

## STAND STRUCTURE OF A NATURAL *PINUS-CUNNINGHAMIA* FOREST IN ANHUI, EASTERN CHINA

XIPING CHENG<sup>1,2</sup>, YANFANG WANG<sup>1</sup>, XIAOJUN YANG<sup>1</sup>, HEDE GONG<sup>1,\*</sup>

<sup>1</sup> Southwest Forestry University, Faculty of Ecotourism, Kunming, 650224, P. R.. China

<sup>2</sup> Chiba University, Graduate School of Horticulture, Matsudo 648, Chiba, 271-8510, Japan

### Abstract

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The aim is to determine the ecological characteristics of *Pinus massoniana* Lamb and *Cunninghamia lanceolata* (Lamb) Hook, which co-dominate a natural coniferous forest in the Huangshan region of Anhui Province, eastern China, we examined the spatial patterns, size structure, and tree height-diameter relationship of both species. *P. massoniana* dominated the canopy layer, but smaller individuals were scarce. In contrast, *C. lanceolata* co-dominated the sub-canopy layer and had a considerable number of saplings and sprouting from the root collar of larger individuals. The spatial pattern of *P. massoniana* tended to be overdispersed at small scales, but became random-overdispersed at intermediate to larger scales. The spatial pattern of *C. lanceolata* was clumped at small scales. In a young stand, tree height at a given stem diameter was larger for *P. massoniana* than for *C. lanceolata*. Based on these results, we inferred several ecological characteristics of these two dominant species: *Cunninghamia lanceolata* is a relatively slow-growing shade-tolerant species. *P. massoniana* is a fast-growing shade-intolerant species that has high mortality rates if suppressed and regenerates only after large-scale disturbances.

*Key words:* Natural forest, size structure, spatial pattern, tree height-diameter relationship

*Abbreviations:* *Pinus massoniana* Lamb (*P. massoniana*); *Cunninghamia lanceolata* (Lamb) Hook (*C. lanceolata*)

### Introduction

Natural coniferous forests dominated by *P. massoniana* are widely distributed throughout southern and eastern China, including the Huangshan region of Anhui Province. This species is a valuable forestry resource because of its high quality timber used for multiple purposes (Hu and Liang, 1996; Zhou, 2000). *P. massoniana* forests are sometimes co-dominant with *C. lanceolata* (Sun, 1992; Zhou, 2000), and we hereafter refer to this type of forest as a *Pinus-Cunninghamia* forest. *C. lanceolata* is also widely used for a variety of products in China. It is a major plantation and commercial tree species in China (Wu, 1984). Because the two dominant species of *Pinus-Cunninghamia* forests

are valuable both commercially and ecologically, this forest type should be managed as a mixed forest by focusing on both of these important species.

The management of mixed-species forest stands is a challenge for forestry efforts, because interactions between species are often complex (Kelty et al., 1992; Smith et al., 1997). At present, the local government's management policy for natural forests, is to protect them from excessive cutting (Zhang et al., 2000). However, forests cannot be maintained in a desirable condition and excluding all types of human activity on a long-term. For example, partial cutting may be necessary to promote natural regeneration of pioneer tree species.

The key to the appropriate management of mixed-species forests is to understand the ecological charac-

\*E-mail: xipingcheng@yahoo.co.jp

teristics of component species (Bartelink, 2000; Oliver, 1992). In this paper, we examined the size structure, spatial patterns, and tree height-diameter relationship of *P. massoniana* and *C. lanceolata* to understand the ecological traits of these dominant species. From size structure, several important ecological characteristics of a species can be inferred, such as growth, mortality, and regeneration (Masaki, 2002; Umeki, 1997). Investigations of spatial patterns are a current topic of forestry research, because spatial variability is now recognised as a ubiquitous ecological characteristic of ecosystems. (Batista and Maguire, 1998; Kenkel et al., 1997; Kubota et al., 2007). The relationship between tree height and diameter can also provide valuable information concerning the growth strategy of tree species (Eerikäinen, 2003; Sharma and Parton, 2007).

