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**Spatial variation in tree seedling density after the site preparation for  
planting in a cleared coniferous plantation in Hokkaido,  
northern Japan**

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**Abstract** To study spatial variation in natural tree seedling density and the relationship between variation in seedling density and seed dispersal mode at a cleared site, we surveyed natural tree seedlings after the site preparation for planting in a coniferous plantation cleared by a typhoon disturbance in 2004. The site was located near Sikotsuko Lake, Hokkaido, northern Japan. Twenty-five tree seedling species were found and the mean seedling density was 9.8 seedlings/m<sup>2</sup>. Seedlings of non-animal-dispersed species (7.2 seedlings/m<sup>2</sup>) were approximately five times more abundant than those of animal-dispersed species (1.4 seedlings/m<sup>2</sup>), and 87% of all seedlings were current. The seedling density of non-animal-dispersed species (almost all: wind-dispersed) decreased with distance from a natural forest; however, this trend did not hold for animal-dispersed species (almost all: bird-dispersed). The spatial variation in seedling density was lower in animal-dispersed species than in non-animal-dispersed species. Seed dispersal patterns and the viability duration of buried seeds likely affected the variation in seedling density by seed dispersal mode.

**Key words:** Cleared site, Occurrence frequency, Seed dispersal, Seedling density, Tree species

## **Introduction**

Since the 1950s, more than 40% of forest in Japan has been replaced with coniferous plantations for the purpose of expansive reforestation for wood production (Sakai et al. 2005). However, natural regeneration was implemented recently for cleared plantations to increase the species diversity of resulting stands via the regeneration of various tree species (Sato and Sakai 2003; Ishibashi et al. 2004). At such sites, it is assumed that the species composition of the resulting stand is greatly affected by both the species composition of surrounding stands and the ecological characteristics inherent in the natural regeneration of each tree species (Nakashizuka 2004).

Sources of natural regeneration of tree species at a cleared site include advanced seedlings, sprouts from stumps, and seedlings derived from dispersed and buried viable seeds (Sakai et al. 2005). The spatial distribution and density of natural seedlings are assumed to primarily depend on the distribution pattern and density of propagation sources. Hamada and Kuramoto (1994) showed that the spatial distribution of seedlings was associated with seed-dispersal patterns, the presence of parent trees, and seed longevity. Furthermore, Sakai et al. (2005) reported that soil seed banks in a mature coniferous plantation affected the establishment of secondary vegetation after a clear-cut. Because forest floor vegetation and the soil surface are disturbed in clear-cut areas, it is presumed that seedlings are primarily derived from dispersed and buried seeds at these sites.

Spatial patterns of seed dispersal differ depending on the mode of seed dispersal. The density of non-animal-dispersed (mainly wind-dispersed) seeds decreases with distance from the parent (Begon et al. 1990; Tanaka et al. 1998; Clark et al. 1999). In

contrast, the density of animal-dispersed seeds is affected by the behavior and mobility of the animal (Murray 1988). For example, frugivorous birds disperse plant seeds over several tens of meters (Iida and Nakashizuka 1998) to several hundred meters (Murray 1988; Fukui 1995) from the parent, and the decrease in dispersal density with distance from the parent is very moderate (Murray 1988). Furthermore, Masaki et al. (1994) found that the spatial distribution of viable seeds of bird dispersal was relatively homogeneous compared to non-animal-dispersed seeds. Buried, bird-dispersed seeds of some tree species, such as *Magnolia*, *Phellodendron*, and *Cornus* spp., can remain viable for greater than 10 years (Ozawa 1950; Watanabe and Mizui 2000). These seeds are expected to accumulate in forest soils over long periods of time. Consequently, seedling spatial distribution at cleared sites should differ among tree species and should depend on seed dispersal density and the viability duration of buried seeds (Murray 1988). However, few studies examined the spatial variation in natural seedling density by species or by seed-dispersal mode at cleared sites with forestry operations.

