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DBH, height, and crown radius growth of some component species of Nopporo National Forest, central Hokkaido, Japan.

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Abstract

A survey on the relationships between age and size in some component trees of mixed forests was conducted in Nopporo National Forest, central Hokkaido. The relationship between age and DBH (diameter at breast height – 1.3 m –) was well represented in seventeen species by linear regression equation. Power function regression showed the best fit to the age and height data in them. The relationship between age and crown area was well represented in eleven species by linear regression, although the scatters of data points were larger than those in other cases. According to the linear relationship between age and crown area, annual growth rates of crown radius were able to be estimated for six species. They decreased simply as trees grew older, and ranged from 2.4 cm/year (*Tilia japonica* Simonkai) to 1.3 cm/year (*Ostrya japonica* Sarg.) when each tree reached the canopy layer. The regressions by extended relative growth law showed better fits to the DBH and height data than the linear regression.

The results of the present study indicated that the maximum height and longevity determining the dominance of trees in canopy layers did not wholly correlate to their shade tolerance.

Key Words: age, annual growth rate of crown radius, DBH, gap, height, Nopporo National Forest, regression analysis.

1. Introduction

The dynamics of forests are able to be assessed from the age structures of them (Kanzaki 1984, Lorimer 1980, Nakashizuka and Numata 1982a, 1982b, Suzuki 1979, 1980, etc.). When we find the relationships between age and size of trees, we can discuss the forest dynamics based on the size structures of trees. Stewart (1986) showed that power function regression fitted in the relationship between age and DBH (diameter at breast height) of trees. He stated that this relationship was often spurious because there was a wide range in DBH against a narrow range of age. Therefore, in the present study, we firstly concern whether or not there are some relationships between age and size of trees. DBH is the only parameter by which we can measure accurately in old-growth forests without cutting trees. We firstly investigate the relationship between age and DBH of trees. In addition, correlations between age and height, between age and crown area, and between

DBH and height are also examined.

There have been several studies on the correlations between DBH and height growth, shade tolerance, photosynthesis, and canopy dominance of trees (Koike 1987, Oga 1985, Williamson 1975). In general, DBH and height growth patterns of trees are regarded to reflect their successional status; early-successional species can photosynthesize effectively under full sun light and grow fast; late-successional species can photosynthesize effectively at low light intensity but grow slowly. However, there have been many exceptions in detail. Therefore, the second objective of the present study is the comparison of the above mentioned age and size relationships among species. We examine the relationship between height growth and the dominance in canopy layers, and discuss some important characteristics determining the dominance in canopy layers.

2. Study area

Nopporo National Forest, the area of the present study, is located near Sapporo city (43°25'N, 141°32'E), central Hokkaido, Japan. This forest is 2,040 ha in area and is roughly rectangular in shape with elevations from 100 to 20 meters (Fig. 1). Soil parent material is the Konopporo geologic formation composed of an alternation of clay, silt, and sand layers (Akamatsu and Yamada 1980). Soils are predominantly brown forest soils with thick impermeable C horizon composed of the Konopporo formation (Ishikawa et al. 1986). For 27 years from 1954 to 1980, the mean annual precipitation and the mean annual temperature are 1,170mm and 6.6°C, respectively (Sapporo Meteorological Observatory 1982).

Forest communities in Nopporo National Forest are alternately predominated by several trees (Tatewaki and Igarashi 1973, Ishikawa et al. 1986). These tree species are arranged in the following order from dry to wet habitat; *Quercus mongolica* var. *grosseserrata* Rehd. et Wils. - *Abies sachalinensis* Masters - *Tilia japonica* Simonkai - *Acer mono* Maxim. - *Ulmus laciniata* Mayr - *Cercidiphyllum japonicum* Sieb. et Zucc. - *U. davidiana* var. *japonica* Nakai - *Fraxinus mandshurica* var. *japonica* Maxim. - *Alnus japonica* Steud. The depth of the impermeable C horizon of soils strongly affects the soil water gradient and causes the distinct mosaic arrangement of the dominant trees (Ishikawa et al. 1986).

3. Methods

3.1 Sampling

Seventeen species were examined in the present study. As mentioned already (Ishikawa et al. 1986), nine dominant trees were recognized in Nopporo National Forest; *Abies sachalinensis*, *Acer mono*, *Alnus japonica*, *Cercidiphyllum japonicum*, *Fraxinus mandshurica* var. *japonica*, *Quercus mongolica* var. *grosseserrata*, *Tilia japonica*, *Ulmus davidiana* var. *japonica*, and *U. laciniata*. Among them *Alnus japonica* was excluded from the present study, because young trees of it were scarcely observed. Data were obtained from sixteen permanent plots established from 1981 to 1985 (Fig. 1). Eleven of them are the same plots as those reported by Ishikawa and Ito (1989). Among them, two plots were 50 m × 50 m

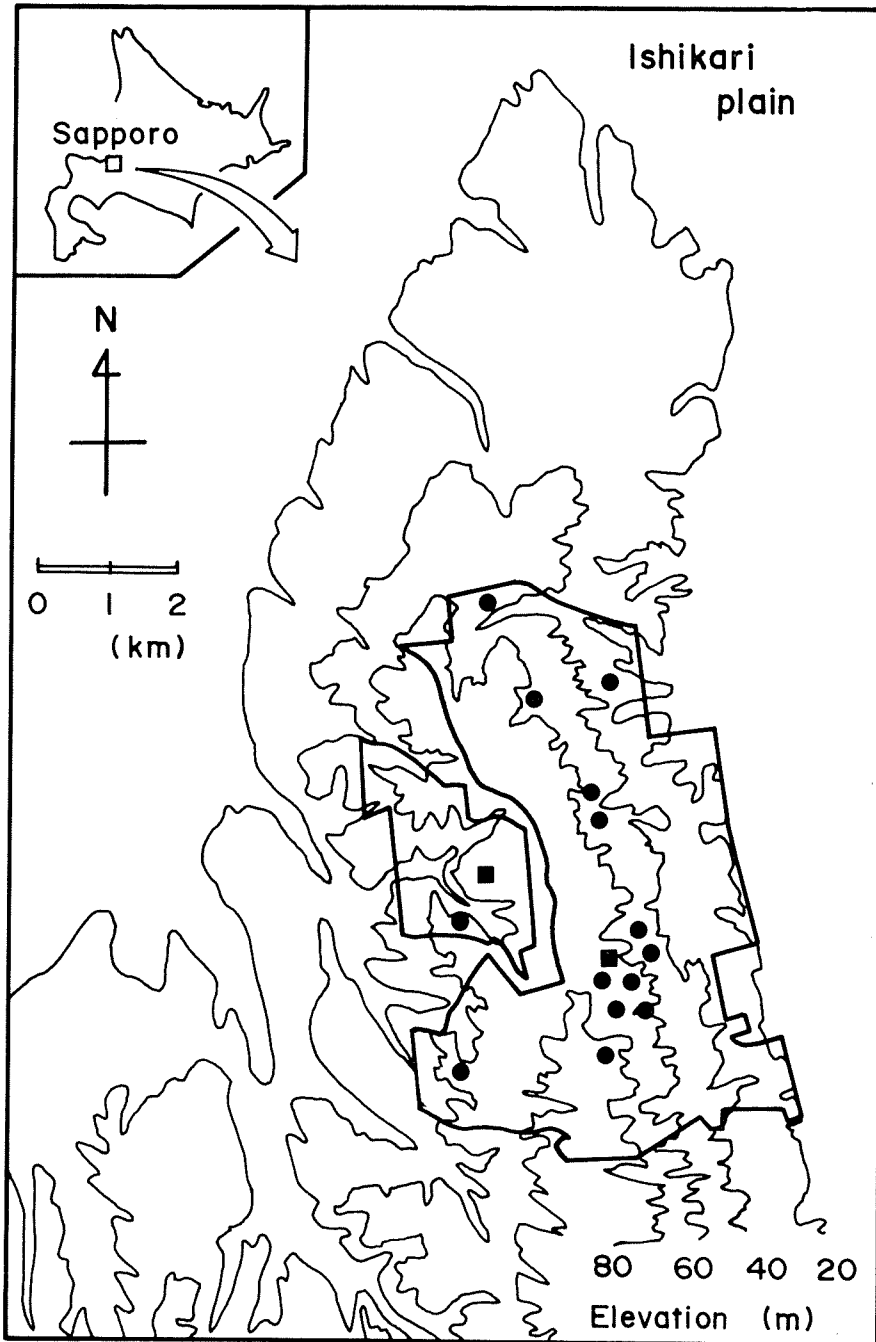


Figure 1. Location of Nopporo National Forest. Solid squares show the larger two permanent plots. Solid circles show fourteen smaller plots.

and 80 m × 80 m, respectively. No records of cuttings are available in the area where those two plots were located (Sapporo Regional Forest Office unpubl.). The canopy layers of them were composed of mature individuals of *Abies*, *Acer*, *Quercus*, *Tilia*, etc. The remaining fourteen plots were 20 m × 20 m, and were scattered over the forest.

