

Population structure and dynamics of *Pinus taiwanensis* Hayata at Songyang county, Zhejiang Province, China

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Abstract

Pinus taiwanensis is a widely distributed species in the southeastern China (Zhejiang, Anhui, Hubei, Hunan, Jiangxi, Fujian, Taiwan provinces) at an elevation of 700–2000 m. This pine is a pioneer in forest succession and is often used as a species for afforestation in this region at an elevation above 700 m. This study was carried out at Guanshanyuan, Zhejiang province, at a latitude of N 28° 18', a longitude of E 119° 16' and an altitude of 800–1502 m above sea level. On the basis of a census of all individuals of *Pinus taiwanensis* at different successional stages and various habitats, age structure, spatial pattern, density, biomass of population and their dynamics were described. Considering the population dynamics throughout the successional process, three phases could be recognized. Until about 9–10 years after *Pinus taiwanensis* invaded the stands, the density of population was increased by the recruitments along with increase of the mean tree weight and population biomass (phase I). Thereafter, the population was in full density state, the biomass of population and the mean tree weight increased exponentially, while the density was decreased drastically by the self-thinning and the invasion of other broad-leaved trees (phase II). The $-3/2$ power law of natural thinning was applicable to the populations in this phase. When the broad-leaved trees reached the canopy, although the mean tree weight increased slowly, the density and biomass of *Pinus taiwanensis* population decreased gradually (phase III) until the population senesced and retreated from the successional series completely. The population dynamics of *Pinus taiwanensis* during the successional process was in common with pioneer species in forest succession. At some special habitats such as rocky steep slopes and ridges, however, *Pinus taiwanensis* population could form such an edaphic climax community that the population density, biomass and the mean tree weight in phase III could be in a stable state for very long period.

Nomenclature: Iconographia Cormophytorum Sinicorum (1985).

Introduction

Pinus taiwanensis is a widely distributed tree species in the southeastern China (Zhejiang, Anhui, Hubei, Hunan, Jiangxi, Fujian, Taiwan

provinces) at an elevation above 600–700 m. Its upper distribution limit can reach an elevation of ca. 2800 m in the Central Mountains, Taiwan province. At an elevation of 500–700 m in this region, *Pinus taiwanensis* is often adjacent to *Pinus*

massoniana. There is often a natural interspecific hybrid at the transition zone. *Pinus taiwanensis* is a heliophyte. It can endure drought, soil poverty and wind. The seed is light and small which has one wing and can be easily dispersed. The natural regeneration is by seeds only (Wu Zhonglun 1963).

According to the System of «Chinese Vegetation», *Pinus taiwanensis* forest is one of the representative formations of the middle mountain vegetation along the vertical zones in the subtropics of East China (Wu Zhengyi 1980). Several Chinese researchers studied the types and composition of this pine forest. It was controversial as to its position in the vertical vegetation zones and in forest succession (Wang Liangping *et al.* 1989). In this paper the structure and dynamics of *Pinus taiwanensis* forest were studied on a population level and knowledge of its population structure and dynamics was valuable to the themes mentioned above (van der Maarel 1984).

The study area and methods

The study was carried out in Guanshanyuan, Songyang county, Zhejiang province, at a latitude of N 28° 18' and a longitude of E 119° 16'. The area had a subtropical monsoon climate. The mean annual temperature was 16.8 °C; the warmest month was July with 27.7 °C and the coldest was January with 5.3 °C. The average annual precipitation and evapotranspiration amounted to 1532 mm and 1294 mm, respectively. The average annual relative humidity was 77%. The zonal vegetation was subtropical evergreen broad-leaved forests dominated by *Castanopsis eyreii* and *Schima superba*.

Due to the diversity of topography (an elevation from 600 to 1502 m), low population density and inconvenient transportation, the vegetation was kept fairly well in the study area. The main plant community types at an elevation of 600–1300 m were evergreen broad-leaved forests dominated by *Castanopsis eyreii*, *Schima superba* or *Cyclobalanopsis nubium*; the needle and evergreen broad-leaved mixed forest with *Pinus taiwanensis*

and *Cunninghamia lanceolata*; *Liquidambar formosana* forest which occurred in gullies. At an elevation above 1300 m, there were *Schima superba* – *Carpinus fargesii* – *Cyclobalanopsis multinervis* evergreen and deciduous mixed forest; *Carpinus fargesii* deciduous forest; *Fagus longipetiolata* deciduous forest; *Rhododendron simiarum* dwarf forest, etc.. There were many types of shrubland and man-made economic forest.