In this study, we hypothesized that the natural seedling density of tree species should be spatially heterogeneous and should be different depending on seed-dispersal mode in a cleared forest site. To examine this hypothesis, we surveyed the spatial distribution of tree seedlings after the site preparation for planting in a coniferous plantation cleared by a typhoon disturbance near Shikotsuko Lake in Hokkaido, northern Japan. In particular, we explored the relationship between the spatial distribution of seedlings and the ecological characteristics of tree species (i.e., seed-dispersal mode and viability duration of buried seeds).

## **Materials and methods**

## Study site

The study was conducted in a coniferous plantation located in the 5283 forest compartment in the Chitose region of the Isikari District Forest Office of Japanese National Forest (42° 46' N, 141° 46' E; altitude 140 m; Fig. 1). The plantation was planted with *Abies sachalinensis* (65%) and *Picea jezoensis* (35%) in 1934. The plantation is surrounded by natural forests at the western and northern boundaries and undisturbed, young *Picea glehnii* plantations at the eastern and southern boundaries. In early September 2004, the plantation suffered from intensive windthrow during a typhoon and was almost completely cleared. At the time of the typhoon, the stand was 71 years old. The topography of the site is flat, and the surface soil is derived from the volcanic ash and pumice of Mt. Eniwa and Mt. Tarumae. The depth of soil available to plants is shallow, being approximately 10 cm (personal observation in an undisturbed natural forest neighboring the study site).

Mean tree volume ( $\sim 0.9 \text{ m}^3$ ) and stand stock ( $\sim 200 \text{ m}^3/\text{ha}$ ) were estimated from lumber data collected at the plantation in 2005. Prior to our tree seedling survey in September and October 2005, the bucking and hauling of trees fallen in 2004 and site preparation for planting had already been completed. The surface soil ( $A_0$  layer and upper part of A layer) was disturbed during these forestry operations and was covered by 2–5 cm of pumice.

## Methods

The site preparation area runs linearly from the northwest to the southeast at the cleared site. We established 20 plots (20 or 25 m<sup>2</sup>) in three transects on the site preparation area (Fig. 1). The interval between plots was 40–50 m and the interval within a transect was constant. All of the plots were scarified and leveled off in the site preparation, and were covered by the pumice layer. Secondary vegetation, including herbs, shrubs, and tree seedlings, occurred in the plots with the mean coverage of 60% at our survey.

We identified the species and measured the height and age of tree seedlings, including current and advanced seedlings and sprouts. Because current seedlings of *Betula* spp. and *Salix* spp. were difficult to identify, we classified them as *Betula* spp. and *Salix* spp. To examine the species composition of seed trees, we identified the species and measured the diameter at breast height (DBH) for trees greater than 20 cm in DBH, which were assumed to be seed trees, in the area of 3.38 ha (dotted area in Fig. 1) of a natural forest along the northern border of the site, which was the closest natural forest to our plots.

The seed-dispersal modes of the trees were classified as non-animal-dispersed and animal-dispersed depending on seed morphology, such as winged seeds and fruits as non-animal-dispersed, and fleshy fruits and acorns as animal-dispersed (following Kikuzawa 1983).

## Statistical analyses

Relationships between the numbers of current and total seedlings and the number and basal area (BA) of seed trees by species, as well as relationships between seedling

density and plot distance from the natural forest, were analyzed using Spearman rank correlation ( $\rho$ ), using SPSS 12.0 J (Chicago, IL, USA). The coefficient of variation (CV) of seedling density among plots was calculated as  $CV (\%) = \text{standard deviation} / \text{mean} \times 100$ . The frequency of occurrence of current seedlings by species was calculated as the number of plots in which seedlings occurred out of all 20 plots.

## Results

### Species composition of seed trees and seedlings

Thirty-one species were identified as seed trees (591 trees, 175 trees/ha; Table 1) in a neighboring natural forest. Species with large BA included *Betula maximowicziana* (BA proportion: 26.0%), *Ulmus davidiana* var. *japonica* (12.1%) and *Picea jezoensis* (8.7%). *Fraxinus mandshurica* var. *japonica*, *Magnolia obovata* and *Acer mono* also occurred frequently.

