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ORIGINAL PAPER

Evaluation of regeneration potential of *Pinus koraiensis* in mixed pine-hardwood forests in the Xiao Xing'an Mountains, China

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Abstract: Large scale harvest of Korean pine (*Pinus koraiensis)* seeds as a food product in the mixed Korean pine-hardwood forest of northeastern China poses a serious threat to the sustainability and restoration of this endangered regional ecosystem. Seed collection over past decades greatly reduced the seed bank and subsequent seedling and sapling recruitment, and impacting a wide array of granivorous animals that rely on the pine seeds. We surveyed Korean pine seeds, including solid seeds (SS), insect consumed seeds (ICS) and other (animal) consumed (OCS) kernels, of the seed bank (forest floor and the top 10 cm of mineral soil), the seedlings and saplings from 1 m^2 sample plots in five forest types in Liangshui Nature Reserve (LNR) of the southern Xiao Xing'an Mountains in northeastern China to provide accurate information for assessing the Korean pine regeneration potential. The average number of pine seeds in the seed bank were 11.2 seeds/m^2, 9.1 seeds/m^2, 4.6 seeds/m^2, 1.1 seeds/m^2, and 0.2 seeds/m^2 in Korean pine-basswood forest, mixed Korean pine-hardwood forest, mixed conifer-hardwood forest, white birch forests, and oak forests, respectively. In the first three forest types, percentages of SS (potentially viable seeds) were 11.2%, 3.5% and 27.8%, respectively. The percentages of ICS (not viable seeds) were consistent at around 35%. The higher but variable percentages of OCS (not viable seeds) indicated high seed predation in these forests. Compared with other studies, we recorded higher percentages of seed damage, probably due to our survey approach and the increased depth of seed bank sampled in our study. Depletion of pine seeds in the seed bank greatly reduced seedling and sapling recruitment. Densities of pine seedlings varied from about 180 trees/ha in the mixed Korean pine-hardwood forest to about 5,400 trees/ha in the mixed conifer-hardwood forests and showed a high degree of spatial variation. Saplings were rare in the mixed Korean pine-hardwood forest, but ranged in the thousands in other forests. Large scale pine seed harvest has seriously threatened the sustainability of the mixed Korean pine-hardwood forest ecosystem. Scaling down the seed harvest or supplemental planting of pine saplings are urgently needed to maintain the health of the existing Korean pine forests and to restore this endangered ecosystem.

Keywords: *Pinus koraiensis*; seed bank; pine regeneration; seed predation

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Introduction

Mixed Korean pine (*Pinus koraiensis* Sieb. et Zucc.)-hardwood forests, the regional vegetation of Northeast Asia temperate zone, possess perhaps the highest plant diversity among the temperate forest ecosystems at similar latitudes in the northern hemisphere (Wang 1995). The forest distribution extends from 34°N in the south to 52°N in the north, and from 124°E in the east to 140°E in the west, and includes scattered distribution of forests on the Korean peninsula and in Japan (Kira 1991). Coverage of this forest ecosystem has declined and fragmented since the late 19th century due to large scale industrial logging, fire, agriculture development, and urbanization along with rapid human population increase and economic development of the region (Tian et al. 2008). Recent studies using remote sensing showed that more than 60% of the original mature mixed Korean pine-hardwood forests have been transformed to various stages of secondary succession, farmland, human settlements, roads and other land-use types, with a much higher percentage of loss in China than in neighboring countries (Li 1997). Because of its rapid decline/fragmentation, the mixed Korean pine-hardwood forest has been recognized as an endangered forest ecosystem (Yang and Xu 2003).

To restore this ever shrinking, highly fragmented forest ecosystem, regeneration ecology, including seed dispersal, germination and establishment, are research and management priorities. As a long lived, late successional species, Korean pine relies on rodents and birds to disperse its large, energy concentrated seeds (Xu 2001). Hutchins et al. (1996) reported that Korean pine seeds are dispersed mainly by red squirrels (*Sciurus vulgaris*) and Eurasian nutcrackers (*Nucifruga caryocatactes*). Both species hoard pine seeds in the shallow litter cover on the forest floor and in the organic matter rich top soil often less than 10 cm deep. The hoarded seeds are destined for dormancy, decay, consumption by animals, and germination (Baskin and Baskin 2001). Only those seeds hoarded in the top few centimeters of soil (<10 cm) achieve the best germination after varying lengths of dormancy, mostly about two winters (Liu 1988). The newly germinated seedlings are moderately shade tolerant, but suffer high mortality by grazers and other causes resulting in low survival to the sapling stage (Li et al. 1989). It takes 80−120 years for an established seedling to reach the canopy layer and mature (Wang 1995). To fully restore this ecosystem will require an even longer time for the forest to reach the uneven aged, mixed species structure and to achieve maximum biodiversity (Jin et al. 2005).

