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The Determination and Prediction of Pine to Oak Forest Succession in Sugadaira, Central Japan

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ABSTRACT : In order to analyze the succession process from a pine forest to an oak forest, the tree growth of *Pinus densiflora* and *Quercus mongolica* ssp. *crispula* was monitored in a permanent quadrat for 23 years. The measurements were carried out for the stem diameter (DBH) of *Pinus densiflora* between 1977 and 1999 and for the height of *Quercus mongolica* ssp. *crispula* saplings between 1998 and 2000. The floristic composition and the locations of the individual *P. densiflora* and *Q. mongolica* ssp. *crispula* trees and saplings in the quadrat were recorded. *P. densiflora* and *Q. mongolica* ssp. *crispula* individuals were randomly distributed within the quadrat. The relative growth rates (RGR) of DBH in *P. densiflora* were 0.085 yr^{-1} for large trees and 0.056 yr^{-1} for small trees in 1977. The RGR of height for *Q. mongolica* ssp. *crispula* was 0.122 yr^{-1}. The growth curve for DBH of *P. densiflora* was approximated by the logistic equation:

$$DBH(t) = 30\ [1+1.16\exp(-0.13\ t)]^{-1}$$

where DBH (t) is the DBH (cm) in year t and t is the number of years since 1977.

The growth in height of *P. densiflora* and *Q. mongolica* ssp. *crispula* was described by following equations:

$$H(t) = 20.2\ [1+0.407\exp(-0.137\ t)]^{-1} \quad (P.\ densiflora)$$

$$H(t) = 30\ [1+20.7\exp(-0.122\ t)]^{-1} \quad (Q.\ mongolica\ \text{ssp.}\ crispula)$$

Where H (t) is the tree height (m) in year t and t is the number of years since 1977 in *P. densiflora* and 1998 in *Q. mongolica* ssp. *crispula*.

With these equations we predicted that the height of *Q. mongolica* ssp. *crispula* increases from 2 m in 1999 to 20 m in 2029. Therefore, *Q. mongolica* ssp. *crispula* and *P. densiflora* will be approximately the same height in 2029. The years required for succession from a pine forest to an oak forest are expected 33 with the range between 23 and 44 years.

Key words : Long term experiment, *Pinus densiflora, Quercus mongolica* ssp. *crispula*, Succession, Tree growth

INTRODUCTION

Succession is a unidirectional temporal change in the vegetation cover of a stand (Cowles 1899, Clements 1916). To study plant succession in detail, long-term observation in permanent quadrats is required. Primary succession of several sites has investigated on volcanic substrates of known age (Tagawa 1964, Tsuyuzaki 1989, Whittaker *et al.* 1989), and many studies of secondary succession have been conducted on old abandoned fields (Smith 1939, Oosting 1942, Bard 1952, Numata and Yamai 1955, Bazzaz 1968). Since the 1950s, experimental studies on succession have also been initiated in artificially prepared bare ground (Numata and Yamai 1955, Bornkamm 1985, Hayashi 1991, Schmidt and Brubach 1993).

However, these studies mainly focused on the herbaceous stages of succession. Only a few experimental studies on the arboreal stages with the permanent quadrat have been carried out in secondary succession (Peet and Christensen 1980, Toyohara and Fujiwara 1998). A theoretical consideration on forest succession was made for implication of forest succession models (Shugart 1984).

We conducted an experimental study in a pine stand, hypothesizing that succession is driven by interactions between the constituent species of the plant community. In this study, we documented quantitative aspects of a *Pinus densiflora* stand that has developed from *Miscanthus sinensis* grassland in Sugadaira, Nagano Prefecture, central Japan. By monitoring the growth and relative growth rates of the component species, we were able to estimate the time when *Q. mongolica* ssp. *crispula* will replace *Pinus densiflora* as the do-

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minant species in the stand.

STUDY SITE AND METHODS

The study site at Sugadaira Montane Research Center, Tsukuba University (SMRT) is located at 36°30' N, 137°27' E and at an altitude of 1300 m. The area experiences a cool climate, with an annual mean temperature of 6.9℃ and a total annual precipitation of 1200 mm. The soil developed from volcanic ash.