The objectives of this study were to analyse the population structure of the two dominant species in *Pinus-Cunninghamia* forests, we examined the spatial patterns, size structure, and tree height-diameter relationship of both species. Based on these analyses, we inferred the stand development history of these two coniferous species and several ecological characteristics.

## Materials and Methods

### Study site

Our study site was located in the Huangshan region of Anhui Province, eastern China (29°51' N, 117°37' E; Figure 1). This area is within the northern subtropical zone characterised by a monsoon climate. The annual

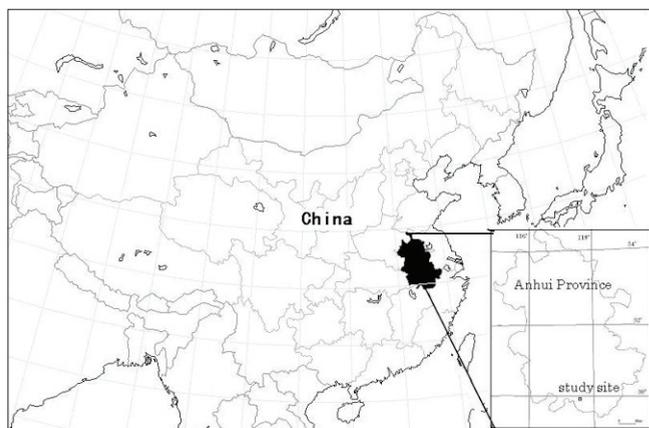


Fig. 1. Location of the study site

mean temperature is 15.7°C, and annual precipitation is 1800 mm (Han, 1981).

In 2006, we established three permanent rectangular plots in three *Pinus-Cunninghamia* forest stands. Two plots were located in mature stands (plots 1 and 2), and the third was established in a young stand (plot 3). Plots 1, 2, and 3 measured 0.12, 0.075, and 0.06 ha in size, respectively.

### Tree measurements

In 2006, we recorded the girth at breast height (GBH) for all stems ( $\geq 15$  cm in GBH) in the plots and identified them to the species level. We mapped the positions of the stem bases using a theodolite with an ultrasonic range finder (Vertex compass, Haglof, Långsele, Sweden). In 2009, we re-measured GBH and measured the height of all target stems. For the two dominant coniferous species, we measured heights of small trees (<15 cm in GBH), including all sprouts emerging from the root collars of large trees and most saplings on the forest floor.

### Data analysis

#### *Spatial patterns and spatial correlations*

To analyse spatial patterns for each of the dominant species, we calculated Ripley's K function (Diggle, 1983; Ripley, 1976). The function  $\hat{K}(r)$  is defined as the expected number of stems within a radius  $r$  of a randomly chosen stem as:

$$\hat{K}(r) = \frac{A}{n^2} \sum_{i=1}^n \sum_{j=1}^n W_{ij}^{-1} I_r(|X_i - X_j|),$$

where  $n$  is the number of stems in an analysed plot,  $A$  is the area of the plot, and  $X_i$  is the location of the  $i$ th stem. The quantity  $|X_i - X_j|$  is the distance between the  $i$ th and  $j$ th stems, and  $I_r(|X_i - X_j|)$  is a counter variable:  $I_r = 1$  when  $|X_i - X_j| < r$  and is otherwise 0.  $W_{ij}$  is a weighting factor to correct for edge effects and was calculated using the edge correction method of Getis and Franklin (1987), Goreaud, and Pélissier (1999).

We then calculated  $\hat{L}(r)$ , a standardised function of  $\hat{K}(r)$ , to facilitate the interpretation of results.  $\hat{L}(r)$  was defined by Dale (1999) as:

$$\hat{L}(r) = \sqrt{\hat{K}(r)/\pi} - r.$$

If  $\hat{L}(r) > 0$ , the spatial pattern is clumped; if  $\hat{L}(r) = 0$ , it is random; and if  $\hat{L}(r) < 0$ , it is over dispersed. To determine whether the spatial arrangement of trees significantly differed from a random distribution, we used a Monte Carlo simulation method to calculate the confidence envelope. To obtain 99% confidence envelopes, 99 permutations of random points were generated, and values of  $\hat{L}(r)$  were calculated.

