Hardwood recruitment into conifer plantations in Japan: Effects of thinning and distance from neighboring hardwood forests

Etsuko Utsugi, Hiroshi Kanno, Naoto Ueno, Mizuki Tomita, Tomoyuki Saitoh, Megumi Kimura, Kenich Kanou, Kenji Seiwa *

Laboratory of Forest Ecology, Graduate School of Agricultural Science, Tohoku University, Naruko-onsen, Miyagi 989-6711, Japan

Abstract

Conservation of plant species diversity in managed and natural forests is a concern worldwide. To clarify the effects of thinning and distance from neighboring hardwood forests on hardwood establishment in conifer plantations, we measured the abundance and diversity of hardwoods at different life stages (seed-fall, soil seed bank, seedling, sapling) and environmental conditions (light, soil temperature, litter accumulation, and composition) from -2 to 40 m from the hardwood-coniferous forest boundary into the coniferous forest interior in five unthinned and four thinned stands in *Cryptomeria japonica* plantations in Japan. In unthinned stands, hardwood abundance and diversity decreased with increasing distance into the coniferous forest interior for all life stages, perhaps because of a distance-dependent decrease in seed-fall and the subsequent soil seed bank for wind- and bird-dispersed seeds. Higher light and soil temperatures and shallower litter accumulation were observed at the hardwood-coniferous forest boundary compared to the coniferous forest interior, suggesting favorable environmental conditions for germination, emergence, and seedling growth for hardwood species, and resulting in higher species diversity near the boundary. In thinned stands, hardwood abundance and diversity also decreased with increasing distance into the coniferous forest interior for seed-fall and the soil seed bank, but did not decrease for seedlings and saplings, probably because of distance-independent improvement of environmental conditions due to thinning. Higher light availability and soil temperature and lower litter accumulation in thinned stands enhance seedling establishment for not only shade-tolerant but also shade-intolerant and light-demanding species. Our results suggest that distance-dependent diversity of juvenile hardwoods in dense coniferous plantations is closely related to distance-dependent gradients in both seed-fall and environmental conditions, but thinning enhances diversity, even in the forest interior.

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1. Introduction

The maintenance of biodiversity has become an increasingly important management goal, to provide a broad array of ecosystem services that directly or indirectly benefit human endeavors, such as maintaining the hydrological cycle, sustaining and/or increasing primary production, and storing and cycling nutrients (Tilman et al., 1996; Callaway et al., 2003; Hooper et al., 2005). Maintaining and/or increasing plant species diversity in conifer plantations is also a concern (Hansen et al., 1991; Roberts and Gilliam, 1995; Moore and Allen, 1999; Simberloff, 1999; Nagaike, 2002; Gotmark et al., 2005). In Japan, conifer plantations (i.e., *Cryptomeria japonica*, *Chamaecyparis obtusa*, *Pinus densiflora*, *Larix leptolepis*) were established for timber production after intensive clear-cutting of natural forests, particularly from the 1950s through the 1970s, and now occupy one-quarter of the area of Japan (10 million ha; Forestry Agency, 2000). These monocultures generally have low value for wildlife (Yui, 1999; Osawa, 2004) and timber production, particularly at high elevations (Krauchi et al., 2000; Masaki et al., 2004). Even-aged coniferous forests may also be susceptible to pest and wind damage and effects of global warming (e.g., Lugo, 1997; Bradshaw et al., 2000), and may acidify the soil (Nordborg and Olsson, 1999). Thus, forest managers require techniques to create mixed hardwood-coniferous forests from these monocultures.

Although old plantations have functions comparable to natural forests, thinning is an effective option to create biodiversity sooner and with more consistency. Thinning,

* Corresponding author. Tel.: +81 229 847399; fax: +81 229 846490.
  E-mail address: seiwa@bios.tohoku.ac.jp (K. Seiwa).

followed closely by underplanting an understory consisting of several native tree species, is a useful tool for increasing stand structural diversity and plant and wildlife diversity (e.g., Maas-Hebner et al., 2005). To preserve genetic diversity and reduce management costs, the conversion of plantations by spontaneous colonization of hardwood species (i.e., natural regeneration) is more suitable and sustainable than underplanting. However, natural regeneration may not produce the desired species composition, distribution, and density in a timely manner because of spatial and temporal variability in seed sources.

Many studies have explored the patterns and mechanisms of hardwood species recruitment in conifer plantations and have found that hardwood abundance and diversity are closely associated with thinning, stand age, previous land-use history, fertilization, and topography (e.g., Guariguata et al., 1995; Halpern and Spies, 1995; Kohli et al., 1996; Allen, 1997; Keenan et al., 1997; Thomas et al., 1999; Ito et al., 2003, 2004; Nagaike et al., 2003; Ramovs and Roberts, 2003; Jobidon et al., 2004). Forest thinning usually allows a greater number of understory species to persist (e.g., Thomas et al., 1999) because canopy disturbance usually increases available resources (e.g., light, nutrients) and fluctuations in temperature, which enhance seed germination and seedling establishment (Washitani and Takenaka, 1987; Tappeiner and Zasada, 1993; Seiwa, 1997; Sakai et al., 2005). Alternatively, thinning may result in increased dominance by one or a few understory species, thereby reducing understory diversity (Alaback and Herman, 1991; Jobidon et al., 2004). However, the mechanisms and processes underlying hardwood recruitment are not fully understood.

In long-lived tree species, the most drastic changes in population demography occur during the early life stages, particularly at the seed and seedling stages (Harper, 1977; Harcombe, 1987; Seiwa and Kikuzawa, 1996). Spatially heterogeneous demographic events at the juvenile stages strongly affect the abundance and composition of forest communities (e.g., Nakashizuka, 2000; Nagamatsu et al., 2002). Thus, to improve hardwood diversity in conifer plantations through natural regeneration, knowledge of the regeneration processes, including seed dispersal, development of the seed bank, germination, and seedling establishment, is important. However, few studies have monitored the early stages of regeneration (but see Halpern et al., 1999).

Recruitment of hardwood trees into conifer plantations largely depends on seed dispersal via dispersal agents such as wind, birds, and small mammals. Although the number of dispersed seeds usually decreases with increasing distance from the seed source, irrespective of dispersal agents (Hoppes, 1988; Nathan and Muller-Landau, 2000), dispersal agents, particularly birds and small mammals, show different dispersal behavior (i.e., dispersal distance, dispersal stand preference) in response to stand conditions, such as vegetation composition and abundance (e.g., Kikuzawa, 1988; Restrepo et al., 1999; Seiwa et al., 2002). Few researchers have investigated the patterns of seed colonization from hardwood forests to coniferous plantations (but see White et al., 2004), although

distance-dependent hardwood seed abundance and diversity is expected.

In fragmented forests, moderate to dramatic differences in light availability, temperature, soil moisture, litter accumulation, and abundance and activity of seed dispersal agents occur in the edge and interior environments. Most of these environmental conditions strongly affect seed germination and seedling recruitment (e.g., Murcia, 1995; Laurance et al., 1998; Wolf and Batzli, 2004), resulting in distance-dependent diversity and growth of understory vegetation (e.g., Williams-Linera, 1990; Chen et al., 1992; Matlack, 1994; Laurance et al., 1998; McDonald and Urban, 2004). Environmental conditions in conifer plantations change with the distance from the boundary with the neighboring hardwood forest in a manner analogous to fragmented forests, which should affect the regeneration of hardwood species.