Pinus taiwanensis population was widely distributed in this region at an elevation of 900–1500 m. At an elevation below 1300 m, it was mixed with *Castanopsis eyreii*, *Schima superba*, *Lithocarpus hancei*, *L. henryi*, *Cyclobalanopsis gracilis*, *C. myrsinaefolia*, etc. evergreen broad-leaved tree species. And at an elevation above 1300 m, it was mixed with *Cyclobalanopsis multinervis*, *Carpinus fargesii*, *Acer* spp., *Viburnum nigrum*, etc. evergreen or deciduous broad-leaved tree species. At some special habitats such as rocky steep slopes or ridges, there was open pine forest which was usually in mature phase. The understory was rather dense and the main species were *Eurya rubiginosa* var. *attenuata*, *Lyonia ovalifolia* var. *elliptica*, *Rhododendron simsii*, *R. latoucheae*, *Stranvaesia davidiana* var. *undulata*, etc.. On clearing or burning lands, there were pine shrub-grassland and pine juvenile forest.

To sum up, *Pinus taiwanensis* population could be found in nearly all stages of secondary forest succession and a variety of habitats in the study area.

Eleven plots were set up on different habitats and plant communities of various successional stages, which included one evergreen broad-leaved forest sample plot, two needle and broad-leaved plots (by point-centred quarter sampling method, each consisted of 30 points), one open pine forest sample plot (consisted of 2 × 2 m small quadrats), three pine juvenile forest sample plots (each consisted of 1.5 × 1.5 m small quadrats) and four pine shrub-grassland sample plots (each consisted of 1 × 1 m small quadrats). The data of these sample plots were listed in Table 1.

In each plot a census of all individuals of *Pinus taiwanensis* was made. The stem diameter at breast height or at basal height (for individuals

Table 1. Data of *Pinus taiwanensis* populations and their environmental conditions in eleven plots at Guanshanyan, Zhejiang province, China.

Plot nr	Plot size (m ²)	Site	Community type	Elevation (m)	Aspect	Slope	Age range (yr)	Density (ind/ha ⁻¹)	LT (%)	Community height (m)	Community coverage (%)
1	30	Qipanshi	S	1100	NW30	42	1-6	11250	33.5	2	40-60
2	80	Qipanshi	S	1060	SW20	25	1-7	12250	46.0	2	20-30
3	36	Qipanshi	S	1050	SW30	35	1-8	14445	25.3	2	40-50
4	51	Qipanshi	S	1070	SW20	40	2-9	16863	21.7	2.5	50-60
5	225	Qipanshi	PT	1020	NW45	15	10-21	2533	21.1	10	50-60
6	90	Qipanshi	PT	1150	NW35	42	9-17	10200	19.5	6	70-80
7	125	Ruoliaoxian	PT	1370	SW25	25	10-24	4222	13.7	10	70-80
8	320	Ruoliaoxian	PTO	1360	SW3	45	1-110	3531	18.3	16	40-50
9	2500	Qipanshi	CSP	1060	NW15	40	35-103	224	8.8	19	80-90
10	2500	Ruoliaoxian	CSCCP	1350	NW40	25	30-90	410	9.7	15	70-80
11	625	Qipanshi	CS	1050	SE30	35	57-100	64	8.4	15	70-80

S: *Pinus taiwanensis* shrub-grassland; PT: pine juvenile forest; PTO: open pine forest; CSP: *Castanopsis eyrei* + *Schima superba* + *Pinus taiwanensis* mixed forest; CASP: *Castanopsis eyrei* + *Schima superba* + *Cyclobalanopsis multinervis* + *Carpinus fargesii* + *Pinus taiwanensis* mixed forest; CS: *Castanopsis eyrei* + *Schima superba* forest; LT: Light throughfall.

less than 2.5 m in height) and tree height for each pine tree were measured. Its age was measured by counting the number of whorls of branches and scars for the individuals aged less than 20 years or by counting the rings in an increment core taken at the root collar.

The aboveground weight per individual (wt) was estimated from following allometrical relation:

$$wt = a(D^2H)^b \quad (1)$$

where a and b are coefficients. D and H are diameter at breast height and tree height, respectively.

In the destructive plot, sixteen sample pine trees in different size were measured and weighted. Coefficients a and b were determined by the least squares method.

