Rupr.) P. S. Green & M. C. Chang	SR	1,3	–	✓		✓	✓
<i>Sambucus williamsii</i> Hance	SW	1	–	✓		✓	
<i>Tilia mandshurica</i> Rupr. et Maxim	TM	1,3	–	✓	✓		✓
<i>Ulmus davidiana</i> var. <i>japonica</i> (Rehd.) Nakai	UD	1	–	✓	✓	✓	✓
<i>Ulmus laciniata</i> (Trautv.) Mayr	UL	1,3	3.7	✓			✓

The type of value is determined according to Flora of China (www.iplant.cn). 1 = the economic tree species; 2 = the national protected plants; 3 = the ornamental tree species. Importance values in study area are cited from Mao et al. (2007)

* The importance value of CC is < 0.03, but it is also a major tree in study area (Zhu et al. 2010)

from splashing down and keep the seeds dry (Yan et al. 2016b). To determine the composition of the soil seed bank, composite samples (three combined samples per site) of forest floor litter and soil at 0–5 cm depth were collected within a distance of 0.5 m from each seed rain trap using a cutting ring with 70 mm diameter (Fig. 1). In total, 270 litter and soil samples were collected (90 samples per treatment).

From 2017 to 2019, seed rain traps and soil seed banks were monitored seven times, namely in October (the end of seed falling) 2017, 2018, 2019; May (at the beginning of the growing season) and August (at the peak of seed falling) in 2018 and 2019. After each monitoring, litter (collected from traps and from the ground) and soil samples were transported to the laboratory. Then, all seeds in the samples were separated, counted, and identified to

species level on the basis of our previous study (Yan et al. 2019).

Seedling recruitment investigation

To monitor seedling emergence, survival and growth, 270 quadrats were monitored. We randomly selected 10 seed traps in each line transect of three treatments to arrange three 1 × 1 m quadrats (30 quadrats in each transect) on the ground in three different directions (left, right, and downhill) at the distance of 0.5 m from each trap (Fig. 1). In August 2017, all 1-year-old seedlings germinated from seeds produced in the previous year were identified and tagged. The same investigation and review of seedling quadrats was performed in August 2018 and 2019. Missing seedlings were presumed dead.

Table 2 Basic information of pre- and post-logging stands in secondary forests

Pre-logging		Total stands	
Age (year)		~ 60	
Mean DBH (cm)		21.26 ± 0.72	
Diameter range (cm)		6.1–48.4	
Density (trees ha ⁻¹)		597	
Basal area (m ² ha ⁻¹)		21.18	
Tree species composition (%)		AM (30), QM (20), JM (20), FM (10), Other species (20)	
Post-logging immediately in March 2017	Logging intensity		
	0% (Control)	25%	50%
Geographic information	41° 50' 19" N, 124° 47' 56" E	41° 50' 20" N, 124° 48' 6" E	41° 50' 18" N, 124° 47' 49" E
Slope (%)	16–29	14–42	12–32
Logging area (ha)	9.1	4.3	4.8
Mean DBH (cm)	20.9 ± 1.12	19.6 ± 0.92	19.2 ± 1.11
Diameter range (cm)	5.4–40	5.2–40	5.3–34.3
Density (trees ha ⁻¹)	608	473	305
Basal area (m ² ha ⁻¹)	20.36	15.98	10.34
NG ratio	–	0.85	0.96
Logging time	–	2017.03	2017.03
Tree species composition (%)	AM (40), QM (17), FR (12), BD (7), FM (6), Other species (18)	PK (23), JM (15), AM (16), CC (8), FM (8), Other species (30)	QM (31), AM (17), FR (11), SA (9), JM (6), Other species (26)

DBH: diameter of trees at breast height. The values of DBH are presented as means ± S.E.

The tree species composition is determined by percent of density (trees ha⁻¹)

AM = *Acer mono*; QM = *Quercus mongolica*; FR = *Fraxinus rhynchophylla*; BD = *Betula dahurica*; FM = *Fraxinus mandshurica*; PK = *Pinus koraiensis*; JM = *Juglans mandshurica*; CC = *Cornus controversa*; SA = *Sorbus alnifolia*

Sprout regeneration investigation

Only a few other sprout forms (root suckers, water sprouts, and layering) were found in a previous investigation, we thus considered only stump sprouts produced in logging stands. In August 2017, all stumps produced through logging were identified to species level and were permanently marked using aluminum foil. The basal diameter at the height of the stump and height of the stump above the ground were recorded. Then, the stumps were categorized as alive or dead (i.e., having at least one living sprout or not), and sprouts of all living stumps were counted. Sprout regeneration was monitored at the same time as seedlings were monitored. We only used stumps located within 2.5 m from the seed rain line transects for analysis (Fig. 1).

Environmental condition monitoring

In each treatment, we evenly placed two data loggers (WatchDog 1650 Micro Station; Spectrum Technologies Inc., USA) along every line transect to continuously monitor the environmental conditions from June 2018 to June 2019: photosynthetically active radiation (PAR), air temperature and relative air humidity 1.0 m above the

forest floor, and soil temperature and water content at 5 cm below the surface. The data of these environmental conditions were recorded once per hour during the non-growing season and twice per hour during the growing season. While investigating seedlings in August, we also measured litter depth at three points (i.e., at a centre point and two points along diagonal) in each seedling monitoring quadrat.

Data analysis

Variations in environmental conditions among the different logging intensities were tested using a one-way ANOVA.

The number of seeds (regarding both seed rain and soil seed banks) and seedlings was recorded and expressed as densities (seeds m⁻² or individuals m⁻²). To ensure sufficient sample size, the relationship between the density of seed rain and soil seed bank in 2018 (the year for seed masting) was determined by fitting a linear regression for each logging intensity. Seeds of all species and of three major trees accounting for the major proportion in seed rain (Tables 1, 4; *Cornus controversa* (CC), *Fraxinus*



mandshurica (FM) and *Quercus mongolica* (QM)) were assessed.

