Ecological Research (1995) **10**, 53–64

Comparative study of leaf carbon gain in saplings of *Thujopsis dolabrata* var. *hondai* and *Quercus mongolica* var. *grosseserrata* in a cool-temperate deciduous forest

RYOJI HASHIMOTO AND MANABU SHIRAHATA

Department of Agronomy and Forestry, Faculty of Agriculture, Iwate University, Ueda 3, Morioka, 020 Japan

Seasonal courses of leaf CO_2 gas exchange in a growing season were examined in saplings of *Thujopsis dolabrata* var. *hondai* and *Quercus mongolica* var. *grosseserrata* in a cool temperate deciduous forest. Between the two tree species there were no large differences in the light compensation point of leaf photosynthesis, except for the season of new leaf expansion. However, light-saturated rates of net photosynthesis were obviously high in *T. dolabrata* var. *hondai*. Evergreen *T. dolabrata* var. *hondai* saplings had large photosynthetic production in two seasons, before the emergence of new foliage and after foliage fall of the overstory deciduous trees, because of the significantly high solar radiant energy penetrating under the forest canopy during the seasons. Saplings of deciduous *Q. mongolica* var. *grosseserrata* were heavily shaded throughout the growing season by foliage of the overstory trees, which resulted in a low daily surplus production. The annual surplus production of leaves in the growing season was estimated to be 2300 mmol CO_2 m^{-2} in *T. dolabrata* var. *hondai* and − 100 mmol CO_2 m^{-2}, slightly negative, in *Q. mongolica* var. *grosseserrata*. These results supported the high survivability of *T. dolabrata* var. *hondai* saplings and the high mortality of *Q. mongolica* var. *grosseserrata* in the deciduous forest.

Key words: leaf carbon gain; light regime; *Quercus mongolica* var. *grosseserrata*; sapling survival; *Thujopsis dolabrata* var. *hondai*.

INTRODUCTION

Forests of *Fagus crenata* Blume and *Quercus mongolica* var. *grosseserrata* Rehd. et Wils. accompanied by *Thujopsis dolabrata* var. *hondai* Makino are widely distributed in and around the Ou Mountains (Murai 1951). Saplings of *T. dolabrata* var. *hondai* are abundant under canopies of these forests. Part of the saplings produce new individuals by a vegetative propagation method, the so called creeping branch propagation (Yamanouchi 1936; Hashimoto & Ishii 1990). *Thujopsis dolabrata* var. *hondai* has been regarded as a typical shade-tolerant tree species capable of surviving in heavily shaded light regimes (Fujishima 1948). It contrasts with broad leaved trees such as *F. crenata, Q. mongolica* var. *grosseserrata* and *Quercus serrata* Thunb. whose seedlings apparently tend to disappear in much shorter periods after germination (Kanazawa 1982; Matsuda 1985; Nakashizuka 1988; Hashizume 1991).

The establishment and survival of seedlings or saplings of trees under a forest canopy has important implications for the regeneration process of the forest, which is generally understood to proceed through canopy openings caused by treefalls or larger scale disturbances (Lorimer 1989; Spies & Franklin 1989). Mortality of seedlings or saplings under forest canopies depends both on biological factors such as disease and insect attacks and environmental factors such as deficit of solar radiant energy and drought. In a cool temperate climate without distinct dry seasons, the light environment has a crucial effect on survival and abundance (Kozlowski *et al.* 1991).

The light regime beneath a forest canopy is heterogeneous in space and time (Pearcy 1990; Washitani & Tang 1991). In particular, in forests dominated by deciduous trees, the solar radiant

---

Received 8 June 1993.
Accepted 17 August 1994.

energy reaching the floors changes drastically with the effects of foliage emergence and foliage fall of the overstory trees. Thus, the seasonal resource availability of plant individuals on such forest floors would greatly differ from that in open sites (Hinckley *et al.* 1981), and the duration of the growing season and the times of leaf expansion and leaf fall would also be important factors in the annual photosynthetic productivity.

In this study photosynthetic responses to light intensity at various temperatures were measured over two growing seasons for saplings of *T. dolabrata* var. *hondai* and *Q. mongolica* var. *grosseserrata* in a deciduous forest dominated by *Q. mongolica* var. *grosseserrata*. By combining these experimental results of CO_2 gas exchange and the meteorological data measured on the forest floor, the seasonal courses of photosynthesis and respiration in leaves were estimated. Based on these ecophysiological examinations, the survivorship and the growth of *T. dolabrata* var. *hondai* saplings are discussed.