To examine spatial correlation between the dominant species, we calculated bivariate  $\hat{K}(r)$ . The bivariate  $\hat{K}_{12}(r)$  defined as the expected number of stems of species (2) that occur within the radius  $r$  of stems of species (1) as:

$$\hat{K}_{12}(r) = \frac{A}{n_1 n_2} \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} W_{ij}^{-1} I_r(|X_i - X_j|),$$

where  $n_1$  and  $n_2$  are the number of stems of *P. massoniana* and *C. lanceolata* respectively.  $X_i$  is the location of the  $i$  th stem of *P. massoniana*, and  $X_j$  is the location of the  $j$  th stem of *C. lanceolata*.

A standardised version of  $\hat{K}(r)$ , as follows:

$$\hat{L}_{12}(r) = \sqrt{\hat{K}_{12}(r) / \pi} - r.$$

To calculate  $\hat{L}(r)$  and  $\hat{L}_2(r)$ , we used the 'Kest()' function in the 'spatstat' library of the statistical software R (Baddeley and Turner, 2005).

### Size structure

Using the tree height data, we depicted the size structure of the two dominant species for each plot. To quantify size structure, we calculated the size distribution index (SDI) as the third moment of the height distribution around the midpoint of the height range (Masaki, 2002). SDI was defined as:

$$SDI = \frac{1}{n} \sum_{i=1}^n (X_i - 0.5)^3$$

$$X_i = (h_i - m) / (H - m)$$

where  $X_i$  is the standardised height of the  $i$  th stem,  $h_i$  is the height of the  $i$  th stem,  $H$  is the maximum height of the analysed species, and  $m$  is the possible minimum value of the measurement. When smaller trees are abundant, SDI takes on negative values, and when smaller trees are scarce, SDI becomes larger.

### Tree height-diameter relationship

Because the relationship between diameter at breast height (DBH) and tree height is correlative and not causative, we used reduced major axis (RMA) regression to analyse the relationship between the two variables. We used the Standardised Major Axis Tests & Routines (SMATR; Warton et al., 2006), to fit the following allometric equation to the tree height-diameter relationship and to compare parameters for the two target species:

$$\log(y) = \log(A) + h \log(x),$$

where  $y$  is tree height,  $x$  is DBH of the analysed species, and  $A$  and  $h$  are parameters. We used 5% as the critical level of significance.

## Results

### Species composition

Overall stem density was higher in the young stand (plot 3) than in the mature stands (plots 1 and 2), whereas basal area and average DBH were smaller in the young stand. The dominant species in all plots was *P. massoniana*, which accounted for 50.1–82.3% of basal area. *C. lanceolata* was the second most dominant species among the three plots, accounting for 9.7–34.2% of basal area (Table 1). Broad-leaved species also occurred in the understorey layer in all plots. The most abundant broad-leaved species were *Loropetalum chinense* (R. Br.) Oliver, *Castanopsis eyrei* (Champ. ex Benth.) Tutch. and *Castanopsis sclerophylla* (Lindl.) Schottky.

### Spatial patterns and spatial correlations

The two dominant coniferous species exhibited distinct spatial patterns. In all plots, the spatial patterns of *P. massoniana* were overdispersed at small scales but became random or approached aggregation at intermediate to larger scales. In all plots, the spatial patterns of *C. lanceolata* were clumped at small scales, whereas they became more random at intermediate to larger scales in plots 1 and 3 (Figure 2). The distributions of the two dominant conifers tended to segregate small scales in the young stand (Figure 3). No clear spatial correlation was found in the mature plots.