The density data from the small quadrats sampled in the pine juvenile forest, open pine forest and shrub-grassland were used to determine the spatial pattern in these stands by applying the ratio of variance to the mean (s^2/\bar{x}) method. The deviation of the value of that ratio from 1.00 was t-tested (Cox 1972).

The data from the point-centred quarter sampling plots in the mixed forest were analysed by assuming the binomial distribution of individuals.

$$P(x) = \frac{4!}{x!(4-x)!} * q^{(4-x)} * p^x \quad (p + q = 1) \quad (2)$$

Where p is the relative density of a population in the community, and P(x) the probability of the sampling point containing x individuals of the populations (x equals to 0, 1, 2, 3, 4). The deviation between the expected frequency of a sampling point containing 0, 1, 2, 3, or 4 individuals from the observed frequency was tested on significance by using the Chi-square test (Cox 1972).

Results and discussion

Age structure and its dynamics

The age structures of *Pinus taiwanensis* population in eleven plots are shown in Fig. 1. The population age distributions were presented as relative frequencies in each age class. Four types of age structure could be recognized: Growing population: age structure showed a peak distribution, and the age of all individuals was <9 yr (plots 1–4), which occurred in shrub-grassland; Declining population: the age structure showed a peak distribution and the age of all individuals was between 9 to 25 yr (plots 5–7), which occurred in pine juvenile forest; Residual population: the age structure showed a strong peak of ageing trees and the age of all individuals was over 30 yr (plots 9–10), which occurred in needle and broad-leaved mixed forest; Stationary population: the age structure showed a reverse J distribution with

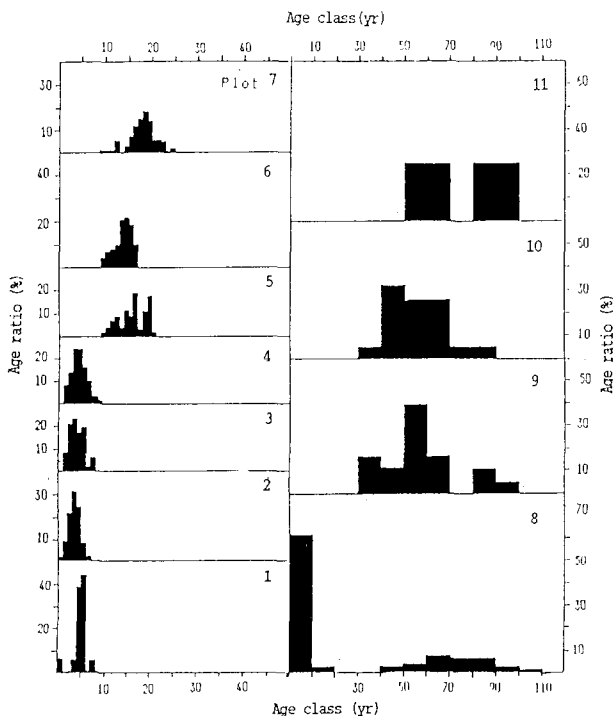


Fig. 1. Age structure of *Pinus taiwanensis* populations in eleven plots (each age class in the left is one year, in the right is ten years).

individuals of all age classes (plot 8), which occurred in open pine forest on rocky steep slopes or ridges.

It was interesting to correlate the population age structures of *Pinus taiwanensis* with different stages of community succession and different habitats (see Table 2). *Pinus taiwanensis* is a heliophyte. It can endure drought and soil poverty, and can be easily dispersed by wind. It thus became the pioneer tree species on clearing or burning lands. The relationship between the stages of community succession, the habitats and the types of age structure of the pine population seemed to result from the biological features and ecological requirement of the species as well as its action on the habitats.

From these data it emerged that the age structure of *Pinus taiwanensis* population changed from a growing type to a declining type and finally to a residual type through the forest succession process. When the tree canopy formed, it created conditions for the establishment and development of shade-tolerant broad-leaved trees, while the pine could not regenerate itself under the shade. At an elevation below 1300 m in this region, the succession would end in *Castanopsis eyreii*-*Schima superba* evergreen broad-leaved forest and at an elevation above 1300 m, in evergreen and deciduous broad-leaved mixed forest or deciduous broad-leaved forest.

On rocky steep slopes or ridges, however, the environmental conditions was very severe for other tree species to establish and develop. Thus, *Pinus taiwanensis* could form an open pine forest which was rather stable and persistent. The open canopy allowed regeneration of pine seedlings to take place. The reverse J age structure meant the pine population could maintain itself for very long period with a high probability.