The seedlings of 25 tree species occurred in the 20 study plots (total area of 430 m<sup>2</sup>; Table 1), all of which were also found as seed trees in the natural forest, with the exception of *Morus bombycis*. The total number of seedlings was 4234 (9.8 seedlings/m<sup>2</sup>), 87% of which were current seedlings (total number = 3695, 8.6 seedlings/m<sup>2</sup>). Advanced individuals included seedlings and sprouts. Seedlings of nonanimal dispersal accounted for 83% (3514 seedlings) in number, and almost all of these were from wind dispersal (3483 seedlings). In animal-dispersed seedlings (720 seedlings), bird-dispersed species accounted for 98% in number. The most abundant species were *Betula* spp. (43.0% in number), *Fraxinus lanuginosa* (34.5%), *M.*

*bombycis* (7.4%), *Phellodendron amurense* (4.7%) and *M. obovata* (3.3%; Table 1). For *F. lanuginosa* and *M. bombycis*, a considerable portion of their total seedlings occurred in one plot (*F. lanuginosa* : 1195 of 1462 seedlings occurred in Plot II-7; *M. bombycis* : 157 of 312 seedlings occurred in Plot II-6; Fig. 1). *Fraxinus lanuginosa* (54.7%) and *Betula* spp. (11.3%) were also abundant as advanced individuals.

The relationships between species composition of seed trees expressed by BA and the individual number and species composition of current and total seedlings are shown in Table 2. We found no significant correlations between any of the seed tree and seedling variables ( $p=0.20-0.51$ ; Table 2).

#### Variation in density and spatial distribution of seedlings

The total number of species in each plot ranged from 6 to 17, and the densities of all seedlings and current seedlings were 1.3–54.4 seedlings/m<sup>2</sup> (CV=132.8%) and 0.3–49.2 seedlings/m<sup>2</sup> (CV=141.8%), respectively. The mean and density ranges of the current seedlings of non-animal-dispersed species were 7.2 seedlings/m<sup>2</sup> and 0.1–47.8 seedlings/m<sup>2</sup>, respectively, whereas those of animal-dispersed species were 1.4 seedlings/m<sup>2</sup> and 0.2–7.4 seedlings/m<sup>2</sup>, respectively. The mean density of non-animal-dispersed species was five times larger than that of animal-dispersed species, although the variation in seedling density among plots was large. In 16 of 20 plots, the current seedling density of non-animal-dispersed species was higher than that of animal-dispersed species. The numbers of species in each plot did not differ greatly between dispersal modes and ranged from 2 to 10 and from 3 to 8 for non-animal-dispersed and animal-dispersed species, respectively.

There was a trend in the density of current seedlings with distance from the natural forest by seed dispersal mode and transect (Fig. 2). At transects I and II, the density of non-animal-dispersed species tended to decrease with distance from the natural forest, but the correlation was significant for only transect II (Fig. 2). In contrast, no significant correlations were found for animal-dispersed species (Fig. 2).

The mean density of current seedlings was high in *Betula* spp., *F. lanuginosa*, *M. bombycis*, *P. amurense*, *M. obovata* and *P. jezoensis* (Table 3). The CV of seedling density was small in *P. amurense*, *M. obovata* and *Betula* spp. The CVs for *M. bombycis* and *F. lanuginosa* were 89.1% and 140.7%, respectively, when dense plots of their seedlings (II-6 and II-7) were omitted. The CV for *M. bombycis* was smaller than that for *P. amurense*. *Betula* spp., *M. obovata*, *M. bombycis*, and *P. amurense* exhibited high frequencies of occurrence ( $\geq 0.9$ ), and their seedlings occurred throughout the study site. Except for *Betula* spp., these species are bird-dispersed. *Magnolia obovata* had the eighth and *P. amurense* had the eleventh largest BA of seed trees in the neighboring natural forest (Table 1); no seed trees of *M. bombycis* were found in the forest (Table 1).