A permanent quadrat (20 m×40 m) was established in a *Pinus densiflora* forest that had developed from a *Miscanthus sinensis* grassland. After recording the species composition of the tree, shrub and herb layers, we measured stem diameter at breast height (DBH) of the trees and tree height of *Pinus densiflora.* And we also recorded the location of individual trees in the quadrat. These data were collected from the permanent quadrat between 1977 and 1999. The measurements provided us the information on trunk increment, relative growth rate (RGR) of DBH, and change in tree density of *P. densiflora* over the 23-year period. We also measured height and recorded the location of *Quercus mongolica* ssp. *crispula* saplings and seedlings in the quadrat.

We marked all the trees with numbered plastic tags. The height and location of saplings and seedlings of all species were measured from 1998 onwards. The floristic composition of herb layer was sampled using five 1 m×1 m quadrats and the species were quantified with *v*-value (Hayashi 1990, Hayashi *et al.* 1996).

We measured the solar energy at a height of 1 m at five points, regularly spaced across the stand, using a Panteon Pyrano Counter Foglia 21. The accuracy of the equipment was confirmed by the Japan Meteorological Agency. Meteorological data collected at the nearby Sugadaira Automatic Meteorological Data Station of the Japan Meteorological Agency were also used.

RESULTS

Environmental features

Seasonal variation in solar radiation in the *P. densiflora* forest is presented in Fig. 1. The mean solar radiation at 1 m above the forest floor from August 25 to September 27, 1998 was 31.5 MJ m^{-2}, equating to 9.5% of the solar radiation received above the canopy. Solar radiation at a height of 1 m fluctuated seasonally. In June, it averaged 10~14 % of that reaching the top of the canopy. The relative light intensity decreased at most within August and September according to the development of dense leaf layers and recovered when the leaves began to fall in October and November.

Species composition and individual distribution

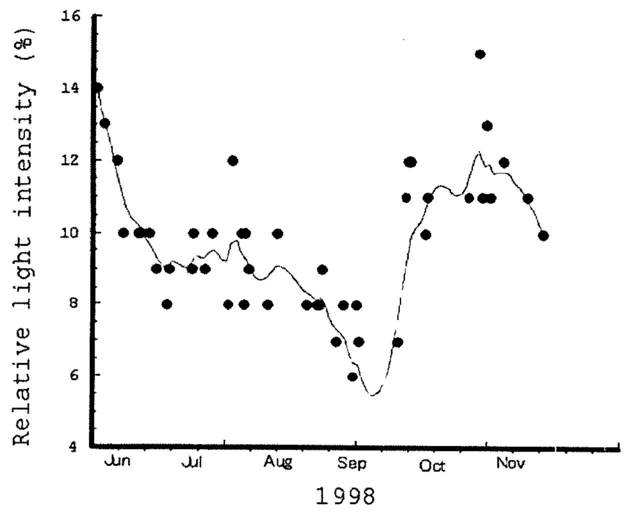

Fig. 1. Seasonal change of relative light intensity (percents of solar radiation at the canopy) in the stand of *Pinus densiflora* from June 1 to November 30, 1998.

The species composition of the *Pinus densiflora* forest in 1999 is shown in Table 1. The quadrat contained 63 individuals of *P. densiflora*, eight of *Betula platyphylla* var. *japonica* and two of *Quercus mongolica* ssp. *crispula* in the tree layer. The mean DBH in the tree layer was 17 cm for *P. densiflora*, 12 cm for *B. platyphylla* and 14 cm for *Q. mongolica* ssp. *crispula*. Forty-two saplings and seedlings of *Q. mongolica* ssp. *crispula*, with a mean height of 119 cm, were recorded. The tree species *Prunus maximowiczii*(mean height 263cm) was also common in the sub-tree and shrub layers with *Rhus trichocarpa*(236cm), *Cornus controversa* (438cm), *Malus toringo*(227cm) and *Clethra barbinervis*(427cm). The shrub species *Rhododendron japonicum* grew in association with *Viburnum opulus* var. *calvascens*. A total of 290 individuals in the sub-tree and shrub layers were recorded in the quadrat. The dominant species in the herb layer were *Hosta sieboldiana, Rosa multiflora* and *Vitis coignetiae.*

Although the *P. densiflora* trees were mature enough to produce seeds, no saplings of this species were observed in the herb or shrub layers. In contrast, many saplings of *Q. mongolica* ssp. *crispula* were observed in the forest ground flora, though no adult trees producing acorns grew in the stand. Toyohara and Fujiwara (1998) reported that the saplings of *Quercus* species were present in the *Pinus densiflora* stands in Hiroshima, Southwestern Japan. Nakamura (1984) reported that jays (*Garrulus glandarius*) stored the acorns of *Q. mongolica* ssp. *crispula* in stands of *P. densiflora* (Mosandl and Kleinert 1998, Suyama and Nakamura 1988).