The importance value (IV) was calculated as follows to examine species compositions among different logging intensities and years after logging:

$$IV = (\text{relative density} + \text{relative frequency} + \text{relative coverage})/3 \times 100\%, \tag{2}$$

$$\text{Relative density} = \text{density of a species (individuals m}^{-2}\text{)}/\text{total density of all species (individuals m}^{-2}\text{)}, \tag{3}$$

$$\text{Relative frequency} = \text{frequency of a species (the number of times)}/\text{total frequency of all species (the number of times)}, \tag{4}$$

$$\text{Relative coverage} = \text{coverage of a species (m}^2\text{ha}^{-1}\text{)}/\text{total coverage of all species (m}^2\text{ha}^{-1}\text{)} \text{ (Lu et al.2019)}. \tag{5}$$

The conversion rate of 2- or 3-year-old seedlings was calculated as the density of 2- or 3-year-old seedlings divided by the density of 1- or 2-year-old seedlings in the previous year. Sokal and Sneath similarity indices regarding species composition between seed rain

Table 3 Basic information and survival condition of predominant stumps (stump number ≥ 4) for the 25% (25% of the basal area removal) and 50% (50% of the basal area removal) logging intensities

Species	Abbre- viation	25% logging intensity						50% logging intensity						
		Mean stump diameter (cm)	Mean stump height (cm)	Number of stumps	Stump sprout rate (%)	Number of survival stumps		Mean stump diameter (cm)	Mean stump height (cm)	Number of stumps	Stump sprout rate (%)	Number of survival stumps		
						2017	2018					2019	2017	2018
<i>Acer mono Maxim</i>	AM	9.5	14.6	25	92	23	23	23	6.8	17.4	22	22	21	21
<i>Acer pseudobaldianum</i> (Pax) Komarov	AP	9.0	6.4	6	100	6	6	6	11.8	14.8	4	4	4	3
<i>Fraxinus rhynchophylla</i> (Hance) E. Murray	FR	21.8	14.4	4	75	3	3	2	19.8	43.1	6	6	6	6
<i>Juglans mandshurica</i> Maxim	JM	34.5	39.6	12	33	4	4	3	28.1	56.8	6	5	3	3
<i>Quercus mongolica</i> Fischer ex Ledebour	QM	14.9	10.5	10	80	8	6	6	21.3	29.5	26	20	16	13
All species		16.3	20.7	81	74	60	55	53	21.7	27.4	79	65	55	49
Living stumps survival rate		–	–	–	–	100%	92%	88%	–	–	–	100%	83%	74%

and contemporaneous soil seed bank in 2017 and 2018, respectively, and between soil seed bank and correspondingly germinated seedlings (using the data of seeds in May and seedlings in August of the same year in 2018 and 2019, respectively) were calculated as follows:

$$I = 2c/(a + b), \quad (6)$$

where I is the similarity index. a is the total number of species in seed rain/soil seed bank, b is the total number of species in soil seed bank/germinated seedlings, and c is the number of common species in both seed rain and seed bank or in both soil seed bank and germinated seedlings (Sokal and Sneath 1963).

The mean density of sprouts (individuals m^{-2}) per year was calculated using data obtained from each transect (150 m long and 5 m wide) (Fig. 1). Stump sprout rate, stump survival rate, and sprouting probability of each species were calculated only for the predominant stumps (stump number ≥ 4) at each logging intensity (Table 3).

$$\text{Stump sprout rate} = \frac{\text{number of living stumps of one species}}{\text{total number of stumps of this species}}. \quad (7)$$

$$\begin{aligned} \text{Stump survival rate} \\ = \frac{\text{number of living stumps in 2018 or 2019}}{\text{number of living stumps in 2017 when the experiment began}}. \end{aligned} \quad (8)$$

Logistic regressions were used to analyse the relationships between the probability of an individual tree sprouting and stump diameter, stump height, and logging intensity in one growing season after logging.

Before analyses, all data were tested for normality and homogeneity of variances, and data were transformed if necessary. We used a two-way ANOVA to examine the effects of logging intensity, time effects of logging, and their interaction on the density of seed rain, soil seed bank, seedlings (with regard to all species and to CC, FR, QM) and sprouts, the similarity indices of species composition, and the number of sprouts per stump regarding the predominant stumps (stump number ≥ 4). When the effect was significant, a least significant difference post-hoc test was used to test differences between logging intensities and investigation times, and Student's t -test was used to compare differences in density of seedlings and sprouts. All statistical analyses were performed using with IBM SPSS (version 24.0; IBM Corp., Armonk, NY, USA), and differences were considered significant at $P < 0.05$.

Results

Environmental conditions

PAR and soil temperature varied significantly between treatments ($P < 0.05$) (Fig. 2a). PAR was significantly

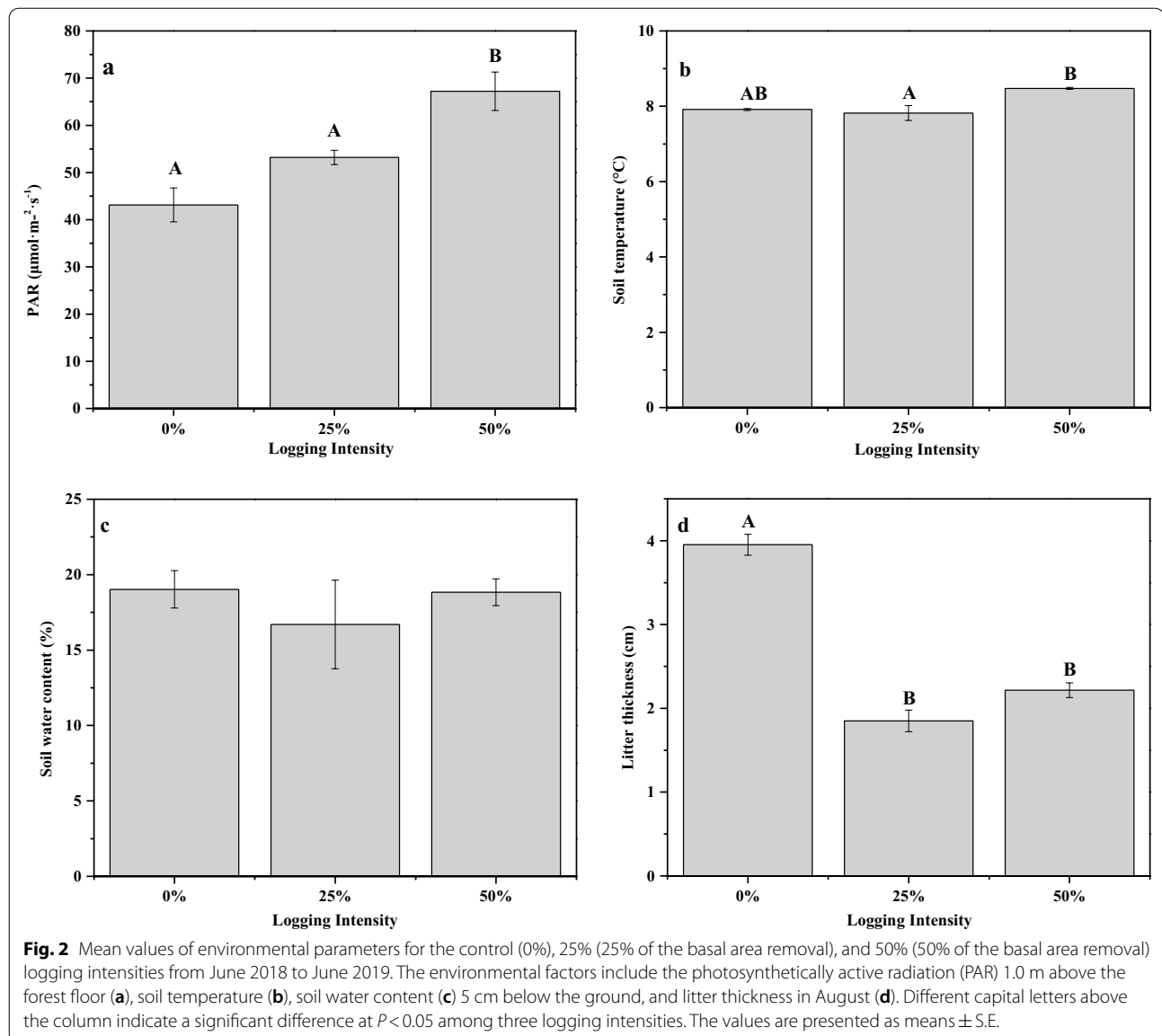
higher under 50% logging ($67.22 \mu\text{mol m}^{-2} \text{s}^{-1}$) than under 25% logging ($53.20 \mu\text{mol m}^{-2} \text{s}^{-1}$; $P = 0.023$) and the control treatment ($43.14 \mu\text{mol m}^{-2} \text{s}^{-1}$; $P = 0.002$) (Fig. 2a). Soil temperature was the highest under 50% logging (8.47°C), which was significantly higher than that in the 25% logging treatment (7.82°C ; $P = 0.014$) (Fig. 2b). No significant difference in soil water content was observed between the three treatments (Fig. 2c). The litter layer was significantly thicker in the control stands than in the two logging treatments ($P < 0.001$) (Fig. 2d).