METHODS

Study area

The study area was located at the transition zone from the Shizukuishi basin to the Ou Mountains, 25 km west of Morioka (39°40′N, 140°55′E) in the North Tohoku district. The study site belonged to the Experimental Forest of Iwate University and had a south-facing slope with an inclination of 20–28° at an altitude of 350–480 m, along the Akasawa River. The annual mean temperature and precipitation measured from 1977 to 1985 at a meteorological observation spot, about 3 km east of the study site, were 9.2°C and 1600 mm, respectively.

A plot of about 0.20 ha was established in order to survey the stand structure. The major tree species comprising the canopy were *Q. mongolica* var. *grosseserrata* and *T. dolabrata* var. *hondai*; these species occupied the upper and lower layers, respectively. The density of trees over 6 cm in diameter at breast height (d.b.h.), and basal area per hectare were 208 trees and 31.0 m^2 for *Q. mongolica* var. *grosseserrata*, 1250 trees and 22.6 m^2 for *T. dolabrata* var. *hondai*, and 475 trees and 12.2 m^2 for the other tree species such as *Acer japonicum* Thunb. and *Carpinus laxiflora* Blume.

Two sub-plots each of 120 m^2 (30 m × 4 m) were set along the slope to investigate the survivorship and recruitment of saplings of *T. dolabrata* var. *hondai* and *Q. mongolica* var. *grosseserrata*. The individuals shorter than 80 cm in height were treated as saplings. The census of the saplings was repeated late in autumn from 1988 to 1991. Evergreen dwarf shrubs such as *Aucuba japonica* var. *borealis* Miyabe et Kudo and *Cephalotaxus harringtonia* subsp. *nana* Kitagawa were seen in the forest floor although they were less frequent.

Measurements

Air temperature and photosynthetically active photon flux density (PPFD) in the forest floor, at heights of 60–80 cm above the ground, were measured in the plot from March to December of 1991. The air temperature was measured at one place by using a thermistor rod and PPFD was measured at four places by using quantum sensors (IKS-25, Koito, Tokyo). By using a data logger (1200 series, Grant, Cambridge, UK) the measurements were made at 10 s intervals and the data averaged for 10 min intervals were stored. Air temperature and PPFD data obtained at the meteorological observation spot of the Experimental Forest, 3.5 km east of the plot, were used for the open site.

Four individuals of each tree species of *T. dolabrata* var. *hondai* and *Q. mongolica* var. *grosseserrata* were sampled at about a 1 month interval in 1990 and 1991: from April to November for *T. dolabrata* var. *hondai* and from May to October for *Q. mongolica* var. *grosseserrata*. The aboveground part was detached at the stem base for *T. dolabrata* var. *hondai* and the whole plant was dug out for *Q. mongolica* var. *grosseserrata*. These materials, being well supplied with water through the cut end of the stem or the root system, were immediately carried to the university in Morioka and photosynthesis and respiration were measured within 48 h after sampling. The experimental materials were kept under a dense canopy of pine trees in the experimental nursery on the campus. Size of the sample individuals was 15–30 cm in height and 0.5–1 cm in stem diameter at the ground for *T. dolabrata* var. *hondai*, and 15–20 cm in height and 0.2–0.3 cm in stem diameter for *Q. mongolica* var. *grosseserrata*. In *T. dolabrata* var. *hondai* a well-developed primary branch attached around the middle of the stem was selected and part of the leaves (80–150 cm^2) were used as measurement material. The measurement material included leaves of different ages, mostly less than 5 years old. In *Q. mongolica* var. *grosseserrata* all leaves (30–50 cm^2) attached to the stem were used for the measurement.

The leaves, water-supplied through the cut end of the branch or the root system, were put into a micro-chamber equipped with a temperature control-unit (MC-A3-W, Koito, Tokyo) and CO_2 gas exchange was measured using an infrared gas analyzer (VIA 300, Horiba, Kyoto). Light was supplied by an electric discharge lamp (HGI-TS, Mitsubishi, Tokyo). A filter, made with a water layer of 8 cm, was placed between the light source and the chamber to absorb heat radiation. Light intensity was changed in the range of 5–600 μmol $q \cdot m^{-2}\ s^{-1}$ by inserting black Saran shading cloth screens between the water filter and the chamber (the photosynthetic rate reached saturation point at below 500 μmol $q \cdot m^{-2}\ s^{-1}$). Leaf temperature was monitored by attaching a thin thermocouple to an abaxial side of the leaf. The concentration of CO_2 in the chamber was kept within a range of 340–360 $\mu L\ L^{-1}$ during the measurement.