In these plots, the species of all living trees larger than 5 cm in DBH were identified, and their DBH and height were measured. Increment cores of them were taken 0.3 m above ground to measure their age. The years needed to reach 0.3 m in height were estimated by using a linear relationship between age (year) and the logarithm of height (cm): *Abies sachalinensis*, $\text{Age} = 15.0865 \log(\text{Height}) - 9.2448$ ($n=12$, $P<0.01$); Deciduous broad-leaved species, $\text{Age} = 5.5270 \log(\text{Height}) - 3.2509$ ($n=642$, $P<0.001$). Based on these equations, we calculated the years of saplings at 0.3 m in height: *A. sachalinensis* is 13 years; deciduous broad-leaved species are 5 years. Therefore, the true age of a tree was obtained by adding the above value to the age obtained from increment core of the tree. In the present study, we excluded the data of the trees which suffered from a disease or were seriously suppressed.

In the two large plots, crown projection diagrams were drawn. The long and short axes of tree crowns were also measured to calculate crown areas.

Nomenclature of species names follows Ohwi and Kitagawa (1983).

3.2 Analysis

Although linear regression is adequate for many biological needs, non-linear regressions are also useful in some cases. Exponential function regression, logarithmic function regression, and power function regression are the most common non-linear regressions. However, logarithmic function regression was excluded from the present study, because the dependent variable y inevitably takes negative values as the independent variable x approaches zero. Therefore, we applied the least squares linear and two non-linear regression models to the age and DBH data, the age and height data, and the age and crown area data of each species. These models are as follows;

linear regression:	$y = ax + b$
exponential function regression:	$y = a(b^x)$
power function regression:	$y = a(x^b)$

where a and b are constants.

In the age and height data, and the age and crown area data, height and crown area are 0 when age is 0. Therefore, according to Snedecor and Cochran (1980), we carried out the operation which made the linear regression go through the origin for these two data.

In the DBH and height data, the relative growth law is theoretically established (Ogawa 1980). Therefore, generalized allometric function model was fitted to the DBH and height data. This model is

$$\frac{1}{H} = \frac{1}{aD^h} + \frac{1}{b}$$

where D and H are DBH and height of a tree. The a , b and h are constants; b is equal to the maximum height of a species; h is 1 in climax forests and for shade tolerant species, but is only known to be larger than 1 in seral forests and for shade intolerant species

(Ogawa 1980). In the present study, we assumed h to be 1 for all species.

In these non-linear regressions, the significance of departures from the linear regression was tested by using F test (Snedecor and Cochran 1980).

4. Results

4.1 Relationship between age and DBH

For the age and DBH data the linear regression and two non-linear regressions were all significant at 1% level (Table 1). However, for all species the sums of squares of deviations due to non-linear regressions were larger than those due to the linear regression. This means that non-linear regressions do not provide better fit to the age and DBH data than the linear regression. This result can be ascertained by Fig. 2. Therefore, the hypothesis of the linearity can not be rejected for all species.

4.2 Relationship between age and height

For the age and height data the linear regression and two non-linear regressions were all significant at 1% level (Table 2). For almost all of the cases departures from linearity were highly significant. *Abies sachalinensis* was the only exception. This result is ascertained by Fig. 3. Therefore, the hypothesis of linearity is rejected for almost all of the species. The numbers of species which non-linear regressions provide better fit to the data than the linear regression are as follows; twelve species are fitted to the exponential function regression, *Acer mono*, *Betula maximowicziana* Regel, *Cornus controversa* Hemsl., *Fraxinus lanuginosa* Koidz., *Kalopanax pictus* Nakai, *Magnolia kobus* var. *borealis* Sarg., *M. obovata* Thunb., *Ostrya japonica*, *Quercus mongolica* var. *grosseserrata*, *Sorbus commixta* Held., *Tilia japonica*, *Ulmus laciniata*; sixteen species are fitted to the power function regression, *Acer mono*, *Betula maximowicziana*, *Cornus controversa*, *Cercidiphyllum japonicum*, *Fraxinus lanuginosa*, *F. mandshurica* var. *japonica*, *Kalopanax pictus*, *Magnolia kobus* var. *borealis*, *M. obovata*, *Ostrya japonica*, *Prunus ssiori* Fr. Schm., *Quercus mongolica* var. *grosseserrata*, *Sorbus commixta*, *Tilia japonica*, *Ulmus davidiana* var. *japonica*, *U. laciniata*.

4.3 Annual growth rate of crown radius

Assuming that the shape of a tree crown was an ellipse, we calculated crown areas in the present study. There was a highly significant linear relationship between calculated crown areas (C) and actual crown areas (A) of randomly selected 108 tree individuals growing in the larger plots ($A = 0.7452C + 2.3419$, $r = 0.9828$, $P < 0.001$, Fig. 4). Actual crown areas were obtained from the crown projection diagram of the plots by using a digital leaf area meter. By using this linear relationship, we estimated the actual crown area from the calculated area. Eleven species analyzed are as follows; *Abies sachalinensis*, *Cornus controversa*, *Fraxinus lanuginosa*, *F. mandshurica* var. *japonica*, *Magnolia kobus* var. *borealis*, *M. obovata*, *Prunus ssiori*, *Ostrya japonica*, *Sorbus commixta*, *Tilia japonica*, and *Ulmus laciniata*.

The linear regression and two non-linear regressions were all significant at 1% level

Table 1. Regression equations and correlation coefficients of the age and DBH data of seventeen species. All of the correlation coefficients are significant at 1% level. Abbreviations of species names are as follows: Am, *Acer mono*; As, *Abies sachalinensis*; Bm, *Betula maximowicziana*; Cc, *Cornus controversa*; Cj, *Cercidiphyllum japonicum*; Fl, *Fraxinus lanuginosa*; Fm, *Fraxinus mandshurica* var. *japonica*; Kp, *Kalopanax pictus*; Mk, *Magnolia kobus* var. *borealis*; Mo, *Magnolia obovata*; Oj, *Ostrya japonica*; Ps, *Prunus ssiori*; Qm, *Quercus mongolica* var. *grosseserrata*; Sc, *Sorbus commixta*; Tj, *Tilia japonica*; Ud, *Ulmus davidiana* var. *japonica*; Ul, *Ulmus laciniata*.