Korean pine seeds are a traditional food that is sold at attractive market prices by local people. With increasing human population in the region and the development of local economies, demand for pine seeds as market goods has constantly increased, and seed collection has intensified. Many trees of the remnant primary forests, even within protected areas, have been damaged during seed harvest. To halt further tree and forest damage, forest managers contract the trees to seed collectors in exchange for their protection of the trees (Ji et al. 2002). The high intensity of seed harvest is a direct threat to the restoration and sustainability of the ecosystem.

Some surveys revealed severe declines in pine regeneration caused by seed harvest (Ji et al. 2002; Jin et al. 2010). Liu (2004) reported that Korean pine seeds in seed banks located in areas where seeds are collected numbered less than 0.5% of that in control forests. Jin et al. (2010) estimated that solid pine seeds numbered about 14,000−34,000 seeds/ha in seed-collection forests, while more than 95% of the seed bank was consumed by animals. However, the results of many earlier studies varied, possibly due to differences in analyses or insufficient descriptions. Therefore, their reference value in restoring the ecosystem and further comprehending the consequences of this ecosystem alteration are limited. To evaluate regeneration potential of Korean pine under the current intensive seed harvest, and to provide support for sustaining and conserving the endangered forest ecosystem, we surveyed five forests, including both primary and secondary communities, by evaluating the current seed banks and the regeneration of Korean pine. We also estimated the intensity of consumption of pine seeds in the seed banks.

Material and methods

Site description

Field survey was conducted in the Liangshui Nature Reserve (LNR) located in the southern Xiao Xing'an Mountains in north-central Heilongjiang province, China (47°11'N, 128°52'E, Fig. 1). Our study area was located in the transitional area from the temperate to the cold temperate zone with a typical continental monsoon climate characterized by warm-humid summers and cold-dry winters. Average annual precipitation is 710 mm, mostly concentrated from May to September, and the annual mean evaporation is 805 mm. Winter is mostly snow covered from early November to early April, and snow depths reach 40 cm on average. The annual mean temperature is -0.4°C with the summer maximum of 38.7°C in July and the winter minimum of -43.9°C in January. The annual frost-free period ranges from 100 to 120 days (Li and Li 2003).

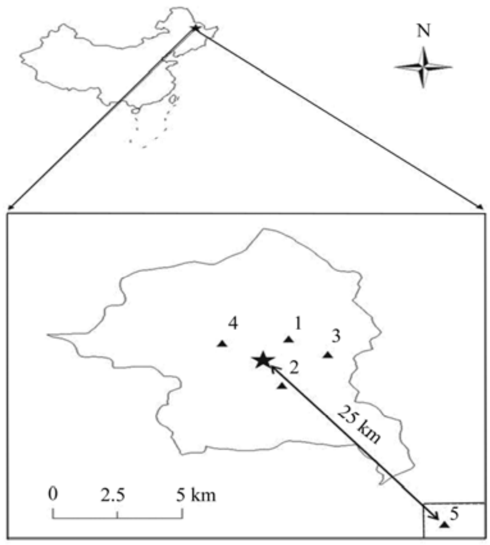

Fig. 1 Forest survey sites in Liangshui Nature Reserve (LNR), China: (1) mixed Korean pine-basswood forest, (2) mixed Korean pine- hardwood forest, (3) mixed conifer-hardwood forest, (4) white birch forest, and (5) oak forest located 25 km southeast of LNR.

The local topography is characterized as ridge and valley with mild slopes. The elevation in LNR (about 100 km^2 of protected area) varies from 280−707 m.a.s.l. The dominant soils are moderately well drained, deep, high organic matter content, fertile Dark-Brown soils in the Chinese Soil Classification System (equivalent to Mollisols of US soil classification system) on the slopes and foot-slopes. Localized permafrost pockets are scattered in some valley bottoms and basins (Ma et al. 1993).

The primary vegetation in the area is mixed Korean pine and hardwood forests, dominated by Korean pine. The associated coniferous and deciduous tree species include spruces (*Picea koraiensis* Nakai and *P. jezoensis* Carr.), fir (*Abies nephrolepis* (Trautv.) Maxim.), basswood (*Tilia amurensis* Rupr.), birch (*Betula costata* Trautv.), walnut (*Juglans madshurica* Maxim.), ash (*Fraxinus mandshurica* Rupr.), Amur cork tree (*Phellodendron amurense* Rupr.), oak (*Quercus mongolica* Fisch, ex Turcz.) and several maple species (*Acer* spp.). Based on the relative dominance of the associated tree species, the forest can be subdivided into pure Korean pine forest, mixed Korean pine-oak forest, mixed Korean pine-basswood forest, mixed Korean pine-birch forest, and mixed Korean pine-spruce/fir forest in LNR. Isolated spruce-fir forests are found in valley bottoms and high elevation areas. In addition, various types of the secondary forests derived from the post-harvest and other disturbances, and patches of tree plantations are scattered in the landscapes. About half of LNR supports primary forest while half supports secondary forests and tree plantations (Chou and Li 1964).