Spatial pattern

The result of spatial pattern analysis for *Pinus taiwanensis* populations in shrub-grassland and pine juvenile forest (plots 1–7) is listed in Table 3). The s^2/\bar{x} ranged from 0.747 to 1.189 and

Table 2. Dynamics of age structure for *Pinus taiwanensis* populations in different habitats and successional stages. Population age structure types: G = growing type; D = declining type; R = residual type; S = stationary type.

Habitats	Types of population age structure						
Rocky steep slopes or ridges at an elevation above 900 m	G	→	D	→	S	→	Open pine forest
Clearing or burning lands at an elevation above 1300 m	G	→	D	→	R	→	Deciduous forest or evergreen and deciduous mixed forest
Clearing or burning lands at an elevation of 800–1300 m	G	→	D	→	R	→	Evergreen broad-leaved forest
Stage of community succession	Shrub-grassland		Pine juvenile forest		Needle and broad-leaved mixed forest		Climax community

Table 3. Analysis of spatial pattern of *Pinus taiwanensis* populations in the shrub-grassland, pine juvenile forest and open pine forest sample plots.

Plot No.	Community type	Number of quadrats	\bar{x}	s^2	s^2/\bar{x}	p
1	S	30	1.125	1.05	0.933	> 0.05
2	S	80	1.225	1.392	1.136	> 0.05
3	S	36	1.444	1.618	1.120	> 0.05
4	S	51	1.686	1.260	0.747	> 0.05
5	PT	25	2.28	2.71	1.189	> 0.05
6	PT	40	2.55	2.41	0.945	> 0.05
7	PT	100	0.95	0.726	0.764	> 0.05
8a	PTO	20	1.85	1.084	0.586	> 0.05
8b	PTO	20	3.8	21.75	5.72	< 0.05

Same symbols of community types as Table 1.

8a: Individuals of age > 30 yr.

8b: Individuals of age < 20 yr.

p = Significant probability of t-test.

did not significantly deviate from unit ($p > 0.05$), hence the spatial pattern was random. For the open pine forest (plot 8), the spatial pattern was analysed separately for mature individuals (age > 30 yr) and juvenile ones (age < 20 yr), because of their big differences in size and quantity. The result showed that the spatial pattern for the

mature individuals was random ($p > 0.05$), while for juvenile ones was contagious ($p < 0.05$), which occurred mainly in the gaps (around the standing dead pine trees, also see Fig. 2).

The analysis of the data obtained with point-centred quarter method from two mixed forest plots is listed in Table 4. The spatial pattern of

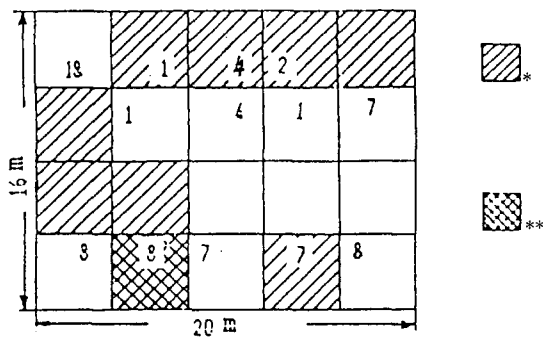


Fig. 2. The relationship between regeneration of *Pinus taiwanensis* and gaps in plot 8. The figures in each quadrat represent the number of seedlings (<15 yr).

* Each quadrat has one standing dead pine tree (>30 yr).
** Each quadrat has two standing dead pine tree (>30 yr).

Pinus taiwanensis population in plot 9 was random ($p > 0.05$) and in plot 10 was contagious ($p < 0.05$), since the observed values were higher, lower and higher than the expected values.

On clearing or burning lands, the environmental conditions were more or less uniform; the initial seed and seedling populations of *Pinus taiwanensis* might be expected to be randomly distributed in most cases, since the seeds were easily dispersed by wind. After growth up of the pine and the invasion of shade-tolerant broad-leaved tree species (intraspecific and interspecific competitions), the spatial pattern might become contagious or keep random. A similar result was mentioned by Wang Bosun (1989) for declining populations in forest succession at the southern subtropics of China.