Species	Function	Regression equation	r	Sum of square	F-value	N
Am	Linear	DBH = 0.2472Age - 2.2266	0.9000	2390.47		38
	Exp.	= 4.2772 × 1.0129 ^{Age}	0.9243	2565.18	—	
	Power	= 0.1355 × Age ^{1.0943}	0.9339	2477.08	—	
As	Linear	DBH = 0.4361Age - 8.9274	0.8978	7105.48		110
	Exp.	= 3.9857 × 1.0198 ^{Age}	0.8800	29630.80	—	
	Power	= 0.0279 × Age ^{1.5325}	0.9250	7822.83	—	
Bm	Linear	DBH = 0.7463Age - 11.5646	0.9653	783.58		24
	Exp.	= 5.7856 × 1.0237 ^{Age}	0.8618	2047.48	—	
	Power	= 0.0723 × Age ^{1.4680}	0.8902	852.15	—	
Cc	Linear	DBH = 0.3074Age + 0.8907	0.7875	785.85		50
	Exp.	= 4.8043 × 1.0228 ^{Age}	0.7862	1124.35	—	
	Power	= 0.2522 × Age ^{1.0627}	0.8472	817.96	—	
Cj	Linear	DBH = 0.3058Age - 1.9273	0.9580	992.74		34
	Exp.	= 6.4853 × 1.0119 ^{Age}	0.8219	12862.50	—	
	Power	= 0.0451 × Age ^{1.3930}	0.9388	3429.90	—	
Fl	Linear	DBH = 0.1713Age + 0.1184	0.7976	583.24		69
	Exp.	= 3.3466 × 1.0172 ^{Age}	0.8343	584.41	—	
	Power	= 0.2588 × Age ^{0.8920}	0.8426	613.64	—	
Fm	Linear	DBH = 0.3296Age - 0.0237	0.9484	958.95		48
	Exp.	= 7.1276 × 1.0140 ^{Age}	0.8529	10152.30	—	
	Power	= 0.3321 × Age ^{0.9915}	0.9304	999.96	—	
Kp	Linear	DBH = 0.2779Age + 2.4452	0.9467	1159.20		31
	Exp.	= 9.1295 × 1.0096 ^{Age}	0.8270	2405.65	—	
	Power	= 0.2145 × Age ^{1.0719}	0.8960	1470.42	—	
Mk	Linear	DBH = 0.2520Age + 3.3374	0.9203	1009.96		43
	Exp.	= 6.9230 × 1.0118 ^{Age}	0.7788	5202.03	—	
	Power	= 0.2447 × Age ^{1.0634}	0.9191	1916.84	—	
Mo	Linear	DBH = 0.2849Age + 0.7283	0.9400	791.91		51
	Exp.	= 5.3785 × 1.0156 ^{Age}	0.8329	4791.04	—	
	Power	= 0.2243 × Age ^{1.0663}	0.9262	913.17	—	
Oj	Linear	DBH = 0.2071Age + 5.5571	0.9603	1357.04		34
	Exp.	= 9.4765 × 1.0070 ^{Age}	0.8128	14066.30	—	
	Power	= 0.2278 × Age ^{1.0222}	0.9198	2437.43	—	
Ps	Linear	DBH = 0.2963Age - 4.7368	0.9178	1392.89		38
	Exp.	= 3.3862 × 1.0169 ^{Age}	0.8963	9094.07	—	
	Power	= 0.0335 × Age ^{1.4160}	0.9331	1913.30	—	
Qm	Linear	DBH = 0.4588Age - 4.5927	0.9570	2359.26		36
	Exp.	= 7.1866 × 1.0136 ^{Age}	0.8494	19920.70	—	
	Power	= 0.0748 × Age ^{1.3632}	0.9358	4737.55	—	
Sc	Linear	DBH = 0.2358Age - 0.9192	0.8779	171.84		43
	Exp.	= 3.0918 × 1.0228 ^{Age}	0.8377	221.16	—	
	Power	= 0.2173 × Age ^{0.9832}	0.8242	188.85	—	
Tj	Linear	DBH = 0.3070Age + 1.6195	0.9352	1687.19		50
	Exp.	= 7.0153 × 1.0130 ^{Age}	0.8283	14679.10	—	
	Power	= 0.2053 × Age ^{1.1064}	0.9292	2380.08	—	
Ud	Linear	DBH = 0.4059Age - 4.5812	0.9702	1215.65		53
	Exp.	= 5.2526 × 1.0165 ^{Age}	0.8870	17747.20	—	
	Power	= 0.0592 × Age ^{1.3888}	0.9514	2796.35	—	
Ul	Linear	DBH = 0.2657Age - 0.0517	0.8855	1820.53		44
	Exp.	= 5.7947 × 1.0120 ^{Age}	0.7693	5863.03	—	
	Power	= 0.1092 × Age ^{1.1971}	0.8589	2465.40	—	

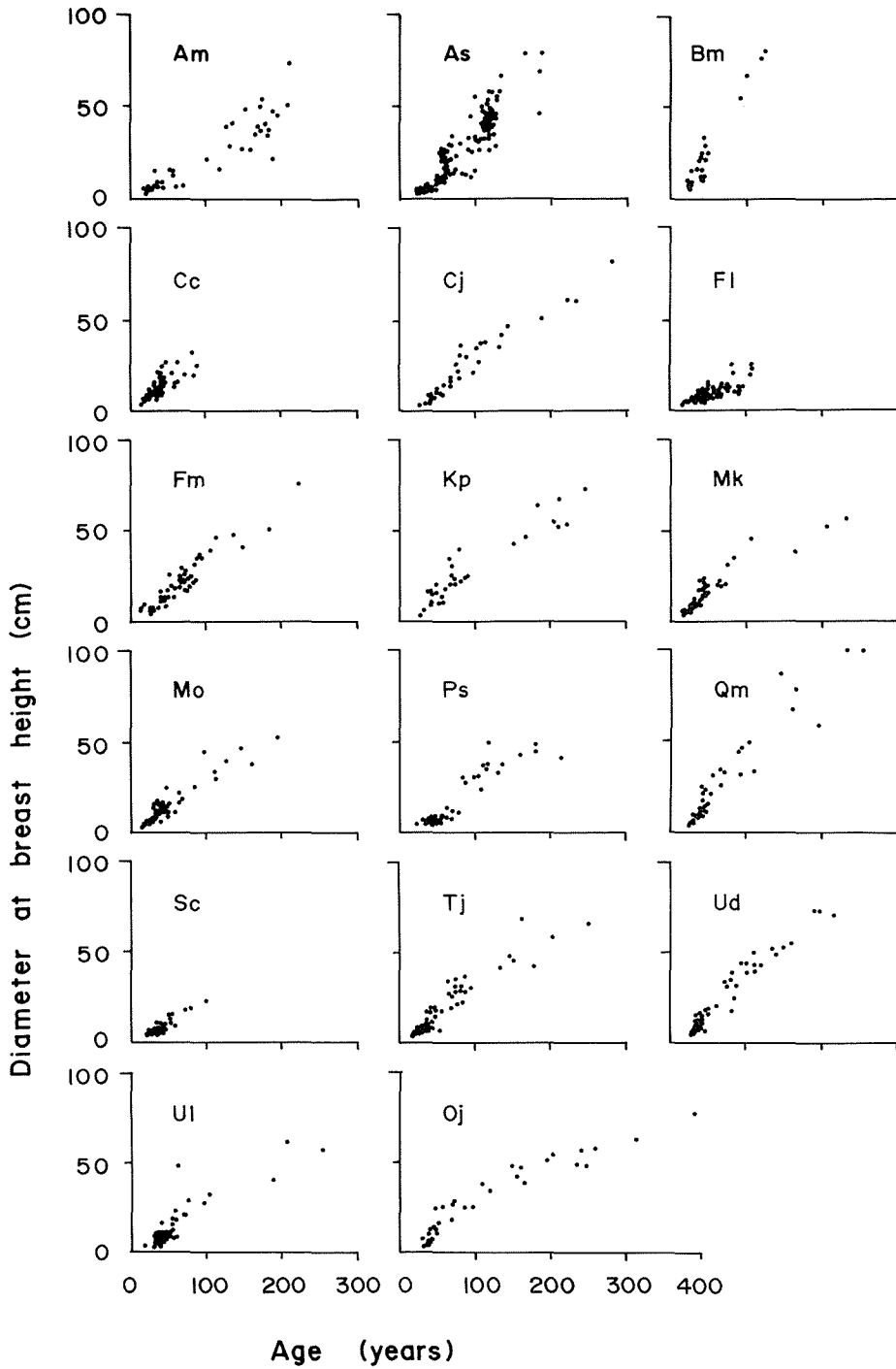


Figure 2. Relationship between age and DBH of seventeen species. Abbreviations of species names as in Table 1.

Table 2. Regression equations and correlation coefficients of the age and height data of seventeen species. All of the correlation coefficients are significant at 1% level. F-values with one asterisk are significant at 1% level. Abbreviations of species names as in Table 1. Numbers of samples as in Table 1.