The measurements were repeated, with a change of leaf temperature at 5 °C intervals in the range of 5–30 °C. First, the measurement was made at a temperature closest to the mean daytime temperature in the habitat (after the 30–50 min pre-illumination of about 150 μmol $q \cdot m^{-2}\ s^{-1}$). After that the temperature was first lowered to the lowest temperature, and then returned to the original one. After checking the photosynthesis recovery, the temperature was raised to the maximum temperature.

After the measurement was made of CO_2 gas exchange, leaves in the chamber were detached to determine the leaf area, by leaf area meter (AAM-7, Hayashi, Tokyo), and dry weight. In branches of *T. dolabrata* var. *hondai*, the leading shoots and lateral branchlets consist of numerous small scale-like leaves. The projected area of such a branch covered with scale-like leaves was defined as the leaf area. The individual sample was divided into leaves, stems and so forth and the dry weight was determined. The respiration of the photosynthetic plant parts (leaves) and non-photosynthetic plant parts (branches and stem) of *T. dolabrata* var. *hondai* were measured for four individuals in June and September in 1991.

Steady-state model on leaf carbon gain simulation

The rectangular hyperbola function (Tamiya 1951), with respect to the photosynthesis/light intensity relationship, often gives a poor fit. In particular, estimates of light-saturated photosynthesis tend to be higher than the observed data. So, the monomolecular equation was used to overcome this problem according to Causton and Dale (1990; Fig. 1):

$$p = a(1 - e^{b-ci}) \qquad (1)$$

Here, p (μmol CO_2 $m^{-2}\ s^{-1}$) is the rate of net photosynthesis at light intensity i (μmol $q \cdot m^{-2}\ s^{-1}$); a is the upper asymptotic maximum, showing the light-saturated rate of net photosynthesis (p_{max}), and b and c are the two other parameters. The initial slope of the curve (ϕ; μmol CO_2/μmol q.) is given by ace^b. The light compensation point (i_c) is obtained as b/c. As dark respiration rate (r) is $-a(1 - e^b)$, gross photosynthesis is determined by $(p + r)$. Equation (1) was fitted to data by iterative non-linear regression to estimate parameter values.

A simple steady-state model of CO_2 gas exchange based on the photosynthetic light response curve was used to simulate CO_2 gas exchange of the leaves in the forest floor; it functioned with inputs of meteorological data of air temperature and PPFD. The parameters a, b and c of the photosynthetic light curve were determined at a given temperature, to obtain the rate of gross photosynthesis, from the graphs showing their temperature dependency (in which mean values at measurement temperatures were connected with straight lines). The rate of dark

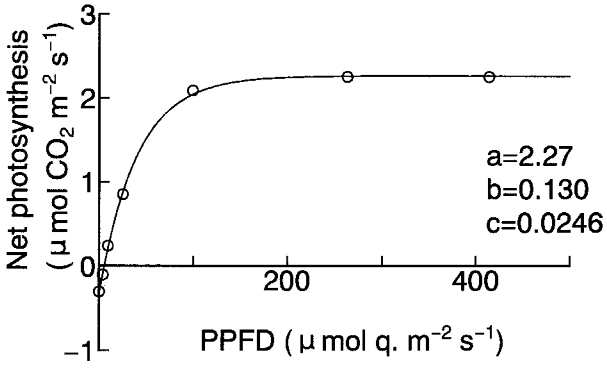

Fig. 1. An example of photosynthetic light response curve for leaves of a sample individual of *T. dolabrata* var. *hondai*. See Equation (1) in text for the regression equation.

respiration at a temperature was similarly determined using measured data. The computation was carried out at 10 min intervals, assuming that the leaf temperature was equal to air temperature since the difference between leaf and air temperatures could not become so great under canopies of dense forests including evergreen trees as treated here. No consideration was paid to the effects of other environmental factors such as atmospheric vapor pressure deficit and soil water conditions on leaf conductance or photosynthetic performance. The computed data were summed up to obtain the daily gross photosynthesis and daily dark respiration. To calculate daily light compensation points for each month, the relation between daily PPFD and daily gross photosynthesis was regressed in the form of rectangular hyperbola.