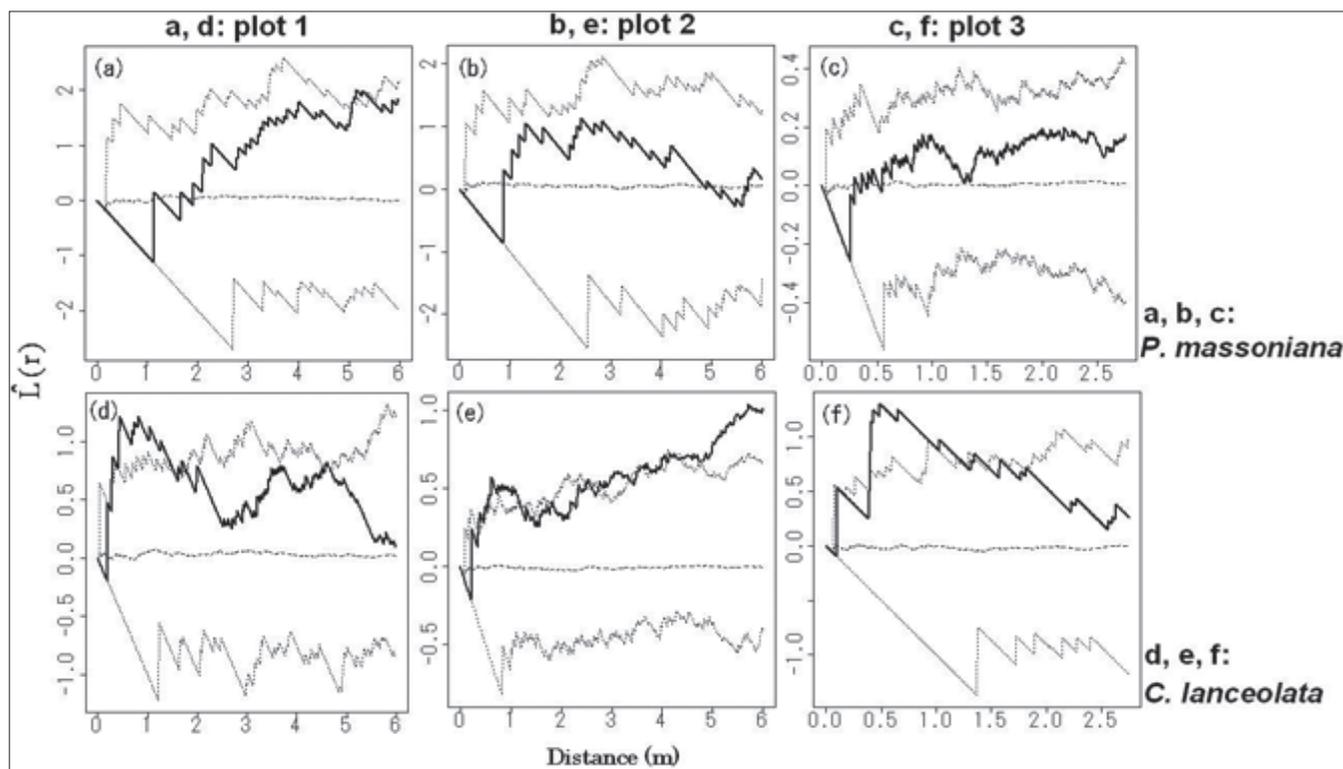
### Size structure

In all plots, *P. massoniana* dominated the canopy layer (Figure 4). However, in the mature stands, smaller individuals of *P. massoniana* were scarce. The young stand was primarily composed of *P. massoniana* individuals in the intermediate-size class.

The heights of *C. lanceolata* were bimodally distributed in each plot (Figure 4). The first mode in the smallest size class comprised saplings and sprouts. The second mode ranging from an intermediate size class to a large size class comprised older individuals that regenerated just after stand initiation. Three stem cores