Early stages of seed regeneration

The seed rain comprised 14 woody species belonging to 9 families and 9 genera, and the soil seed bank contained 9 species of 6 families and 6 genera. Regarding seedlings, 21 woody species were observed which belonged to 13 families and 18 genera (Tables 4 and 5). *Betula dahurica* (BD) was well represented in seed rain, and QM was one of the most common seedlings (Tables 4 and 5). FM, FR, and CC were also dominant in the early regeneration stages (Tables 4 and 5). The species number of seedlings was the lowest in the control stand and increased after logging (Tables 4 and 5).

The fluctuation tendency of density was similar in the soil seed bank and seed rain among different logging intensities and years of investigation. Only seed rain density was significantly affected by logging intensity and years after logging ($F = 13.125$, $df = 2$, $P < 0.001$; $F = 23.916$, $df = 2$, $P < 0.001$). The seed density in the seed rain of 2018 (mast seeding) was the highest among all treatments, followed by those of 2017 and 2019 ($P < 0.001$) (Fig. 3). Regarding logging treatments, seed densities were ranked as follows: control $> 50\% > 25\%$, and the difference between 0% and 25% logging was significant ($P < 0.001$) (Fig. 3). Only the factor 'years after logging' significantly influenced seedling density ($F = 7.190$, $df = 2$, $P < 0.001$), and seedling density in 2018 and 2019 was higher than that in 2017 (Fig. 4). In 2019, 1-year-old seedling density was the highest in the control stands and by far exceeded those of the 25% and 50% logging treatments (7.6% and 49.2% of the control, respectively) (Fig. 4). Conversely, the rank of 3-year-old seedling densities was 50% (16.2%) $> 25\%$ (1.34%) $> 0\%$ (1.13%) (Fig. 4). The 2-year-old seedling conversion rate increased with logging intensity, from 15.35% in the control to 44.65% under 25% logging to 72.01% under 50% logging. The 3-year-old seedling conversion rate was 37.50% in control stands and 100% and 80.95% under 25% and 50% logging, respectively.

Significant positive correlations were observed between seed rain and soil seed bank for all woody species under 25% and 50% logging, CC in the control and 25% logging, QM in the control and 50% logging, and FM in the control stand (Fig. 5). No significant correlation of seedling

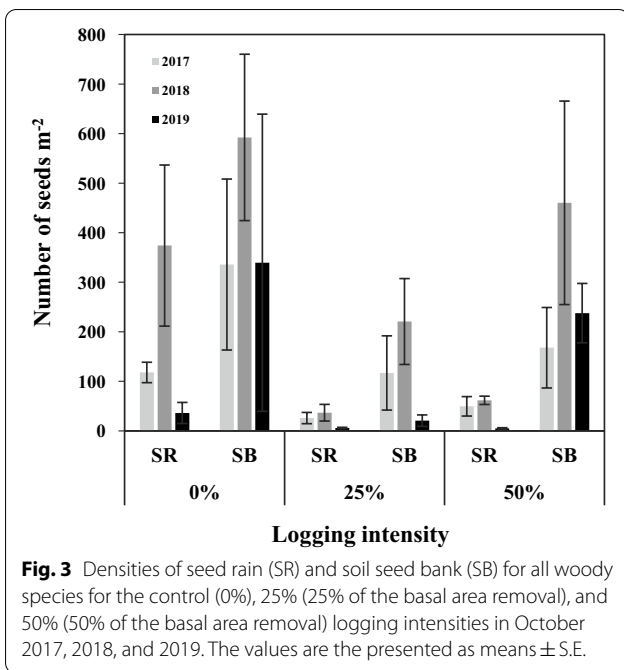


and soil seed bank density was observed. According to the two-way ANOVA, the Sokal and Sneath similarity index in species composition between seed rain and soil seed bank was significantly affected by logging intensity ($F=3.901$, $df=2$, $P=0.049$), thus the similarity index decreased with increasing logging intensity, from 0.75 in the control stand to 0.52 under 50% logging. The factor ‘years after logging’ significantly affected on the similarity index between the soil seed bank and regenerated seedlings ($F=5.294$, $df=1$, $P=0.040$), that is, the similarity index in 2019 (0.53) was substantially higher than that in 2018 (0.35).

Early stage of sprout regeneration

In total, 160 stumps were recorded in the two logging treatments, which belonged to 10 families, 12 genera, and

15 species, and AM, QM, JM, AP, and FR stumps were predominated (at >4 stumps). The stump sprout rates were high ($>75\%$), except for those of JM under 25% logging (33%), and stump sprout rates under 50% logging were almost consistently higher than those under 25% logging (Table 3). Of the 126 living stumps, 125 produced sprouts in 2017, but only one stump produced sprouts in 2018 (Table 3). Stump survival rates under 25% logging were higher than those under 50% logging in 2018 (92% vs. 83%) and 2019 (88% vs. 74%) (Table 3). The logistic regression of stump sprouting probability was used only regarding QM and AM, and stump diameter, stump height, and logging intensity did not significantly predict stump sprouting probability ($P > 0.05$). ‘Years after logging’ significantly influenced the density of sprouts



($F=4.042$, $df=2$, $P=0.046$), that is sprout density decreased by years, and the density in 2017 was significantly higher than that in 2019 ($P=0.016$) (Fig. 4).

