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RESEARCH ARTICLE

Effect of stand density and humus removal on regeneration of *Pinus densiflora* seedlings in a mixed conifer and broad-leaved forest

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Abstract We studied the impact of stand density and forest floor humus removal on regeneration of *Pinus densiflora* in a mixed conifer and broad-leaved forest on the Daimonji-Yama Mountain, Kyoto, Japan. Three levels of stand density were set, i.e., a clear-cut site, a heavily thinned site and a lightly thinned site. In each density treatment, comparisons were carried out between humus removal (A_0-free) and humus intact (A_0-intact) subplots. We counted the emergence of sown pine seeds and measured survival and growth of pine seedlings over the next four years. In addition, light conditions and the recovery of understory were monitored. Results show that thinning intensity and humus removal promoted the establishment and growth of seedlings. One exception, however, was that seedling growth was minimal in the heavily thinned A_0-intact subplots. This was due to a strong response of understory vegetation growth on the treatment combination, which hindered the pine seedling growth. Furthermore, we found that the canopy openness measured at 1.3-m height remained at least 35% for the heavily thinned site in 2008. The results suggest that the removal of the A_0 layer after heavy thinning is the most effective and labor-saving operation for *P. densiflora* regeneration.

Key words *Pinus densiflora*, regeneration, understory vegetation, thinning, forest operation

1 Introduction

Due to pine wilt disease and long-term lack of effective management, *Pinus densiflora* forests have sharply declined in Japan since the 1990s and their forest composition has changed significantly (Wu and Ando, 2010a). After the decline of *P. densiflora* in forests, parts of these forests have successfully recovered as broad-leaved forests; however, other parts had vegetation without successful regeneration of trees (Hattori et al., 1995; Morishita and Ando, 2002; Wu and Ando, 2010b). In particular, forests located in the dry and poor ridge areas became the so-called "degraded forests due to pine wilt disease", where shrubs flourished because environmental conditions hindered the regeneration of taller, broad-leaved trees. According to previous reports, forest degradation caused by pine wilt disease results in environmental deterioration (Yamase, 1998a) and a decline in forest water conservation (Nakane, 2000) due to the lack of tall trees. Therefore, it is important to recover high forests.

In many locations where *P. densiflora* survived pine wilt disease, forest operations have been carried out to recover *P. densiflora* trees (Yamase, 1998a; Sakamoto et al., 2004). Iwasaki et al. (1997) and Sakamoto et al. (2004) reported that in forests degraded by pine wilt disease, thinning of the intermediate and lower-layer trees and removal of the humus (A_0) layer boosted the initial establishment and growth of *P. densiflora* seedlings. However, thinning intensities have various effects on the recovery of understory vegetation (De Grandpré and Bergeron, 1997; Wolk and Rocca, 2009) and the target plants for vegetation recovery (Berkowitz et al., 1995; Zald et al., 2008). In earlier research, increased canopy openness due to different thinning intensities promoted the establishment and growth of *Pinus thunbergii* (Zhu et al., 2003). However, it has also been reported that heavy thinning promotes the growth of understory vegetation and in turn restricts the growth of pine trees (Wetzel and Burgess, 2001; Boucher et al., 2007).

Further, Iwasaki et al. (1997) and Sakamoto et al.

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(2004) reported seedling growth only in the initial two years. Generally, it is believed that at least four years are required to evaluate the regeneration of *P. densiflora* in competition with understory vegetation (Ogasawara and Ishibashi, 1986). To our knowledge, there has been no research on the impact of thinning on the regeneration of *P. densiflora* in competition with understory vegetation for periods longer than four years.

Our present study included subplots with two ground treatments of different thinning intensities in forests degraded by pine wilt disease. We conducted a four-year survey to analyze the emergence, survival and growth of sown *P. densiflora* seedlings. Changes in the light environment and the recovery of understory vegetation were also studied for four years after seeding in order to elucidate their relationship with seedling growth. Through these surveys, we studied the impact of different thinning intensities and the removal of the A_0 layer on the initial regeneration of *P. densiflora* in forests affected by pine wilt disease.