**Table 1**  
Basic characteristics of the two dominant coniferous species

	Plot 1	Plot 2	Plot 3
Stem density (number of stems ha <sup>-1</sup> )	1475.0	2266.7	4066.7
<i>C. lanceolata</i>	308.3	920.0	833.3
<i>P. massoniana</i>	191.7	280.0	2033.3
Mean DBH (cm)	14.0	14.0	10.8
<i>C. lanceolata</i>	19.0	14.6	7.9
<i>P. massoniana</i>	33.0	36.5	14.7
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	34.9	54.8	45.1
<i>C. lanceolata</i>	9.7	18.8	4.4
<i>P. massoniana</i>	17.4	30.7	37.2
<b>SDI</b>			
<i>C. lanceolata</i>	-0.08119	-0.07950	-0.04174
<i>P. massoniana</i>	0.04150	0.02975	0.03369



**Fig. 2.**  $\tilde{L}(r)$  function for the two dominant species in the three study plots. The thick line represents

taken from a stand near plot 1 indicated that intermediate (DBH = 10.6 cm) and large-sized (DBH = 17.1 cm) individuals of *C. lanceolata* and large-sized individuals of *P. massoniana* (DBH = 28.7 cm) were of similar ages (38, 41, and 43-years-old, respectively).

The SDI was positive for *P. massoniana* and negative for *C. lanceolata* (Table 1). Using these values, the size structures of the populations were evaluated. Populations of *P. massoniana* included few small individuals or lacked them entirely, whereas populations of *C. lanceolata* included many small individuals.