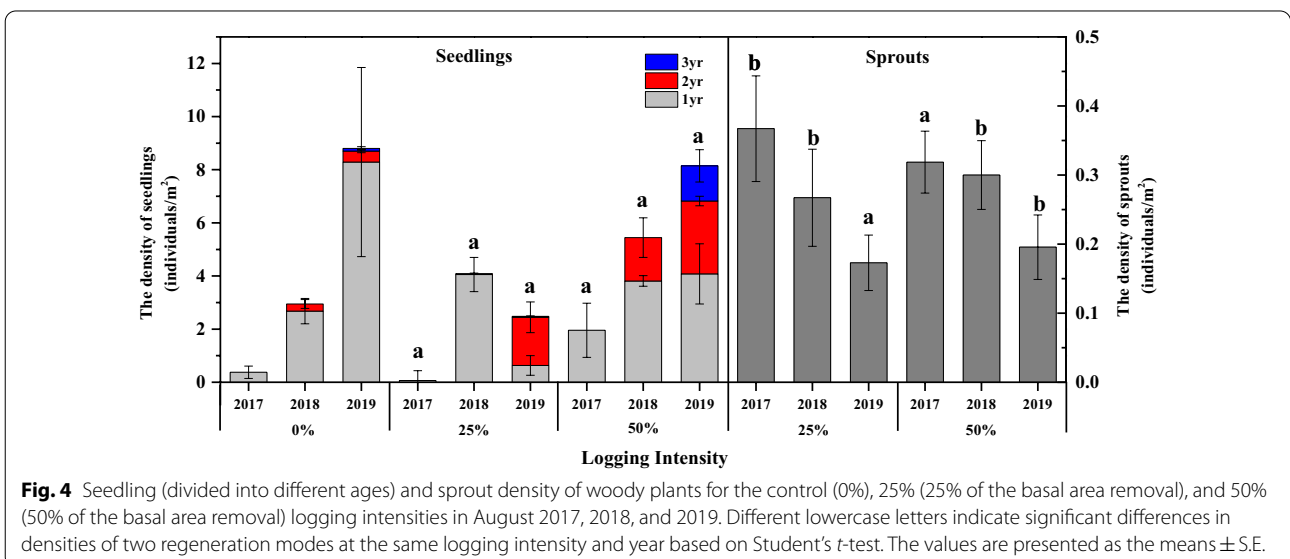
Relative importance of two regeneration modes after logging

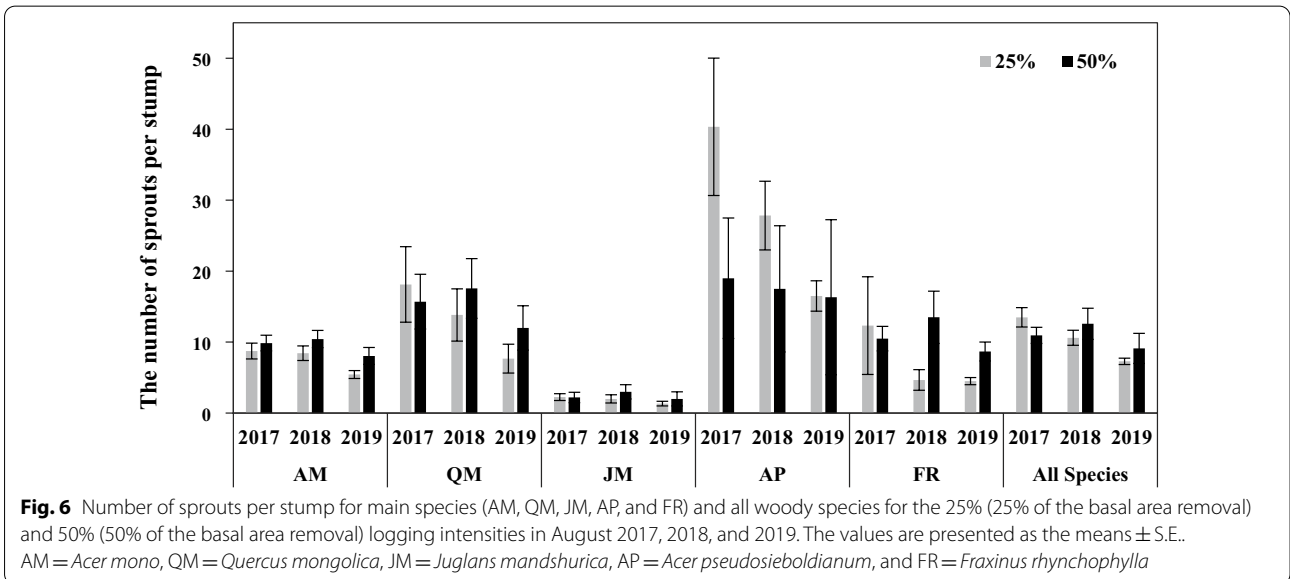
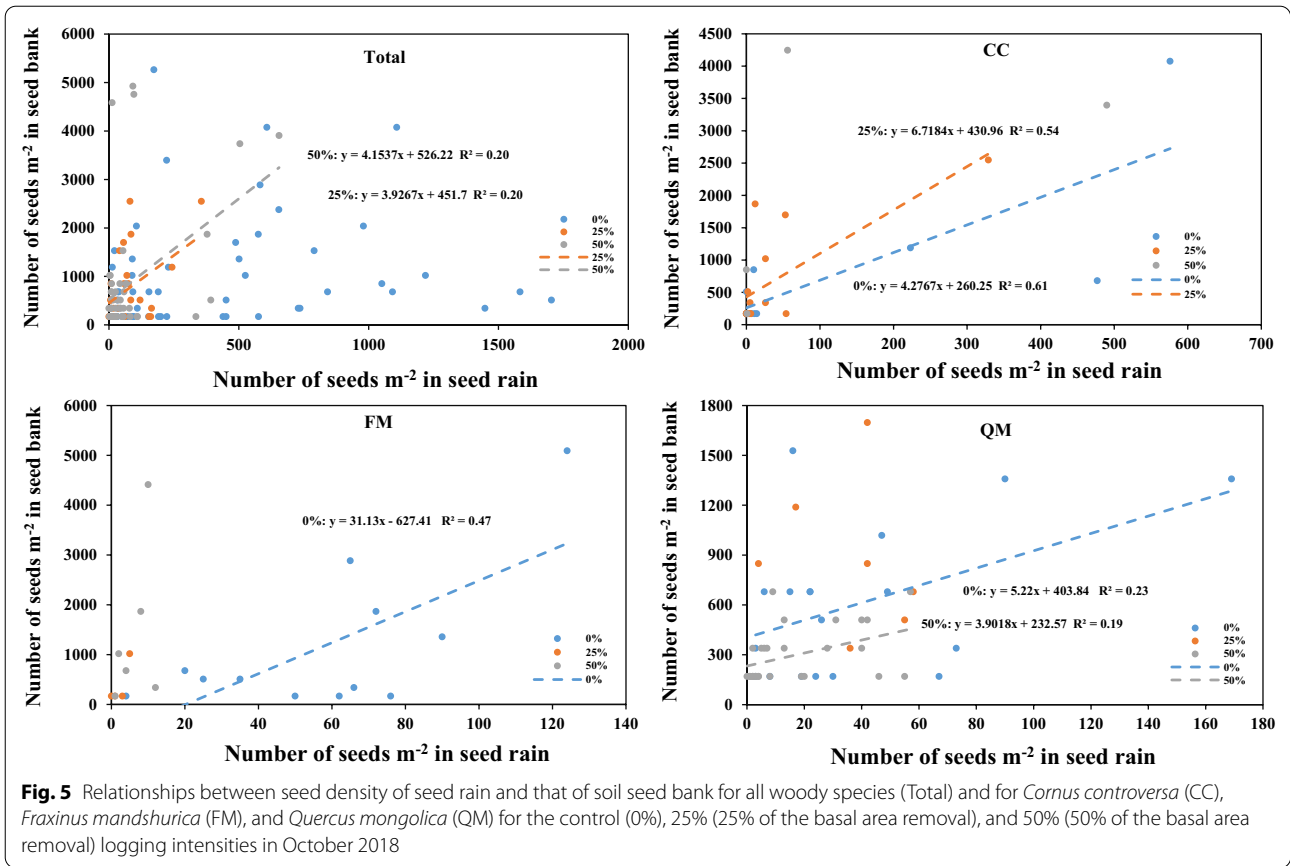
Student’s t test showed that except for 25% logging in 2017 and 2019 and 50% logging in 2017, the density of seedlings was significantly higher than that of stump sprouts ($P=0.005$ under 50% logging in 2017; $P<0.001$ in other cases). During the 3 years of investigation, the