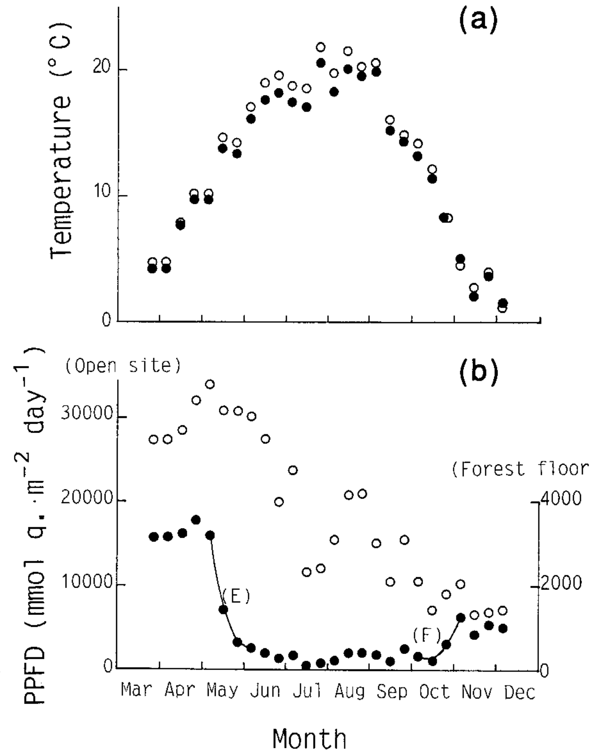

Fig. 2. Seasonal courses of (a) air temperature and (b) PPFD in the open site and forest floor. ○, open site; ●, forest floor; (E), leaf expansion; (F), leaf fall.

RESULTS

Climate and phenology

The snow fall in the study area started from early to middle December and the snow cover disappeared in early April. In 1991, the snow cover almost disappeared on 7–11 April and the snowfall began on 3–4 December. The snow depth in midwinter was estimated to be 80–100 cm around the plot according to the observations from 1988 to 1993.

The value of PPFD in the forest floor drastically changed by new foliage emergence in spring and foliage fall in autumn of the overstory deciduous trees (Fig. 2). The new leaves emerged from the beginning of May and their expansion was completed at the end of the month. The leaf fall started from September, but it was most concentrated in late October. The values of PPFD in the forest floor were approximately 10–15% of that of the open site in the winter season, while they were reduced to only 1–3% during the leafy season.

Leaves of *T. dolabrata* var. *hondai* saplings on the forest floor seemed to remain alive for more than 5 years. The current year's leaves emerged over a relatively long period from the beginning of May to the end of June, and the formation of new leaves was most active during the middle of May to the middle of June. Consequently, the period of photosynthetic production of the saplings in the year was defined as 34 weeks from the snow disappearance on 9 April to the first snow fall on 2 December for *T. dolabrata* var. *hondai*. In saplings of *Q. mongolica* var. *grosseserrata*, the leaf expansion was concentrated in a short period in the middle of May. The discoloration of leaves began from the middle of October and most of the saplings shed their leaves by the end of the month. The period of photosynthesis was consequently defined as 24 weeks from 14 May to 28 October for *Q. mongolica* var. *grosseserrata*.

Survivorship of saplings

Mortality of the saplings of *T. dolabrata* var. *hondai* was negligible in the period from 1988 to 1991, and a few individuals were recruited by the creeping branch propagation method (Table 1). The density was about three individuals m^{-2}, where those less than 40 cm in height occupied more than 90% (Table 2). All saplings of *Q. mongolica* var. *grosseserrata* were individuals which had germinated in the autumn of 1987. Sapling density was about one individual m^{-2} in 1988, but the mortality was high, reaching 70% for 3 years after germination. There

Table 1. Number of saplings (height < 80 cm) in two 120 m^2 sub-plots.

	T. dolabrata var. *hondai*					*Q. mongolica* var. *grosseserrata*				
	Found in	Recruited in			Total	Found in	Recruited in			Total
Year	1988	1989	1990	1991		1988	1989	1990	1991	
1988	401				401	122				122
1989	401	1			402	72	0			72
1990	401	1	5		407	59	0	0		59
1991	401	1	5	2	409	37	0	0	0	37

were no seedlings exceeding 20 cm in height in the period.

Photosynthetic and respiratory properties of leaves

The values of ϕ (*ace*^{b}) *and* $p_{\max}$ (*a*) of the photosynthetic light response curve in each month varied with the leaf temperature and showed a convex curve (Tables 3, 4). The optimum temperature increased from spring to summer and then decreased towards autumn; for example, around 15 °C from April to May, 15–20 °C from July to September, and 10–15 °C from October to November in ϕ of *T. dolabrata* var. *hondai*. The value of r exponentially increased with increasing temperature and Q_{10} differed with the season (Table 5).