Study forests and sampling

Five forests were selected for sampling (Fig. 1, Table 1): (1) mixed Korean pine-basswood forest (MPBF) with >70% of the main canopy trees being 250−270 year-old Korean pines and about 12%, basswood; (2) mixed Korean pine-hardwood forest (MPHF) with about 60% of the main canopy trees being 220−250 year-old Korean pines plus various other old-growth coniferous and hardwood trees including *A. nephrolepis, Ulmus japonica,* and *B. costata*. The forests were high-graded at low intensity in the 1960s; (3) secondary mixed conifer-hardwood forest (MCHF) with about 50% of the main canopy trees being Korean pines and fir (*A. nephrolepis*), plus numerous hardwood species, resulting from seed-tree harvest in 1965−1968; (4) white birch (*Betula platyphylla* Suk.) forest (BF), with >90% of canopy trees being 25 year-old white birch, developed from the clear cut sites of MPHF on bottom lands; (5) oak (*Q. mongolica*) forest (OF), resulting from repeated disturbances, dominated by about 30 year-old oaks. There is no oak forest within LNR so our sampling forest was located about 25 km southeast of LNR (Table 1). The first three forests, MPBF, MPHF and MCHF, are representatives of the local pine forests, while the remaining two, BF and OF, represent two common post-disturbance secondary forests.

Table 1. Species composition of the overstory, shrub and herbaceous layers, and topographic features of the five study forests in the Liangshui Nature Reserve or nearby. The information is from survey of one 50 × 50 m plot in each forest.

Vertical layer	Species	Forest Types				
		Korean pine -basswood forest	Korean pine -Harwood forest	Coniferous-Hardwood forest	White birch forest	Oak forest
Overstory (BA m^2/ha¥ % relative frequency)	*Pinus koraiensis*	42.93\58.82	27.98\19.08	9.35\6.47	0.04\1.09§	1.05\12.08$
	Tilia amurensis	6.06\11.76	0.58\0.76	0.79\1.18§		0.10\0.67
	Ulmus japonica	0.90\7.35§	5.11\25.19^	1.54\5.88§		
	Acer mono	1.08\9.56§		0.06\0.59§		
	Acer tegmentosum	0.68\10.29§		1.71\15.29§		
	Picea koraiensis	0.28\0.74§	0.25\1.53§		0.15\1.64§	
	Phellodendron amurense	0.27\0.74§	0.72\0.76§			
	Fraxinus mabdschurica	0.15\0.74§	0.78\7.63§	0.11\0.59§		
	Abies nephrolepis		5.39\35.88	5.73\10.00		0.29\0.67
	Betula costata		5.99\9.16	4.03\34.7	0.59\6.01§	
	Acer ukurunduense			4.28\19.41§	0.29\3.28§	0.10\3.36§
	Betula platyphylla			0.72\2.36§	16.37\84.7	
	Popolus cathayana			0.50\2.35§		
	Prunus maackii			0.42\1.18§	0.52\1.64§	
	Alnus sibirica				0.22\1.64§	
	Quercus mongolica					18.12\83.22
	Tot. BA (m^2/ha)//Tot. FQ	**58.29//100**	**46.80//100**	**29.24//100**	**18.18//100**	**19.66//100**
Shrub layer (% cover)	*Corylus mandshurica*	60±6	83±13	62±19		90±10
	Euonymus paucifloru	32±24	20±6		19±10	
	Lonicera edulis	20±10	39±10	29±7		
	Philadelphus schrenkii		53±9			
	Acer tegmentosum			23±13		
	Sorbaria sorbifolia				35±5	
	Quercus mongolica					59±7
Herbaceous layer (% cover)	*Carex spp.*	15±2	10±5	40±1	94±2	40±8
	Athyrium spp.		33±13	37±6	28±8	
	others	3±0.9	2±0. 4	11±4	20±6	6±1
Understory	**Total cover (%)**	**77±6**	**82±5**	**62±38**	**92±5**	**73±4**
Site features	slope	SE	S	N		SE
	slope aspect	<10^o	<10^o	<10^o	<10^o	<20^o
	slope position/landform	top & backslope	ridge top	top & backslope	bottom land	top & backslope
	elevation (m)	390	430	450	370	250

§: subcanopy trees, ^: mostly subcanopy trees, a few in the main canopy, $: young non-fruiting Korean pine trees in the canopy layer.

In 2010, Korean pine seeds in the seed banks of the five forests were surveyed seasonally (early June, late July, and mid-September). During each season, 10−12 sampling plots of 1 m^2 were randomly sited in each forest type. We recognized that there was no true replication at the forest level because it was difficult to find replicates with the same species composition, forest age, management history, soil condition and history of disturbance in LNR. To avoid the potential problems of pseudo-replications, we tried to locate our sample plots covering a large enough area representing a large spatial variation of seed banks in each forest type. We did not establish control plots (without seed harvest) because we could not find a Korean pine forest where seeds were not harvested.