Fig. 2 shows the distribution of individual trees of *P. densiflora* including *B. platyphylla* and *Q. mongolica* ssp. *crispula* in the tree

Table 1. Species composition, DBH (cm), density (stems/400 m^2) and v-value (0.001 m^3/m^2) of the *Pinus densiflora* stand

Species	Tree layer		Sub-tree and shrub layers	Herb Layer
	Density	DBH	Density	v-value
Pinus densiflora	63	17		
Betula platyphylla var. *japonica*	8	12		
Quercus mongolica ssp. *crispula*	2	14	42	0.9
Rhus trichocarpa			88	9.1
Prunus maximowiczii			34	3.6
Rhododendron japonicum			24	
Ligustrum tschonoskii			15	5
Lonicera gracilipes var. *glandulosa*			12	2.7
Cornus controversa			7	
Acer rufinerve			6	2.2
Malus toringo			5	0.7
Euonymus sieboldianus			5	
Prunus incisa			5	
Viburnum opulus var. *calvescens*			5	
Acer crataegifolium			4	
Sorbus commixta			3	
Prunus grayana			3	
Clethra barbinervis			2	
Acanthopanax sciadophylloides			2	
Fraxinus sieboldiana			2	
Juglans ailanthifolia			2	
Hydrangea paniculata			2	
Viburnum wrightii			2	
Fraxinus mandshurica var. *japonica*			2	
Ilex macropoda			1	
Toisusu urbaniana			1	
Fraxinus lanuginosa f. *serrata*			1	
Aralia elata			1	11.3
Acer ginnala var. *aidzuense*			1	
Prunus jamasakura			1	
Magnolia praecocissima			1	
Acer mono f. *marmoratum*			1	
Viburnum dilatatum			1	
Pourthiaea villosa var. *laevis*			1	0.3
Chaenomeles japonica			1	
Euonymus alatus f. *ciliato-dentatus*			1	
Abies veitchii			1	
Prunus apetala			1	
Rosa multiflora			1	1.3
Salix bakko			1	
Acanthopanax spinosus			1	
Vitis coignetiae			1	10.6
Hosta sieboldiana				23.9
Rhus ambigua				18.6
Schisandra chinensis				12.2
Celastrus orbiculatus				5.4
Solidago virgaurea var. *asiatica*				1.8
Miscanthus sinensis				1.2
Tripterospermum japonicum				0.8
Liparis kumokiri				0.5
Kalopanax pictus				0.2
Carex lanceolata				0.2
unidentified sp.				0.2
Sanguisorba officinalis				0.1
Epipactis thunbergii				0.1
Pyrola japonica				0
Total 56 species	73		290	

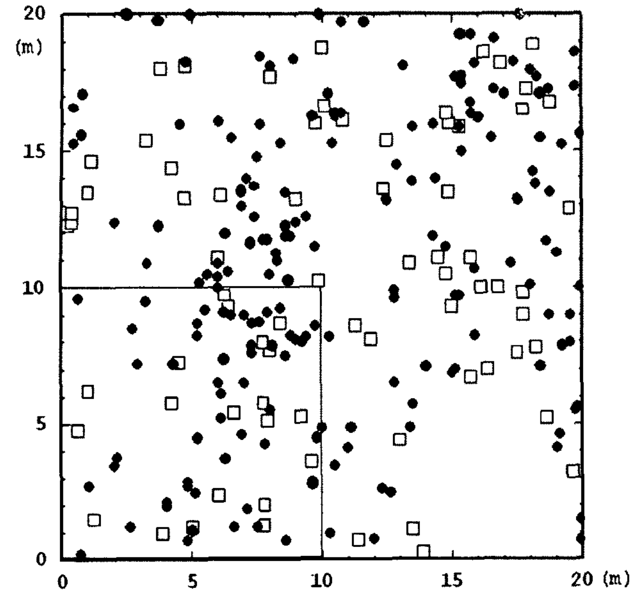

Fig. 2. Spatial Distribution of tree individuals of *P. densiflora, B. platyphylla* var. *japonica* and *Quercus mongolica* ssp. *crispula* in the tree layer (open square). Saplings (solid circle) of *Q. mongolica* ssp. *crispula* in the sub-tree and shrub layers in the 20m×20m subplot. The three dimensional graph of left and lower quarter of the subplot is shown in Fig. 3.