Species	Function	Regression equation	r	Sum of square	F-value
Am	Linear	Height = 0.1092Age	0.9695	471.75	
	Exp.	= $5.7588 \times 1.0067^{Age}$	0.9082	290.66	23.05*
	Power	= $0.9066 \times Age^{0.5802}$	0.9124	205.02	48.14*
As	Linear	Height = 0.1669Age	0.9735	1497.42	
	Exp.	= $4.5003 \times 1.0124^{Age}$	0.7899	2905.71	—
	Power	= $0.1605 \times Age^{1.0120}$	0.8746	1528.34	—
Bm	Linear	Height = 0.2634Age	0.9424	671.22	
	Exp.	= $9.7928 \times 1.0079^{Age}$	0.7030	214.66	48.91*
	Power	= $2.1890 \times Age^{0.5003}$	0.7353	190.26	58.14*
Cc	Linear	Height = 0.2491Age	0.9568	560.78	
	Exp.	= $7.1384 \times 1.0101^{Age}$	0.5957	265.03	54.68*
	Power	= $1.6312 \times Age^{0.5188}$	0.6999	219.88	75.97*
Cj	Linear	Height = 0.1329Age	0.9530	718.73	
	Exp.	= $6.1778 \times 1.0073^{Age}$	0.7249	1129.39	—
	Power	= $0.2366 \times Age^{0.9034}$	0.8780	598.25	6.65*
Fl	Linear	Height = 0.1471Age	0.9670	356.39	
	Exp.	= $5.1393 \times 1.0090^{Age}$	0.7388	157.74	85.62*
	Power	= $1.2730 \times Age^{0.4814}$	0.7683	146.19	97.77*
Fm	Linear	Height = 0.1957Age	0.9554	1120.23	
	Exp.	= $7.8900 \times 1.0085^{Age}$	0.7764	1365.16	—
	Power	= $0.9438 \times Age^{0.6666}$	0.9263	353.31	102.03*
Kp	Linear	Height = 0.1352Age	0.9381	1001.55	
	Exp.	= $8.9355 \times 1.0050^{Age}$	0.8583	390.37	46.97*
	Power	= $1.1482 \times Age^{0.5808}$	0.8565	273.32	79.93*
Mk	Linear	Height = 0.1472Age	0.8715	1383.75	
	Exp.	= $7.2120 \times 1.0060^{Age}$	0.6405	608.46	53.52*
	Power	= $1.1764 \times Age^{0.5700}$	0.7981	377.81	111.83*
Mo	Linear	Height = 0.1605Age	0.9048	1154.72	
	Exp.	= $6.7967 \times 1.0071^{Age}$	0.6759	471.93	72.34*
	Power	= $1.4141 \times Age^{0.5199}$	0.7955	292.91	147.12*
Oj	Linear	Height = 0.0866Age	0.8853	1893.20	
	Exp.	= $9.6663 \times 1.0029^{Age}$	0.6879	682.53	58.53*
	Power	= $1.7387 \times Age^{0.4608}$	0.8492	351.68	144.65*
Ps	Linear	Height = 0.1376Age	0.9673	410.23	
	Exp.	= $5.0558 \times 1.0090^{Age}$	0.8466	577.97	—
	Power	= $0.4512 \times Age^{0.7450}$	0.8660	291.55	15.06*
Qm	Linear	Height = 0.1513Age	0.9287	1183.56	
	Exp.	= $7.8010 \times 1.0064^{Age}$	0.7251	797.33	16.95*
	Power	= $0.7828 \times Age^{0.6787}$	0.8421	448.89	57.28*
Sc	Linear	Height = 0.2130Age	0.9811	127.87	
	Exp.	= $4.3949 \times 1.0160^{Age}$	0.8137	106.03	8.65*
	Power	= $0.6727 \times Age^{0.6941}$	0.8041	103.05	10.12*
Tj	Linear	Height = 0.1636Age	0.9417	1161.67	
	Exp.	= $7.0394 \times 1.0077^{Age}$	0.7674	992.06	8.38*
	Power	= $0.7803 \times Age^{0.6832}$	0.8938	401.46	92.79*
Ud	Linear	Height = 0.1664Age	0.9551	993.85	
	Exp.	= $6.1874 \times 1.0090^{Age}$	0.7996	1291.77	—
	Power	= $0.4572 \times Age^{0.7977}$	0.8977	575.44	37.81*
Ul	Linear	Height = 0.1472Age	0.8988	1255.39	
	Exp.	= $7.8414 \times 1.0054^{Age}$	0.6656	444.66	78.40*
	Power	= $1.1290 \times Age^{0.5772}$	0.7983	296.77	138.89*

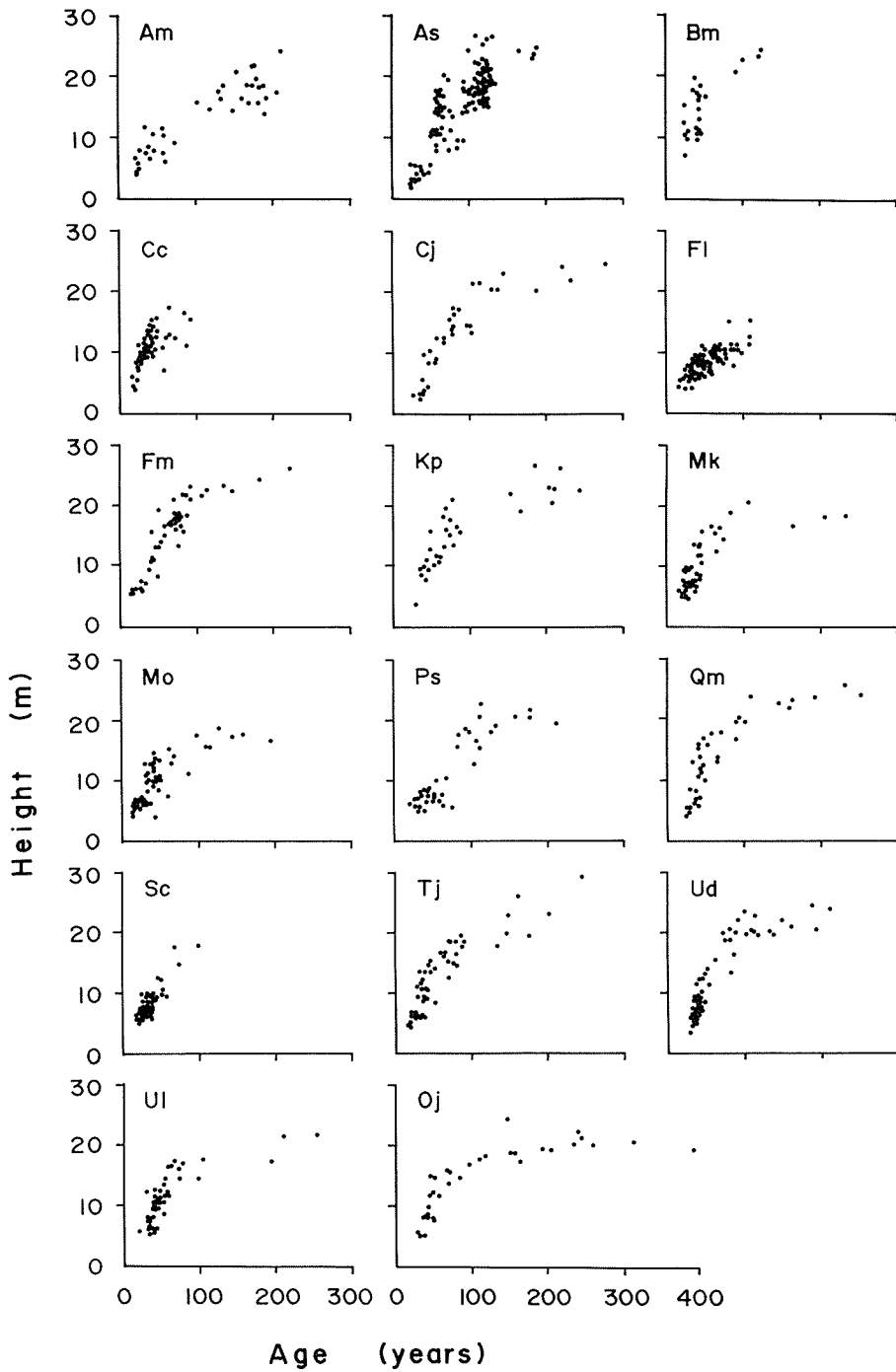


Figure 3. Relationship between age and height of seventeen species. Abbreviations of species names as in Table 1.

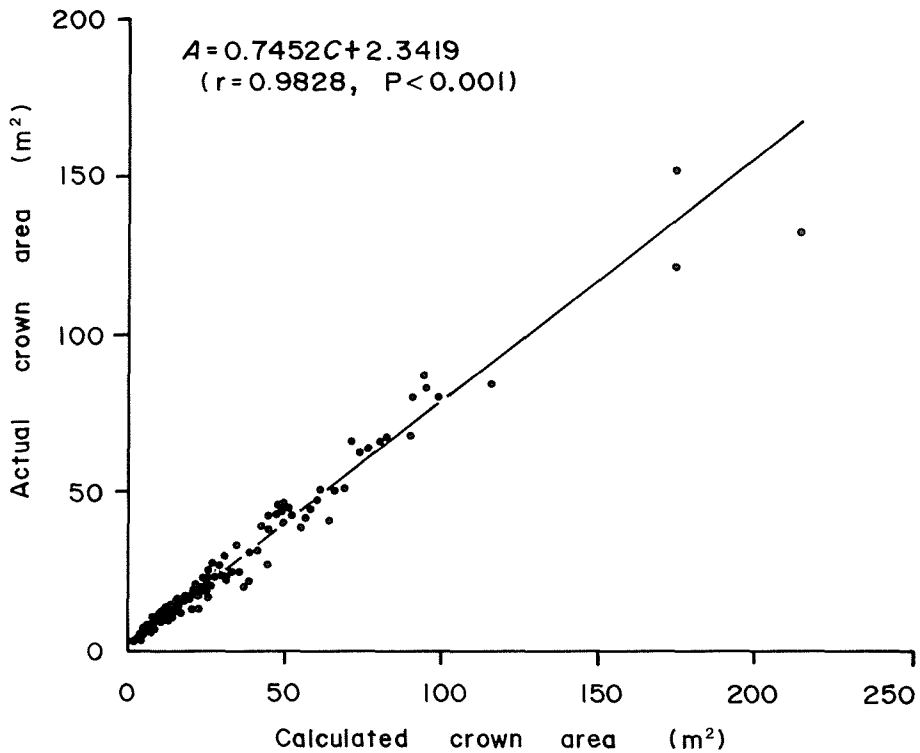


Figure 4. Relationship between actual crown areas and calculated crown areas of randomly selected 108 individuals growing in the larger plots. A and C in the regression equation represent actual crown areas and calculated ones, respectively.