2 Materials and methods

2.1 Study site

This study was conducted in the *P. densiflora* and broad-leaved mixed forest on the Daimonji-Yama Mountain, Kyoto City, Japan (35.02°N, 135.80°E). Three levels of stand density were established in a clear-cut site (CT), a heavily thinned site (HT) and a lightly thinned site (LT). The three stand density treatments were conducted by the Kyoto-Osaka District National Forest Office in December 2003, February 2004 and October 2004; the areas were 0.05, 0.11 and 0.29 ha in size, respectively. Details of the study site are shown in Fig. 1 and Table 1. The elevation is around 260 m above sea level. The meteorological data for the study sites had not been collected. However, the mean annual temperature and mean annual precipitation in 2005–2008 were 15.5°C and 1358 mm, respectively, at the Kitashirakawa Experimental Station of the Field Science Education and Research Center of Kyoto University (60 m a.s.l.), approximately 2 km west of the study sites.

In order to determine the forest composition of the study sites before the experimental thinning, we set up six 10 m × 10 m plots in October 2003 and measured the diameter at breast height (DBH) of all trees taller than 1.3 m. As shown in Table 2, the basal area (BA) of upper-story trees with a DBH ≥ 4.5 cm was 33.9 $m^2 \cdot ha^{-1}$. These included surviving *P. densiflora* trees, which accounted for 32.8% of BA. Among the broad-leaved trees, *Castanopsis cuspidata* and *Quercus serrata* were seen as tall trees and *Ilex pedunculosa* accounted for an extremely high percentage of sub-trees. The density of intermediate-story trees with a height ≥ 1.3 m and a DBH < 4.5 cm was 6000 trees per ha.

After thinning, the BA of the remaining upper-story trees in HT and LT was 17.4 and 18.5 $m^2 \cdot ha^{-1}$, respectively, and except for *P. densiflora*, their BA was 6.3 and 10.3 $m^2 \cdot ha^{-1}$, respectively. In HT and LT, the densities of intermediate-layer trees were 736 and 2034 trees per ha, respectively. All shrub-layer trees

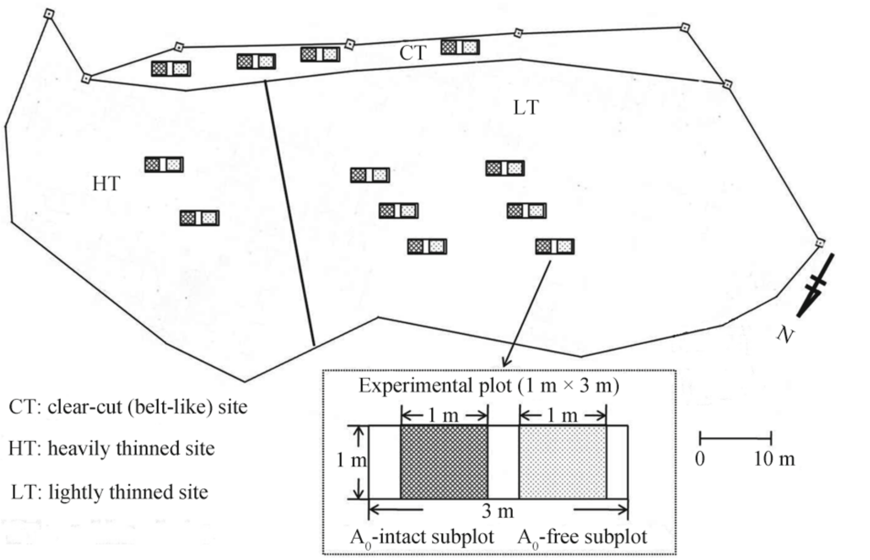

Fig. 1 Details of the study sites. At the clear-cut, belt-like site (CT), the heavily thinned site (HT) and the lightly thinned site (LT), four, two and six experimental plots of 1 m × 3 m were randomly established, respectively. In each experimental plot, we set two 1 m × 1 m subplots. In one of the subplots, the entire A_0 layer was removed (the A_0-free subplot), while in the other, only the litter layer was removed without any further ground treatment (the A_0-intact subplot).