layer and saplings of *Q. mongolica* ssp. *crispula* in sub-tree and shrub layers. The randomness of the tree distribution was tested by comparing it to the theoretical binomial distribution. The results suggested that the trees were distributed randomly (chi-square = 0.34, degrees of freedom = 3, $p < 0.9$). The spatial distribution of 165 *Q. mongolica* ssp. *crispula* saplings on the forest floor was also determined in the same figure (Kenkel 1988, Mosandl and Kleinert 1998, Lookingbill and Zavala 2000).

The mean heights of the saplings and seedlings of *Q. mongolica* ssp. *crispula* were 298 cm and 45 cm, respectively under the canopy of *P. densiflora* stand. The three-dimensional structure of the shrub and herb layers of the stand is presented in Fig. 3. The figure shows that the saplings of *Q. mongolica* ssp. *crispula* grew below the shrubs of *Rhus trichocarpa, Prunus maximowiczii* and *Cornus controversa* in the shrub layer. Hence, three strata were identified in the *P. densiflora* forest.

Yearly changes in DBH of P. densiflora

The mean diameter at breast height (DBH) of the *P. densiflora* population was 9.6 cm in 1977 and 18.8 cm in 1999. The mean DBH increased 9.2 cm over the 23-year study period. The DBH

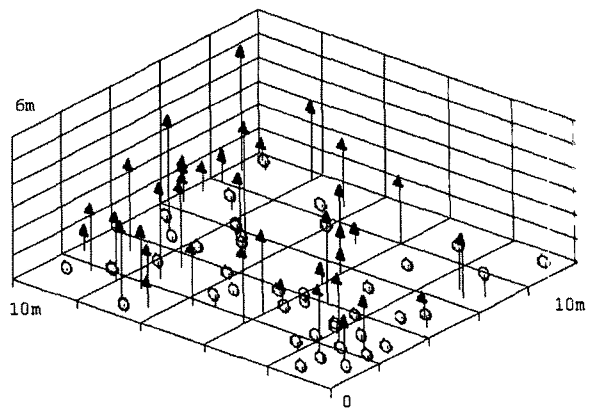

Fig. 3. Three dimensional graph of sub trees (solid triangle) and oak saplings (open circle) in the 10m×10m sub-plot shown in Fig. 2.

increased by 0.41 cm per year. In 1999 DBH ranged from 4.5 to 32.2 cm. The Spearman's coefficient of rank correlation for DBHs of 1977 population and 1999 population was 0.66 ($p < 0.05$). This suggests that the rank of individual's DBH within the population is maintained over a long period of time. The individual trees in the population were classified into five groups according to their size such as 25~32cm, 21~24 cm, 19~20 cm 15~18 cm and 5~14cm; each group contained 26 tree individuals. Similar growth rates were maintained within groups over the study period.

The increase in DBH of the trees in the largest size-class was approximated by the following equation:

$$\mathrm{DBH}\ (t) = 30\ [1+1.16\exp(-0.13\ t)]^{-1} \qquad (1)$$

Where DBH (t) is the DBH (cm) in year t and t is the number of years since 1977.

Yearly changes in the density of the *P. densiflora* population

In the tree layer, the quadrat contained 317 individuals in 1977 and 141 individuals in 1999 per 800 m^2. Over the 23-year study period, there was a net loss of 176 trees. In 1999, the living trees per 800 m^2 were 126 in *P. densiflora*, 13 in *B. platyphylla*, and 2 in *Q. mongolica*, ssp. *crispula*.

The tree density decreased exponentially as shown Fig. 4. The decrease in density from 1977 to 1999 was approximated by the following equation:

$$N = 315\exp(-0.036\ t) \qquad (2)$$

Where N is the density (number of individuals per 800 m^2), and the t is the number of years since 1977.