density of seedlings in the 50% and 25% logging treatments exceeded that of sprouts by more than 41.65- and 15.31-fold, respectively. Seedling density increased with growth rate from 679% in 2018 to 199% in 2019 in the control treatment, 6033% in 2018 and – 40% in 2019 under 25% logging; and 178% in 2018 and 50% in 2019 under 50% logging (Fig. 4). The decrease rate of sprout density under 25% and 50% logging was 27% and 6% in 2018, and 37% and 33% in 2019, respectively (Fig. 4). The number of sprouts per stump constantly decreased with years after logging ($F=4.078$, $df=2$, $P=0.045$), and were ranked as follows: third year (8.20) < first year (12.22) < second year (11.60) (Fig. 6).

Seedling densities of CC and QM differed significantly between logging intensities ($F=27.173$, $df=2$, $P<0.001$; $F=10.751$, $df=2$, $P=0.001$, respectively) and years ($F=17.118$, $df=2$, $P=0.001$; $F=5.190$, $df=2$, $P=0.017$, respectively), i.e. for CC: 25% ≈ 50% > 0% and 2018 > 2019; for QM: 50% > 25% > 0% and 2019 > 2018 ≈ 2017. The interactions between logging intensity and years were significant for FR ($F=3.928$, $df=4$, $P=0.049$), and FR seedling density in control stands was higher than that in logging stands in 2019.

The combination of stump survival rates and sprout number per stump was used to characterise sprout regeneration ability. The stump survival rate was maintained at a higher level and ranked as follows in 2019: AM (97.8%) > AP (90%) > FR (88.9%) > QM (67.9%) > JM (66.7%). Sprout numbers decreased by year and markedly differed between woody species, ranging from 31.8 ± 7.3 (AP) to 2.2 ± 0.4 (JM) in the first year after logging, from 23.7 ± 4.6 (AP) to 1.56 ± 0.5 (JM) in 2018, and from 14.8 ± 3.5 (AP) to 0.89 ± 0.35 (JM) in 2019 (Fig. 6). Separate analysis of sprout numbers per stump showed that





only AM was significantly affected by logging intensity and by ‘years after logging’ ($F = 4.257$, $df = 1$, $P = 0.041$; $F = 4.412$, $df = 2$, $P = 0.014$, respectively), that is, the

number of sprouts per stump in the 25% treatment (6.11) was significantly lower than that in the 50% treatment (8.80), and 2017 (7.64) \approx 2018 (7.99) > 2019 (5.39) (Fig. 6).

Discussion

Early stages of seed regeneration responding to logging

Logging directly changes the stand structure and micro-environmental conditions and consequently, influences forest regeneration (Zhang et al. 2018). The NG ratios indicated a slight tendency towards a selective logging from above, which indicated that relatively more dominant trees had been removed (Sukhbaatar et al. 2019) and more environmental resources had been released. In the present study, the responses of each stage of early seed regeneration (i.e., seed rain, soil seed bank, and seedling emergence/survival) to logging intensity were inconsistent. Logging tended to decrease the densities of seed rain and soil seed bank, but increased seedling density by promoting seedling survival. This facilitating effect lasted longer after high-intensity logging (i.e., 50%).

1. Compared with the control treatment, in secondary forests, the density of seed rain decreased substantially after logging, and the lowest density of seed rain occurred under 25% logging intensity (Fig. 7A). This finding was consistent with the research of Huang et al. (2016) showing that logging led to a decrease in total seed production per hectare. Although logging can increase the seed production in some woody species, it reduces the number of masting trees at the same time (Lombardo and McCarthy 2008). In the current study, this increase in seed production did not balance the seed decrease caused by the reduction of masting trees. The annual density change of seed rain is due to seed masting, which depends on annual fluctuations affected

by the climate and biological rhythms rather than by logging intensity (Koenig et al. 2010; Tiebel et al. 2020). Furthermore, the species composition of stands also plays a crucial role in the variation of seed rain density at different logging intensities (Gioria et al. 2012). The density of residual BD trees was higher in unlogged stands than in logging stands (Table 2), and BD seeds were minute and numerous, which led to the highest seed density of BD in seed rain of unlogged stands in the masting year (317.52 seeds m⁻² in 2018, Table 4).