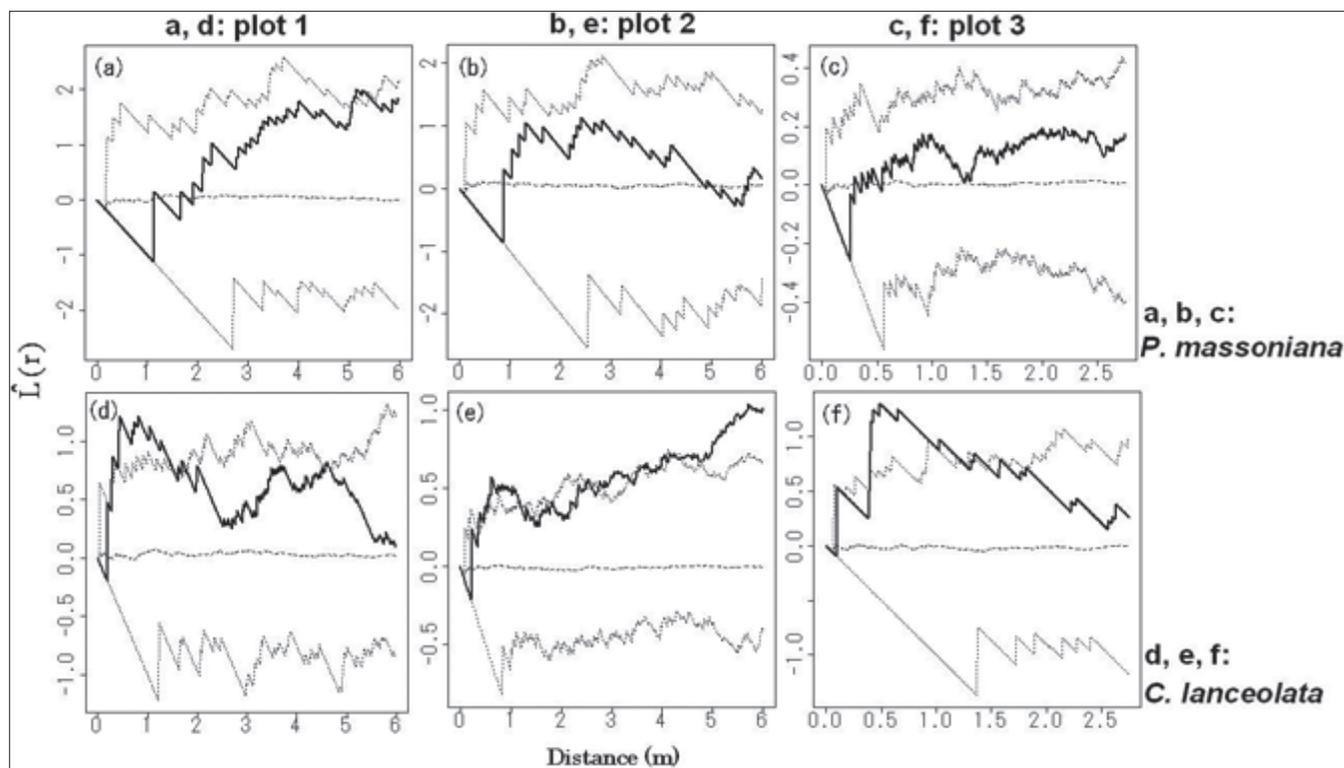
### Tree height-diameter relationship

In the mature stands (plots 1 and 2), the slope  $h$ , did not differ between the two species. In plot 2, the intercept  $\log(A)'$  was larger for *C. lanceolata* than for *P. massoniana*, indicating that the former species was approximately 60 cm larger than the latter, given the same DBH. However, these results do not imply that

*P. massoniana* occurred underneath *C. lanceolata*, because the size ranges of both species only slightly overlapped in the mature stands (Figures 4 and 5). In the young stand (plot 3), the slope of the regression line differed between the two dominant species ( $p < 0.001$ ; Figure 5; Table 2), and the allometry coefficient  $h$  was smaller for *P. massoniana* than for *C. lanceolata*. At the same DBH, *P. massoniana* was taller than *C. lanceolata* for the range of observed values of DBH.

### Discussion

The lack of seedlings and smaller individuals of *P. massoniana* in the mature stands indicates that this species cannot regenerate under a closed canopy. Given these regenerative traits and size distributions of *P. massoniana* in the study plots, the *Pinus-Cunninghamia* forests were likely initiated after large-scale disturbances. Stem cores collected from a stand near plot



**Fig. 3.**  $L_{12}(r)$  function for the spatial correlation of the two dominant species in the three study plots. The thick line represents  $L_{12}(r)$ , and thin envelopes represent the 99% confidence interval of the null hypothesis of no spatial relatedness

1 indicated that a large-sized individual of *P. massoniana* and intermediate- to large-sized individuals of *C. lanceolata* regenerated almost simultaneously in the mid 1960s.

Based on the bimodal size distribution of *C. lanceolata*, populations of this species were likely comprised of multiple cohorts: one cohort regenerated at stand initiation and formed the mode composed of larger size classes, and other cohorts regenerated some time after stand initiation and formed the mode in the smallest

height class. The cohort that regenerated at stand initiation includes intermediate-sized stems of ages similar to the dominant individuals of *P. massoniana*. This result indicates that the growth rates of *C. lanceolata* were slower than those of *P. massoniana* and that the mortality rate of suppressed *C. lanceolata* stems was not high. The existence of many small saplings and sprouts within the smaller size distribution mode (Figure 4) in-