Population density dynamics

By treating population age as the time after invasion of *Pinus taiwanensis* population into secondary barelands, which was estimated by the largest age class in each plot, the change of population density with population age could be considered to be a population density dynamics in the successional process (Fig. 3). During the initial successional stage, pine seeds annually invaded, germinated and established themselves. Thus, the

Table 4. Analysis of spatial pattern of *Pinus taiwanensis* populations in the mixed forest.

Individuals per point	Plot 9 (30 points)		Plot 10 (30 points)	
	$p = 0.15$ Ox	$P > 0.05$ Ex	$p = 0.16$ Ox	$P < 0.05$ Ex
0	16	15.56	17	15.06
1	10	11.05	10	11.33
2	4	2.93	0	3.20
3	0	0.34	3	0.40
4	0	0.02	0	0.01

p = Relative density of the population.
 P = Significant probability of Chi-square test.
Ox = Observed frequency.
Ex = Expected frequency.

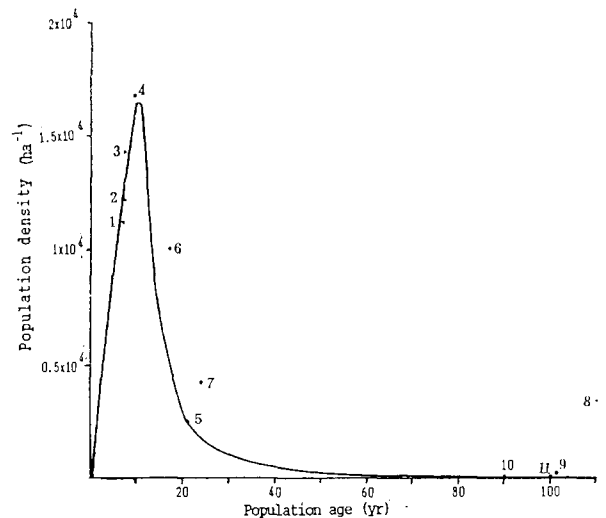


Fig. 3. Change of the population density (d) with the population age (A) for *Pinus taiwanensis*. The line shows the approximation by Eq. (3) and the figures are plot number.

stand density in the initial 1–9 years increased rapidly. When the stand density was in full density state and self-thinning took place as a consequence of the rapidly increasing size of the individuals, the density decreased exponentially with a high mortality until ca. 30 years after their invasion. When the stand had developed the mixed forest stage, the pine individuals were all part of the upper canopy stratum and self-thinning was stopped. During this stage the mortality

became lower afterward until all individuals of the pine retreated from the community.

Considering these facts, the curve for change of population density with population age was determined:

$$d = \begin{cases} 1786.47A^{1.0107} & (0 < A \leq 9, p < 0.05) \\ 976826.9A^{-2.681} & (A > 9, p < 0.05) \end{cases} \quad (3)$$

where d is the density (trees/ha⁻¹) and A is the population age (yr). The values of d and A for each plot is listed in Table 3. The coefficients were determined by the least squares method.

Aboveground biomass dynamics

In the study area, the individual tree weight (wt) of *Pinus taiwanensis* could be calculated from the following regression equation:

$$wt = 1.3831(D^2H)^{0.9358} \quad (p < 0.05) \quad (\text{g, cm}) \quad (4)$$

And the biomass of the pine population (BT) in each plot could be estimated as follows:

$$BT = \frac{1}{S} \sum_{i=1}^n 1.3831 (D_i^2 H_i)^{0.9358} \quad (5)$$

Table 5. The population age (A), basal area (BA'), density (d), biomass (BT), and mean tree weight (\bar{wt}) of the pine populations in eleven plots.

Plot nr	Age structure	A (yr)	d (ind/m ⁻²)	BT (ton/ha ⁻¹)	BA' (cm ⁻² /m ⁻²)	\bar{wt} (g)
1	G	6	1.1250	3.1230	6.2875	277.60
2	G	7	1.2250	1.8729	3.7738	152.89
3	G	8	1.4445	6.6560	10.4744	460.78
4	G	9	1.6863	7.8694	12.0477	463.70
5	D	21	0.2533	67.2737	25.1816	26 558.91
6	D	17	1.0200	67.4325	32.9258	6 611.03
7	D	24	0.4222	110.0134	43.5642	26 057.18
8a	S	110	0.3531	227.0390	50.4123	64 298.79
8b	S	110	0.1156	226.8616	50.1359	196 247.03
9	R	103	0.0224	50.5793	12.3150	210 747.18
10	R	90	0.0410	94.0415	23.7805	229 369.53
11	R	100	0.0064	21.4363	5.2175	334 941.90

The explanation for population age structure types see Table 2.