## Discussion

Current seedlings dominated the cleared site and accounted for 87% of the total number of seedlings (Table 1). This result was likely affected by forestry operations on the site, such as the bucking and hauling of fallen trees and site preparation for planting, which are generally conducted at a site after clear cutting. Therefore, it is probable that seedlings occurring after such forestry operations would be dominant at cleared sites.

Seed trees of all species, of which seedlings occurred in the surveyed plots, were found in the neighboring natural forest (except for *Morus bombycis*; Table 1). Seed trees are particularly important to the natural regeneration of trees at cleared sites. Seed trees of *M. bombycis* may have occurred near plot II-6 before the 2004 typhoon disturbance because the *M. bombycis* seedling density was extremely high in this plot (6.3 seedlings/m<sup>2</sup>). However, we found no significant correlations between seed tree and seedling species composition (Table 2), indicating that seed tree species composition did not immediately affect that of seedlings. Furthermore, because frugivorous birds disperse seeds over several hundred meters (Murray 1988; Fukui 1995), tree seeds might be dispersed from seed trees beyond the neighboring natural forest and plantation (Fig. 1). *Betula* spp. seedlings accounted for 43% of the total number of seedlings (Table 1), which was likely the result of the abundant seed dispersal of this species (Tsutsumi 1994). In 41–51-year-old *Larix kaempferi* plantations located in the same district as our study area, Hanada et al. (2006) reported that *Betula* spp. tree density was low, whereas the tree density of shade-tolerant, broad-leaved species such as *Acer* and *Sorbus* spp. was high. Although the plantation species were different between Hanada et al. (2006) and our study, it is possible that the identity of broad-leaved trees that invade coniferous plantations is dependent on the growth stage of the plantation, and that pioneer tree species, such as *Betula* spp., dominate expansive open sites just after clear-cutting.

Spatial variation in seedling density was dependent on the seed-dispersal mode. The seedling density of non-animal-dispersed species in transects I and II tended to decrease with distance from the natural forest, but the density of animal-dispersed species did not (Fig. 2). The extremely high density of *Fraxinus lanuginosa* in plot II-7

may have affected the distance-dependent decrease in non-animal-dispersed seedlings in transect II. However, this trend remained constant when *F. lanuginosa* was omitted from the correlation ( $\rho=-0.821$ ,  $p=0.023$ ,  $n=7$ ). Seedling density was primarily dependent on seed density; thus, it is evident that the seed dispersal of animal-dispersed species was spatially homogeneous (Fig. 2). A similar trend was reported by Masaki et al. (1994) for bird-dispersed species.

The species with high frequencies of occurrence were *Betula* spp., *M. bombycis*, *Magnolia obovata*, *Phellodendron amurense*, and *F. lanuginosa* (Table 3). *Betula* spp. occurred in all survey plots, probably because of their abundant and long-distance seed dispersal (Mori 1991). *Morus bombycis*, *M. obovata* and *P. amurense* are bird-dispersed, and their seed trees in the neighboring natural forest (*M. bombycis*: 0 trees/3.38ha, *M. obovata*: 46 trees/3.38ha, *P. amurense*: 19 trees/3.38ha) were less abundant than those of *Betula* spp. (Table 1). Therefore, the annual amount of seed dispersal of these three species was low compared with that of *Betula* spp., but seed dispersal is expected to be relatively spatially homogeneous (Masaki et al. 1994). Furthermore, the duration of seed burial for *M. obovata* and *P. amurense* can be considerably long (Ozawa 1950; Watanabe and Mizui 2000), and it might contribute to increased frequency of occurrence and density of their seedlings at cleared sites (Murray 1988; Table 3). The duration of seed burial of *M. bombycis* seeds is unknown, yet our results suggest that it is considerably long, similar to *M. obovata* and *P. amurense*.