(Table 3). In general, the scatter of the data points (Fig. 5) was larger in this case than those in other cases mentioned already. Except for *Abies sachalinensis* the sums of squares due to the power function regression were larger than those due to the linear regression. In *Sorbus commixta* the sum of squares due to the exponential function regression was smaller than that due to the linear regression, and F-value due to this regression was significantly large at 5% level. For other species the sums of squares due to the exponential function regression were larger than those due to the linear regression. From this the hypothesis of linearity could not be rejected to almost all of the species. It indicates that annual growth rates of crown areas may be constant for almost all of the species. However, judging from the wider scatter of the data points, it needs further investigation to reveal this question.

Based on the linear regression equations obtained above, annual growth rates of crown radius in six species whose scatters of data points are relatively small are obtained as follows;

in year t ,

$$\pi R^2 = at$$

Table 3. Regression equations and correlation coefficients of the age and crown area data of eleven species. All of the correlation coefficients are significant at 1% level. The level of significance of F-values are as follows:*, $P < 0.01$; **, $P < 0.05$. Abbreviations of species names as in Table 1.

Species	Function	Regression equation	r	Sum of square	F-value	N
As	Linear	Crown=0.2271Age	0.9197	7554.42		85
	Exp.	$=1.1799 \times 1.0258^{Age}$	0.8309	29058.60	—	
	Power	$=0.0018 \times Age^{1.9985}$	0.8762	7381.25	1.97*	
Cc	Linear	Crown=0.4013Age	0.8863	3091.79		42
	Exp.	$=2.9286 \times 1.0347^{Age}$	0.5850	5329.95	—	
	Power	$=0.0358 \times Age^{1.5942}$	0.6525	3634.83	—	
Fl	Linear	Crown=0.1601Age	0.8594	1835.61		53
	Exp.	$=2.6150 \times 1.0173^{Age}$	0.5527	1912.09	—	
	Power	$=0.2030 \times Age^{0.8940}$	0.5466	2046.93	—	
Fm	Linear	Crown=0.3356Age	0.9443	2610.77		23
	Exp.	$=3.5549 \times 1.0175^{Age}$	0.9056	9291.66	—	
	Power	$=0.1068 \times Age^{1.1944}$	0.9233	2735.05	—	
Mk	Linear	Crown=0.2778Age	0.9087	3119.39		36
	Exp.	$=5.3572 \times 1.0127^{Age}$	0.7183	7647.08	—	
	Power	$=0.1653 \times Age^{1.1064}$	0.8004	3411.90	—	
Mo	Linear	Crown=0.2086Age	0.8553	2766.34		39
	Exp.	$=2.7927 \times 1.0171^{Age}$	0.6218	4886.35	—	
	Power	$=0.0333 \times Age^{1.4075}$	0.7518	3371.02	—	
Oj	Linear	Crown=0.3041Age	0.9565	5746.94		21
	Exp.	$=8.3365 \times 1.0081^{Age}$	0.8099	39441.50	—	
	Power	$=0.0985 \times Age^{1.2175}$	0.9100	8574.16	—	
Ps	Linear	Crown=0.2098Age	0.8831	2475.01		23
	Exp.	$=2.5280 \times 1.0163^{Age}$	0.6953	5279.87	—	
	Power	$=0.0228 \times Age^{1.4398}$	0.7311	2911.09	—	
Sc	Linear	Crown=0.1650Age	0.9135	333.51		33
	Exp.	$=1.9211 \times 1.0246^{Age}$	0.6398	310.41	2.38**	
	Power	$=0.1037 \times Age^{1.0772}$	0.6232	359.71	—	
Tj	Linear	Crown=0.4569Age	0.8910	15460.00		32
	Exp.	$=5.0068 \times 1.0168^{Age}$	0.7716	74015.90	—	
	Power	$=0.0278 \times Age^{1.5672}$	0.8588	19807.10	—	
Ul	Linear	Crown=0.2749Age	0.9202	3102.98		35
	Exp.	$=4.1644 \times 1.0138^{Age}$	0.7096	9708.06	—	
	Power	$=0.0263 \times Age^{1.4917}$	0.7854	5020.17	—	

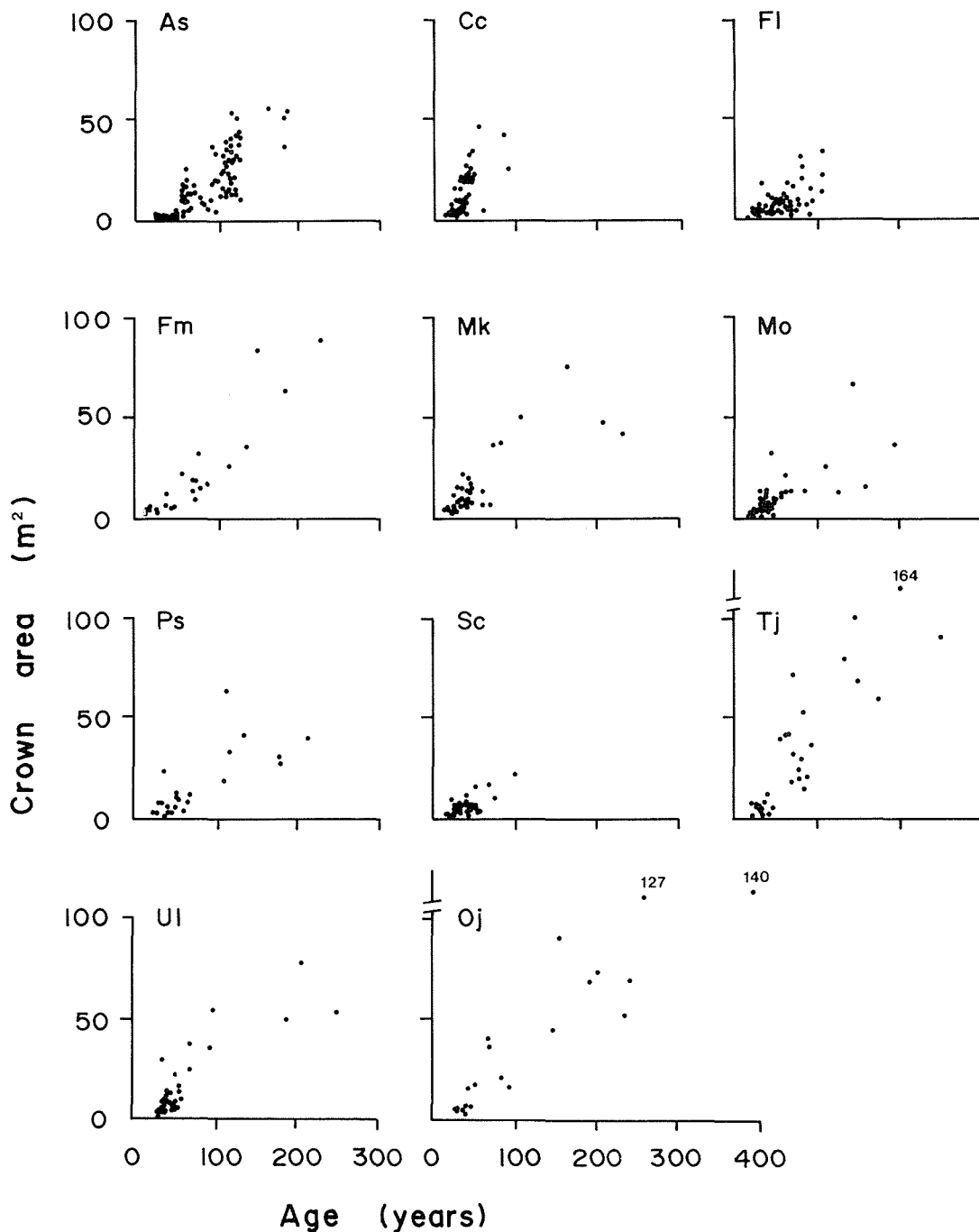


Figure 5. Relationship between age and crown area of eleven species. Abbreviations of species names as in Table 1. Crown areas were firstly calculated assuming that the shape of a tree crown to be an ellipse. Then actual crown areas were estimated from the calculated ones by using the regression equation in Figure 4.