In *T. dolabrata* var. *hondai*, ϕ at mean temperature of each month ranged from 0.065 to 0.08 µmol CO$_2$/µmol q., showing high values from late summer to autumn (Fig. 3). The value of $p_{\max}$ was in the range of 2.2 to 3.4 µmol CO$_2$ m^{-2} s^{-1}, apparently low at the new leaf expansion season. In *Q. mongolica* var. *grosseserrata*, ϕ was low at the early growing season and then increased to around 0.09 µmol CO$_2$/µmol q. The value of $p_{\max}$ ranged from 1.7 to 2.6 µmol CO$_2$ m^{-2} s^{-1}, showing obvious decline after summer.

The value of r at the mean temperature of each month in *T. dolabrata* var. *hondai* was already at a high level in April and May and reached a peak in June (Fig. 3). It then declined rapidly in July and was relatively stable between 0.15 to 0.25 µmol CO$_2$ m^{-2} s^{-1} from July to November. For *Q. mongolica* var. *grosseserrata*, r was slightly higher in the early growing season and then decreased to 0.15–0.25 µmol CO$_2$ m^{-2} s^{-1}. The value of i_c at the mean temperature of each month showed almost the same seasonal course as r in both tree species. It rose to 8–10 µmol q · m^{-2} s^{-1} during the new leaf expansion season in *T. dolabrata* var. *hondai* but was less than 6 µmol q · m^{-2} s^{-1} in other seasons. In *Q. mongolica* var. *grosseserrata*, i_c was less than 6 µmol q · m^{-2} s^{-1} over the whole growing season.

Daily photosynthesis and respiration

The daily gross photosynthesis in leaves (P_g) changed largely with the season through the effect of daily PPFD (Figs 4, 5); the seasonal change of P_g almost agreed with that of daily PPFD in the forest floor. In saplings of *T. dolabrata* var. *hondai*, P_g was significantly higher during April to the middle of May and averaged about 80 mmol CO$_2$ m^{-2} day^{-1}. It then declined to 10–20 mmol CO$_2$ m^{-2} day^{-1} in summer but increased to about 30–40 mmol CO$_2$ m^{-2} day^{-1} in late autumn. In saplings of *Q. mongolica* var. *grosseserrata* P_g was slightly higher in May but then showed lower values of 10–20 mmol CO$_2$ m^{-2} day^{-1} until the end of the growing season.

The daily dark respiration in leaves (R) also changed with the season (Figs 4, 5), but the seasonal

Table 2. Sapling density (m^{-2}) in each height class.

Species	Year	Height class (cm)				
		0–20	20–40	40–60	60–80	Total
T. dolabrata var. *hondai*	1991	1.69 (50)	1.47 (43)	0.21 (6)	0.04 (1)	3.41 (100)
Q. mongolica var. *grosseserrata*	1991	0.31 (100)				0.31 (100)

Figures in parentheses show percentages.

Table 3. Seasonal courses of initial slope (ϕ) and light-saturated net photosynthesis (p_{max}) of photosynthetic light response curve in leaves of *T. dolabrata* var. *hondai* saplings.

Season	Sample size	Leaf temperature (°C)					
		5	10	15	20	25	30
ϕ (μmol CO_2/μmol q.)							
April (M)	8	0.067 (0.010)	0.066 (0.005)	0.067 (0.012)	0.065 (0.008)		
May (E)	4	0.060 (0.010)	0.063 (0.011)	0.070 (0.013)	0.071 (0.011)	0.064 (0.009)	
May (L)	8	0.059 (0.005)	0.064 (0.002)	0.066 (0.005)	0.061 (0.003)	0.061 (0.003)	
June (M)	8	0.055 (0.003)	0.064 (0.006)	0.075 (0.008)	0.067 (0.013)	0.058 (0.005)	0.053 (0.016)
July (M)	8		0.057 (0.007)	0.061 (0.005)	0.065 (0.010)	0.052 (0.003)	0.048 (0.009)
August (M)	8		0.067 (0.007)	0.071 (0.009)	0.080 (0.013)	0.068 (0.007)	0.063 (0.007)
Sept. (M)	8	0.066 (0.005)	0.074 (0.003)	0.081 (0.007)	0.081 (0.003)	0.071 (0.005)	0.058 (0.003)
Oct. (M)	8	0.069 (0.003)	0.079 (0.009)	0.088 (0.012)	0.076 (0.009)	0.071 (0.008)	
Nov. (M)	8	0.066 (0.012)	0.068 (0.009)	0.063 (0.009)	0.060 (0.008)	0.064 (0.006)	
p_{max} (μmol CO_2 m^{-2} s^{-1})							
April (M)	8	2.61 (0.23)	3.05 (0.30)	2.90 (0.27)	2.93 (0.30)		
May (E)	4	2.49 (0.30)	3.09 (0.20)	3.21 (0.21)	3.23 (0.26)	2.95 (0.23)	
May (L)	8	1.99 (0.17)	2.49 (0.15)	2.57 (0.18)	2.51 (0.12)	2.17 (0.12)	
June (M)	8	1.87 (0.18)	2.43 (0.24)	2.68 (0.22)	2.51 (0.33)	2.20 (0.21)	1.86 (0.19)
July (M)	8		2.05 (0.08)	2.24 (0.11)	2.28 (0.09)	1.90 (0.07)	1.66 (0.05)
August (M)	8		2.54 (0.46)	2.72 (0.46)	2.83 (0.33)	2.69 (0.24)	2.07 (0.29)
Sept. (M)	8	2.33 (0.12)	2.92 (0.16)	3.17 (0.22)	3.07 (0.14)	2.79 (0.21)	2.77 (0.22)
Oct. (M)	8	2.79 (0.16)	3.34 (0.35)	3.49 (0.42)	3.42 (0.48)	3.33 (0.44)	
Nov. (M)	8	2.16 (0.25)	2.38 (0.31)	2.39 (0.30)	2.16 (0.26)	1.82 (0.30)	