In each plot, after counting all Korean pine seedlings (<2 years) and saplings (>2 years and <1.3 m height: Due to non-destructive seedling/sapling survey, exact ages of older saplings were not measured, and the young trees >1.3m height were excluded), the forest floor was carefully searched and all Korean pine seeds were collected. Then, the top 10 cm of mineral soil was sieved to collect pine seeds. Seeds were sorted as solid seeds and hollow/damaged kernels and stored separately. Seeds and kernels with mold were excluded. Soil depths greater than 10 cm were not sampled because pine seeds hoarded deeper than 10 cm by rodents are unlikely to germinate (Xu et al. 1980; Zong et al. 2007).

Seedlings and saplings of Korean pine were surveyed a second time in summer 2011. In each forest, 30 plots of 1 m^2 were randomly sited and sampled. All seedlings and saplings of Korean pine were carefully counted and recorded.

In the lab, collected pine seeds were counted according to the following criteria: (1) a complete seed without insect damage was counted as one solid seed (SS, i.e. potentially viable); (2) a complete hollow kernel with evidence of insect damage (a hole bored by an insect), as one insect consumed seed (ICS); (3) damaged kernels, i.e., missing less than 1/4 of the kernel shell, as one seed consumed by other animals (rodent, wild boar, bird etc.) (OCS); (4) one half of a kernel shell, as 1/2 OCS; (5) a kernel shell smaller than 1/2 but larger than 1/4, as 1/4 OCS, and (6) kernel shells smaller than 1/4 were not counted.

In 2010, the yield of Korean pine seeds was 15−20 kg/ha, which was abnormally low as reported during a survey of local seed collectors. Though the seed banks that we surveyed represented the accumulated results of the past few years (Korean pine seeds generally rot in about three years depending on conditions (Liu 1988)), the surveys in September 2010 included few current year seeds.

Data analysis

We examined the effects of forest type and season, and their interaction on the seed bank pine seeds using two-way ANOVA. Except the OCS category, season and forest type × season interaction did not show significant effects (Table 2). We then pooled the data of all seasons to compare the pine seed quantities among different forests using one-way ANOVA. Because most of the data failed variance homogeneity tests, even after transformation, we used ANOVA results as references to determine whether further multiple comparisons were needed. As the ANOVA of a category tested significant, non-parametric Dunnett's T3 multiple comparison was conducted (Dunnett 1980). For the OCS category, Dunnett's T3 approach was conducted to compare the seasonal means for each forest type.

Table 2. p-values of two-way ANOVA examining the effects of forest type and season on total Korean pine seed, solid seeds (SS), other consumption (OCS) and insect consumption (ICS)

Impact factors	p-value			
	Total seeds	SS	OCS	ICS
Forest type	<0.0001***	0.003**	<0.0001***	<0.0001***
Season	0.136	0.407	0.006**	0.233
Forest type × Season	0.445	0.390	0.145	0.892

Because quantifying seasonal and yearly variation of seed germination was not the aim of this study, we pooled the seedling and sapling data together and used the same analytical strategy mentioned above because the data were neither normally distributed nor were the variances homogeneous. One-way ANOVA was used to compare numbers of Korean pine seedlings and saplings between the five forests. Dunnett's T3 multiple comparisons were conducted when ANOVA tests were significant. All statistical analyses were conducted using SPSS version-18 (IBM® SPSS® software).

Results

Soil seed bank

Mean densities of pine seeds in seed banks varied from about $0.2/m^2$ in OF to $11.2/m^2$ in MPBF (Fig. 2). There were significant differences in total numbers of seeds, SS, ICS and OCS between forest types (Fig. 2). Multiple comparisons tests showed that MPBF and MPHF had the highest total seed numbers, followed by MCHF, then BF, and finally OF had fewest seeds (Fig. 2).

Numbers of OCS showed significant seasonal variation and season × forest interaction basically due to the high OCS number in MPBF in spring. The number of OCS in spring was significantly higher than in summer and autumn for all five forest types (Fig. 3), and this raised the mean density of OCS across forest types and caused significant season × forest interaction.

Density of SS varied from 0.09 seeds/m^2 in OF to 2.51 seeds/m^2 in MPHF. Densities of SS in MPBF and MCHF were significantly greater than in BF and OF, while in MPHF, SS density did not differ significantly from that in any other forest due to high variation, though its mean was the highest (Fig. 2). OF had the highest percentage (~43%) of solid seeds (SS), followed by MPHF (27.8%), MCHF (13.6%), MPBF (11.2%) and BF (3.5%) (Table 3).