8a: For all individuals of *Pinus taiwanensis* in plot 8.

8b: For the individuals of age > 30 yr and DBH > 10 cm in plot 8.

where s is the size of the plot and BT the biomass of the pine population in ton/ha⁻¹.

The age, basal area (BA' , calculated from DBH), density and biomass of the populations as well as the mean tree weight (\bar{wt}), for each plot are listed in Table 5.

A simple logistic curve was applied to the change of population biomass (BT) from shrub-grassland to the initial stage of mixed forest (plots 1–7) as shown in Fig. 4:

$$BT = \frac{227}{1 + 370.3 e^{-0.2627A}} \quad (p < 0.01) \quad (\text{ton/ha}^{-1}, \text{yr}) \quad (6)$$

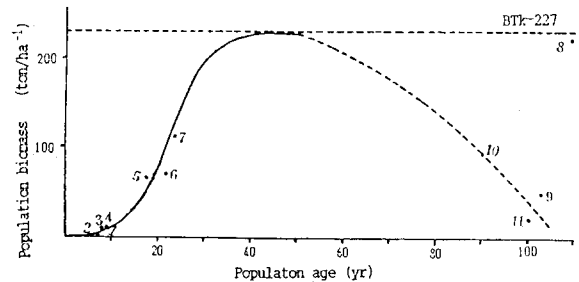


Fig. 4. Change of the population biomass (BT) with the population age (A). The line shows the approximation by Eq. (6) and the figures are the same as in Fig. 3.

where A is the population age. The coefficients were determined by the least squares method. The asymptote was 227 ton/ha⁻¹ and was estimated from plot 8 which had a stationary population structure and a maximum population biomass.

The broken line showed the decline in biomass during and after the mixed forest stage. When the community developed into a broad-leaved forest, the biomass of the pine would be reduced to zero.

A simple logistic curve (Fig. 5) was also applied to the change of basal area (BA') with population age (A):

$$BA' = \frac{50.4}{1 + 19.519 e^{-0.169A}} \quad (p < 0.05) \text{ (cm}^{-2}\text{/m}^{-2}\text{, yr)} \quad (7)$$

where the asymptote was 50.4 cm⁻²/m⁻² and was estimated from plot 8.

The change of BA' with population age was the same as the change of BT (see Fig. 4 and Fig. 5).

The change of frequency distribution of the individual tree weight (wt) with population age for *Pinus taiwanensis* is shown in Fig. 6. The frequency distribution for the population in plot 8 had another mode, which was formed by many under-

growing seedlings. But it was excluded from Fig. 6 and only the individuals of age > 30 yr was shown.

Two time trends could be seen from Fig. 6: (1) The individual tree weight (wt) of the pine increased with time; (2) the range of frequency distribution was wider for the populations in the early successional stages, which showed a more or less normal distribution. With the increase of the population age, the range became narrower. Such a process was similar to that illustrated by Nakashizuka (1984).

The change of the mean tree weight (\bar{wt} , derived from population biomass/population density) for the populations during the successional process is shown in Fig. 7, which shows a simple logistic change:

$$\bar{wt} = \frac{334\,941.9}{1 + 9809.9 e^{-0.2995A}} \quad (p < 0.01) \quad (8)$$

where \bar{wt} is the mean tree weight in g for the populations in each plot and A is the population age. The asymptote was estimated by the largest \bar{wt} in plot 11. The \bar{wt} increased exponentially in the initial stages and approached the asymptote more slowly than the change of the population