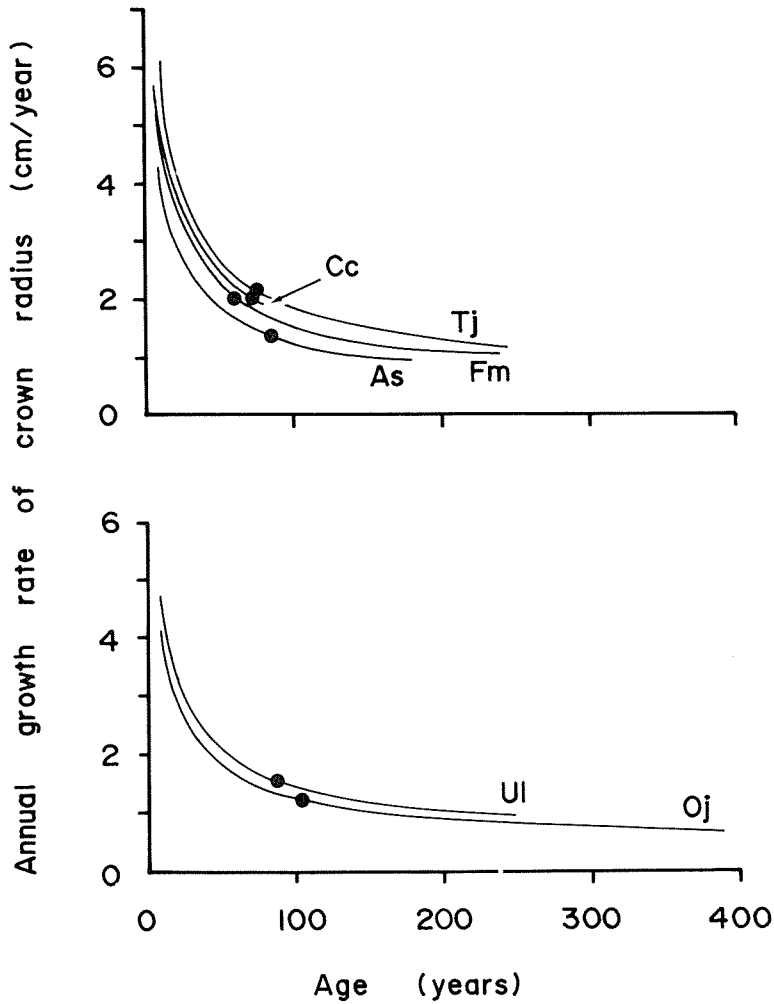


Figure 6. Annual growth rates of crown radius of six species whose scatters of the data were relatively small. Abbreviations of species names as in Table 1. Solid circles show the estimated values at the year when each species reaches canopy layers (15 m in height).

where R is crown radius at year t and a is the constant of the linear regression equation; the crown radius at year t is given by

$$R = \sqrt{at/\pi}$$

therefore annual growth rate (r) of crown radius from year $t-1$ to t is:

$$r_{(t-1 \sim t)} = \sqrt{at/\pi} - \sqrt{a(t-1)/\pi}$$

Fig. 6 shows r s of the six species analyzed. The end points of ages are based on the data of the present study. Annual growth rates of crown radius simply decrease with the age.

Except for *Cornus controversa* (Cc), annual growth rates of crown radius approach ca. 1 cm as they become older. Solid circles show the estimated values at the year when each species reaches canopy layers of the plots (15 m in height). The ages when trees reach canopy layers are calculated by using the power function regression equations mentioned in 4.2. The values range from 2.4 cm/year (*Tilia japonica*) to 1.3 cm/year (*Ostrya japonica*).

4.4 Relationship between DBH and height

A height growth curve of a tree generally levels off antecedently to the stagnation of DBH growth: the relation between height growth and DBH growth is asymptotic (Ogawa 1980, Yoda 1971). This tendency was also ascertained in the present study (Fig. 7). The linear regression and extended relative growth regression are significant at 1% level (Table 4). Except for *Cornus controversa*, *Kalopanax pictus*, *Magnolia obovata*, *Prunus ssiori* and *Sorbus commixta*, the extended relative growth regression gave significantly better fits to the data than the linear regression.

5. Discussion

5.1 DBH, height and crown radius growth

Yajima and Matsuda (1978) stated that there was no significant relationship between age and DBH of several dominant tree species in their studies of a primeval mixed forest of northern Hokkaido. In contrast, in the present study at least one regression model was significant for each relationship, respectively. This is probably because we excluded the data of diseased or suppressed trees whose growth were reduced. In other words, the equations obtained in the present study correspond to the potential of growth under favourable conditions.

(1) DBH growth

It is well known that the growth curve of individuals is usually sigmoidal (Ogawa 1980). Stewart (1986) stated that, as a tree becomes older, the DBH growth rate decreases and power function regression empirically provides the best fit to the age and DBH data. By using a simulation model, Mitchell (1975) predicted that DBH and height growth in the process of time tended to level off. In the present study, however, linear regression provides the best fit to the age and DBH data (Fig. 2, Table 1). It is probably due to the fact that the number of mature trees in Nopporo National Forest has diminished by wind damage and partial cuttings, and may be due to the difficulty of sampling of increment cores: in older trees, increment cores could not be sampled and annual growth rings could not be counted. Thus, the linear regression equations obtained in the present study may be reliable within the range of values from 0 to the maximum size of DBH as follows; *Quercus mongolica* var. *grosseserrata*, ca. 100 cm; other dominant species, *Betula maximowicziana*, *Kalopanax pictus*, and *Ostrya japonica*, ca. 80 cm; *Magnolia kobus* var. *borealis*, *M. obovata*, and *Prunus ssiori*, ca. 50 cm; *Cornus controversa*, *Fraxinus lanuginosa*, and *Sorbus commixta*, ca. 30 cm.

(2) Height growth

Although the exponential function regression provides better fit to the age and height