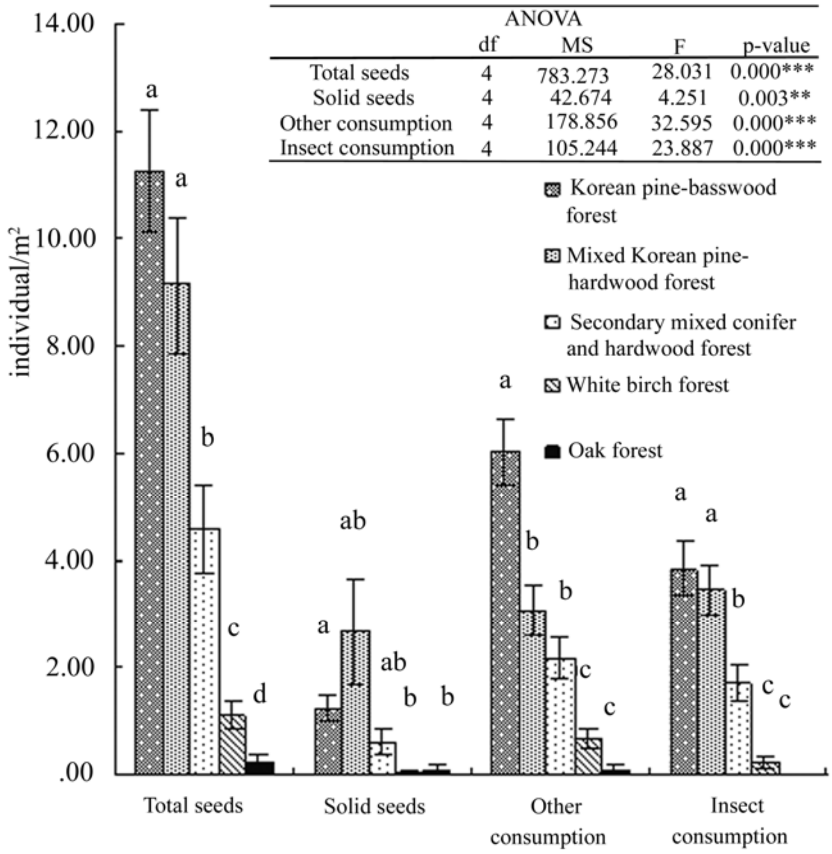

Fig. 2 Comparison of the seed bank Korean pine seeds, illustrated as total seeds, solid seeds (SS), other consumption (OCS) and insect consumption (ICS) among five forest types in LNR. The table in the up-right corner shows one-way ANOVA results for the variation of pine seed numbers by class among the five forest types.

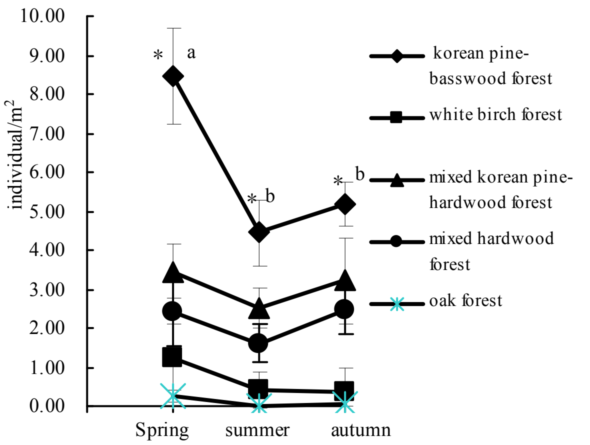

Fig. 3 Seasonal variation of the other consumption (OCS) category of the seed bank pine seeds in five forest types. The mixed Korean pine-basswood forest is the ONLY one with significant seasonal variation indicated by (*). Different letters indicate significant difference.

Most seeds were consumed kernels (i.e., ICS + OCS), and MPBF had the highest number of consumed kernels, followed by the MPHF, MCHF, BF, and OF (p< 0.0001, Fig. 2). BF and OF had significantly fewer consumed kernels than did MPBF and MCHF. Although MPHF had the second highest percentage of consumed kernels, it did not differ from MPBF or MCHF (Fig. 2).

Table 3. Percentages of solid seeds (SS), other consumption (OCS), and insect consumption (ICS) in the total seed bank (TS=SS+ICS+OCS)

Forest type	Percentages of the total seed bank (TS)		
	SS/TS	OCS/TS	ICS/TS
Mixed Korean pine- basswood	11.18	53.65	33.27
Mixed Korean pine- hardwood	27.76	33.43	36.54
Mixed conifer- hardwood	13.58	48.39	38.03
White birch	3.45	68.97	24.14
Oak	46.15	53.85	0.00

OCS (i.e., consumption by rodent, bird and/or wild boar) density varied significantly by forest type. OCS density was greatest in MPBF, followed by MPHF and MCHF, and least in BF and OF (Fig. 2). ICS densities in both MPBF and MPHF were greatest, followed by MCHF, and BF, while density was least in OF (Fig. 2). However, the relative amount of the two consumption categories showed varied by forest type. The three forests with mature pines had comparable ICS percentages, but OCS percentages varied (Table 3). BF was characterized by a high percentage of OCS and low percentage of ICS. OF had no ICS (Table 3).