The equation exhibits also the relationship between mean DBH

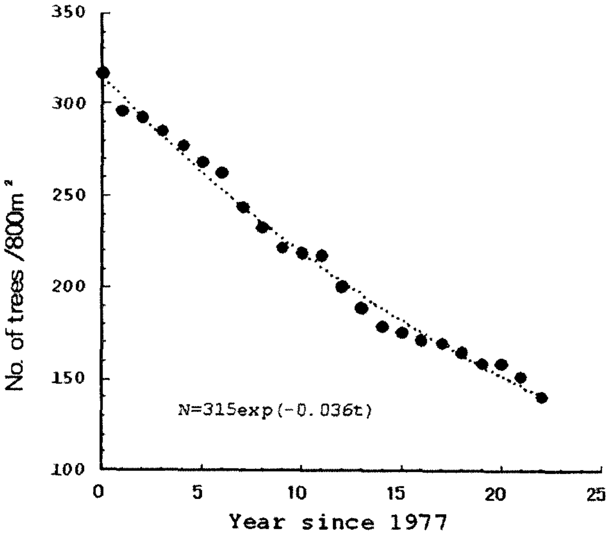

Fig. 4. Change in tree density since 1977.

of trees and the tree density of the stand, because the DBH is determined by the time t. A similar relationship between mean DBH and density was reported by Yamashita and Hayashi (1987) in *Pinus densiflora* stands and by Hayashi *et al.* (1996) in *Quercus mongolica* ssp. *crispula* stands.

Yearly changes in the DBH histogram for the *P. densiflora* population

The changes in DBH histograms within the *P. densiflora* population between 1977 and 1999 are shown in Fig. 5. In 1977 and 1981, the DBH histogram exhibited a normal distribution (chi-square = 8.55, degrees of freedom = 7, $p > 0.05$). However, in 1982, 1985 and 1989, the distribution was significantly different from the normal (for example in 1982, chi-square= 17.14, degrees of freedom = 7, $p < 0.05$).

The growth and death of the smaller trees due to competition, accounted for the changes in the DBH distribution. The results suggest that the DBH distribution naturally alternated between normal and non-normal distributions during growth in *P. densiflora* population.

Yearly changes in the relative growth rate (RGR) of *P. densiflora*

Yearly changes in the mean RGR of *P. densiflora* in the DBH ranges of 25~32 cm is presented in Fig. 6. The RGR decreased as the trees aged. The mean *RGR* was 0.078 in 1977, and 0.019 in 1999.

The change in averaged *RGR* was approximated by the following equation:

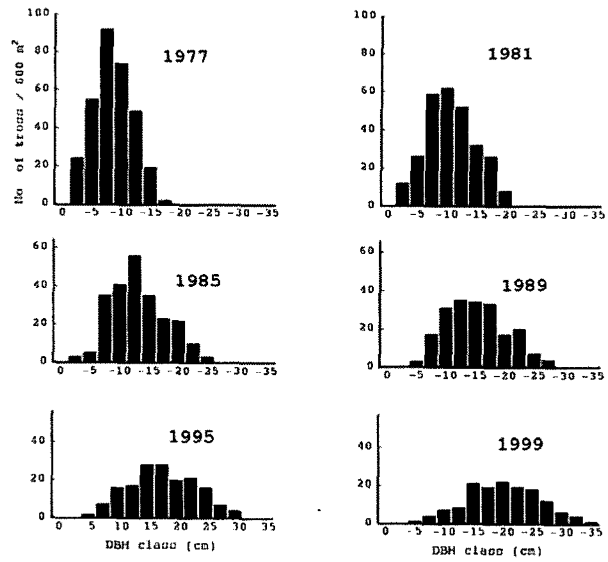

Fig. 5. Yearly change of the histograms of DBH in the *Pinus densiflora* stand from 1977 to 1999.

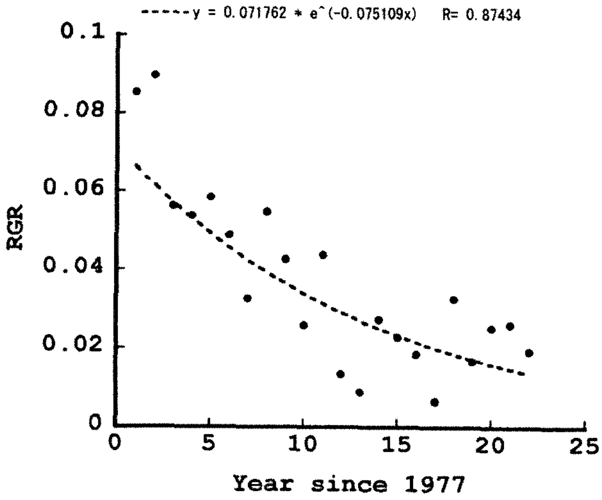

Fig. 6. Change in RGR for large size class during the growth period of *Pinus densiflora* from 1977 to 1999.

$$RGR\ (t) = 0.072\exp(-0.075\ t) \qquad (3)$$

Where $RGR\ (t)$ is RGR in year t and t is the number of years since 1977.