The aim of this study was to evaluate the effects of thinning and the distance from the hardwood-coniferous forest boundary on hardwood recruitment success and species diversity in *C. japonica* plantations. We investigated environmental conditions (i.e., light, soil temperature, litter accumulation) and hardwood abundance and diversity at different stages of the regeneration process (i.e., seed-fall, soil seed bank, seedling, and sapling) at various distances from neighboring hardwood forests in both thinned and unthinned *C. japonica* stands. We addressed the following questions: To what extent is hardwood abundance and diversity affected by thinning and the distance from the hardwood-coniferous forest boundary into the interior of the *C. japonica* forest? How do environmental conditions vary with distance and thinning, and how do they affect hardwood regeneration?

2. Materials and methods

2.1. Study area

This study was conducted in *C. japonica* plantations adjacent to deciduous broad-leaved stands in the Experimental Forest of the Integrated Field Research Center of Tohoku University (38°45′N, 140°45′E, 330–540 m asl), northeastern Japan. Most of the forest area had previously been utilized as fuelwood coppices or hay meadows, but beginning in the 1950s, some of these were replanted with *C. japonica*. Other remnant coppices and meadows were abandoned in the 1960s and have regenerated naturally as secondary forests consisting of deciduous broad-leaved trees. The current landscape pattern of the study site is composed of plantation components (each 0.5–20 ha) as a mosaic in the secondary hardwood forests. In 2000, the mean annual temperature and rainfall were 10.7 °C and 1733 mm, respectively. Snow cover lasted from mid-December 2000 to mid-April 2001, with a maximum depth of 1.0 m. The soil is a well-drained Melanic Andosol (FAO-UNESCO, 1998).

We chose four stands in which thinning had been performed 2–3 years before the investigation, and five control (unthinned) stands with dense, closed canopies (Table 1). In both the thinned and control stands, hardwood trees were absent from

Table 1

Characteristics and management history of the study sites of five unthinned and four thinned stands in *Criptomeria japonica* plantations, and characteristics of neighboring hardwood forests

	Control sites					Thinned sites			
	C1	C2	C3	C4	C5	T1	T2	T3	T4
Cryptomeria japonica stands									
Aspect	SW	S	E	E	S	E	N	–	SSW
Slope (%)	25	40	25	35	35	25	35	0	10
Transect aspect (boundary-interior)	SE-NW	E-W	W-E	W-E	N-S	W-E	W-E	NW-SE	N-S
Years after thinning	–	–	–	–	–	2	2	3	3
Years after planting	35	33	25	23	23	23	30	23	38
Density (number ha^{-1})	1725	2050	1675	1800	1475	1175	1900	1500	975
Mean tree height (m)	17.1	20.8	14.5	15.6	13.2	12.5	7.7	10.1	17.4
Ry index[a]	0.88	1.00	0.86	0.91	0.82	0.72	0.63	0.73	0.68
Neighboring hardwood forests									
Basal area of trees with wind-dispersed seeds (m^2 ha^{-1})	0.17	4.08	17.73	1.97	5.32	11.65	11.25	17.24	0.66
Basal area of trees with bird-dispersed seeds (m^2 ha^{-1})	0.20	7.07	0.22	9.47	5.97	1.73	6.93	3.39	6.12
Basal area of trees with small mammal dispersed seeds (m^2 ha^{-1})	9.48	3.88	27.52	30.17	33.73	27.09	36.68	0.28	1.01
Total basal area	9.85	15.03	45.48	41.60	45.01	40.47	54.86	20.91	7.79
Number of tree species, including shrubs[b] (400 m^{-2})	10	9	11	12	14	14	19	16	12

[a] The Ry index is a measure of tree crowding relative to full density at a given stand volume; Ry of 1.00 indicate full density.

[b] Trees ≥5 cm in diameter at breast height and shrubs >1.5 m in height.

the canopy layer, and the slope was gentle (<5°). Precommercial thinning had been conducted at least once in all stands. To estimate crowding, we calculated the Ry index (Ando, 1968), which has been used as an index to assess the density of conifer plantations:

$$Ry = \frac{V_{Rc}}{V_{Rfc}},$$

where V_{Rc} and V_{Rfc} are the observed and expected total stem volume (m^3 ha^{-1}) at full density, respectively. The Ry index was similar among the five control and four thinned stands (Table 1), indicating comparable crowding within the control and thinned stands. In each of the neighboring hardwood forests, a 20-m × 20-m quadrat was established along the boundary edge, and the diameter at breast height (DBH) was measured for all trees >5 cm in DBH and all shrubs >1.5 m in height. The hardwood forest canopy was typically dominated by *Quercus serrata*, *Q. mongolica* var. *grosseserrata*, *Castanea crenata*, and *Carpinus laxiflora*; the subcanopy layer included *Ilex macropoda*, *Cornus controversa*, *Acer amoenum* var. *matsumurae*, and *A. mono*. *Enkianthus perulatus*, *Viburnum dilatatum*, and *V. furcatum* dominated the shrub layer. The total basal area of hardwood forests neighboring to the control stands did not differ statistically from that neighboring to thinned stands (Table 1; one-way ANOVA, $F = 0.0009$, $P = 0.98$).

2.2. Measurement of seed-fall, seedlings, and saplings

In each thinned and unthinned stand, a straight edge was delimited at the hardwood-coniferous forest boundary. Three parallel transects (45 m × 2 m), separated by more than 5 m, were established perpendicular to the boundary, with the exception of one thinned stand (T1) in which only two transects were established. Each transect began 5 m inside the edge of the hardwood forest and extended 40 m into the interior of the

managed *C. japonica* forest. In each transect, nine 2-m × 2-m quadrats were established at −2, 0, 2, 5, 10, 15, 20, 30, and 40 m from the edge of the hardwood-coniferous forest boundary. All woody stems in each quadrat were identified as seedlings (<0.3 m in height) or saplings (>0.3 m in height). The measurements were conducted from July to August in 2000 and 2001.

Three replicate seed traps were placed beside each of the nine quadrats in two control (C1, C2) and two thinned (T1, T2) stands in early August 2000 for a total of 108 traps. Each trap consisted of a 0.5-m^2 circular wire frame supporting a 0.2-mm mesh bag. Each frame was suspended 1.5 m above the ground on three polyvinyl chloride posts. We collected seeds and counted the number of sound seeds monthly from August 2000 to December 2001. During the winter (October 2000–April 2001), all traps were placed on the ground to reduce snow pressure.

2.3. Measurement of the soil seed bank

To estimate the buried viable seed population, we used the seedling emergence method (Halpern et al., 1999; Sakai et al., 2005) and counted the number of seedlings that emerged from sampled soil in a greenhouse. Twelve soil samples (0.5 m × 0.5 m, 25 mm depth) were collected from quadrats 0, 5, 10, and 30 m from the hardwood-coniferous forest boundary in three control (C1–C3) and three thinned (T1–T3) stands in late May 2001. Stones and roots were removed, and each sample was spread in a plastic tray (28 cm × 58 cm, 30-mm depth) at a 3–5-mm thickness within 24 h of collection. To prevent drying, silica fiber mattresses were placed in each tray. We identified and counted all hardwood seedlings until no new seedlings emerged (24 August 2001). The trays were occasionally watered to capacity. The minimum and maximum temperatures during the experiment were 9.5 and 45.5 °C, respectively. The range of temperature in the greenhouse was

almost identical to that observed in a thinned stand (T1) of *C. japonica* plantations (10.0–48.1 °C).

