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# Roles of thinning intensity in hardwood recruitment and diversity in a conifer, *Criptomeria japonica* plantation: A 5-year demographic study

Kenji Seiwa [a,*], Yukino Etoh [a], Masahiro Hisita [a], Kazuhiko Masaka [b], Aya Imaji [a], Naoto Ueno [a], Yoichi Hasegawa [a], Miki Konno [a], Hiroshi Kanno [a], Megumi Kimura [a]

[a] *Laboratory of Forest Ecology, Graduate School of Agricultural Science, Tohoku University, Naruko-onsen, Miyagi 989-6711, Japan*
[b] *Forestry Research Institute, Koshunai, Bibai, Hokkaido 079-0198, Japan*

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ABSTRACT

To evaluate the role of thinning intensity in increasing hardwood diversity in managed coniferous forests, we investigated the effects of environmental changes caused by thinning on the seedling demography (i.e. seedling emergence, survival, and growth) of hardwood species for 5 years after thinning in 67% thinned (Intensive), 33% thinned (Weak), and unthinned treatments (Control) in a *Cryptomeria japonica* plantation in northern Japan. Intensive thinning strongly increased light and soil temperature but reduced litter accumulation, thus facilitating seed germination, seedling emergence, and seedling survival of primarily early- and mid-successional species compared to late-successional species. As a result, more early- and mid-successional species were observed in Intensive compared to Weak and Control, whereas the number of late-successional species did not differ among thinning intensities. Thus, the number of species was greatest in Intensive but lowest in Control throughout the 5 years. However, Shannon's diversity index ($H'$) did not strongly differ among thinning intensities, largely due to the predominance of the mid-successional species *Cornus controversa*, particularly in Intensive. In Control and Weak, both seedling survival and height were often greater for advance regeneration than for seedlings newly emerged in the year following thinning, whereas neither variable differed between advance regeneration and seedlings newly emerged in Intensive, mainly due to selective predation of advance regeneration by mammalian herbivores. These results suggest that the future composition of hardwoods can be roughly predicted by the composition of advance regeneration in Weak but by the composition of both advance regeneration and seedlings newly emerged in Intensive. When comparing large individuals (height >1.5 m), the number of species was greatest in Intensive in 2008, 5 years post-thinning, primarily due to rapid vertical growth regardless of successional status. These results suggest that within a *C. japonica* plantation, a canopy-level mixed conifer-hardwood forest would be more probable and occur more rapidly in Intensive compared to Weak. In Weak, enhanced species diversity would likely be restricted to the understorey layer because of the slower growth rate and lower survival rate of hardwood seedlings caused by the more rapid deterioration of favourable environmental conditions.



## 1. Introduction

In conifer plantations, the recovery of species diversity has become an increasingly important goal of forest management (Hansen et al., 1991; Roberts and Gilliam, 1995; Lugo, 1997; Simberloff, 1999; Hooper et al., 2005; Brockerhoff et al., 2008; Widenfalk and Weslien, 2009). Recent studies have suggested that compared to even-aged managed plantations, forests with higher species diversity may provide a broader array of ecosystem functions, such as maintaining the hydrological cycle, sustaining and/or increasing primary production, storing and cycling nutrients, reducing negative effects of global warming, and enhancing wildlife habitats (Lugo, 1997; Garcia-Gonzalo et al., 2007; Ohsawa, 2007; Steffan-Dewenter et al., 2007; Smith et al., 2008; Lei et al., 2009; Taki et al., 2010). Improving ecosystem functioning may also facilitate more sustainable timber production (Seiwa et al., in press). In addition, knowledge of the mechanisms involved in the maintenance of species diversity in natural forests has motivated forest managers to convert monoculture plantations to species-rich forests. Recent studies have clearly shown important roles of both abiotic factors (e.g. heterogeneity of light, water, nutrients) and biotic interactions between plants and between plants and natural enemies such as pathogens and herbivores (e.g. Paccala et al., 1996; Givnish, 1999; Sheil and Burslem, 2003; Seiwa, 2007; Imaji and Seiwa, 2010) for maintenance of species diversity.

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

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Furthermore, compared to abiotic factors, biotic interactions facilitate the coexistence of tree species at much smaller scales within forest communities (e.g. Packer and Clay, 2000; Seiwa et al., 2008; Konno et al., 2011). An increasing body of evidence strongly suggests that the recovery of diversity via a fine–scale mixture of species is necessary for forest managers to more sustainably maintain forest production and to effectively increase ecosystem services. Thus, forest managers should utilise techniques to generate mixed hardwood-conifer forests from planted coniferous monocultures.

Thinning, followed closely by underplantings of an understorey consisting of several native tree species, is a useful tool for increasing stand structural diversity and plant and wildlife diversity (e.g. Parker et al., 2001; Maas-Hebner et al., 2005). To preserve genetic diversity and reduce management costs, the conversion of plantations via the spontaneous colonisation of hardwood species (i.e. natural regeneration) is more suitable and sustainable than underplanting. In conifer plantations, thinning usually increases species diversity, particularly during younger stages (Thomas et al., 1999; Ito et al., 2006; Lindgren et al., 2006; Utsugi et al., 2006; Wilson and Puettmann, 2007; Ishii et al., 2008; Widenfalk and Weslien, 2009; Ares et al., 2010). Furthermore, several thinning experiments have demonstrated that species diversity usually increases monotonically with the level of thinning (Thomas et al., 1999; Parker et al., 2001; Moya et al., 2009; but see Ares et al. (2010)); however, intensive thinning or clear cutting occasionally facilitates the dominance of one or a few understorey species, due to the dominance of herbs and shrubs that strongly inhibit the regeneration of hardwoods, thereby reducing understorey diversity (Alaback and Herman, 1991; Ito et al., 2006; Nagai and Yoshida, 2006; Sabo et al., 2009). Together, these studies suggest that an optimal thinning intensity exists for maximising species diversity in conifer plantations (see Jobidon et al., 2004), although the mechanism by which diversity is maximised has not yet been fully elucidated, primarily due to the lack of monitoring during the process of hardwood recruitment at different thinning intensities.