2. The density of the soil seed bank was more stable after logging than seed rain. We detected no difference in density in the soil seed bank among the three treatments, which was consistent with previous research on secondary forests with gap treatment: the preponderance of the control treatment regarding seed rain was not reflected in the soil seed bank (Yan et al. 2012). This is because selective logging can promote species diversity and increase the proportion of dispersed seeds in the soil compared to those in control stands (Bordon et al. 2019), as observed in the relationship between seed rain and soil seed bank of all species (Fig. 5). The similarity index in species composition between seed rain and soil seed bank decreased with logging intensity for the same reason; the open stands formed by logging facilitated seed dispersal. In addition, seed dispersal characteristics differed between species, leading to various relationships between seed rain and soil seed bank (Fig. 5). Moreover, populations of PA, one of the national secondary protected species, regenerated faster in 25% logging stands because of

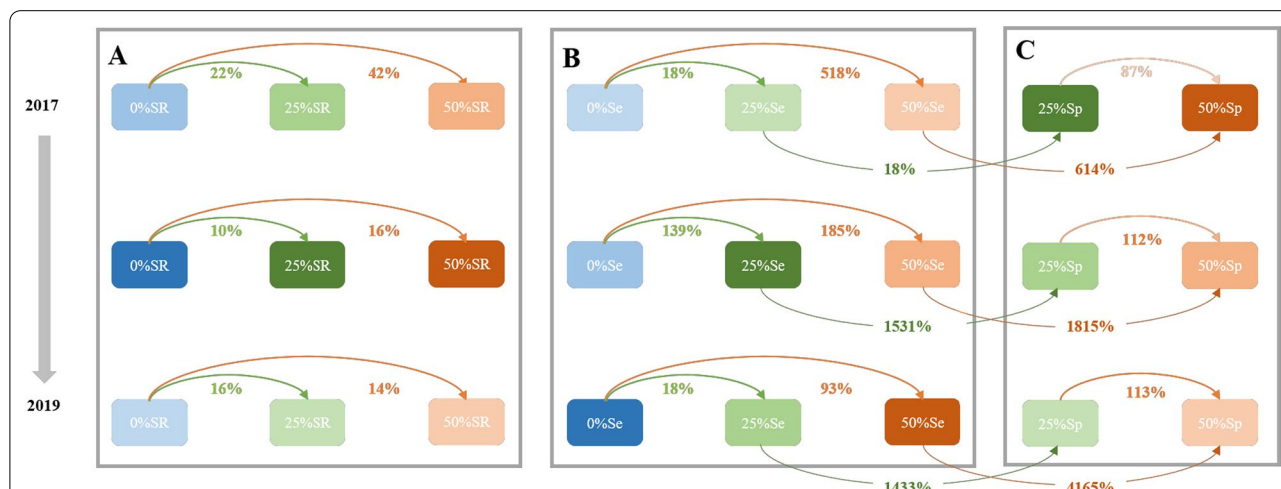


Fig. 7 Conceptual framework of the conclusion. Only results that differ between logging treatments are shown in this figure. **A–C** are the effects of logging intensity on the density of seed rain (SR), seedlings (Se) and sprouts (Sp), respectively. Blocks from top to bottom represent the different years after logging (from 2017 to 2019), and the color gradation of blocks from dark to light color indicates decreasing size of density in the same logging intensity treatment. The percent on pointers is a ratio between the density of seed rain/seedlings/sprouts in control (0% logging intensity), 25% logging intensity (25% of the basal area removal) and 50% logging intensity (50% of the basal area removal), and the proportional relationships between seedling and sprout density at the same logging intensity

the contribution of the soil seed bank after logging disturbance, according to the IV (Table 5). Seedlings may thus germinate from the permanent soil seed bank to a substantial extent, as we did not observe PA in the seed rain and soil seed bank during the study period.

3. According to Lu et al. (2019) and Donoso et al. (2020), selective logging exerts a positive effect on forest recruitment by increasing seedling density in hardwood forests compared to unlogged treatments. However, in the present study, seedling density of broadleaved woody species in both unlogged and 50% logged stands continuously increased during the investigation years and was higher compared with that under 25% logging intensity (Figs. 4 and 7B). In unlogged stands, high seedling density may be due to sufficient seed production (i.e. the highest density of seed rain and soil seed bank, Fig. 3); however, only a few seedlings survived in the control stands with lower light availability, greater litter depth, and competing vegetation (Fig. 2) (Lu et al. 2018). This result indicated that the recruitment limitation of secondary forests without management (e.g., logging) was the establishment limitation of seedlings and not source limitation or dissemination limitation, which was in line with the results of Zhu et al. (2012). In the 50% logging treatment, brighter microsite conditions (in relation to PAR), higher soil temperatures, and reduced litter depth favored seed germination and seedling establishment (Fig. 2) (de Avila et al. 2017). In 25% logging stands, the lack of seed availability was the primary reason for the low seedling density (Figs. 3 and 4), and a second reason was fast closure of the canopy after low-intensity logging. Furthermore, the limitation of light availability and increasing competition for limited resources resulted in low survival rates; therefore, seedling recruitment at 25% logging intensity was short-lived (de Avila et al. 2017). The tree species composition may also lead to different regeneration states between two logging intensities. For example, Sukhbaatar et al. (2019) found that lower logging intensity promoted Scots pine regeneration while higher logging intensity promoted broadleaved tree regeneration. Thus, more attention should be paid to different regeneration requirements of each tree species. Seedling species richness increased with logging intensity, which may be attributed to post-logging environmental conditions which are more favourable (e.g., higher light availability) for seed germination of different woody species in the study area (Gang et al. 2015). It is worth noting that the relationship between the soil seed bank and seedlings was irrelevant, even though the density of seeds and seedlings showed a certain relationship. A study of Yan et al. (2012) in the same area also found that the contribution of the seed bank to seedlings was less than 10%, with significant differences between spe-

cies, which is contributed to fact that the determination factors of seed germination are associated with micro-environment, rather than with seeds abundance. Thus, despite logging greatly decreased seed rain and soil seed bank density, it helped to reduce limitations of seedling survival.

Early stages of sprout regeneration responding to logging

Sprouting is an extremely common life history stage in woody angiosperms, and disturbance is one of the main elicitors of sprouting (Splichalova et al. 2012). Tredici (2001) found that many woody species can produce sprouts at the stem of living trees in undisturbed forests, however, this phenomenon is so rare that it can be ignored in our investigation. Xue et al. (2014) suggested that these sprouts at stem base are accidental events and are likely a survival strategy rather than a regeneration strategy. In general, secondary forests exhibited powerful sprouting ability, and only approximately 22% of the stumps did not produce sprouts in the present study. The high stump sprout rate may partly ascribe to the fact that the logging season (March) was during the dormant period of the trees, which benefited to preserve more NSC in the root system to support sprouts germination (Xue et al. 2014). Although all species examined in the current study can produce sprouts, not all stumps did. This is because environmental conditions and tree species characteristics of woody species exert combined effects on stump sprouts (Keyser and Loftis 2015). The brighter light condition and higher soil temperature have proved to stimulate stump sprouting (Knapp et al. 2017); thus, the stump sprouting rate under 50% logging was higher than that under 25% logging intensity. The stump survival rate was shown in many studies to be affected by logging intensity (Atwood et al. 2009); however, the stump survival rate under 25% logging intensity was only slightly higher than that under 50% logging in current study, and these inconsistent results were related to specific site conditions. The density of stump sprouts showed no evident differences between 25 and 50% logging intensity but decreased markedly with time (Figs. 4 and 7C), suggesting that this decline is mainly caused by self-thinning (Escandón et al. 2013). Stump sprouts self-thinning occurred over time, and the number of sprout clumps finally remained constant, due to the exhaustion of carbohydrate reserves of the parent plant and competition for nutrients during sprout development (Moyo et al. 2015). For example, the number of water oak sprouts decreased during the first 4 years and stabilised at approximately four sprouts per stump (Li et al. 2013).