2.4. Microenvironment measurements

To estimate light conditions in the forest understory, hemispherical canopy photographs were taken at a height of 1.0 m from the ground at the center of each quadrat at 0, 5, 10, and 30 m from the hardwood-coniferous forest boundary in all study stands. Photographs were taken using a digital camera with a fish-eye lens (Nikon FC-E8 0.21x) before (5 April) and after (July–August) canopy closure occurred in the neighboring hardwood forests. Canopy openness was calculated using Winphoto (ter Steege, 1996). Photosynthetic photon flux density (PPFD) was measured at a height of 0.3 m from the ground beside quadrats at 0, 5, 10, and 30 m from the forest boundary in one control (C2) and one thinned (T2) stand using a photo-sensor (MDS-MkV-L; Alec Electronics Co., Ltd., Kobe, Japan). Measurements were taken at 20-min intervals for 1 month (12 July–11 August 2001). Each sensor recorded the average and cumulative daily PPFD during the census period.

The soil temperature was measured in quadrats 0, 5, 10, and 30 m from the hardwood-coniferous forest boundary in one control (C2) and one thinned (T2) stand. Measurements were taken at a depth of 5 mm at 20-min intervals for 1 month (11 June–12 July 2001) using a thermo-recorder TR-52 (T&D Co., Nagano, Japan). Each sensor recorded the average and cumulative daily soil temperature during the census period.

Litter depth was measured at five points (four corners and the center) in all quadrats using a steel shovel with an engraved scale, and averaged for each quadrat. In June and July, the percent cover of *C. japonica* litter, including needles and woody material (twigs, cones, branches), was estimated at 0.1% increments.

2.5. Grouping of species by habitat and life-history traits

For comparative analyses, plant species were divided into predetermined categories describing their life-history traits (i.e., dispersal agents, seed size, clonality, successional status) according to several previous studies (Appendix A; Kikuzawa, 1983, 1984; Ishizuka and Sugawara, 1989; Seiwa and Kikuzawa, 1991, 1996; Abe et al., 1995; Seiwa et al., 2006). Dispersal agents were classified into three categories: wind, birds, and small mammals. Seed size was classified as small (<0.5 mg), medium (<300 mg), and large (>300 mg). Our broad definition of clonality included species with rhizomes or runners and those that characteristically layer. Successional status was based on shade tolerance or environmental light availability in the common habitat of the species, and was classified into two categories: early and late successional.

2.6. Species diversity and richness

The species diversity and richness were quantified using Shannon's species diversity index (H'; Margurran, 1988) and the number of species in each stand.

2.7. Data analysis

To evaluate whether hardwood abundance and diversity in *C. japonica* forests were affected by those of the neighboring hardwood forests, Spearman's rank correlations were calculated between the woody plant basal area of the neighboring hardwood forest (400 m^{-2}) and the number of hardwoods in the study stand (100 m^{-2}), and between the number of species in the neighboring hardwood forest (400 m^{-2}) and the number of species of juveniles (seedlings and saplings) in the study stand (100 m^{-2}). The correlations were calculated separately for control ($n = 5$) and thinned ($n = 4$) stands.

To evaluate the effects of thinning and distance from the hardwood-coniferous forest boundary on the measured environmental conditions and hardwood diversity at each life stage, we used analysis of covariance (ANCOVA) with distance as the covariate. To evaluate the effects of season (i.e., before and after canopy closure), thinning, and distance on canopy openness, we used a two-factor ANCOVA with distance as the covariate. The effects of thinning and distance from the hardwood-coniferous forest boundary on hardwood abundance were also analyzed separately for each life stage, using ANCOVA with distance as the covariate. To determine whether distance-dependent patterns of hardwood abundance differed among species grouped by life-history traits, separate ANCOVAs were conducted for control and thinned stands, with distance as the covariate.

Table 2
ANCOVA results for the effects of thinning, season, and distance from the hardwood-coniferous forest boundary into the coniferous forest interior on environmental variables in *Cryptomeria japonica* plantations

Environmental variable	Distance F	Thinning F	Season F	Distance × thinning F	Distance × season F	Thinning × season F
Canopy openness	12.34[**]	0.31	18.08[****]	1.17	4.65[*]	0.74
Photosynthetic photon flux density	1.02	63.95[*]		0.02		
Soil temperature	0.00	1.58		0.96		
Litter depth	82.26[****]	0.66		14.85[***]		
Percent cover of coniferous litter	212.60[**]	0.30		12.42[***]		

[*] $P < 0.05$.
[**] $P < 0.01$.
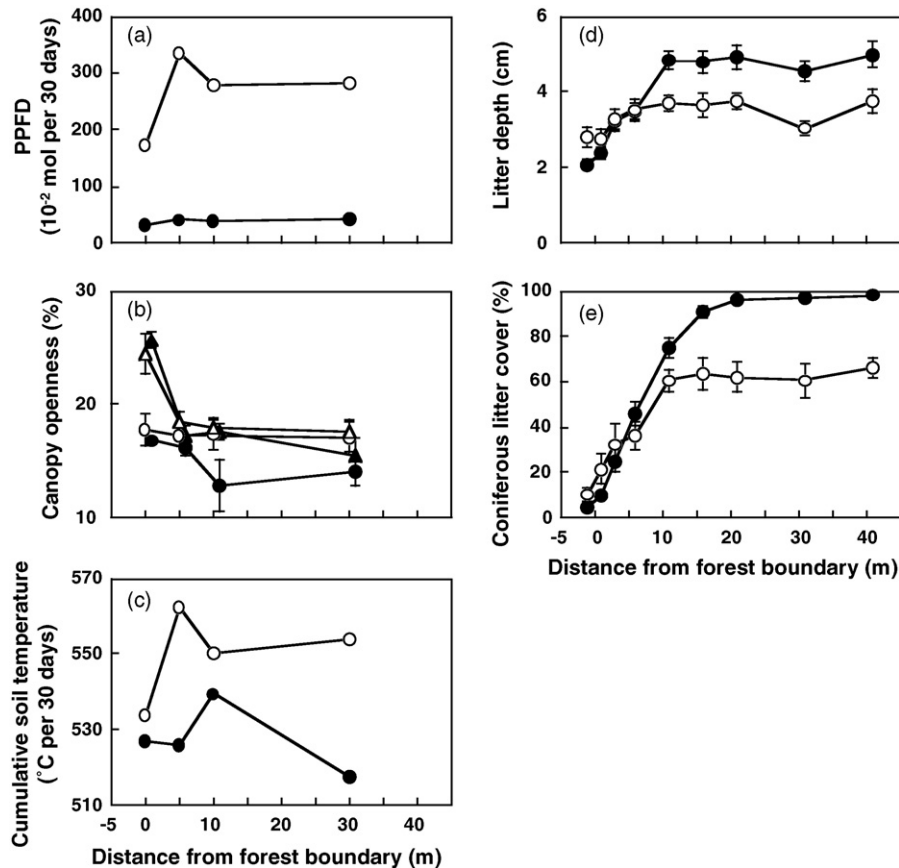[***] $P < 0.001$.
[****] $P < 0.0001$.

Fig. 1. Changes in understory environmental conditions with distance from the hardwood-coniferous forest boundary into the coniferous forest interior in *Cryptomeria japonica* plantations. (a) Photosynthetic photon flux density (PPFD) after canopy closure; (b) canopy openness before (C, H) and after (E, J) canopy closure in the neighboring hardwood forests; (c) cumulative soil temperature; (d) depth of coniferous litter; and (e) percent cover of coniferous litter (%). Open and closed symbols indicate thinned and unthinned stands, respectively.

When necessary to meet the assumptions of the ANOVA, the data were square-root-transformed for litter cover; ln-transformed for soil temperature, litter depth, number of individuals, and number of species; and arcsine square-root-transformed for canopy openness and species diversity index (H').

To evaluate the effects of litter on seedling establishment, Spearman's rank correlations were calculated between the number of seedlings and litter depth or coniferous litter percent cover for all quadrats.

All analyses were conducted using data pooled across the three replicated quadrats at each distance for each study stand. The number of seeds from seed traps was also pooled across 2 years (2000 and 2001) because of poor seed-fall in 2001. All statistical analyses were performed using JMP (SAS Institute Inc., Cary, NC, USA).