Table 1 Characteristics of study sites

Variable	Study site		
	CT	HT	LT
Thinning date	Dec. 2003	Feb. 2004	Oct. 2004
Area (ha)	0.05	0.11	0.29
Elevation (m)	265	260–265	260–265
Topography	Ridge	Ridge-slope	Ridge-slope
Aspect (°)	N26E	N23E	N33E
Slope (°)	3	23	22

Note: CT (clear-cut site), HT (heavily thinned site), LT (lightly thinned site).

Table 2 Forest composition of study sites before thinning

Species	Number of trees (per ha)	Basal area ($m^2 \cdot ha^{-1}$)	Relative basal area (%)
Ilex pedunculosa	2000	13.1	39.0
Pinus densiflora	317	11.1	32.8
Castanopsis cuspidata	67	3.2	9.4
Symplocos prunifolia	267	2.7	8.2
Quercus serrata	150	1.8	5.2
Clethra barbinervis	117	0.8	2.4
Lyonia ovalifolia	283	0.7	2.2
Eleutherococcus sciadophylloides	33	0.2	0.5
Rhus trichocarpa	17	0.1	0.1
Evodiopanax innovans	17	0.1	0.1
Cleyera japonica	17	0.1	0.1
Total	3285	33.9	100.0

Note: the mean values of upper-story trees with a DBH ≥ 4.5 cm in six 10 m × 10 m plots are shown.

with a height of 0.1–1.3 m were removed and the litter layer in the forest was accumulated. In CT, removal of understory vegetation was conducted on May of each of the four years until 2008. This removal was not carried out at the other two study sites.

2.2 *P. densiflora* seeding test

In May 2005, we set up four, two and six experimental plots of 1 m × 3 m in CT, HT and LT (Fig. 1). In each experimental plot, we established two 1 m × 1 m subplots. In one of the subplots, the A_0 layer (humus) was entirely removed (A_0-free subplot), while in the other, only the litter layer was removed without any further ground treatment (A_0-intact subplot). When the A_0 layer was removed from the A_0-free subplot, the roots and some stumps of understory vegetation were also removed.

Futai and Nakai (1993) reported that the resistance of *P. densiflora* to pine wilt disease is genetic. Although pine wilt disease generally attacks large trees, we selected *P. densiflora* seeds resistant to pine wilt disease in order to avoid the effect from pine wilt disease in the seeding test. The seeds were provided by the Shiga Prefecture Forest Center. Fifty seeds were sown on each 1 m^2 subplot and each seed was individually positioned. Emergence and survival data for the *P. densiflora* seedlings were recorded once a week from June–July 2005 and once a month from August 2005 to November 2008. The number of seeds sown at the study sites with various thinning intensities and ground treatments was taken as our basic data. The proportion of seedlings that emerged until November 2005 was recorded to calculate the rate of emergence. Compared with the cumulative number of emergent seedlings, the proportion of seedlings that survived in November 2008 was taken as the survival rate. In November 2008, we measured the height and diameter of the seedlings at ground level (D_0) as the fourth year data.

In November 2008, we also measured the cover of understory vegetation in all the subplots of each site. The measurement surveys were recorded in percentages by rounding off to the nearest 1% for 1%–10%, 5% for > 10%. The values for plants < 1% were taken as 0.5% and the values for other plants were added together to calculate the total cover of one subplot. Understory vegetation, other than the sown *P. densiflora* seedlings, was cut off at ground level and dried at 80°C for 72 h. Then, the weight of aboveground parts was measured.

The understory vegetation in HT (February 2004–November 2008, five years) had recovered one year earlier than that in LT (October 2004–November 2008, four years), because thinnings in HT and LT were conducted in February and October 2004, respectively. In order to compare the recovery of understory vegetation correctly after thinning for four years with that of other thinned sites for consistency, we used data from a different series of tests conducted in HT. In this different series of tests, we set up another five 1 m × 3 m experimental plots in May 2004, including A_0-free subplots and A_0-intact subplots at random in HT. In October 2007, we measured the cover of understory vegetation and weight of the aboveground parts in all subplots (May 2004–October 2007, four years).

2.3 Environment of the study site

In August 2005, we measured the thickness of the A_0 layer of the study site. These measurements of the A_0 layer were conducted on 50 points in each A_0-intact subplot.