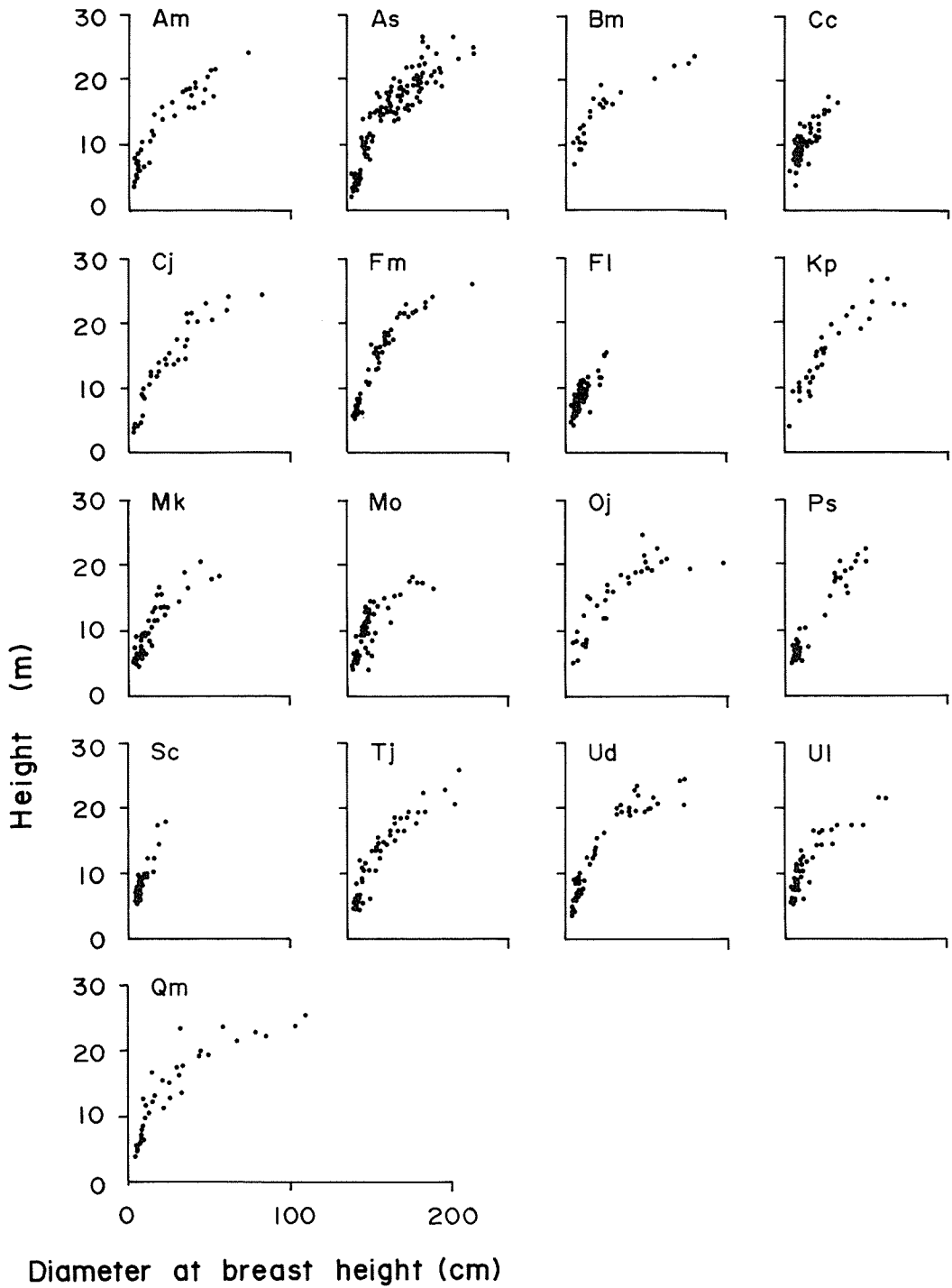


Figure 7. Relationship between DBH and height of seventeen species. Abbreviations of species names as in Table 1.

Table 4. Regression equations and correlation coefficients of the DBH and height data of seventeen species. All of the correlation coefficients are significant at 1% level. F-values with one asterisk are significant at 1% level. Abbreviations of species names as in Table 1. Numbers of samples as in Table 1.

Species	Function	Regression equations	r	Sum of squares	F-value
Am	Linear	Height = 0.2871DBH + 6.1479	0.9350	149.25	
	RG	$\frac{1}{\text{Height}} = \frac{1}{1.5952\text{DBH} + 24.2895}$	0.9484	103.16	16.53*
As	Linear	Height = 0.3045DBH + 6.1411	0.8913	879.36	
	RG	$\frac{1}{\text{Height}} = \frac{1}{0.9873\text{DBH} + 39.5726}$	0.9484	523.40	74.13*
Bm	Linear	Height = 0.1858DBH + 10.4850	0.8845	110.25	
	RG	$\frac{1}{\text{Height}} = \frac{1}{2.0964\text{DBH} + 25.5102}$	0.9293	44.72	33.71*
Cc	Linear	Height = 0.3460DBH + 6.5110	0.8039	135.62	
	RG	$\frac{1}{\text{Height}} = \frac{1}{1.8822\text{DBH} + 20.9644}$	0.7219	134.22	0.51
Cj	Linear	Height = 0.3066DBH + 5.8265	0.9168	215.18	
	RG	$\frac{1}{\text{Height}} = \frac{1}{0.9975\text{DBH} + 39.4166}$	0.9809	87.43	48.22*
Fl	Linear	Height = 0.3624DBH + 5.2261	0.7775	137.77	
	RG	$\frac{1}{\text{Height}} = \frac{1}{1.9818\text{DBH} + 17.0940}$	0.7845	129.47	4.36*
Fm	Linear	Height = 0.3546DBH + 7.3455	0.8957	298.73	
	RG	$\frac{1}{\text{Height}} = \frac{1}{1.2252\text{DBH} + 41.6667}$	0.9682	82.50	123.21*
Kp	Linear	Height = 0.2757DBH + 7.5444	0.9152	164.53	
	RG	$\frac{1}{\text{Height}} = \frac{1}{1.6287\text{DBH} + 25.0000}$	0.9534	193.46	—
Mk	Linear	Height = 0.3091DBH + 5.6624	0.8694	203.83	
	RG	$\frac{1}{\text{Height}} = \frac{1}{1.5795\text{DBH} + 20.0000}$	0.8254	191.07	2.80*
Mo	Linear	Height = 0.2724DBH + 6.3868	0.8082	267.93	
	RG	$\frac{1}{\text{Height}} = \frac{1}{2.0674\text{DBH} + 16.8577}$	0.7751	268.73	—
Oj	Linear	Height = 0.2022DBH + 8.6884	0.8421	292.68	
	RG	$\frac{1}{\text{Height}} = \frac{1}{1.8632\text{DBH} + 22.8363}$	0.9031	167.58	24.63*
Ps	Linear	Height = 0.3715DBH + 4.7506	0.9680	81.96	
	RG	$\frac{1}{\text{Height}} = \frac{1}{1.7176\text{DBH} + 21.9154}$	0.8962	187.06	—
Qm	Linear	Height = 0.1931DBH + 8.3766	0.8589	371.15	
	RG	$\frac{1}{\text{Height}} = \frac{1}{1.2763\text{DBH} + 30.3030}$	0.9645	144.85	54.68*
Sc	Linear	Height = 0.6435DBH + 3.2539	0.9242	53.03	
	RG	$\frac{1}{\text{Height}} = \frac{1}{1.6385\text{DBH} + 25.2525}$	0.8741	65.27	—
Tj	Linear	Height = 0.3101DBH + 6.1348	0.9151	251.20	
	RG	$\frac{1}{\text{Height}} = \frac{1}{1.3173\text{DBH} + 27.7008}$	0.8967	160.32	27.78*
Ud	Linear	Height = 0.2989DBH + 6.1091	0.9255	309.56	
	RG	$\frac{1}{\text{Height}} = \frac{1}{1.2318\text{DBH} + 32.7869}$	0.9334	103.93	102.87*
Ul	Linear	Height = 0.2600DBH + 7.4298	0.8639	193.77	
	RG	$\frac{1}{\text{Height}} = \frac{1}{1.9865\text{DBH} + 21.6169}$	0.8438	148.64	13.06*

data than the linear regression for ca. two-thirds of the species analyzed, height growth curves expressed by this function are not suitable for the actual height growth (Fig. 3). This is due to the operation which makes the linear regression go through the origin: this operation increases the sums of squares of deviations in the linear regression: and this makes F-values of the exponential function regression significant in the twelve species. In fact, without this operation, the sums of squares due to the exponential function regression were larger than those due to the linear regression. Therefore, in this case the exponential function regression is not adequate to the age and height data. In contrast, the sums of squares due to the power function regression were significantly smaller than those due to the linear regression for eleven species even when the linear regression does not go through the origin. Thus, the power function regression is generally more adequate to the data than the linear regression.

(3) *Crown radius growth*

Little is known about the process of crown radius growth. Inose (1982) stated that the growth of branch length against branch age was not linear but tended to level off. This suggests that the annual growth rate of crown radius decreases in the process of time. Although it is not possible to formulate the growth of crown radius theoretically with the present knowledge, the result of the present study coincides with Inose's (1982) result.

Annual growth rates of crown radius have remarkably varied among previous studies. For example, Runkle and Yetter (1987) found that annual growth rate of crown radius of trees which grow on the border of gaps was on average 18 cm/year. They estimated the value based on the measurements of crown radius in 1976 or 1977 and the remeasurement of them in 1983. By using a regression analysis, Runkle (1982) estimated that annual growth rate of crown radius of canopy trees was on average 4.1 cm/year. It is known: once a gap created, repeated disturbances occur on the border of the gap, and destroy gap bordering trees or at least branches of them; as a result, the area of the gap expands (Foster and Reiners 1986). The value obtained by Runkle and Yetter (1987) may be applicable to the short-term condition when no repeated disturbances have occurred. On the other hand, the value obtained by Runkle (1982) should be applied to the long-term condition when repeated disturbances have occurred, and killed trees around gaps. Moreover, in the present study trees growing under canopies were also included. This means that the values obtained in the present study correspond to the lateral crown growth under undisturbed condition. The annual growth rates of crown radius of the trees growing under canopies is presumably lower than those in gaps because of shade condition. Those are probably the reason why the value of ours, 2.0 cm/y on average, is smaller than not only that of Runkle and Yetter's (1987) but also that of Runkle's (1982). Phares and Whilliams (1971) reported the same value (2.0 cm/y) for *Juglans nigra* under undisturbed condition.

5.2 *Height growth and dominance in canopy layers*

It goes without saying that light is one of the most important factors affecting plant growth. Every plant individuals competitively grow taller in order to be exposed to enough sun light. Based on the height growth curves obtained in 4.2, the second discussion concerns with the relationship between height growth and dominance of trees in canopy layers.