3. Results

3.1. Microenvironment

In the *C. japonica* forests, summer PPFD was higher in thinned than control stands, but did not change with distance into the forest interior (Table 2, Fig. 1a). In both stand types, canopy openness was greatest at the edge and decreased toward the interior in winter, before canopy closure occurred

in the neighboring hardwood forests. Little difference was observed with distance in summer, after canopy closure, resulting in a significant interaction between season and distance (Table 2, Fig. 1b). Soil temperature was not affected by distance, but was higher in thinned than in control stands (Fig. 1c), although not significantly so (Table 2). Both litter depth and coniferous litter percent cover increased with increasing distance into the coniferous forest interior in both control and thinned stands (Table 2, Fig. 1d and e). The increase was much greater in control than in thinned stands, resulting in a significant interaction between thinning and distance (Table 2).

3.2. Hardwood abundance and diversity

We recorded 28,101 individuals of 95 tree species, including 17,653 trapped seeds of 35 species, 3868 buried viable seeds of 18 species, 3436 seedlings of 80 species, and 3255 saplings of 81 species (Table 3).

3.2.1. Seed-fall and soil seed bank

For trapped and buried viable seeds in both control and thinned stands, the number of individuals and number of species were greatest in quadrats at the hardwood-coniferous forest boundary and decreased with increasing distance into the

Table 3
Total number of seeds, viable seeds in the soil, seedlings and saplings per 100 m^2 in each of control and thinned sites

Life stage	Number of hardwoods									Total
	Control stands					Thinned stands				
	N1	N2	N3	N4	N5	T1	T2	T3	T4	
Seed	2549	52246				9224	6032			17653 (35)
Viable seeds in the soil	6460	4928	75158			13520	9091	19647		3868 (18)
Seedling	661	269	790	347	359	326	124	225	331	3436 (80)
Sapling	285	41	486	152	205	51	197	57	1786	3255 (81)

Numerals in parentheses are number of species observed.

coniferous forest interior, whereas H' did not show distance-dependent patterns (Table 4, Fig. 2a and b).

In both control and thinned stands, decreasing patterns of distance dependency were also observed for most of the dominant species (Fig. 3). The exceptions were three species with small, wind-dispersed seeds: *Alnus hirsuta* var. *sibirica*, *Betula grossa*, and *B. maximowicziana* showed little decline with distance in the number of seeds trapped in both stand types (Fig. 3a). Most bird-dispersed seeds were disseminated near the hardwood-coniferous forest boundary, whereas wind-dispersed seeds showed moderate declining patterns with distance into the coniferous forest interior (Fig. 3 a and b), although the extent of the decline was not statistically different between the two dispersal modes in either control or thinned stands (ANCOVA, control: $F < 0.52$, $P > 0.47$; thinned: $F < 0.07$, $P > 0.79$). In *Q. serrata*, the largest-seeded species, the number of acorns trapped decreased drastically with distance, and all acorns were trapped within 10 m of the forest boundary in the thinned stands (Fig. 3c). As a result, we found a significant difference in the distance-dependent declining patterns among seed sizes in thinned stands, but not control stands, because no acorns were trapped in the control stands (ANCOVA, control: $F < 1.92$, $P > 0.16$; thinned: $F < 5.44$, $P > 0.007$).

3.2.2. Seedlings and saplings

For both seedlings and saplings, the number of individuals, number of species, and H' were greatest in quadrats at the hardwood-coniferous forest boundary and decreased with increasing distance into the coniferous forest interior in control

stands, except in thinned stands (Table 4, Fig. 2c and d). The differences between thinned and control stands were few for seedlings but large for saplings, particularly in the forest interior, compared to the hardwood-coniferous forest boundary (Fig. 2c and d), resulting in a significant interaction between distance and thinning (Table 4).

For most of the species studied, distance-dependent and distance-independent patterns were also observed in control and thinned stands, respectively (Fig. 4). The exceptions were *Lindera umbellata* var. *membrancea* (distant-independent pattern) in control and *V. dilatatum* (distant-dependent pattern) in thinned stands.

In both control and thinned stands, few differences (ANCOVA, $F < 0.55$, $P > 0.58$) in distance-dependent changes among species grouped by life-history traits (dispersal mode, seed size, successional status), were observed in any of the groups for any variable (number of individuals or species, H').

The number of seedlings was negatively correlated with litter depth ($r = -0.423$, $P < 0.0001$) and coniferous litter percent cover ($r = -0.441$, $P < 0.0001$) in control stands, but not in thinned stands (litter depth: $r = -0.053$, $P = 0.624$; coniferous litter percent cover: $r = -0.026$, $P = 0.810$; Fig. 5a and b).

3.3. Effects of neighboring hardwood forests

In both control and thinned stands, neither the number of individuals per 100 m^2, nor the number of species of seedlings and saplings was correlated with the basal area or

Table 4
ANCOVA results for the effects of thinning and distance from the hardwood-coniferous forest boundary into the coniferous forest interior on the number of individuals, number of species, species diversity index (Shannon's H') at different life stages (seed, seed bank, seedling, and sapling) in *Cryptomeria japonica* plantations

	Number of individuals			Number of species			Shannon's H'		
	Distance F	Thinning F	Distance × thinning F	Distance F	Thinning F	Distance × thinning F	Distance F	Thinning F	Distance × thinning F
Seed	3.51[†]	0.42	0.25	3.83[†]	2.78	0.09	0.05	66.44[***]	0.17
Seed bank	7.86[*]	0.03	0.27	10.30[**]	1.17	0.15	0.07	0.24	0.88
Seedling	4.27[*]	2.46	5.78[*]	6.21[*]	2.14	4.08[*]	0.97	0.17	0.38
Sapling	13.70[***]	2.72[†]	10.50[**]	11.91[***]	3.88[*]	7.73[**]	12.14[***]	2.22	3.94[*]

[*] $P < 0.05$.
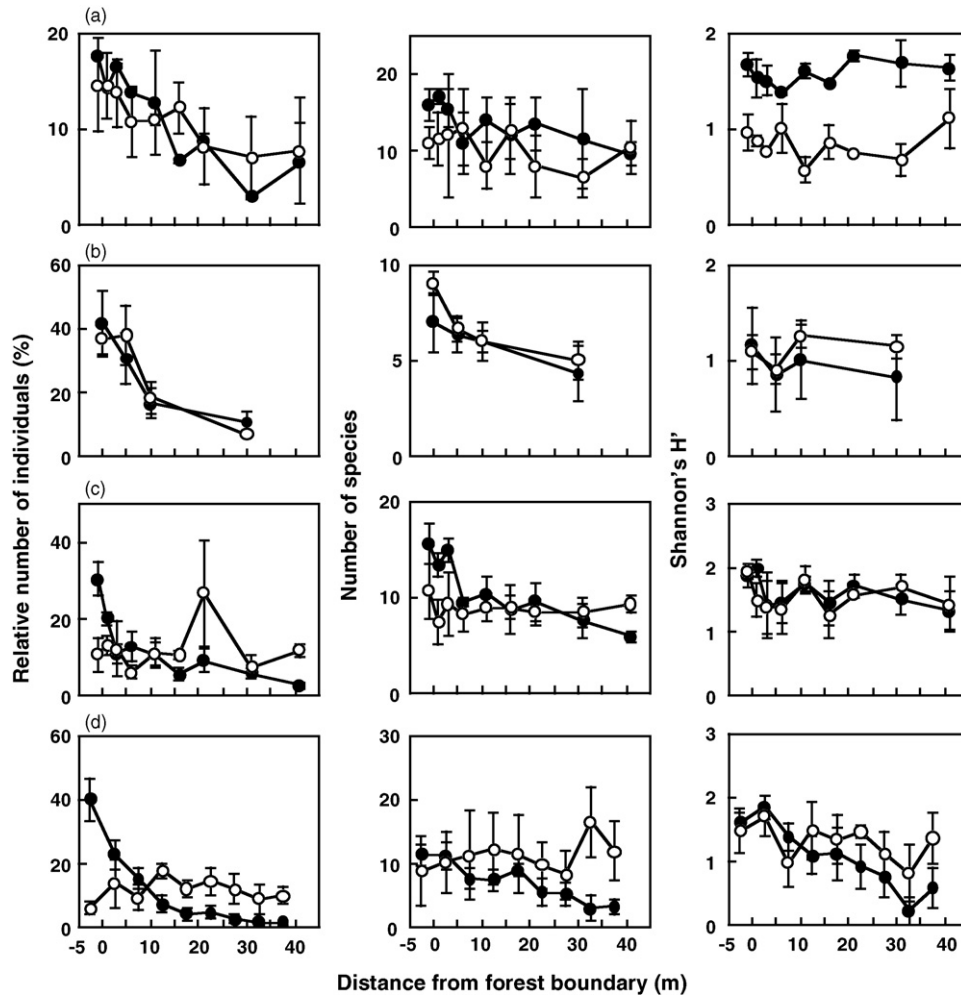[**] $P < 0.01$.
[***] $P < 0.001$.
[†] $P < 0.1$.