Although the CVs of seedling density were large in species with low frequencies of occurrence, those of *P. amurense* (CV: 93.3%), *M. obovata* (99.3%) and *Betula* spp. (111.8%) were small (Table 3). For *M. bombycis* and *F. lanuginosa*, the CVs decreased to 89.1 and 140.7 %, respectively, when plots II-6 and II-7 were excluded from the

calculations. When comparing the CVs of seedling density between the three species with the highest frequencies of occurrence for each seed-dispersal mode, it becomes clear that the spatial variation in seedling density was smaller for animal-dispersed species than for non-animal-dispersed species (Table 3).

In conclusion, tree seedling density was high (mean: 9.8 seedlings/m<sup>2</sup>) at a cleared site 1 year following a typhoon disturbance. Both wind-dispersed (*Betula* spp.) and bird-dispersed (*M. bombycis*, *M. obovata*, *P. amurense*) species were found at high densities and frequencies of occurrence. The natural regeneration of non-animal-dispersed species, especially of wind-dispersed species, will likely continue at this site by seeding from the neighboring natural forest; whereas, the regeneration of bird-dispersed species will not, because there were no perch trees. The seedling density of non-animal-dispersed species was dependent on the distance from seed trees, and consequently, the species composition of seedling cohorts will likely change both spatially and temporally.

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Table 1. Species composition and density of seed trees in a nature forest and seedlings in cleared sites

Species	Seed dispersal type *	In a natural forest			In cleared sites			Density of current seedlings (1/m <sup>2</sup> )
		Basal area (m <sup>2</sup> )	Individual number	Basal area ratio (%)	Seedling number			
					Current	Advanced	Total	
<i>Betula maximowicziana</i>	N	10.507	165	26.01	1758**	61**	1819**	4.088**
<i>Ulmus davidiana</i> var. <i>japonica</i>	N	4.900	62	12.13	14	5	19	0.030
<i>Picea jezoensis</i>	N	3.523	29	8.72	43	9	52	0.100
<i>Fraxinus lanuginosa</i>	N	2.828	49	7.00	0	0	0	0
<i>Tilia maximowicziana</i>	N	2.602	41	6.44	0	0	0	0
<i>Acer mono</i>	N	2.278	41	5.64	1	4	5	0.002
<i>Cercidiphyllum japonicum</i>	N	2.238	13	5.54	24	3	27	0.056
<i>Magnolia obovata</i>	A	1.988	46	4.92	129	10	139	0.300
<i>Quercus crispula</i>	A	1.741	30	4.31	6	11	17	0.014
<i>Alnus hirsuta</i>	N	1.487	17	3.68	23	1	24	0.053
<i>Phellodendron amurense</i>	A	1.030	19	2.55	177	22	199	0.412
<i>Populus sieboldii</i>	N	0.751	4	1.86	0	0	0	0.000
<i>Fraxinus lanuginosa</i>	N	0.658	12	1.63	1167	295	1462	2.714
<i>Kalopanax septemlobus</i>	A	0.489	7	1.21	1	2	3	0.002
<i>Acer palmatum</i> var. <i>matsumurae</i>	N	0.452	5	1.12	5	20	25	0.012
<i>Sorbus alnifolia</i>	A	0.448	9	1.11	0	0	0	0
<i>Betula ermanii</i>	N	0.339	4	0.84	-	-	-	-
<i>Magnolia kobus</i> var. <i>borealis</i>	A	0.323	6	0.80	8	7	15	0.019
<i>Ostrya japonica</i>	N	0.218	3	0.54	0	0	0	0
<i>Carpinus cordata</i>	N	0.198	4	0.49	2	1	3	0.005
<i>Purunus maximowiczii</i>	A	0.194	3	0.48	5	15	20	0.012
<i>Tilia japonica</i>	N	0.194	3	0.48	0	13	13	0
<i>Abies sachalinensis</i>	N	0.182	2	0.45	1	16	17	0.002
<i>Cornus controversa</i>	A	0.174	3	0.43	6	2	8	0.014
<i>Maackia amurensis</i>	N	0.174	3	0.43	2	2	4	0.005
<i>Acanthopanax sciadophylloides</i>	A	0.170	4	0.42	1	1	2	0.002
<i>Betula platyphylla</i> var. <i>japonica</i>	N	0.117	2	0.29	-	-	-	-
<i>Salix</i> spp.	N	0.085	2	0.21	33	2	35	0.077
<i>Prunus sargentii</i>	A	0.044	1	0.11	0	2	2	0
<i>Acer japonicum</i>	N	0.044	1	0.11	2	7	9	0.005
<i>Sorbus commixta</i>	A	0.036	1	0.09	0	3	3	0
<i>Morus bombycis</i>	A	0.000	0	0.00	287	25	312	0.667
Density(per area)		11.960 m <sup>2</sup> /ha	175/ha	100	8.6/m <sup>2</sup>	1.3/m <sup>2</sup>	9.8/m <sup>2</sup>	8.590