Trade-offs between two natural regeneration recruitment modes

The trade-offs between regeneration modes typically depend on environmental conditions, species, and

disturbance characteristics (Ky-Dembele et al. 2007; Wang et al. 2013). Seed regeneration was the dominant recruitment mechanism under logging and in unlogged stands during the first 3 years in our study, and sprout regeneration acted as a recruitment assurance after logging and was rare in unlogged stands. The relative importance of the two regeneration modes in different recovery stages of a logged *Quercus variabilis* forest showed that stump sprouts contributed more to their recovery after disturbance (5, 10 and 20 years after logging) and seedlings were beneficial in the unlogged stands, but the significance of sprout regeneration declined with extended post-logging time (Xue et al. 2014). By contrast, in our study, sprouts density was higher than that of seedlings only in the 25% logging treatment in 2017 (i.e., the first year after logging), but was substantially lower than that of seedlings in the other 2 years, and the difference in relative contribution of these two regeneration modes varied markedly in the 50% logging treatment (Figs. 4 and 7). This difference may be due to the divergence of the investigation period, as our investigation covered the first 3 years after logging, which for seedlings was the period of the highest vulnerability to varying environmental conditions. However, the varying trends of sprout regeneration in these two studies were similar, that is, both sprout density and sprout number per stump declined with increasing time after logging. Understanding the long-term effects of logging intensity based on continuous monitoring is thus urgently required.

The regeneration type strongly affects the early development of disturbed forests, because seedlings and sprouts rely on different energy sources, that is, sprouts absorb nutrients and water through the existing root system of the stump, whereas seedlings obtain resources directly from soil, and thus affect the resources distribution and response to the environment (Pietras et al. 2016). In general, the importance of sprouts will increase over the next few years after logging, because the seedling density growth rate slowed down and the sprout density decrease rate remained stable. In addition, regeneration patterns after logging differed among species because of differences in seed traits, germination characteristics, suitable seed germination, seedling survival conditions, and vigorous sprouting (Yan et al. 2012; Wang et al. 2016; Zhang et al. 2018). According to the relative contributions of seed regeneration and sprout regeneration, dominant woody species were mainly divided into three groups, i.e., seed regeneration preference (BD, CC and FM with high densities of seeds and seedlings after logging), sprout regeneration preference (AM and AP with strong sprouting capacity and failure in seed regeneration), and no preference (QM, FR and JM with relatively good status in both seed regeneration and sprout regeneration).

Study limitations

In the context of the NFPP, one major limitation of this study was the limited number of logging plots, and each treatment level was only allowed to be implemented at one site. To circumvent this limitation, we established three transects per logging treatment to satisfy the analysis requirement. In addition, seed masting occurred at an interval of 3–5 years in the study area, which can result in interannual differences in seed rain and the consequent regeneration process. This was evidenced by significant interannual variation of similar indices in species composition between soil seed banks and seedlings in the first 3 years after logging (i.e., 2017–2019). Thus, a longer investigation period (> 10 years) is required to assess long-term effects of these change factors. Despite these limitations, we believe that the results of the current study allow inferring the impacts of logging on early natural regeneration in secondary forests in Northeast China.

Conclusion

The results of the present study revealed that seed regeneration, rather than sprout regeneration was the predominant regeneration mechanism of woody species after logging in the first 3 years. The promoting effect on seedling recruitment at higher logging intensity (50%) was stronger than that at low logging intensity (25%) and in the control treatment (0%). Sprout regeneration was triggered by disturbance, and sprout density was not affected by logging intensity; however, 50% logging intensity was beneficial for stabilising sprout density with a lower decline rate. These results support our hypothesis that in the first 3 years after logging, higher logging intensity contributes to promoting seed regeneration and sprout regeneration. We found that logging is a key method for promoting seed regeneration of BD, CC, and FM (species with seed regeneration preference), sprout regeneration of AM and AP (species with sprout regeneration preference) and both regeneration modes in QM, FR, and JM (no preference). Our findings provide new insights into restoring of temperate secondary forests under NFPP, for example, to promote sprout regeneration, sprout preference species should be preferentially logged; to promote seed regeneration, logging intensity should be as high as possible to achieve higher seedling recruitment. Overall, our findings demonstrated the effects of logging on seed regeneration, sprout regeneration, and their relative contributions during the first 3 years after logging in secondary forests, and understanding the long-term effects of logging intensity based on continuous monitoring is required.

Appendix

See Tables 4 and 5.

Table 4 The seed density of woody species in the seed rain and soil seed bank in October 2017, 2018 and 2019 (seeds m⁻²)

Species	Abbre-viation	Density of seed rain									Density of soil seed bank								
		0% logging intensity			25% logging intensity			50% logging intensity			0% logging intensity			25% logging intensity			50% logging intensity		
		2017	2018	2019	2017	2018	2019	2017	2018	2019	2017	2018	2019	2017	2018	2019	2017	2018	2019
<i>Acer barbinerve</i> Maxim	AB	-	0.03	-	-	-	-	0.46	-	-	-	-	-	-	-	-	-	-	-
<i>Acer mono</i> Maxim	AM	3.08	8.27	2.31	3.41	8.28	1.57	0.40	1.03	0.01	5.66	13.20	5.66	9.43	16.98	-	-	3.77	-
<i>Acer pseudosieboldianum</i> (Pax) Komarov	AP	-	0.14	0.01	-	1.42	0.03	-	2.20	-	-	-	-	-	5.66	-	-	11.32	-
<i>Acer tegmentosum</i> Maxim	ATe	-	0.14	-	-	0.49	0.36	-	0.13	-	-	5.66	-	-	-	-	-	-	-
<i>Acer triflorum</i> Komarov	ATr	-	5.43	-	-	0.07	-	-	0.01	-	-	-	-	-	-	-	-	-	-
<i>Betula dahurica</i> Pall	BD	52.89	317.52	6.07	6.67	4.92	0.63	4.44	31.14	0.41	11.32	135.81	-	-	-	-	-	-	-
<i>Cornus controversa</i> Hemsley	CC	3.98	6.30	-	10.10	14.97	0.03	0.53	6.59	-	33.95	88.66	1.89	35.84	105.63	-	54.70	96.20	-
<i>Fraxinus mandshurica</i> Rupr	FM	14.97	17.62	22.19	0.43	2.44	1.52	0.14	0.80	0.70	47.16	154.68	122.61	-	16.98	7.55	3.77	94.31	81.11
<i>Fraxinus rhynchophylla</i> (Hance) E. Murray	FR	36.33	6.52	4.93	2.87	0.58	1.48	40.18	8.06	3.68	237.67	73.56	203.72	69.79	5.66	1.89	109.40	160.33	154.68
<i>Juglans mandshurica</i> Maxim	JM	0.07	0.03	0.01	0.30	0.46	0.18	0.24	0.10	0.01	-	-	3.77	1.89	1.89	11.32	-	-	1.89
<i>Quercus mongolica</i> Fischer ex Ledebour	QM	6.53	12.02	0.61	2.18	3.10	0.04	3.63	11.04	0.17	-	120.72	1.89	-	67.91	-	-	94.31	-
<i>Sorbus alnifolia</i> (Sieb. et Zucc.) K. Koch	SA	-	0.03	-	-	-	-	-	0.04	-	-	-	-	-	-	-	-	-	-
<i>Tilia mandshurica</i> Rupr. et Maxim	TM	-	0.04	-	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ulmus davidiana</i> var. <i>japonica</i> (Rehd.) Nakai	UD	0.07	-	-	0.03	-	-	-	-	-	-	-	-	-	-	-	-	-	-