Fig. 2. Changes in the number of individuals, number of species, and species diversity index (H') of hardwood species with distance from the hardwood-coniferous forest boundary into the coniferous forest interior in *Cryptomeria japonica* plantations. (a) Seeds; (b) viable seeds in the soil; (c) seedlings; and (d) saplings. The number of individuals is given as the relative value in each of the thinned and control stands because of large differences among stands. Vertical bars indicate ±S.E. Open and closed symbols denote thinned and unthinned stands, respectively.

number of species in the neighboring hardwood forests ($-0.95 \leq r_{sp} \leq -0.40$, $0.052 \leq P \leq 0.60$).

4. Discussion

4.1. Distance-dependent species diversity in unthinned C. japonica forests

In unthinned *C. japonica* forests, hardwood abundance and diversity were greatest at the hardwood-coniferous forest boundary, but decreased dramatically with increasing distance into the *C. japonica* forest interior. Such distance-dependent patterns in juvenile species diversity were strongly affected by distance-dependent patterns in seed-fall and soil seed banks. Decreasing seed-fall with distance from the parent tree is common in wind-dispersed species (e.g., Augspurger and Franson, 1987; Nathan and Muller-Landau, 2000). However, we observed exceptions for three species that have small, wind-dispersed seeds (*A. hirsuta* var. *sibirica*, *B. grossa*, and *B. maximowicziana*), probably because of their large wing-load (Greene and Johnson, 1995; Houle, 1998), which would enable

them to disperse beyond the traps 40 m from the hardwood-coniferous forest boundary. This would also result in little correlation in species diversity between understory hardwoods in *C. japonica* forests and in neighboring hardwood forests. In contrast, most bird-dispersed seeds were disseminated beneath the neighboring hardwood canopy, probably because of greater avian abundance in hardwood forests than in *C. japonica* plantations (Yui, 1999). Seedlings of *Q. serrata* were observed more than 20 m from the forest boundary, although the acorns were disseminated a very short distance from the forest boundary. Acorns are usually dispersed by wood mice, such as *Apodemus speciosus* and *A. argentius*, but wood mice are rarely active in the absence of vegetative cover, thus inhibiting seed dispersal into open habitats, such as gaps and forest edges, in temperate forests (Kikuzawa, 1988; Miyaki and Kikuzawa, 1988; Wada, 1993; Seiwa et al., 2002). Our results indicate that wood mice cached acorns beneath the dense canopy of unthinned *C. japonica* forests, even though there was little vegetation in the understory. Jays (*Cyanocitta* spp.) are also a probable disperser of acorns. In a heterogeneous landscape, Gomez (2003) found that jays moved acorns nonrandomly,
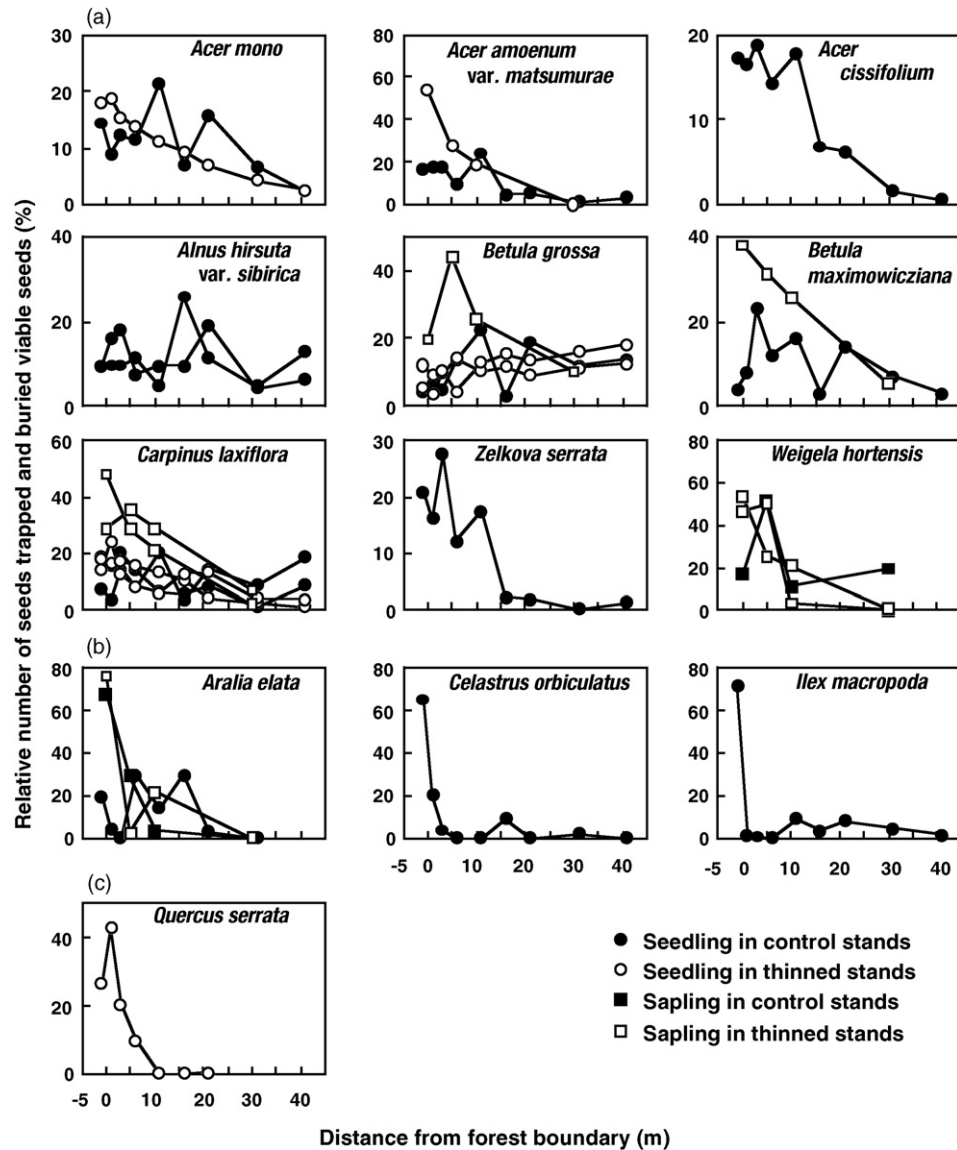
Fig. 3. Changes in the number of seeds trapped and the number of viable seeds in the soil of hardwood species with distance from the hardwood-coniferous forest boundary into the coniferous forest interior in *Cryptomeria japonica* plantations. (a) Wind-dispersed seeds; (b) bird-dispersed seeds; (c) mammal-dispersed seeds. The number of individuals is given as the relative value in each of the thinned and control stands because of large differences among stands. Only the most abundant species are shown (>500 and >1000 individuals per 100 m² for trapped seeds and viable seeds in the soil, respectively). Vertical bars indicate ±S.E.

avoiding shrubland and grasslands, and moving most acorns to pine stands.