The *RGR* decreased exponentially during the growth period. The differences between DBHs of larger and small trees increased progressively with time because the *RGR* of large trees were bigger than that of small trees.

We determined the difference (*rgr*) between an observed *RGR* and that predicted by equation (3). The *rgr* values were then correlated with the monthly mean temperature (T: ℃), monthly solar radiation (E: MJ m^{-2}) and monthly precipitation (R: mm) using the multi variable analysis. The equation is as follows:

$$rgr = 0.41T - 0.27E + 0.42P \quad (4)$$

The coefficient of multiple determination was 0.76 ($p < 0.14$) (Coile 1936, Takahashi 1971).

The values of T (mean temperature of the last July), E (solar radiation in August of the current year) and P (precipitation in April, May and June of the current year) were normalized using their means and standard deviations. According to this equation (4), E and P contributed positively to the tree growth. Solar energy in August affected negatively to the growth.

Growth of saplings of *Q. mongolica* ssp. *crispula*

In 1999, there were 165 saplings of *Q. mongolica* ssp. *crispula* per 400m^2 in the *P. densiflora* forest quadrat. Their mean height of the seedlings was 45 cm. Their height distribution was the L-shaped (Fig. 7), because most seedlings were lower then 45 cm. Twenty-one seedlings less than 27 cm in mean height, disappeared between 1998 and 1999. However, 16 seedlings with a mean height of 14 cm were newly recorded in 1999. Thus, *Q. mongolica* ssp. *crispula* maintained its population by emergence and loss of the seedlings and saplings from the stand during the forest succession.

The mean *RGR* of seedlings and saplings between 1998 and 1999 was 0.127 yr^{-1}. The RGRs of the saplings in 1998 were positively correlated with those in 1999 ($r = 0.336$, $p = 0.004$). This suggests that the value of *RGR* of the seedlings and saplings continued to maintain the value in the following year.

Among this group, there were eight saplings whose height was greater than 2 m. The average height growth of these saplings was 27.8 cm per year (Sano 1988, Hayashi *et al.* 1996).

The relationship between the *RGR* of the sapling height and solar radiation from August 25 to September 27 in 1999 is shown in Fig. 8. The relationship was approximated by following equation:

$$RGR = -0.205(1/E) + 0.42 \quad (5)$$

Where E is solar radiation (MJ $m^{-2}day^{-1}$).

Equation (5) suggests that the saplings of *Q. mongolica* ssp. *crispula* can survive at solar radiation intensities above 0.488 MJ $m^{-2}day^{-1}$. Therefore, saplings of *Q. mongolica* ssp. *crispula* were expected to be able to grow in this forest stand, because the mean solar radiation of this stand was 0.949 MJ $m^{-2}day^{-1}$.

Prediction of the growth of *P. densiflora* and *Q. mongolica* ssp. *crispula*

The DBH growth of *P. densiflora* trees was able to predict using the equation (1). In order to determine the tree height from the DBH data, heights (H: m) of *P. densiflora* trees were estimated using the following equation (Ogawa 1980) derived from the data of Ando (1962), Hatiya *et al.* (1989) and the Japan Forestry Agency (1973) (Fig. 9).

$$1/H = (0.98DBH^{-1.26}) + 0.036 \quad (6)$$

Using equation (6), tree height was estimated from DBH of our data. Then, the following logistic equation of height growth for *P.*