\* N: non-animal-dispersed, A: animal-dispersed.

\*\* : Seedling number of *Betula* spp.

Table 2. Correlations between current and total numbers of seedlings in cleared sites and seed tree basal areas by species and number of individuals by species in a natural forest

	Basal area by species in a natural forest		Individuals by species in a natural forest	
	$\rho^*$	$p$ -value	$\rho^*$	$p$ -value
Number of current seedlings	0.190	0.31	0.243	0.20
Total number of seedlings	0.126	0.51	0.138	0.47

\* Spearman rank correlation coefficient.

Table 3. Mean density of current seedlings and occurrence frequency by species

Dispersal type	Species	Mean density (1/m <sup>2</sup> )	Standard deviation	Coefficient of variation (%)	Occurrence frequency
Non-animal-dispersed	<i>Betula</i> spp.	4.088	4.569	111.8	1
	<i>Fraxinus lanuginosa</i>	2.714	9.600	353.7	0.70
	<i>Picea jezoensis</i>	0.100	0.184	184.0	0.65
	<i>Salix</i> spp.	0.077	0.107	139.4	0.45
	<i>Cercidiphyllum japonicum</i>	0.056	0.076	136.2	0.35
	<i>Alnus hirsuta</i>	0.053	0.116	216.9	0.30
	<i>Ulmus davidiana</i> var. <i>japonica</i>	0.030	0.123	410.0	0.15
	<i>Acer palmatum</i> var. <i>mayrii</i>	0.012	0.026	223.6	0.20
	<i>Acer japonicum</i>	0.005	0.014	301.0	0.10
	<i>Carpinus cordata</i>	0.005	0.022	473.0	0.05
	<i>Maackia amurensis</i>	0.005	0.022	473.0	0.05
	<i>Abies sachalinensis</i>	0.002	0.011	473.0	0.05
	<i>Acer mono</i>	0.002	0.009	387.0	0.05
Animal-dispersed	<i>Morus bombycis</i>	0.667	1.502	225.0	1
	<i>Phellodendron amurense</i>	0.412	0.384	93.3	0.90
	<i>Magnolia obovata</i>	0.300	0.298	99.3	1
	<i>Magnolia kobus</i> var. <i>borealis</i>	0.019	0.039	209.6	0.20
	<i>Quercus crispura</i>	0.014	0.023	164.8	0.30
	<i>Cornus controversa</i>	0.014	0.027	193.5	0.25
	<i>Purnus maximowiczii</i>	0.012	0.024	206.4	0.20
	<i>Acanthopanax sciadophylloides</i>	0.002	0.011	473.0	0.05
<i>Kallopanax septemrobis</i>	0.002	0.011	473.0	0.05	