Distance-dependent recruitment patterns of hardwood species in the coniferous plantations were also largely affected by distance-dependent changes in environmental conditions. Greater accumulation of litter usually inhibits seed germination, particularly for light-demanding species (Seiwa, 1997), because light is reduced exponentially by increasing amounts of litter (Facelli and Pickett, 1991). Litter also inhibits seedling emergence for small-seeded species that cannot penetrate thick layers of litter (Peterson and Facelli, 1992; Seiwa and Kikuzawa, 1996; Kanno and Seiwa, 2004). Therefore, seedling establishment would be strongly inhibited by the greater amounts of litter in the *C. japonica* forest interior than at the forest boundary. Furthermore, favorable light conditions at the hardwood-coniferous forest boundary would promote hardwood

recruitment into the edge of the coniferous forest. Understory light conditions were more favorable for understory hardwoods in the hardwood-coniferous forest boundary than in the coniferous forest interior, particularly in spring before canopy closure, because leaves of the dominant canopy trees (i.e., *Q. serrata*, *Q. mongolica* var. *grosseserrata*, and *C. crenata*) began to unfold approximately 2–6 weeks after those of most hardwood juveniles (Utsugi and Seiwa, personal observation). There is evidence that greater light availability in spring, prior to canopy closure in temperate deciduous forests, strongly enhances the survival and growth of juvenile hardwoods by promoting carbon acquisition and escape from pathogen and/or herbivore attacks (e.g., Seiwa, 1998; Tomita and Seiwa, 2004).

Gradients in the microenvironmental conditions from the forest edge to the interior, or "edge effects," usually cause distance-dependent changes in vegetation (e.g., Matlack, 1994;
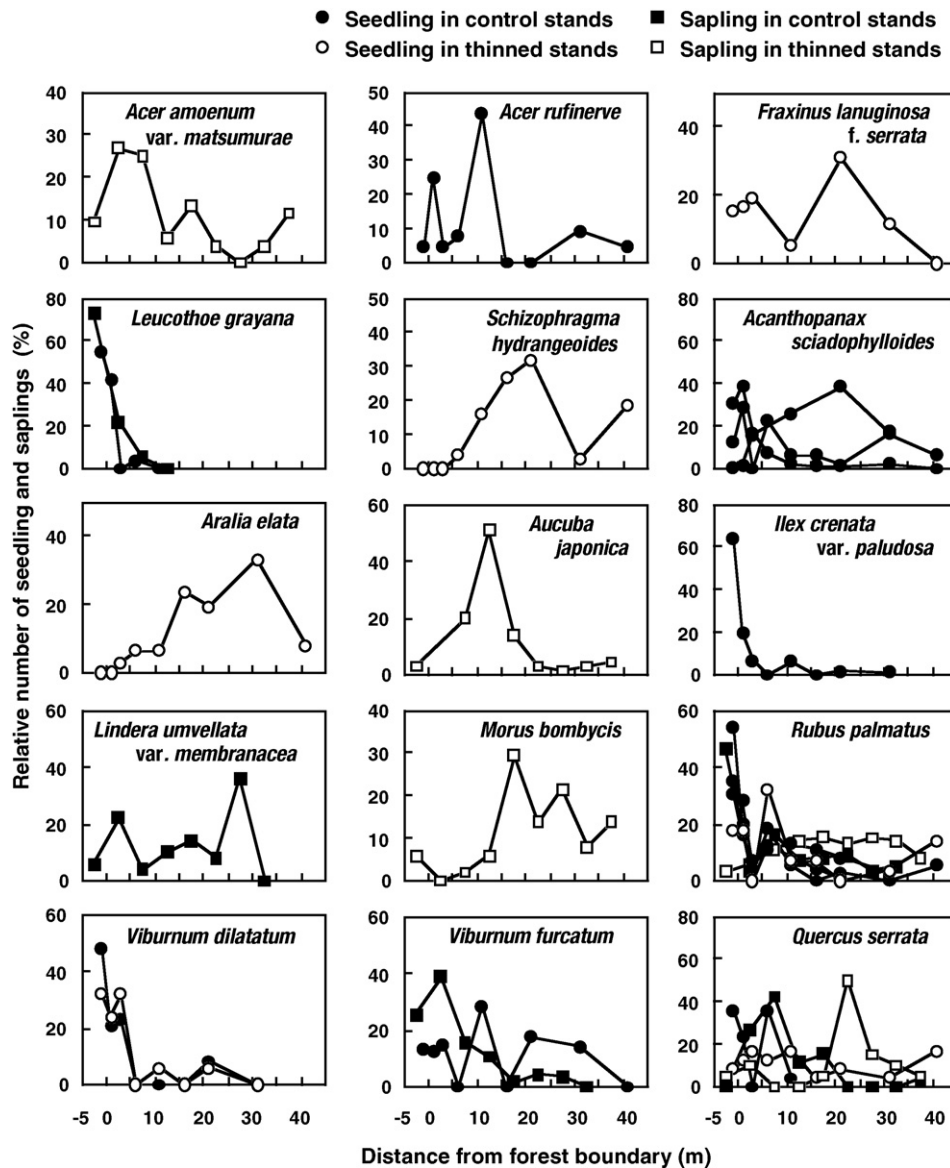
Fig. 4. Changes in the number of (a) seedlings and (b) saplings of hardwood species with distance from the hardwood-coniferous forest boundary into the coniferous forest interior in *Cryptomeria japonica* plantations. The number of individuals is given as the relative value in each of the thinned and control stands because of large differences among stands. Only the most abundant species are shown (>50 individuals per 100 m^2). Vertical bars indicate ±S.E.

Oosterhoorn and Kappelle, 2000; Euskirchen et al., 2001). Most of the distance-dependent patterns we observed were in accordance with edge effects previously reported for hardwood forest edges adjacent to clearings. However, there were some exceptions. In hardwood forests, early successional species are more abundant near edges adjacent to clearings (Matlack, 1994; Euskirchen et al., 2001), but this did not occur at the hardwood-coniferous forest boundary, probably because favorable conditions for understory plants at forest boundaries are more ephemeral and subtle than at forest edges.

4.2. Effects of thinning

In managed forests, thinning often dramatically increases the abundance and diversity of understory vegetation (e.g., Allen, 1997; Halpern et al., 1999; Thomas et al., 1999; Ito et al.,

2003). In this study, we also observed that the number of species was greater in thinned than unthinned *C. japonica* stands for saplings, but not earlier life stages (seed-fall, seed bank, or seedlings). This suggests that the higher species richness of the saplings was caused by thinning, not by favorable conditions intrinsic to the thinned stands, which were characterized by a higher abundance of wind- and bird-dispersed species in adjacent hardwood forests, compared to the unthinned stands. If favorable conditions influenced species richness, a greater number of species would be present in the seed-fall and soil seed bank stages, as well as the sapling stage.