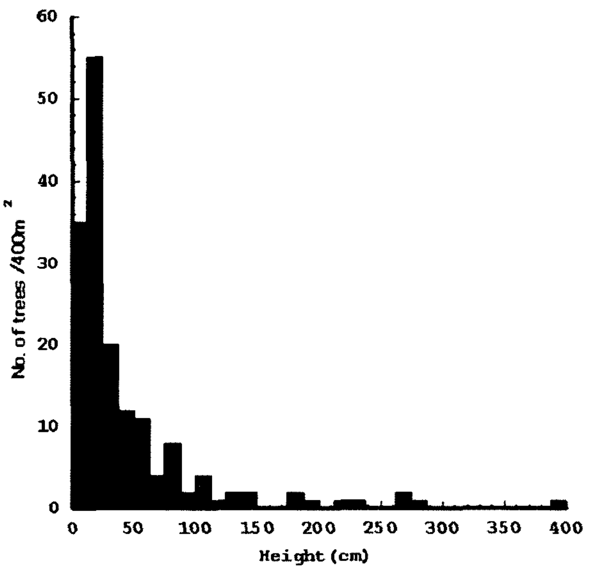

Fig. 7. Height histogram of *Quercus mongolica* ssp. *crispula* seedlings in 1999.

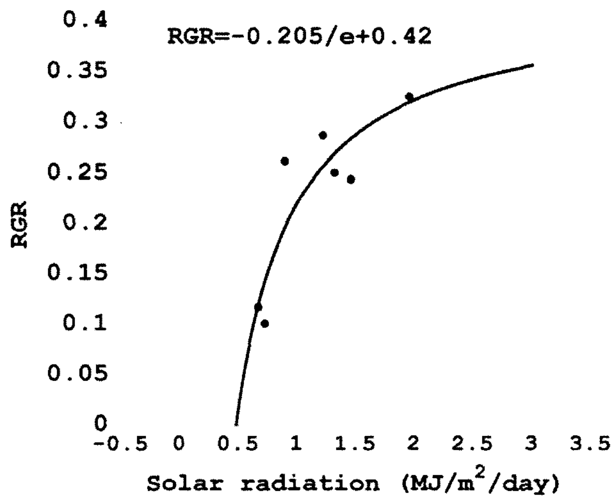

Fig. 8. Relationship between the RGR and intensity of solar radiation in the stand from 25 August to 27 September 1999.

densiflora was derived:

$$H(t) = 20.2\ [1+0.407\exp(-0.137\ t)]^{-1} \quad (7)$$

Where H (t) is the tree height (m) in year t and t is the number of years since 1977. The height of *P. densiflora* can be estimated for any year from equation (7). The growth curve for the height of *Q. mongolica* ssp. *crispula* was obtained using the mean intrinsic growth rate at the study stand based on the measurements between 1998 and 2002. The mean intrinsic rate was 0.122 with a standard deviation of 0.039. Therefore the growth curve was approximated by the equation:

$$H(t) = 30\ [1+20.7\exp(-0.122\ t)]^{-1} \quad (8)$$

Where H (t) is tree height (m) in year t and t is the number of years since 1998.

The growth curves for *P. densiflora* and *Q. mongolica* ssp. *crispula*, based on equations (7) and (8), are shown in Fig. 10. *Q. mongolica* ssp. *crispula* saplings which were 2 m in 1999 are expected to attain a height of 20 m in 2029. This date could vary between 2022 and 2043, by when *Q. mongolica* ssp. *crispula* and *P. densiflora* will be approximately the same height. Since *P. densiflora* is a heliophyte, it is unlikely to survive under shade and will be replaced in the succession by *Q. mongolica* ssp. *crispula*.

DISCUSSION AND CONCLUSIONS

The *P. densiflora* stand consisted of various species with different life cycles. Spatial distribution of individuals within a natural stand is determined by seed dispersion, growth of seedlings,

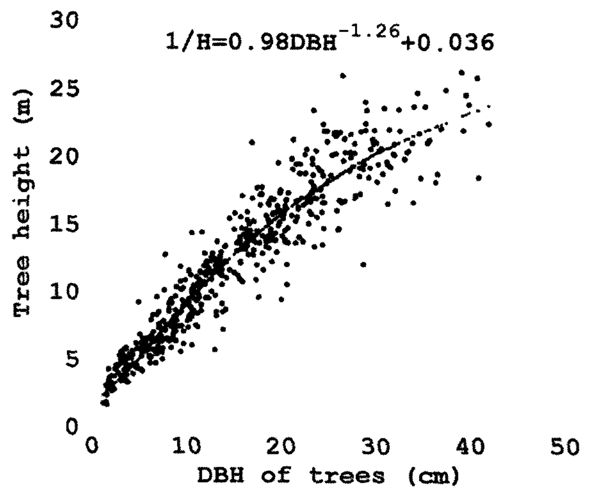

Fig. 9. Relationship between DBH and tree height of *Pinus densiflora*.