Seedlings and saplings

Seedling numbers differed significantly (p = 0.012) by forest type, possibly due to very low seedling numbers in MPHF (only one seedling was found in 56 plots). There was no significant difference in the number of seedlings in MPBF, BF and OF (Fig. 4). The high standard errors (Table 4, Fig. 4) indicated high spatial variation in seedling numbers between forest types. The frequencies of seedlings were 17.3%, 1.79%, 28.85%, 12% and 9.62%, in MPBF, MPHF, MCHF, BF and OF, respectively.

Excluding MPHF, the average sapling densities of four forests ranged from 0.16–0.54 saplings/m^2 with high variability (Table 5). Sapling frequencies were low at 5.77%, 1.79%, 17.31%, 10%, and 5.77% for MPBF, MPHF, MCHF, BF and OF, respectively. ANOVA revealed marginal significance (p=0.054) in sapling numbers among the forests (Fig. 4).

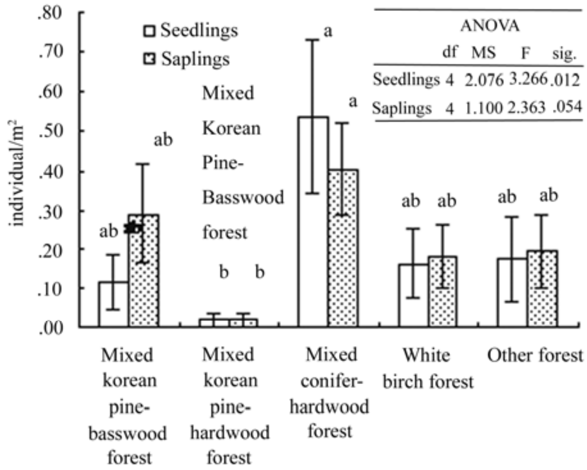

Fig. 4 Comparison of the Korean pine seedlings and saplings between five forest types in LNR. The table in the up-right corner shows one-way ANOVA results.

Table 4. Comparison of mean Korean pine seed numbers (segregated as total seeds [TS] and solid seeds [SS]) in the Korean pine forests between this study and other studies of Korean pine forests in east and northeast China and Japan. Numbers in the table are seeds/ha, and numbers in () are standard errors. Data from pre or no large scale seed harvest are represented with italic letters/numbers.

Forest Type [1]	This study		Xu et al. (1980) [2]		Jin et al. (2010)[3]		Liu, Q. (1988)[4]	Liu et al. (2004)[5]	Zong et al. (2007) [6]	Wang et al. (1959)[7]	Song et al. (2009)[8]	Li et al. (1989)[9]	Miyaki (1987)[10]
	TS	SS	TS	SS	TS	SS	SS	SS	SS	SS	TS	SS	
Mixed Korean pine-basswood forest	112,424 (11,281)	12,424 (2,344)	490,830-536,670	12,500-13,330	291,670	14,292	77,190	218	3,039 (329)	—	564,000	13,750	—
Mixed Korean pine-hardwood forest	91,282 (12,652)	25,128 (9,472)			780,400	33,557		444	1,672 (220)	—		12,500	—
Mixed conifer-hardwood forest	45,757 (8,483)	6,060 (2,258)	506,250	6,250	—	—		850	-	—		15,000	—
White birch forest	11,000 (2,461)	333 (333)	7,500	0	246,620	0	—	—	1,438 (377)	—	—	—	—
Oak forest	2,121 (1,554)	909 (909)	16,000	0	—	—	—	—	—	—	—	—	—
Pine seed production	—	—	—	—	—	—	—	528,000		582,400 Mast yr: 2,492,800 Lean yr: 98,280	—	—	661,123 (26,400)

[1] We matched forest types in different studies based on our knowledge of the forests. If insufficient information was given in the reports, we used the reported number as pooled averages; [2] No detailed method described. Seed numbers were surveyed between litter and mineral soil (at the surface of mineral soil) and collected in the Xiao Xing'an area near LNR in 1963-64 without error terms given; [3] The survey included forest floor and 0–20 cm soil, no error terms given. Data collected in Liangshui Nature Reserve (LNR); [4] Derived from Liu's report (1988), data collected from Liangshui Nature Reserve (LNR); [5] Seeds were collected between litter and mineral soil (at the surface of mineral soil) in Changbaishan National Natural Reserve; [6] Derived from Zong et al. (2007), seed numbers were surveyed between litter and mineral soil (at the surface of mineral soil); [7] Data were from southern Xiao Xing'an. near LNR. No error terms given; [8] Derived from Song et al. (2009), data were the average of the seed banks (litter layer + humus layer) under the canopy gaps of different sizes from Chanbaishan. area. No error terms given; [9] Data were collected from the litter layer in 1963 from Xiao Xing'an area near LNR; [10] Derived from Miyaki's report (1987) on the mixed Korean pine-hardwood forest in Hokkaido, Japan. The seed maturation rate was reported as 0.554.