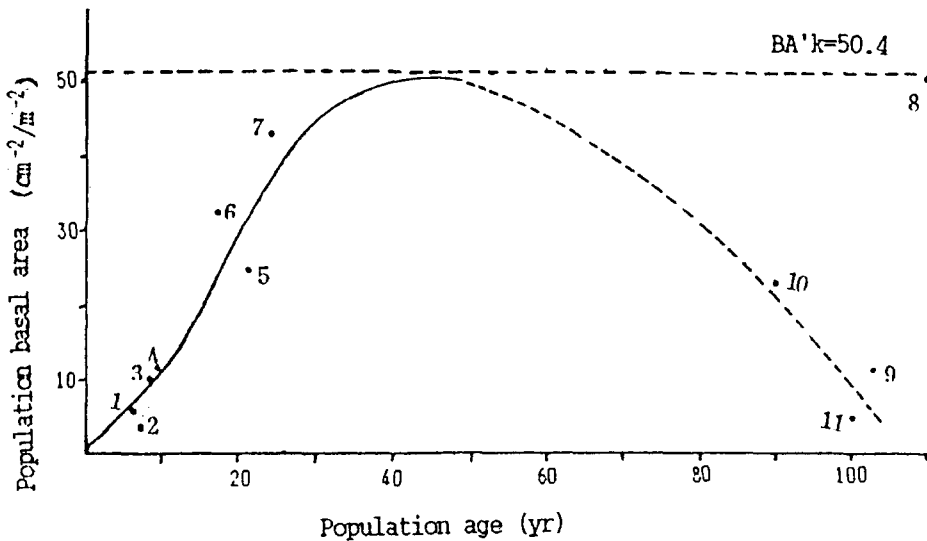


Fig. 5. Change of the population basal area (BA') with the population age (A). The line shows the approximation by Eq. (7) and the figures are the same as in Fig. 3.

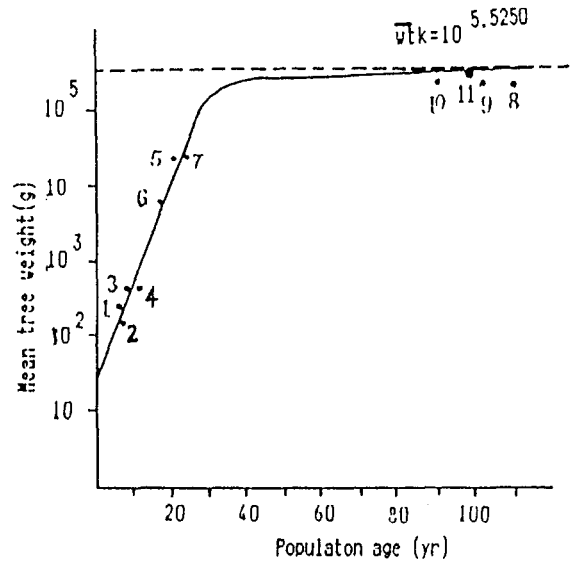
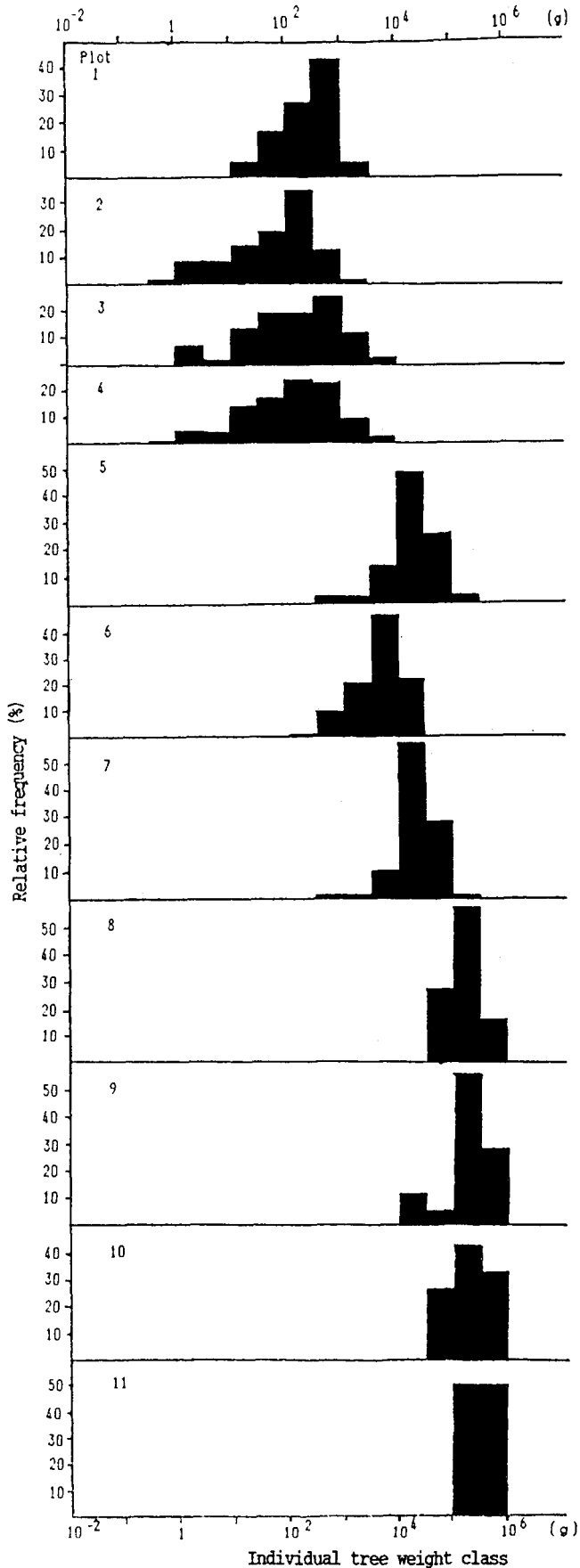