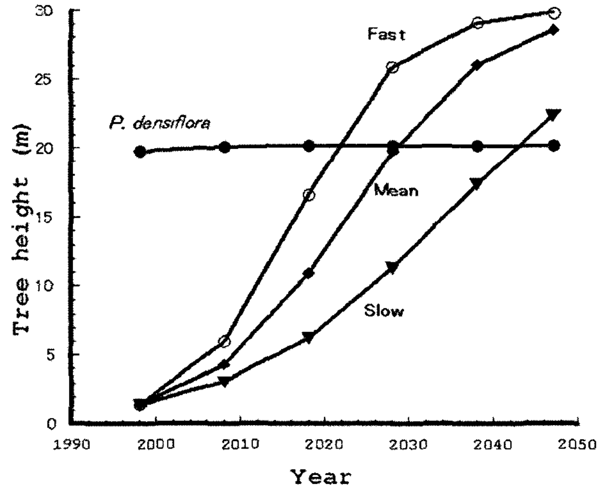

Fig. 10. Predicted height growth of trees of *P. densiflora* and *Q. mongolica* ssp. *crispula*.

competition during the growth period and unexpected disturbances, such as typhoons. The seedling stage is mainly controlled by the physical environment. When individuals reach the sapling stage, the influence of the physical environment is reduced, and as individuals age, their success reflects intra and inter species competition. The location of tree individuals become random distribution when the stand mature (Stoll *et al.* 1989). In our experimental plot, the populations of *P. densiflora* and *Q. mongolica* ssp. *crispula* were randomly distributed in 1981 and 1999 (Fig. 2). With subsequent growth after 1981, the smaller trees are eliminated from the population through interactions with neighboring individuals. As a result of this interactive process, the spatial distribution of the trees changes with time (He and Duncan 2000).

The temporal change in the DBH distribution shown in Fig. 5 suggests the elimination of the smaller individuals from the stand. The tree density was reduced by self-thinning. A gap was formed when a canopy tree died, allowing light to reach the forest floor. However, increased illumination not only favored the growth of *Q. mongolica* ssp. *crispula* saplings, but also promoted the growth of other plants on the forest floor such as *Sasa senanensis*. Therefore, canopy gaps do not necessarily favor *Q. mongolica* ssp. *crispula* saplings.

Multiple regression analysis between the *RGR* of *P. densiflora* and various environmental factors suggested that temperature in the last July and precipitation between April and June in the current year promoted tree growth. Solar radiation in August of the current year was negatively correlated with tree growth. Although it is difficult to explain the inhibitive effect of light, sunny conditions may be linked to drought.

The distribution of the *Q. mongolica* ssp. *crispula* seedlings is initially determined by birds and voles such as jays for example. (Lookingbill and Zavala 2000). The seedlings are only grow at the sites where mean solar radiation exceeds 0.488 MJ $m^{-2}day^{-1}$ from the end of August until the end of September.

Using equation (8), we were able to estimate when the seedlings of *Q. mongolica* ssp. *crispula* had germinated. According to the equation (8), we estimated that the germination date of the seedlings of 14 cm tall had emerged in 1989. In the other hand, the density of *P. densiflora* trees in 1989 estimated using equations (1) and (2), was 253 trees per 800 m^2. In such a dense stand, the light intensity would be too low for *Q. mongolica* ssp. *crispula* to survive. A reduction in the density of *P. densiflora* trees and the consequent increase in light levels was necessary to ensure the success of *Q. mongolica* ssp. *crispula* survive.

We did not find any *P. densiflora* saplings in the sub-canopy and shrub layers in 1999, although the trees of *P. densiflora* were sufficiently mature to produce seeds. In contrast, numerous seedlings and saplings of *Q. mongolica* ssp. *crispula* were found in the stand. *Q. mongolica* ssp. *crispula* was able to grow under the environmental conditions created by the dominant *P. densiflora* cover. It is predicted that the saplings of *Q. mongolica* ssp. *crispula* will reach the same height as the *P. densiflora* canopy after between 23 and 44 years (Fig. 10). At this stage in the forest succession, the dominant *P. densiflora* will begin to be replaced by *Q. mongolica* ssp. *crispula*.

This change in dominance is the result of repeated regeneration of the species with different germination, growth and survival characteristics.

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