The mean and SD values are shown in parentheses.
(E), (M), (L) represent the beginning, middle and end of each month, respectively.

Table 4. Seasonal courses of initial slope (ϕ) and light-saturated net photosynthesis (p_{max}) of photosynthetic light response curve in leaves of *Q. mongolica* var. *grosseserrata* saplings.

Season	Sample size	Leaf temperature (°C)					
		5	10	15	20	25	30
ϕ (μmol CO_2/μmol q.)							
May (L)	4	0.042 (0.005)	0.060 (0.011)	0.061 (0.009)	0.049 (0.006)		
June (M)	4	0.075 (0.010)	0.080 (0.050)	0.082 (0.047)	0.067 (0.011)	0.052 (0.007)	
July (M)	4		0.077 (0.015)	0.080 (0.012)	0.086 (0.015)	0.055 (0.009)	0.044 (0.010)
August (M)	4		0.070 (0.010)	0.074 (0.015)	0.080 (0.016)	0.050 (0.013)	0.040 (0.010)
Sept. (M)	4	0.082 (0.011)	0.086 (0.017)	0.089 (0.019)	0.088 (0.011)	0.065 (0.007)	
Oct. (M)	4	0.087 (0.031)	0.092 (0.024)	0.085 (0.034)	0.057 (0.020)	0.054 (0.009)	
p_{max} (μmol CO_2 m^{-2} s^{-1})							
May (L)	4	1.57 (0.23)	1.94 (0.36)	2.29 (0.51)	2.02 (0.19)		
June (M)	4	1.30 (0.18)	1.84 (0.25)	2.44 (0.38)	2.57 (0.74)	2.31 (0.52)	
July (M)	4		2.37 (0.20)	2.54 (0.35)	2.64 (0.22)	2.28 (0.33)	1.83 (0.41)
August (M)	4		2.17 (0.20)	2.22 (0.35)	2.20 (0.27)	1.34 (0.42)	0.98 (0.34)
Sept. (M)	4	2.09 (0.19)	2.20 (0.22)	2.34 (0.35)	1.87 (0.29)	1.69 (0.36)	
Oct. (M)	4	1.36 (0.32)	1.55 (0.52)	1.81 (0.70)	1.36 (0.79)	1.27 (0.52)	

The mean and SD values are shown in parentheses.
(E), (M) and (L) represent the beginning, middle and end of each month, respectively.

course of R did not always correspond with that of air temperature. In *T. dolabrata* var. *hondai* the averaged value of R was about 20 mmol CO_2 m^{-2} day^{-1} in April and increased to 40 mmol CO_2 m^{-2} day^{-1} in May and June, but decreased to 20 mmol CO_2 m^{-2} day^{-1} in July and August despite the increase of air temperature. It then declined in slow degrees towards the end of the growing season. In *Q. mongolica* var. *grosseserrata*, R was around 20 mmol CO_2 m^{-2} day^{-1} from spring to early

Table 5. Seasonal courses of dark respiration rate (r, μmol CO_2 m^{-2} s^{-1}) in leaves of *T. dolabrata* var. *hondai* and *Q. mongolica* var. *grosseserrata* saplings.