Fig. 7. Change of the mean tree weight (\bar{wt}) with the population age (A). The line shows the approximation by Eq. (8) and the figures are the same as in Fig. 3.

biomass (BT). After BT stopped increasing, \bar{wt} continued to increase.

Phases in successional process

Considering the change of the biomass and density of the population as well as the mean tree weight throughout the successional process, three phases could be recognized (Fig. 8).

Until about 9–10 years after the *Pinus taiwanensis* invaded the secondary barelands, which was the shrub-grassland stage, the density of the population was increased by the recruitment along with increase of the mean tree weight. The population biomass was increased as a whole (phase I).

From about 10 to 30–40 years after the invasion, that was from the pine juvenile forest stage to the initial stage of needle and broad-leaved mixed forest, the stand was in the full density state and the canopy inhibited further recruitment of the pine population. The population biomass increased along with rapid increase

Fig. 6. Time trend of the frequency distribution of tree weight for the pine populations in eleven plots. In plot 8, only the individuals of age > 30 yr and DBH > 10 cm are shown.

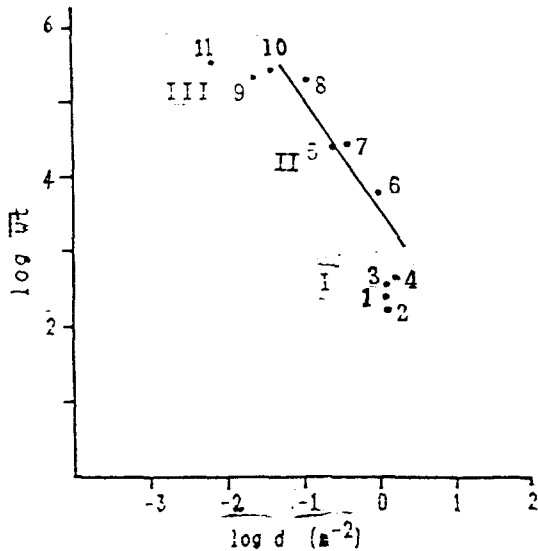


Fig. 8. Relationship between the mean tree weight (\bar{wt}) and population density (d) on log-log coordinates. The solid line shows an approximation by the $-3/2$ power law. I, II, III correspond to the phases in population dynamics explained in the text.

of the mean tree weight, while the density was decreased exponentially by natural thinning. Self-thinning was the most important process during this period, though it decreased in intensity as the pine density decreased (phase II). The $-3/2$ power law of natural thinning was applicable to the populations in this period (White & Harper 1970; Silvertown 1982):

$$\log \bar{wt} = 3.51 - 1.47 \log d \quad (p < 0.05) \quad (9)$$

or

$$\bar{wt} = 3262.35 d^{-1.47}$$

where \bar{wt} is the mean tree weight in g, d is the population density in trees/m⁻².

When the stands developed into mixed forest and the broad-leaved trees entered into the canopy which was ca. 30–40 years after the beginning of the succession, the pine population density further reduced slowly through interspecific competitions or senescence of the ageing individuals. Although the mean tree weight continued to increase, the

population biomass decreased until the pine retreated from the successional series completely (phase III). The population dynamics of *Pinus taiwanensis* during the successional process was in common with another pioneer species *Pinus massoniana* in forest succession (Dong Ming 1987).

On rocky steep slopes and ridges, however, *Pinus taiwanensis* populations could develop into such an stable community (open pine forest) as the population biomass, density and the mean tree weight was in a stable state for very long period. The population dynamics of the pine in these special habitats was more or less in common with that of climax species in forest succession (Whitmore 1982). According to the polyclimax theory (Colinvaux 1973), the open pine forest was an edaphic climax.

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