In natural forests, recent studies have determined the optimal intensity of disturbance to maximise species diversity (i.e. intermediate disturbance hypothesis: Connell, 1978; Sheil and Burslem, 2003) in both tropical (Molino and Sabatier, 2001) and temperate regions (Wang and Chen, 2010). These studies have revealed that excessive disturbance leads to the dominance of light-demanding early-successional species, whereas too little disturbance leads to the competitive exclusion of species adapted to colonisation immediately following a disturbance (i.e. predominance of late-successional species), resulting in the co-existence of the maximum number of species under an intermediate disturbance regime. These results, together with the fact that drastic changes in population size typically occur during the juvenile stage (Paccala et al., 1996; Seiwa and Kikuzawa, 1996; Nagamatsu et al., 2002), strongly suggest that monitoring seedling establishment patterns of tree species of varying successional status in response to different thinning intensities is crucial for evaluating the mechanisms driving species diversity in conifer plantations.

In conifer plantations, the abundance and composition of advance regeneration have been considered good predictors of future regeneration of hardwood species (Nagaike et al., 2003; Ito et al., 2003, 2004; Gotmark et al., 2005; Yamagawa et al., 2008; Igarashi and Kiyono, 2008), although these factors vary widely with stand age, previous land-use history, distance from seed sources, fertilisation, topography, geology, and altitude (Guariguata et al., 1995; Halpern and Spies, 1995; Thomas et al., 1999; Ito et al., 2003; Ramovs and Roberts, 2003; Masaki et al., 2004; Utsugi et al., 2006; Sugita et al., 2008; Widenfalk and Weslien, 2009). In older stages of conifer plantations, substantial numbers of hardwood species usually grow to large sizes as advance regeneration (Ito et al., 2006; Sugita et al., 2008), and thinning does not always enhance species richness (Halpern and Spies, 1995; Wetzel and Burgess, 2001; Widenfalk and Weslien, 2009; but see Moya et al., 2009), likely because advance regeneration can predominate even after thinning. In natural forests, on the other hand, advance regeneration of late-successional species is often suppressed by newly germinated seedlings of early-successional species (i.e. pioneer) after disturbance, especially in systems with intensive and large disturbances, because of the much faster growth rates of pioneers (e.g. Brokaw, 1985). Thus, the relative importance of advance regeneration and newly emerged seedlings in determining hardwood recruitment after thinning and subsequent diversity may differ according to stand age and thinning intensity (i.e. disturbance regime) in conifer plantations. Therefore, empirical studies monitoring the relative establishment success of advance regeneration and newly germinated seedlings at different thinning intensities are important for evaluating the role of thinning in increasing species diversity, particularly for younger stages of conifer plantations.

Natural disturbance or thinning usually facilitates seed germination of early-successional species through the enhancement of environmental signals (e.g. ratio of light in the red to far-red wavelength [R:FR], fluctuations in soil temperatures; Jankowska-Blaszczuk and Grubb, 2006; Jankowska-Blaszczuk and Daws, 2007; Vandelook et al., 2008; Seiwa et al., 2009). Furthermore, recent studies have shown that critical values of the signals inducing seed germination and the relative importance of individual signals often differ even among early-successional species (Daws et al., 2002; Jankowska-Blaszczuk and Daws, 2007; Seiwa et al., 2009). These results suggest that species composition after thinning may be strongly influenced by thinning intensity through varying magnitudes of environmental signals. However, such environmental effects may be ephemeral and rapidly deteriorate, most likely due to the rapid recovery of both canopy foliage and understorey vegetation (Seiwa et al., 2009). If this is the case, temporal (yearly) patterns of seed germination would also be affected by thinning intensity, particularly for light-demanding species. Thus, information regarding the effects of thinning intensity on temporal changes in environmental signals and consequent seed germination of hardwood species is also important for determining the mechanisms and processes of seedling recruitment in conifer plantations.

The objective of the present study was to evaluate the role of thinning intensity in the processes and mechanisms of seedling establishment and subsequent diversity of hardwood species in conifer plantations. We investigated understorey environments (light, soil temperature, soil moisture, height and cover of vegetation, and litter accumulation), annual seedling emergence (i.e. seed germination), seedling survivorship, seedling vertical growth, species richness, and diversity of hardwoods for 5 years after thinning at three different treatment intensities, 67% thinned (Intensive), 33% thinned (Weak), and unthinned (Control), in a *Cryptomeria japonica* plantation in northern Japan. In this study, we focused on canopy and subcanopy (adult height <4 m) tree species, because the full extent of ecosystem functioning (e.g. $CO_2$ fixation, timber production, providing wildlife habitats) is most likely achieved through a canopy-level mixture of hardwoods (see Ohsawa, 2007; Steffan-Dewenter et al., 2007; Brockerhoff et al., 2008; Seiwa et al., in press). Here, we specifically addressed the following questions: (1) To what extent does thinning intensity affect seedling performance (e.g. seedling emergence, seedling survival, seedling growth) of hardwood species by changing the micro-environment? (2) Does seedling performance differ between advance regeneration and newly emerged seedlings after thinning and among species of different successional status? If so, (3) how do these differences affect species diversity? Finally, we evaluated the optimal thinning intensity for maximising species diversity in *C. japonica* plantations.