In thinned stands, seed germination and seedling growth of shade-intolerant species are enhanced by the removal of canopy trees, which increases light availability and soil temperature in the understory, (e.g., *Rhus javanica*, *Ulmus japonica*; Washitani and Takenaka, 1987; Seiwa, 1997). Thinning may also increase
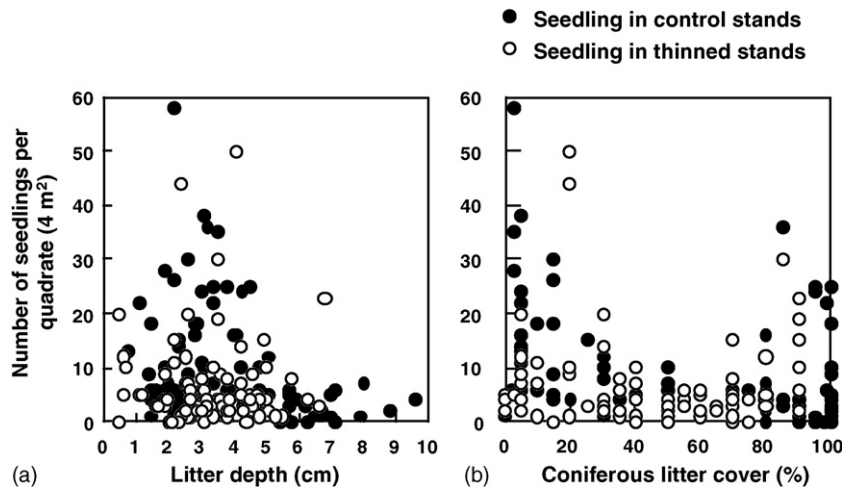
Fig. 5. Relationships between the number of seedlings (per 4 m^2) and (a) litter depth and (b) percent cover of coniferous litter.

the availability of nutrients and water for understory plants (Brix and Mitchell, 1986), enhancing the growth of seedlings, saplings, or both. Although we did not monitor the growth of the cohorts in this study, we observed rapid growth of hardwood seedlings immediately after thinning operations in other experimental stands of *C. japonica* plantations near our study stands (Eto and Seiwa, unpublished data). For example, in thinned stands, *Acer rufinerve*, *Alaria elata*, and *Moms bombycis* seedlings grew 25–48 cm in mean height 1–2 years after thinning, whereas the seedlings grew only 0–5 cm in unthinned stands.

Furthermore, in thinned stands, the negative effects of litter accumulation on seedling abundance were far less than in unthinned stands, most likely owing to less accumulation of coniferous litter, which has stronger negative effects than hardwood litter. Thinning usually disturbs the forest floor, providing favorable substrates such as bare soil and shallow coniferous litter accumulation for seedling establishment, particularly for light-demanding and small-seeded species (Peterson and Facelli, 1992; Seiwa and Kikuzawa, 1996; Seiwa, 1997; Kanno and Seiwa, 2004). Thus, reducing the litter accumulation appears to be an important contribution of thinning to species diversity.

Our results strongly suggest that thinning promotes seedling establishment for a variety of hardwood species by providing favorable environmental conditions for seed germination, seedling emergence, and seedling growth, resulting in species richness in *C. japonica* plantations. We observed improved diversity especially in the forest interior of thinned stands, where thinning improved environmental conditions (i.e., light, litter accumulation) more than at the hardwood-coniferous forest boundary. This increased hardwood recruitment in the forest interior and resulted in distance-independent patterns of species richness.

4.3. Management implications

In Japan, most commercial plantations of even-aged conifers are forest fragments that range in area from 0.1 to 100 ha and are adjacent to natural hardwood forests on at least one side. In recent decades, forest managers have been reluctant to thin

plantations because of decreasing timber prices and increasing harvesting costs. Thus, many coniferous plantations are overcrowded and have low species diversity, particularly in large fragments, because of the abrupt decline in species diversity with distance into the forest interior. In contrast, high diversity would be expected in small fragments because most of the area would experience edge effects. However, we evaluated juvenile, rather than adult, species richness, whereas most of the ecosystem function effects of biodiversity are performed by adult plants (Hooper et al., 2005).

Thinning appears to be a reliable method for restoring adult-level hardwood diversity in *C. japonica* plantations because it promptly and dramatically diminishes edge effects and strongly enhances the growth of understory juveniles, regardless of their successional status. However, in this study, we examined the distribution of seedlings and saplings but did not undertake long-term monitoring of our cohorts. To evaluate the duration of thinning effects, further long-term studies are needed.

To improve the species diversity of adult trees in monoculture forests, periodic thinning should be performed because intensive thinning often results in one or a few dominant species (Jobidon et al., 2004). However, periodic thinning is unrealistic economically, due to low timber prices and high operation costs. To meet this challenge, changes in ecosystem functions as newly recruited hardwoods increase in size should be evaluated. Improving the economic value of hardwoods is also important to determine thinning intensity. Further research is warranted to better understand the full range of management activities (e.g., thinning intensity, rotation age, stand size, configuration, timber price, and operation costs) for conversion of artificial coniferous forests to mixed hardwood-coniferous forests.

Acknowledgements

Appendix A

Mean number of seeds, viable seeds in the soil, seedlings, and saplings in unthinned and thinned stands in *Cryptomeria japonica* plantations, with functional-group classifications.