Season	Sample size	Leaf temperature (°C)						
		5	10	15	20	25	30	Q_{10}
T. dolabrata var. *hondai*								
April (M)	8	0.17 (0.06)	0.29 (0.05)	0.55 (0.06)	0.80 (0.17)			2.6
May (E)	4	0.19 (0.11)	0.23 (0.08)	0.49 (0.12)	0.73 (0.22)	1.01 (0.30)		2.9
May (L)	8	0.18 (0.03)	0.26 (0.09)	0.41 (0.07)	0.58 (0.12)	0.83 (0.19)		2.2
June (M)	8	0.12 (0.04)	0.22 (0.07)	0.37 (0.13)	0.68 (0.16)	0.87 (0.21)	0.86 (0.14)	2.4
July (M)	8		0.09 (0.05)	0.18 (0.03)	0.27 (0.06)	0.48 (0.10)	0.77 (0.08)	3.2
August (M)	8		0.06 (0.04)	0.09 (0.03)	0.13 (0.03)	0.27 (0.04)	0.44 (0.10)	3.3
Sept. (M)	8	0.12 (0.01)	0.10 (0.02)	0.13 (0.03)	0.19 (0.02)	0.60 (0.04)	0.65 (0.13)	2.2
Oct. (M)	8	0.16 (0.04)	0.16 (0.03)	0.25 (0.05)	0.41 (0.11)	0.49 (0.09)		2.0
Nov. (M)	8	0.16 (0.02)	0.20 (0.04)	0.27 (0.06)	0.40 (0.10)	0.60 (0.16)		2.1
Q. mongolica var. *grosseserrata*								
May (L)	4	0.09 (0.02)	0.15 (0.03)	0.31 (0.04)	0.38 (0.06)			2.8
June (M)	4	0.07 (0.02)	0.12 (0.03)	0.22 (0.06)	0.32 (0.06)	0.47 (0.10)		2.6
July (M)	4		0.06 (0.02)	0.21 (0.02)	0.25 (0.03)	0.41 (0.07)	0.74 (0.15)	3.4
August (M)	4		0.03 (0.01)	0.09 (0.04)	0.20 (0.04)	0.38 (0.05)	0.53 (0.10)	4.1
Sept. (M)	4	0.06 (0.03)	0.10 (0.03)	0.20 (0.05)	0.27 (0.06)	0.50 (0.08)		2.6
Oct. (M)	4	0.08 (0.02)	0.11 (0.02)	0.23 (0.04)	0.30 (0.09)	0.39 (0.14)		2.4

The mean and SD values are shown in parentheses.
(E), (M) and (L) represent the beginning, middle and end of each month, respectively.

autumn so no distinct seasonal variations were seen except for the decreases in late autumn.

The daily surplus production (P_n; $P_g - R$) in *T. dolabrata* var. *hondai* averaged 50–60 mmol CO_2 m^{-2} day^{-1} during April to the middle of May (Fig. 6). P_n then declined to negative in June–July. From summer to autumn, P_n increased and changed to positive values. In *Q. mongolica* var. *grosseserrata*, however, there were no seasons when P_n was kept largely positive.

The daily light compensation point (I_c) at which P_g and R equalled each other, ranged from 200 to 900 mmol q · m^{-2} day^{-1} over the growing season in *T. dolabrata* var. *hondai*. The value of I_c was apparently high in the early growing season, reached a peak in June, and then declined to keep values of 200–250 mmol q · m^{-2} day^{-1}. The number of days at which P_g exceeded R was 138, corresponding with 58% of the total days (238 days) in the growing season (Fig. 6). In *Q. mongolica* var. *grosseserrata*, I_c was in the range of 200–450 mmol q · m^{-2} day^{-1} throughout the growing season. The value of I_c reached its maximum in May and then declined to relatively stable values of 300–350 mmol q · m^{-2} day^{-1} until it declined at the end of the growing season. The number of days at which P_g exceeded R was 83, equivalent to 49% of the total days (168 days) in the growing season (Fig. 6).

DISCUSSION

Leaf photosynthetic properties

Plants growing under poor light environments lower the photosynthetic light compensation point in leaves to keep the CO_2 balance between photosynthesis and respiration positive (Schaedle 1975; Boardman 1977; Larcher 1983; Koike 1986). The light compensation point (i_c) is determined by two physiological factors, dark respiration rate (r) and initial slope (ϕ) of photosynthetic light response curve, and is reduced by an increase in ϕ or a decrease in r (Hashimoto 1991). In saplings of *T. dolabrata* var. *hondai* and *Q. mongolica* var. *grosseserrata*, the values of ϕ at mean temperature in each month were almost at the same level except for July in which the latter ones showed higher values (Fig. 3). Accordingly, i_c at the mean temperature of each season changed mainly due to variations of r with each season. Values of r tended to show relatively stable values in summer to autumn; the changes of r from spring to summer could be understood also as the acclimatization process of leaf respiration to changing light regimes after the leaf expansion of canopy trees. The value of r was in the range of 0.15 to 0.23 μmol CO_2 m^{-2} s^{-1} after August, and large differences were not recognized between the two tree