In CT, HT and LT, 4, 13 and 26 experimental plot locations were randomly selected, respectively. In July 2005 and July 2008, a fisheye camera (Fisheye-NIKON 8 mm f/2.8, Japan) was set up at a height of 0.3 m and 1.3 m, respectively, to obtain hemispherical photographs. Two photographs were taken for each plot location. The mean value of canopy openness was calculated by using a software, i.e., the Gap Light Analyzer (GLA), for analysis of hemispherical photography (http://www.ecostudies.org/gla/).

2.4 Statistical analysis

One-way analysis of variance (ANOVA) was performed to analyze the thickness of the A_0 layer and the difference of canopy openness in the study sites and a multiple comparison was conducted using Tukey's test. The emergence and survival rates of *P. densiflora* seedlings were categorized by study sites and ground treatments and the results of the calculations were evaluated using the χ^2 test. To analyze the recovery of understory vegetation after thinning for four years and the growth of seedlings, we conducted two-way ANOVA with thinning intensity and ground treatment as parameters. When the two-way ANOVA revealed a significant relationship, a multiple comparison was conducted by using Tukey's test. If an interaction was found with regard to the recovery of understory vegetation, one-way ANOVA was performed. In order to analyze the effects of canopy openness at 0.3-m height, cover of understory vegetation and ground treatment on seedling growth, a multiple regression analysis was conducted. In the analysis, A_0-intact was taken as 0 and A_0-free was taken as 1 for ground treatment.

3 Results

3.1 Environment of the study site

The mean value of the thickness of A_0 layer in CT was the lowest (3.7 ± 0.3, n = 200), while the difference between HT (5.8 ± 0.6, n = 100) and LT (5.9 ± 0.7, n = 300) was not significant. In 2005, the canopy openness at 1.3-m height decreased in the following sequence: CT (53.6% ± 6.0%, n = 4), HT (39.6% ± 6.4%, n = 13) and LT (32.2% ± 4.0%, n = 26); the canopy openness at 0.3-m height of each study site was similar to that at 1.3-m height (Fig. 2). In 2008, the canopy openness at 1.3-m height of CT and HT remained similar, i.e., 46.6% ± 5.1% and 35.5% ± 5.7%, respectively, while that of LT decreased to 28.4% ± 5.7%. In 2008, the canopy openness of HT at 0.3-m height was 22.3% ± 5.4%, lower than that of LT (25.8% ± 3.2%; Fig. 2).

3.2 Understory vegetation after four-year thinning

The cover of the understory vegetation and weight of the aboveground vegetation in the A_0-intact subplot of HT were the highest (Fig. 3), followed by the A_0-free subplot in the HT treatment, whereas cover in the LT and the A_0-free subplot of HT were not significantly

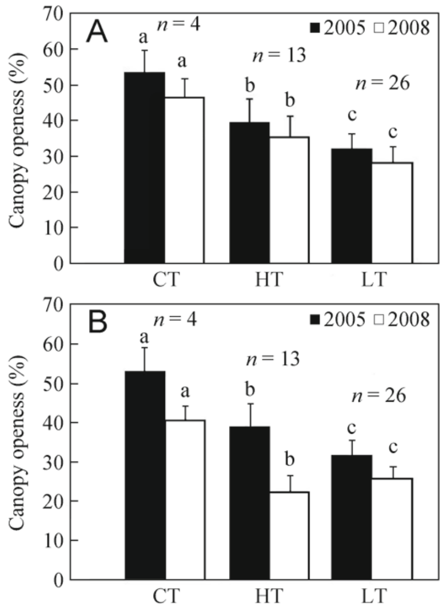

Fig. 2 Canopy openness at 1.3- (A) and 0.3-m (B) height of the study sites, recorded in July 2005 and July 2008. Bars indicate SD. One-way analysis of variance was performed and a multiple comparison was conducted using Tukey's test. Significant differences in expression due to treatment are indicated by different numbers (p < 0.001). The same comments apply to the following figures.