Table 5. Comparison of mean seedlings/saplings numbers in Korean pine forests from this study and other studies of Korean pine forest in east and northeastern China. The numbers in the table are trees per hectare, and the numbers in () are standard errors.

Forest Type [1,5]	This research		Jin, et al. 2010	Cui (1962)[2] unpublished	Zhu, et al. 1958		Li, et al (1988)	Li, et al (1989)		Xu, Z et al. (1980)[3]	Xu, et al. (2001)[4]	
	Saplings (>2yr)	Seedlings	(<5yr)	Saplings	Saplings (>2yr)	seedlings	Seedlings & saplings	Saplings (2-20yr)	seedlings	Saplings (<15yr)	Seedlings (<3yr)	Saplings (>3yr)
Mixed Korean pine-basswood forest	2,885 (1,269)	1,154 (708)	150	—	500	3,000				2500-	—	—
Mixed Korean pine-hardwood forest	179 (179)	179 (179)	54	—	—	—	917 (<5yr old)	544	4,107	2000 -3146	1,688 (638)	830 (339)
Mixed conifer- hard-wood forest	4,038 (1,173)	5,385 (1,931)	—	1,250 (205)	—	—				548 -1702	—	—
White birch forest	1,800 (792)	1,600 (874)	321	—	—	—	—	—	—	570	—	—
Oak forest	1,923 (953)	1,731 (1,089)	—	—	—	—	—	—	—	1,000	—	—

[1] We matched the forest types in different studies with our best knowledge on the forest. If insufficient information was given in the articles, we used the reported number as pooled averages.
[2] Numbers are derived form Li et al. (1988).
[3] IAE refers to the Institute Applied Ecology of China.
[4] Derived from Xu et al. (2001).
[5] Excepted reported, all other mean numbers were given without error terms.

Discussion

Soil seed banks

There were few viable pine seeds remaining in the seed banks after decades of intensive seed harvest. MPBF, MPHF, and MCHF with large seeding pine trees had much higher numbers of total pine seeds and solid seeds in the seed banks than did BF and OF (Fig. 2). The long distances from seed sources limited pine seed accumulation in the seed banks of BF and OF (~2 and ~20 km from large mature pine forests, respectively). Ma et al. (2008) demonstrated that red squirrel and Siberian chipmunk hoard seeds with an average dispersal distance of more than 300 m, while Miyaki (1987) reported less than 600 m of dispersal distance. Eurasian nutcrackers can disperse seeds over greater distances, ranging from to 2−5 km (Lu 2002).

The very small fraction of SS in this study suggested low potential for regeneration. Earlier reports estimated that Korean pine seed production in normal seed years ranged from 530,000 to 661,000 seeds/ha (Wang et al. 1959; Miyaki 1987; Liu et al. 2004; Song et al. 2009). Wang et al. (1959) estimated seed production of about 2.5 million seeds/ha in heavy mast years and less than 100,000 seeds/ha in lean years in the Xiao Xing'an mountains. They also estimated that Korean pine experiences a heavy mast year at intervals of 3−4 years, with a super mast year recurring roughly every 10−12 years. Relative to average annual seed production, SS remained less than 1% of total seed production when the three forests with pines were averaged, assuming that our survey reflected seed bank accumulation during the past 2-3 years.

Our seed density estimations were higher than many post-seed harvest era surveys (Table 4). This is probably because other surveys generally sampled partial seed banks: litter only (Liu 1989) or between the litter layer and the mineral soil (Liu et al. 2004, Zong et al. 2007, Song et al. 2009). Xu et al. (1980) stated that the solid pine seeds between the litter and mineral soil in different Korean pine forests varied from less than 10,000 to about 20,000 seeds/ha based upon surveys during the 1960s. They also found negative effects of understory shrubs and herbaceous cover on the density of pine seeds in the seed banks.

Animal seed hoarding and consumption (Wall and Balda 1977; Christensen et al. 1991; Siepielski & Benkman 2007) resulted in a unique spatial distribution pattern of pine seeds. Liu (1988) reported that SS dispersed by Eurasian nutcracker and Eurasian nuthatch were mostly in clumps of 2-4 seeds, and followed a negative binomial distribution. In this study, we examined the SS data using the approach of Uppreti & Rohatgi (2009) and found that SS were best fitted with a Poisson distribution ($\lambda=0.4557$, $p=0.056$) at the scale of 1 m^2 and largely agreed with the result reported by Liu (1988).

Most pine seeds in the seed banks were consumed by animals. Jin et al. (2010) reported 780,400 pine seeds/ha in the seed bank (litter + top 20-cm soil) of MPHF, with 4.3%, 82.5% and 13.2% for solid, consumed and decayed seeds, respectively. Our data agreed with this composition, but their total seed estimates were much higher: The proportionate approach for partial kernels we adopted probably reduced the estimates of total seeds (Table 4). In addition, our survey depth was 10 cm, which was shallower.