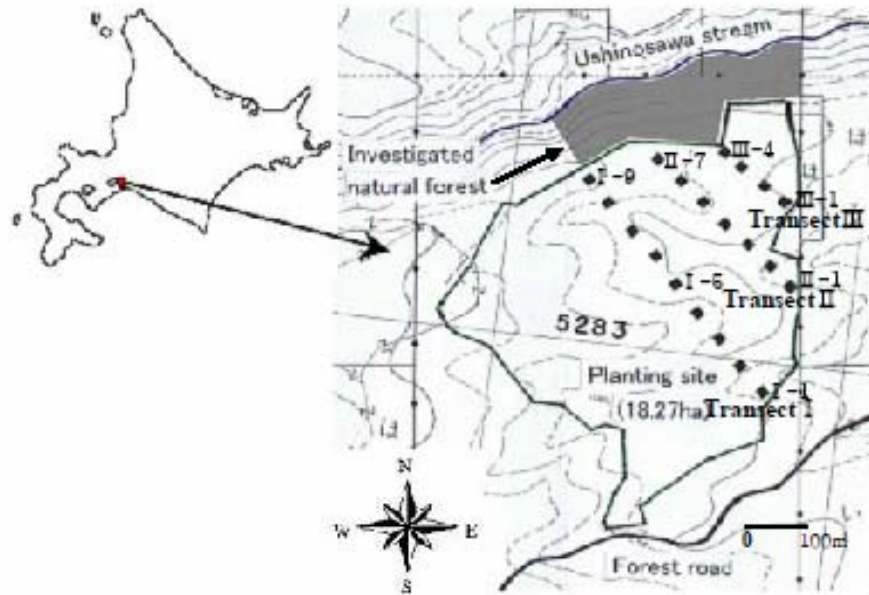


Fig. 1. Map of the study site

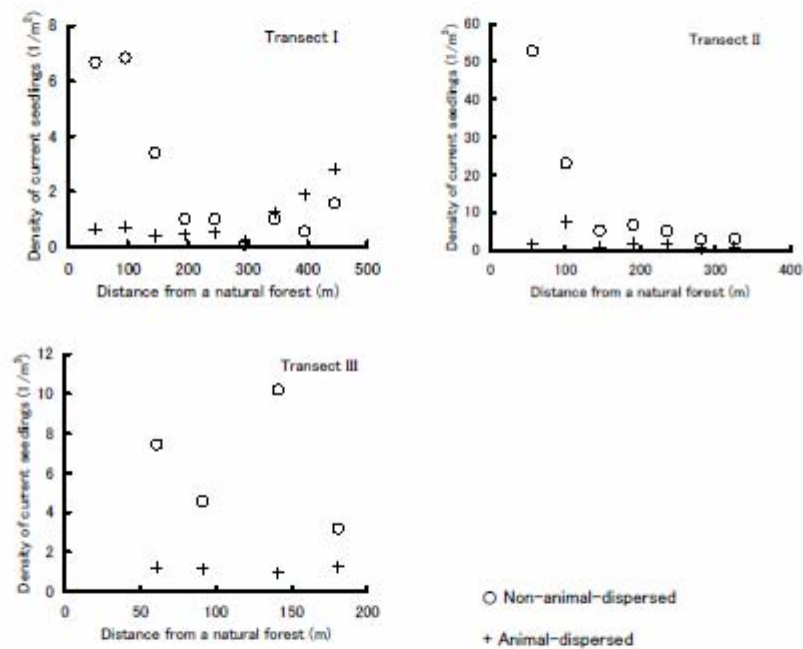


Fig. 2. Relationship between current seedling density by seed dispersal mode and distance from a natural forest; Spearman rank correlations for non-animal-dispersed (*circles*) and animal-dispersed (*plus signs*) species:  $\rho = -0.644$  ( $p=0.06$ ) and  $\rho = 0.500$  ( $p=0.17$ ) in transect I,  $\rho = -0.810$  ( $p=0.03$ ) and  $\rho = -0.571$  ( $p=0.18$ ) in transect II, and  $\rho = -0.400$  ( $p=0.60$ ) and  $\rho = 0.200$  ( $p=0.80$ ) in transect III, respectively.