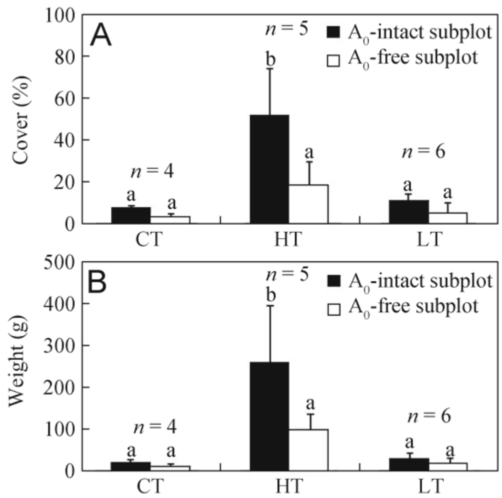

Fig. 3 Cover of understory vegetation (A) and weight of aboveground parts per m² (B) in the thinned subplots four years after thinning

different from that of the continuously managed CT (Fig. 3).

3.3 Emergence and survival of *P. densiflora* seedlings

Whether or not the A_0 layer was removed, the emergence rate of seedlings was the highest in CT, although not significantly different from that in HT (Table 3). In the A_0-intact subplot of LT, the emergence rate was very low (Table 3), which was significantly lower than that in the A_0-free subplot of LT ($p < 0.001$, as evaluated with χ^2).

The survival rate in the A_0-intact subplot decreased in CT, HT and LT sequentially. In HT and LT, the survival rate was higher in the A_0-free subplot than that in the A_0-intact subplot (Table 3).

3.4 Growth of *P. densiflora* seedlings

The seedling height of both subplots (A_0-free and A_0-intact) was the highest in CT and lowest in HT ($p <$ 0.001; Fig. 4). In the thinned sites, the height of seedlings was higher in the A_0-free subplot than that in the A_0-intact subplot ($p < 0.001$). The result of D_0 was very similar.

The height of seedlings in the fourth year (2008) were significantly and positively impacted by canopy openness and ground treatment, but were significantly and negatively impacted by the cover of the understory vegetation (Table 4). The response of D_0 was again very similar.

4 Discussion

4.1 Survival of *P. densiflora* seedlings

Since *P. densiflora* bears light-sensitive seeds, the lower the light intensity, the higher the possibility that the seeds in the A_0 layer will die due to attacks by fungi and bacteria (Vaartaja, 1952). It is inferred that a higher thinning intensity and a larger canopy openness could promote the emergence of seedlings. In addition, previous studies have reported that the emergence rate of seedlings could be increased by removing the A_0 layer (Iwasaki et al., 1997; Sakamoto et al., 2004; Wu and Ando, 2009). We confirmed those results in this study.

Although the thickness of the A_0 layer in the A_0-intact subplot was not significantly different between HT and LT, the survival rate of seedlings was higher in HT (Table 3). This result leads to the conclusion that the increase in canopy openness due to different thinning intensities promotes seedling survival. We believe that the maximum survival rate of seedlings in the A_0-intact subplot of CT is due to the fact that it had the highest canopy openness as well as the thinnest A_0 layer. Sakamoto et al. (2004) reported that under sufficient light environmental conditions, removal of the A_0 layer decreased the death of seedlings caused by fungi and dryness and improved the survival rate. The results of this study lead to the same conclusions for HT and LT.

4.2 Growth of *P. densiflora* seedlings

For forests affected by the pine wilt disease, some reports have indicated that heavy thinning could increase the varieties of plant species and improve the amount and spread of sprouting vegetation in the initial stage of recovery (Yamase, 1998b, 2000). When canopy openness is greater than 35% at 1.3-m height, canopy openness at 0.3-m height was significantly reduced four years after thinning in HT when compared to LT. We think that heavy thinning improves the light environment at 1.3-m height, leads to the recovery of understory vegetation (Fig. 3) and a deterioration of the light environment at 0.3-m height (Fig. 2), which

Table 3 Emergence rates of *P. densiflora* seedlings after seeding and survival rates of its seedlings in the fourth year after seeding (2008)