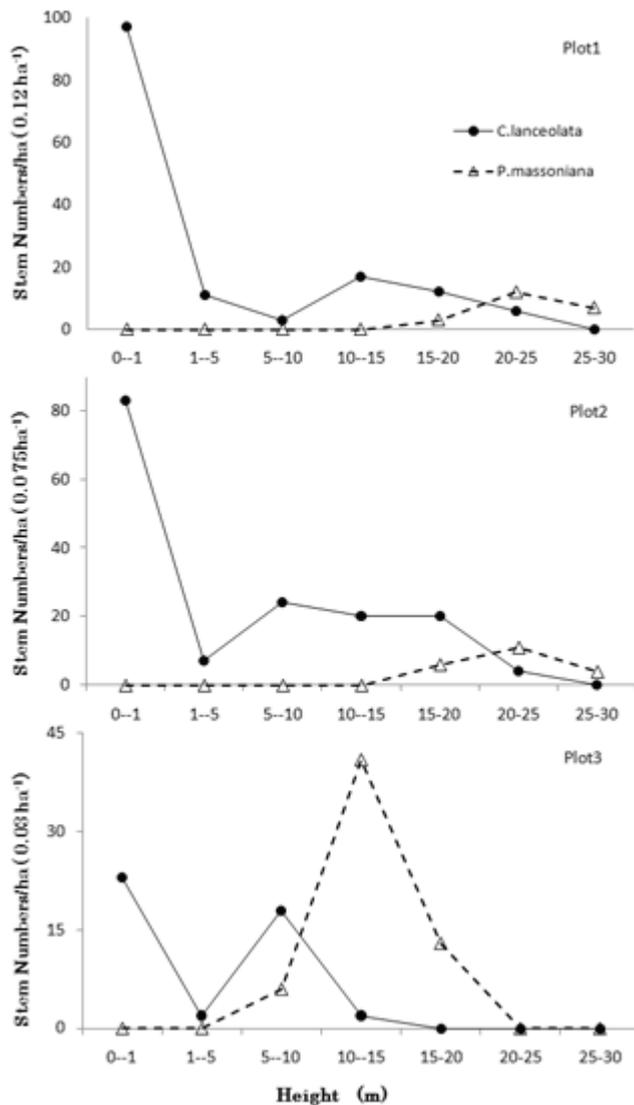


Fig. 4. Tree height distribution of two dominant coniferous species in Pinus-Cunninghamia forests

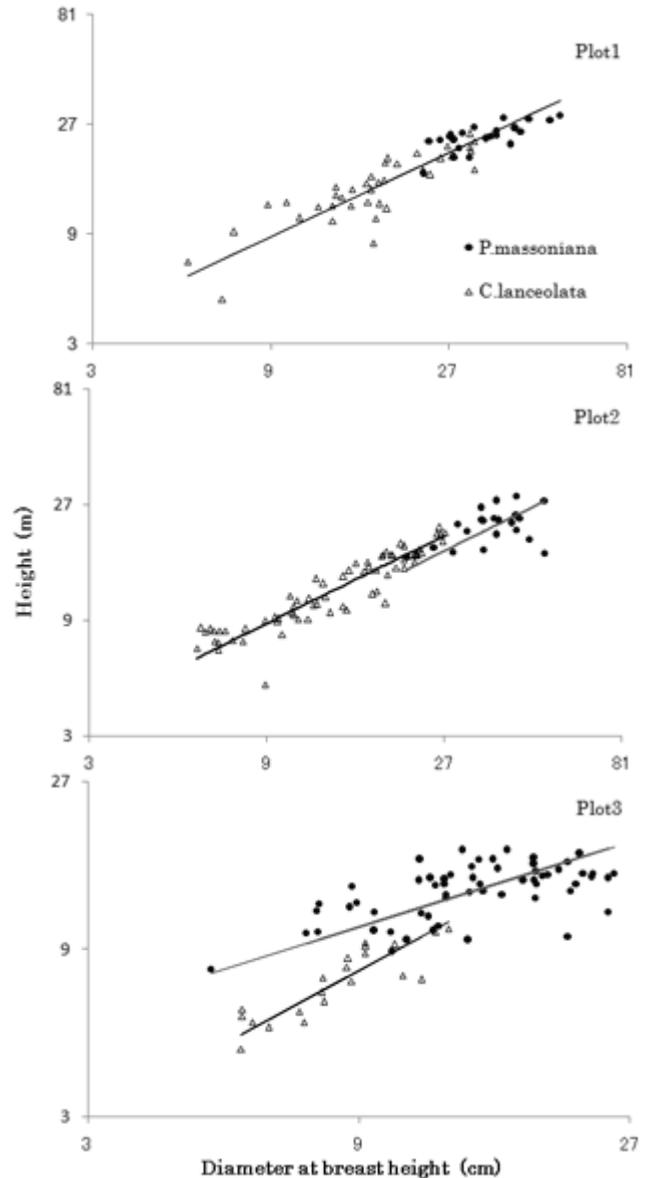


Fig. 5. The relationship between tree height and diameter of two dominant coniferous species

dicates that *C. lanceolata* can germinate or sprout even under the canopy. Sprouting is an important method of regeneration in this species (Wu, 1984).