25% logging intensity = 25% of the basal area removal; 50% logging intensity = 50% of the basal area removal

Table 5 Importance values (%) of seedlings regenerated from seeds for woody species in August 2018 and 2019

Species	Abbreviation	0% logging intensity		25% logging intensity		50% logging intensity	
		2018	2019	2018	2019	2018	2019
<i>Acer barbinerve</i> Maxim	AB ²	–	–	–	0.74	–	–
<i>Acer mono</i> Maxim	AM ²	0.44	–	0.63	0.91	1.02	1.05
<i>Acer pseudosieboldianum</i> (Pax) Komarov	AP ²	0.87	0.77	0.61	0.69	2.42	3.40
<i>Betula dahurica</i> Pall	BD ¹	8.18	0.40	0.66	–	5.56	3.29
<i>Carpinus cordata</i> Bl	CCo ²	–	–	1.42	2.26	–	–
<i>Cornus controversa</i> Hemsley	CC ²	13.60	1.94	42.92	35.72	31.08	20.05
<i>Corylus mandshurica</i> Maxim	CM ¹	–	–	–	–	–	0.57
<i>Cerasus serrulate</i> (Lindl.) G. Don ex London	CS ¹	–	–	–	–	0.24	0.19
<i>Fraxinus mandshurica</i> Rupr	FM ²	6.74	10.39	2.60	4.79	0.92	2.13
<i>Fraxinus rhynchophylla</i> (Hance) E. Murray	FR ²	39.56	48.86	9.92	9.90	6.96	6.75
<i>Juglans mandshurica</i> Maxim	JM ¹	6.26	2.25	29.82	23.87	7.38	5.53
<i>Phellodendron amurense</i> Rupr	PA ¹	–	–	5.04	4.52	0.83	0.88
<i>Padus avium</i> Miller	PAV ³	–	–	0.51	1.66	–	–
<i>Populus davidiana</i> Dode	PD ¹	–	–	0.63	0.79	–	–
<i>Pinus koraiensis</i> Siebold et Zuccarini	PK ¹	–	–	0.36	1.17	–	–
<i>Quercus mongolica</i> Fischer ex Ledebour	QM ¹	22.86	35.38	2.48	8.57	37.22	51.10
<i>Ribes mandshuricum</i> (Maxim.) Kom	RM ³	–	–	–	0.46	–	–
<i>Sorbus alnifolia</i> (Sieb. et Zucc.) K. Koch	SA ¹	0.51	–	–	–	0.24	0.41
<i>Syringa reticulata</i> subsp. <i>amurensis</i> (Rupr.) P. S. Green & M. C. Chang	SR ²	0.49	–	–	0.36	0.55	0.39
<i>Sambucus williamsii</i> Hance	SW ¹	–	–	0.48	–	2.36	–
<i>Ulmus davidiana</i> var. <i>japonica</i> (Rehd.) Nakai	UD ¹	0.50	–	1.91	3.59	3.22	4.26

25% logging intensity = 25% of the basal area removal; 50% logging intensity = 50% of the basal area removal. The superscript numbers of abbreviation refer to the shade tolerance of woody species. 1: shade-intolerant species; 2: intermediate shade-tolerant species; 3: shade-tolerant species (Lu et al. 2019)

Abbreviations

NFPP: Natural Forest Protection Project of China; PAR: Photosynthetically active radiation; IV: Importance value; AM: *Acer mono* Maxim.; QM: *Quercus mongolica* Fischer ex Ledebour; JM: *Juglans mandshurica* Maxim.; FR: *Fraxinus rhynchophylla* (Hance) E. Murray; CC: *Cornus controversa* Hemsley; FM: *Fraxinus mandshurica* Rupr.; BD: *Betula dahurica* Pall.; AP: *Acer pseudosieboldianum* (Pax) Komarov; AB: *Acer barbinerve* Maxim.; Ate: *Acer tegmentosum* Maxim.; Atr: *Acer triflorum* Komarov; BY: *Betula yphylla* Suk.; CCo: *Carpinus cordata* Bl.; CM: *Corylus mandshurica* Maxim.; CS: *Cerasus serrulate* (Lindl.) G. Don ex London; PA: *Phellodendron amurense* Rupr.; PD: *Populus davidiana* Dode; PK: *Pinus koraiensis* Siebold et Zuccarini; PU: *Padus avium* Miller; RM: *Ribes mandshuricum* (Maxim.) Kom.; SA: *Sorbus alnifolia* (Sieb. et Zucc.) K. Koch; SR: *Syringa reticulata* subsp. *amurensis* (Rupr.) P. S. Green & M. C. Chang; TM: *Tilia mandshurica* Rupr. et Maxim.; UD: *Ulmus davidiana* var. *japonica* (Rehd.) Nakai; UL: *Ulmus laciniata* (Trautv.) Mayr.

Acknowledgements

We greatly thank Deliang Lu and Chunyu Zhu for their help in the field and laboratory and statistical analysis.

Authors' contributions

RL and QLY conceived the ideas and designed the study. RL, JX, JW and TZ collected field data. RL analyzed the data and led the writing of first draft of manuscript. QLY and JJZ substantially contributed to revising the manuscript. All authors read and approved the final manuscript.

Funding

This work was financially supported by the Strategic Leading Science & Technology Programme, CAS (XDA23070100), K. C. Wong Education Foundation (GJTD-2018-07), and Liaoning Revitalization Talents Program (XLYC1807102).

Availability of data and materials

The data sets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Received: 10 July 2021 Accepted: 20 January 2022

Published online: 04 February 2022

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