	Unthinned stands			Thinned stands			Functional group			
	S[†] Mean number ± S.D. (n = 2)	VS[‡] Mean number ± S.D. (n = 3)	SL&SA[§] Mean number ± S.D. (n = 5)	S[†] Mean number ± S.D. (n = 2)	SB[‡] Mean number ± S.D. (n = 3)	SL&SA[§] Mean number ± S.D. (n = 4)	SDA[a]	SS[b]	CL[c]	SC[d]
Acanthopanax sciadophylloides	26.0 ± 5.7		43.4 ± 46.9			4.7 ± 5.5	B	M		L
Acanthopanax spinosus			1.0				B	S		L
Acer amoenum var. *matsumurae*	1848.5 ± 2457.2	1931.0	9.0 ± 9.8	148.5 ± 115.3		10.5 ± 9.9	W	M		L
Acer cissifolium	16898.5 ± 23876.9	266.0	6.0	44.0			W	M		L
Acer distylum			7.5 ± 7.8			5.0	W	M	+	L
Acer japonicum	96.0		9.0			2.0	W	M		L
Acer micranthum	27.0		6.1 ± 8.3				W	M		L
Acer mono	2382.0 ± 3348.9	216.5 ± 259.5	5.5 ± 4.2	452.5 ± 586.2	33.0	2.8 ± 1.7	W	M		L
Acer rufinerve	296.0 ± 398.8	33.0	19.0 ± 26.4	152.0 ± 120.2	66.5 ± 47.4	2.3 ± 1.3	W	M	+	L
Acer sieboldianum			3.0 ± 2.8			0.5 ± 0.7	W	M		L
Actinidia arguta	166.5 ± 204.4		6.0	252.0		4.0	B	S	+	L
Actinidia polygama			4.0 ± 1.7			0.8 ± 0.3	B	S	+	L
Akebia trifoliate			44.5 ± 48.8			14.8 ± 18	B	M	+	L
Alnus hirsuta var. *sibirica*	578.0 ± 168.3			70.5 ± 16.3			W	S		E
Aralia elata	278.0 ± 350.7	399.7 ± 547.9	1.3 ± 0.6	92.5 ± 120.9	1399.0	27.8 ± 47.6	B	S		E
Aralia elata						42.0	B	M	+	L
Aucuba japonica var. *borealis*			32.0			13.5 ± 17.7	B	M	+	L
Betula grossa	1476.0 ± 1821.5	410.3 ± 170.9	1.5 ± 0.7	2089.5 ± 2368.1	1543.0 ± 2326.1	2.0	W	S		E
Betula maximowicziana	340.5 ± 461.7	24309.0 ± 41614.3			189.0 ± 101.8		W	S		E
Broussonetia kazinoki			0.2				B	S		E
Callicarpa japonica			1.0			6.2 ± 8.3	B	S		E
Carpinus cordata	7.0			44.0			W	M		L
Carpinus laxiflora	719.5 ± 743.2	277.3 ± 214.2	5.3 ± 4.2	1159.0 ± 886.7	5883.0 ± 4945.2	1.8 ± 1	W	S		E
Castanea crenata	7.0		8.3 ± 11.9			5.0 ± 5.7	M	L		E
Celastrus orbiculatus	63.0 ± 35.4		4.8 ± 3.9			7.0 ± 5.4	B	M		E
Cledendrum trichotomum			9.5 ± 11.2			1.0	W	S		E
Clerodendoron trichotomum				7.0		7.5 ± 3.5	B	M		E
Cornus controversa	181.5 ± 120.9		4.0 ± 4.8	148.0 ± 147.1		2.7 ± 2.1	B	M		E
Corylus heterophylla var. *thunbergii*			1.0				M	L		E
Corylus sieboldiana			0.5			1.0	M	L		E
Enkianthus perulatus			3.0				W	S		L
Euonymus macropterus			0.2			0.4	B	M		L
Euonymus sieboldianus						3.0	B	M		L
Fagus crenata				11.0 ± 5.7			M	L		L
Fraxinus lanuginosa f. *serrata*			10.3 ± 13.5			30.0 ± 36.8	W	M		L
Fraxinus sieboldiana			4.0			3.5 ± 3.5	W	M		L
Hamamelis japonica						10.0	A	M		L
Hydrangea paniculata			7.5 ± 7.3			6.9 ± 7.3	W	S		E
Hydrangea petiolaris			2.2 ± 2.5			1.0	W	S	+	L
Hydrangea serrata var. *megacarpa*			1.5 ± 0.7			1.0	W	S	+	E
Ilex crenata var. *paludosa*			116.0			2.0	B	M	+	L
Ilex macropoda	611.5 ± 738.9		6.3 ± 4.8	59.0 ± 73.5		15.0	B	M		L
Juglans ailanthifolia						1.0	M	L		E
Kalopanax pictus	296.0		0.5 ± 0.7			1.3 ± 0.6	B	S		L
Lespedeza bicolor		100.0 ± 94.8			144.3 ± 138.9	0.2	A	M		E
Leucothoe grayana			43.0 ± 52.3			0.5	W	S	+	E
Lindera pracox						3.0	M	M		L
Lindera umbellata var. *membranacea*			9.8 ± 15.6			3.2 ± 4.2	B	M		L

Appendix A (Continued)

	Unthinned stands			Thinned stands			Functional group			
	S[†] Mean number ± S.D. (n = 2)	VS[‡] Mean number ± S.D. (n = 3)	SL&SA[§] Mean number ± S.D. (n = 5)	S[†] Mean number ± S.D. (n = 2)	SB[‡] Mean number ± S.D. (n = 3)	SL&SA[§] Mean number ± S.D. (n = 4)	SDA[a]	SS[b]	CL[c]	SC[d]
Magnolia hypoleuca			0.8 ± 1	7.0		1.5 ± 0.7	B	M		L
Magnolia praecocissima			1.0				B	M		L
Melisoma myriantha						1.0	B	M		L
Menzeisia purpurea			14.0				W	S		L
Morus bombycis		233.0	1.0	52.0	344.0 ± 538.7	22.0	B	S		E
Ostrya japonica				52.0 ± 52.3			W	M		E
Prunus grayana			6.0 ± 1.4			5.0 ± 5.7	B	M		L
Prunus sargentii			1.5 ± 0.7	38.0		3.0	B	M		L
Prunus verecunda	104.0 ± 73.5		13.0 ± 19.1	33.0 ± 15.6		4.0	B	M		E
Pterocarya rhoifolia				15.0			W	M		E
Pueraria lobata		33.0					A	M	+	E
Quercus mongolica var. *grosserrata*			1.0			2.5 ± 1.9	M	L		L
Quercus serrata	14.5 ± 10.6	33.0	7.4 ± 10.5	2734.5 ± 3793.6	33.0	7.5 ± 5.8	M	L		E
Rhododendron kaempferi			10.9 ± 12.7			1.0	W	S		E
Rhus ambigua			0.8 ± 0.4			1.4 ± 1.3	B	M	+	L
Rhus javanica						0.3	B	M		E
Rhus trichocarpa	22.0		2.8 ± 2.9	44.5 ± 53		6.0	B	M		E
Rubus parvifolius L.						1.0	B	S	+	E
Rubus crataegiofolius						0.0	B	S	+	E
Rubus palmatus var. *coptophyllus*			63.0 ± 41.4			110.0 ± 210.7	B	S	+	E
Salix vulpine			6.0			1.7 ± 1.8	W	S		E
Sambucs sieboldiana			7.0		33.0	10.7 ± 13.3	B	S		E
Schisandra nigra			0.5				B	S	+	L
Schizophragma hydrangeoides			15.8 ± 10.2			23.5 ± 24.7	W	S	+	L
Smilax china			3.4 ± 4.1			3.1 ± 4.3	B	M	+	E
Sorbus alnifolia			0.5 ± 0.5			3.0	B	M		L
Sorbus commixta			2.0			2.0	B	S		L
Sorbus japonica			5.0			0.4	B	M		L
Stachyurus praecox						0.7 ± 0.5	B	S		E
Staphylea bumalda			0.4				A	M		L
Styrax japonica				30.0	133.0	2.7 ± 3.3	M	M		E
Styrax obassia			0.6 ± 0.4			4.5 ± 4.9	M	L		L
Symplocos chinensis			4.0			0.4	B	M		L
Tilia japonica			2.0	30.0			W	M		L
Tripterygium regelii			1.0				B	S	+	L
Ulmus japonica				7.0		0.7 ± 0.4	W	S		E
Ulmus laciniata						2.5 ± 0.7	W	S		L
Vaccinium japonicum			2.0				B	S		L
Vaccinium oldhamii			3.5 ± 3.5				B	S		E
Viburnum plicatum var. *toentosum*				89.0		21.0	B	M	+	L
Viburnum wrightii			8.7 ± 7.5				B	M	+	L
Viburnum dilatatum			20.0 ± 20.3			19.8 ± 17.9	B	M	+	L
Viburnum furcatum			247.0			3.0	B	M	+	L
Vitis coignetiae	25.5 ± 26.2	199.5 ± 94	5.2 ± 7.7	7.0	66.3 ± 57.7	7.0 ± 8.5	B	M		E
Weigela hortensis		3163.5 ± 2260.6	4.0 ± 4.2		3141.3 ± 2077.7	2.4 ± 3.1	W	S		E
Wisteria brachybotrys			1.0			3.1 ± 2.5	A	L	+	E
Zelkova serrata	1156.0 ± 1540.1		3.3 ± 3.9	70.5 ± 4.9	233.0	3.0 ± 2.8	W	M		E

[†] S: seeds.
[‡] VS: viable seeds in the soil.
[§] SL & SA: seedlings and saplings.
[a] Seed dispersal agents (SDA): A: dispersed automatically; B: bird-dispersed; M: mammal-dispersed; W: wind-dispersed.
[b] Seed size (SS): S: small <0.5 mg; M: medium <300 mg; L: large ≧300 mg.
[c] Clonality (CL): + indicate clonal plants which glow clonaly by stron and rhizome.
[d] Successional status (SC): E: early successional; L: late successional.

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