The analyses of spatial patterns support the above discussion. The spatial patterns of *P. massoniana* were over dispersed at smaller scales, indicating that stems of this species cannot survive in close proximity to one another, likely due to competition for light. In contrast, the spatial patterns of *C. lanceolata* were clumped at smaller scales, because this species can sprout and its stems can survive even in close proximity. Because the analysis excluded small stems (GBH <15 cm), which probably regenerated after stand initiation, the clumped spatial patterns indicate that *C. lanceolata* also regenerated by sprouting at stand initiation. The negative spatial correlation observed in the young stand is indicative of competition between the two conifer species.

In the young stand (plot 3), tree heights of *P. massoniana* were larger than those of *C. lanceolata* at the same DBH. These results indicate that suppressed inter-

mediate-sized individuals of *P. massoniana* invest more energy in height growth than in diameter growth, and this pattern of growth may be a strategy for this shade-intolerant species to escape strong shade (Figure 5). Despite this strategy, nearly all intermediate-sized individuals appeared to have died in the mature plots. Compared to *P. massoniana*, *C. lanceolata* exhibited a relatively stable relationship between diameter and tree height.

The ecological characteristics of *P. massoniana* and *C. lanceolata* revealed in this study are summarized in Table 3. Interspecific variation in shade tolerance based on a trade-off between growth in high light and survivorship in low light is often considered a primary factor driving forest succession and explaining species coexistence (Kobe et al., 1995; Nakashizuka, 2001; Tilman, 1990). Our target species represent examples of co-occurring species that differ in ecological traits based on this trade-off: *P. massoniana* is a shade-intolerant species that can grow rapidly in high light but

**Table 2**  
**Allometric relationship [ $\log(y) = \log(A) + h \times \log(x)$ ] between DBH and tree height for the two dominant species**

Plot	Species	n	log(A)	h	r <sup>2</sup>	common h	log(A) <sup>#</sup>	p-value for test of homogeneity	
								h	log(A) <sup>#</sup>
Plot 1	<i>P. massoniana</i>	37	0.462	0.601	0.506***	0.742	0.247	0.138	0.792
Plot 1	<i>C. lanceolata</i>	23	0.182	0.790	0.726***		0.241		
Plot 2	<i>P. massoniana</i>	21	0.087	0.804	0.190*	0.758	0.159	0.754	0.012
Plot 2	<i>C. lanceolata</i>	69	0.223	0.756	0.845***		0.220		
Plot 3	<i>P. massoniana</i>	61	0.534	0.508	0.344***			0.001	
Plot 3	<i>C. lanceolata</i>	25	0.057	0.879	0.747***				

#: intercept was calculated assuming that the slope was the same for the two species

\*\*\*:  $P < 0.001$ ; \*:  $P < 0.05$

**Table 3**  
**Ecological characteristics of the two dominant species**

	<i>P. massoniana</i>	<i>C. lanceolata</i>
Shade tolerance	Low	Relatively high
Growth under unshaded conditions	Fast	Relatively slow
Mortality under shaded conditions	High	Relatively low
Regeneration mode	Seedlings	Seedlings and sprouts
Regeneration under the canopy	Impossible	Possible
Tree form under shaded conditions	High priority in height growth	No clear trends
Seedling bank	No	Yes

cannot survive in low light, whereas *C. lanceolata* is a relatively shade-tolerant species that has a high probability of survival in low light but cannot grow as well as *P. massoniana* in high light.

The potential history of stand development in these *Pinus-Cunninghamia* forests can be described as follows: many seedlings of *P. massoniana* regenerated after a large-scale disturbance. *Cunninghamia lanceolata* regenerated at the same time by seedlings and sprouts. Due to higher growth rates, *P. massoniana* came to dominate the canopy layer; however, its mortality rate was very high under the canopy and only canopy trees survived. *Cunninghamia lanceolata* could survive under the canopy and thus dominated the sub-canopy layer. The regeneration of *P. massoniana* occurred only during a short period after the disturbance, whereas *C. lanceolata* continued to regenerate by sprouting. Some broad-leaved species were also able to regenerate under the canopy.

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