Site	Emergence rate (%)		*p*-value	Site	Survival rate (%)		*p*-value
	A_0-intact	A_0-free			A_0-intact	A_0-free	
CT	43.5 (87/200)	52.0 (104/200)	> 0.05	CT	60.9 (53/87)	55.8 (58/104)	> 0.05
HT	40.0 (40/100)	48.0 (48/100)	> 0.05	HT	57.5 (23/40)	75.0 (36/48)	**< 0.05**
LT	22.7 (68/300)	48.3 (145/300)	**< 0.001**	LT	44.1 (30/68)	62.1 (90/145)	**< 0.05**
	***p* < 0.01**	*p* > 0.05			***p* < 0.05**	***p* < 0.05**	

Note: the differences in the emergence rates of seedlings among study sites and ground treatments were evaluated with the χ^2 test. The numbers of emergent seedlings and sown seeds are shown in left. The number of surviving seedlings and emergent seedlings are shown in right.

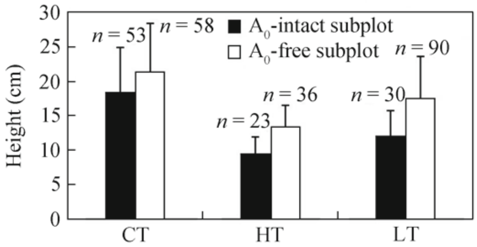

Fig. 4 Height of *P. densiflora* seedlings in the fourth year after seeding. Two-way analysis of variance was performed by thinning intensity and ground treatment. The effects of thinning intensity and ground treatment were significant ($p < 0.001$ and $p < 0.001$, respectively); the interaction effect was not tested.

Table 4 Results of multiple regression for effects

Height	Partial regression coefficient	*p*-value
Regression		**< 0.001**
Canopy openness at 0.3-m height	4.944	**< 0.001**
Cover of understory vegetation	–7.463	**< 0.001**
Ground treatment	1.978	**< 0.05**

Note: effects of canopy openness at 0.3-m height, cover of understory vegetation and ground treatment on the height of *P. densiflora* seedlings in the fourth year (n = 290).

inhibits the growth of *P. densiflora* seedlings (Fig. 4). Results of multiple regression analysis also showed that the growth of *P. densiflora* seedlings was significantly and positively impacted by canopy openness, but was significantly and negatively impacted by the cover of the understory vegetation (Table 4).

Given these facts, we conclude that heavy thinning can improve the light environment, which in turn boosts the growth of *P. densiflora* seedlings. Simultaneously, being a risk factor restricting seedling growth, it also promotes the recovery of understory vegetation and enhances seedling competition.

4.3 Forest management for *P. densiflora* regeneration

On the basis of the findings of the *P. densiflora* seeding tests in the sites with different thinning intensities, we conclude that the growth of seedlings in CT, where the understory vegetation was removed each year, showed the best growth (Fig. 4). This operation is ideal and appropriate and should be carried out if budgets permit.

In HT, the removal of only the litter layer (A_0-intact subplots) after heavy thinning boosted the growth of understory vegetation and restricted the growth of *P. densiflora* seedlings. Consequently, it is necessary to cut the understory vegetation periodically. In LT, canopy openness would decrease quickly over time. It is necessary to cut upper-story trees for the second time, because low canopy openness adversely affects the growth of seedlings (Chiba, 1965; Shidei and Sano, 1973; Table 4). However, re-thinning of the understory vegetation or upper-story trees would not only increase the cost of operations but also cause *P. densiflora* seedlings to disappear (Shelton and Cain, 2000). Therefore, this secondary operation could only be practiced in special cases.

When the A_0 layer was removed in HT, the growth of seedlings was slower than that in the A_0-free subplots of LT. However, the mean values of the seedling height and the mean D_0 value, in particular, were not significantly different from those in LT (Fig. 4). Compared with the A_0-intact subplots, the effects of removal of the A_0 layer were readily apparent; the overgrowth of understory vegetation was significantly reduced, while the growth of seedlings increased. Therefore, we would expect the *P. densiflora* seedlings to out-compete the understory vegetation. Additionally, four years after thinning in HT, canopy openness at 1.3-m height remained at 35% or above (Fig. 2). Therefore, in all likelihood, the most effective and labor-saving method for *P. densiflora* regeneration is to conduct a primary heavy thinning and removal of the A_0 layer.

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