This survey revealed large percentages of ICS and OCS (Table 3). ICS densities in the three forests with pines showed relatively large but consistent (percentage wise) insect predation. As high energy-concentrated propagules with variable annual productivity (Xu et al. 1980, Wang et al. 1959), Korean pine seeds have supported a wide range of herbivores/granivores/omnivores, from insects to large mammals (Liu 1988). High predation on pine seeds (Table 1) suggests their importance in maintaining high heterotrophic diversity of the ecosystem. We observed widespread wild boar tracks and signs of boar consumption in MPBF that may explain the significantly higher OCS percentages there (Fig. 2). Given that this survey was carried out after a poor seed year, assuming that OCS and ICS hold stable, we predict that there should be sufficient seeds for pine regeneration following a normal mast year after the seed eaters are satiated (Silvertown 1980; Kelly and Sork 2002; Fletcher et al. 2010) if the human seed harvest is kept at an average level.

The lower densities of seeds and very different seed consumption patterns (Table 3) in BF and OF might indicate different seed eating guilds or seed eating behavior shifts due to the contrasting environments and the different composition of the seed banks. Folgarait and Sala (2002) suggested that the granivory rates by different granivore guilds were affected by seed composition and seed nutrition and palatability. The survey year (2010) was a big mast year for oaks, more than 100 acorns/m^2 were recorded in OF on average while none were collected in the other forest types (Li unpublished data). However, the specific relationship between seed distribution and consumption, and different granivore guilds in this area needs further study.

Seedlings and saplings

Reduced input of pine seeds to seed banks depresses seedling and sapling recruitment. All five forests had few seedlings with spatial variation was great (Table 5). With sufficient seed sources and prior to large scale seed harvest by humans, densities of Korean pine seedlings in mixed Korean pine-hardwood forests were reported as several thousands to 40,000 per hectare (Xu et al. 1980). Seedling and sapling densities in this study were far below such levels but were comparable to many other reports including some surveys prior to large scale seed harvest (Table 5).

"Few seedlings but many saplings " has long been said of the mixed Korean pine-hardwood forests because of the very low rate of seedling establishment (Xu et al. 1980). However, our data do not support this assessment because we found comparable numbers of seedlings and saplings in our five forest types (Table 5). In a study of white pine (*Pinus strobes* L.), a close counterpart of Korean pine in North America, Dovčiak et al (2003) revealed documented higher densities of saplings than seedlings. The numbers of saplings represents the accumulation of established seedlings over recent years, particularly for species with small, wind-distributed seeds and slow growth rates. For the large-seeded Korean pine, the comparable numbers of saplings and seedlings recorded in this study (Table 5, Fig. 5) suggests that high mortality rates of seedlings and possible high mortality of saplings may both contribute to the low establishment rate of Korean pine.

Several surveys revealed very low numbers of saplings in similar forests (Table 5). Many attributed the low establishment rate of Korean pine seedlings to overstory shading (Zhu et al. 1958; Xu et al. 1980; Xu 2001), rodent predation (Xu 2001), or pine rust (personal communication with Dai, L.). The confounding results of the seedling and sapling numbers in MPBF, MPHF and MCHF in relation to their total basal areas (Tables 1 and 5) painted a complicated picture, especially for the extremely low numbers of both seedlings and saplings in MPHF. It seems that the mechanisms of "seedlings but saplings" are complex. We have not discovered convincing explanations for this phenomenon in the scientific literature.

Dovčiak et al. (2003) listed five hypotheses on pine regeneration, namely, seed-rain limitation, safe-site limitation, shallow soil refugia, negative canopy effect, and shrub recruitment filter. Our results, in conjunction with the previous studies on Korean pine (cited studies in Table 5) seem to support the first three hypotheses, particularly the seed-rain limitation hypothesis. The human caused seed limitation makes it the most critical bottleneck, considering the low rate of seedling establishment and its importance in pine regeneration. In addition, the animal/insect predation filter mechanism should be added as an important factor influencing pine regeneration.

Implications

The depletion of Korean pine seeds in the seed banks suggests a pessimistic restoration future for the endangered Korean pine-hardwood forest ecosystems as many other studies revealed. We documented the extremely high percentages of seed consumption in five forest types, and indicated indirectly that the seed harvest not only limits pine regeneration, but might also limit the productivity and diversity of the granivores/omnivores/herbivores in these forests and consequently interrupt ecosystem trophic structure and biogeochemical functions. To maintain the health and normal functions of the ecosystems, we recommend: (1) reduce the scale of the human seed harvest; (2) set the seed harvest to start in late autumn to enable animal hording and to secure large amounts of seed for wildlife consumption and pine regeneration (Xu et al. 1980); (3) supplement pine regeneration by periodic broadcasting of pine seeds and planting saplings to maintain the uneven age structure of the population in existing Korean pine forests, and to accelerate succession in hardwood forests of the region; and (4) permit commercial tree harvest only at low levels of intensity and following a conservation-driven schedule in commercial Korean pine forests to create safe sites for pine regeneration. In this sense, this study has provided some quantitative references.

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