It is generally believed that species dominating in canopy layers possess high shade tolerance and grow slowly (Numata 1983). The reason of this relationship is usually explained as follows; trees growing slowly are suppressed from fast growing trees; however, high shade tolerance of the former compensates for this disadvantage. The results of the present study, however, do not completely agree with the above hypothesis. Fig. 8 shows the height growth curves obtained in 4.2. It is easy to recognize that several dominant species, *Fraxinus mandshurica* var. *japonica*, *Quercus mongolica* var. *grosseserrata*, and *Tilia japonica*, grow faster in younger stage (<50 years) than the subordinate species (Fig. 8, B)

Furthermore, the shade tolerance and height growth rates of the species analyzed in the present study do not correlate clearly. According to Harada (1942), seedlings of main component species in Nopporo National Forest may be arranged in decreasing order of shade tolerance as follows; *Abies sachalinensis*, *Quercus mongolica* var. *grosseserrata*, *Tilia japonica*, *Fraxinus lanuginosa*, *Kalopanax pictus*, *Magnolia obovata*, and *Prunus ssiori*. The result of the present study shows that not only shade tolerant *Abies sachalinensis* but also less tolerant *Prunus ssiori* grow slowly in younger stage (Fig. 8). Therefore, the hypothesis that dominant trees generally possess high shade tolerance and grow slowly can not be wholly accepted.

The dominance of trees in canopy layers is determined by the two factors; the maximum height and the longevity. Except for *Acer mono* and *Ulmus laciniata*, six dominant species can attain ca. 40 m in height (Table 4, Fig. 8 A). Subordinate species can not exceed in height although some of them grow faster in younger stage than the dominant species. The longevity of each species are also shown in Fig. 8. The height growth curves in Fig. 8 are drawn from age 0 to the maximum age for each species. Note that solid circles show maximum ages obtained by increment cores in the present study. Open circles are those estimated from the DBH of the largest trees in the present study, Ishikawa et al. (1986) or Ishikawa and Ito (1989) by using the linear relationships in 4.1. It is clear that the maximum age of the dominant species are longer than those of others. The two dominant species, *Acer mono* and *Ulmus laciniata* whose maximum height was the same as the subordinate species, can also survive longer than the subordinate ones. The only exception is *Ostrya japonica*, which scarcely attain the canopy dominance but survives about 400 years. If other characteristics are all the same between species, a big tree species with longer longevity can, of course, accumulate in canopy layers and can surpass other small and short living tree species.

It is a matter of course that the shade tolerance, height growth rate, maximum size and longevity of a species correlate each other to some extent. Williamson (1975) stated that the specific gravities of woods in intolerant species are low, and that those in tolerant species are high. According to Koike (1987), this fact is explained as follows; intolerant trees produce cells whose walls are thin; this enables them to grow fast, but reduces the strength of woods and the longevity. However, judging from the results of the present study, the relationship between those parameters is not so clear. For example, *Fraxinus mandshurica* var. *japonica* possesses high photosynthetic ability (Koike 1986) and high growth rate (Fig. 8), and yet they can survive longer and dominate in canopy layers (Fig. 8). Compared with

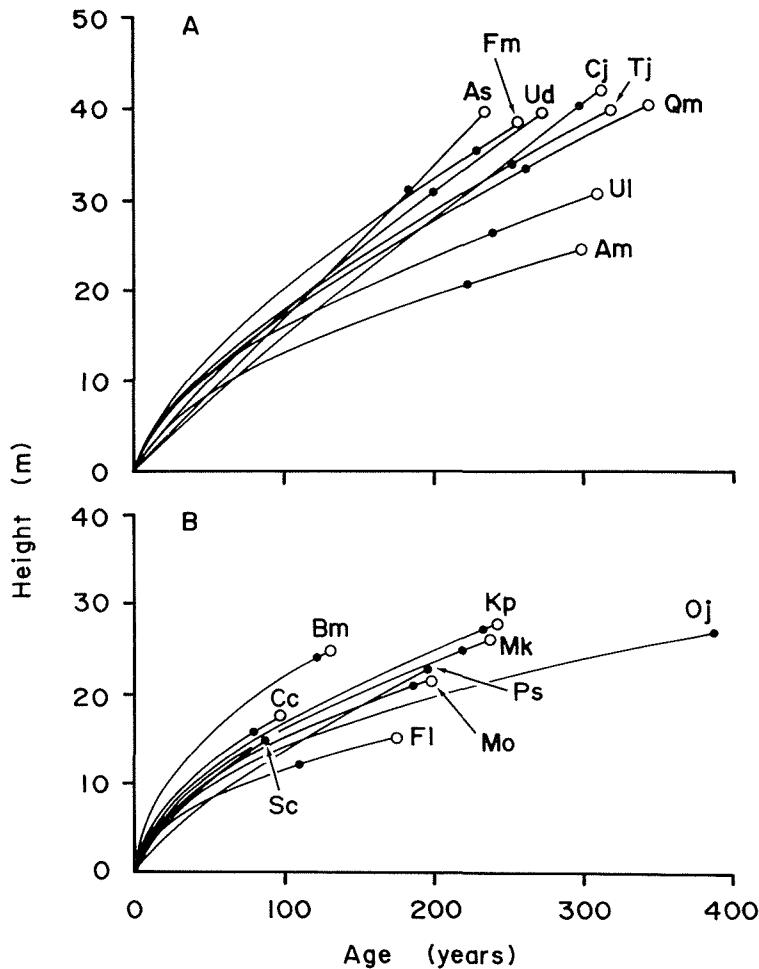


Figure 8. Height growth curves against age drawn by the power function regression equations in 4.2. Abbreviations of species names as in Table 1. A: dominant species, B: subordinate species. Solid circles are maximum ages obtained by increment cores in the present study. Open circles are those estimated from the DBH of the largest trees in the present study, Ishikawa et al. (1986), or Ishikawa and Ito (1989) by using the linear relationship in 4.1. Note that, in subordinate species without open circles, ages obtained by increment cores exceeded the estimated ages.

early-successional species such as *Aralia elata* Seemann and *Betula platyphylla* var. *japonica* Hara, the species analyzed in the present study are all mid-successional or late-successional species. They certainly possess higher shade tolerance and grow more slowly than early-successional species. However, among those mid-successional and late-successional species, the dominance in canopy layers can not be wholly predicted from the differences in shade tolerance or photosynthetic rate. The results of the present study rather indicate that we should find the factors governing the maximum size and longevity of a species. The

photosynthetic ability, i.e., shade tolerance, of a species is not the only factor governing them. It is suggested that conditions of the favourable habitat of a species may affect them. For example, species growing in ravines, such as *Fraxinus mandshurica* var. *japonica*, may be able to survive longer even if the strength of their woods are low, because they are not blown stronger than the species growing on ridges. We can not strictly separate external and internal factors in field observations (White 1979). It is not also clear how short-living smaller size species, such as *Fraxinus lanuginosa*, *Magnolia kobus* var. *borealis*, and *M. obovata*, can survive beneath canopies. The reasons why some species can dominate in canopy layers and why others can survive beneath canopies should be further studied from the correlations between their physiological and life history characteristics, and habitat conditions.

6. Summary

1. Based on the data obtained from 1981 to 1985, seventeen species were analyzed to reveal the relationships between age and size of them in Nopporo National Forest, central Hokkaido. Least squares linear and two non-linear (exponential function and power function) regression models were fitted to the age and DBH data, the age and height data, and the age and crown area data. Another non-linear model, extended relative growth model, was fitted to the DBH and height data.

2. Linear regression provided the best fit to the age and DBH data for all the seventeen species analyzed. This result does not coincide with the former studies which indicated that the DBH growth leveled off in the process of time. This is probably due to past wind damage and cuttings which reduced the number of mature individuals in the forest. The difficulty of samplings of increment cores may also affect the result.

3. Power function regression provided the best fit to the age and height data. This result agrees with former studies.

4. For the eleven species, linear regression provided the best fit to the age and crown area data, although the scatter of the data points was larger than those of other relationships. By using this linear relationship between age and crown area, annual growth rates of crown radius were estimated for six species whose scatters of the data points were relatively small. They decreased simply and approached ca. 1 cm/y as trees became older. Annual growth rates of crown radius ranged from 2.4 cm/year (*Tilia japonica*) to 1.3 cm/year (*Ostrya japonica*) when each species reached canopy layers.

5. The regression by extended relative growth law provided better fit to the DBH and height data than linear regression.

6. It was suggested that the general explanation of the relationship between the dominance, maximum height and longevity of a species, and its shade tolerance was not always hold.

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