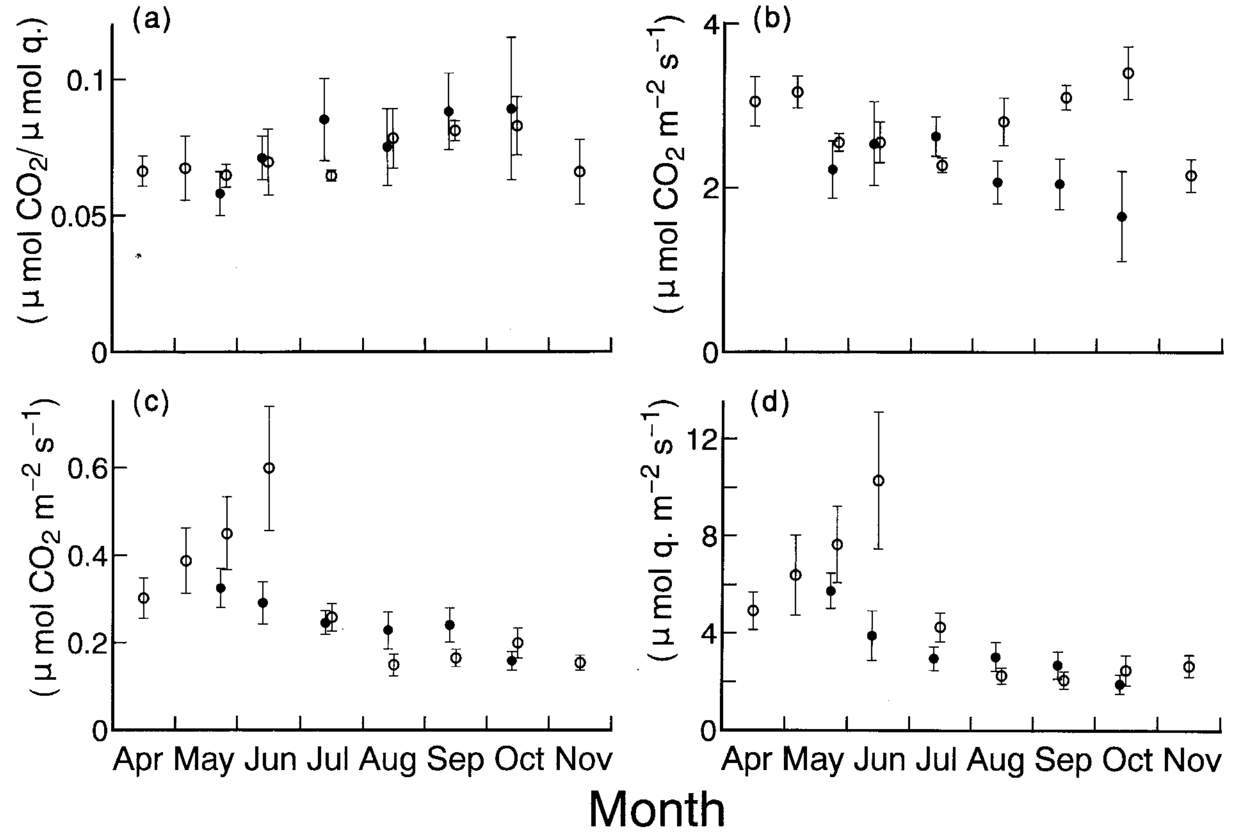

Fig. 3. Seasonal courses of (a) initial slope (ϕ), (b) light-saturated net photosynthesis (p_{max}), (c) dark respiration (r), and (d) light compensation point (i_c) of *T. dolabrata* var. *hondai* (○) and *Q. mongolica* var. *grosseserrata* (●) leaves at the mean temperature of each month. Circles and vertical bars show means and SD, respectively. These values were calculated from the curve fitted to the data (for details, see Methods section). The value of mean temperature at each month was calculated by the interpolation of the values measured at every 5 °C.

species. As a result, the means of i_c after August were almost the same, 2.4 and 2.6 μmol q · m^{-2} s^{-1} in *T. dolabrata* var. *hondai* and *Q. mongolica* var. *grosseserrata*, respectively.

The value of ϕ, directly linked with photosynthetic quantum efficiency in leaf chloroplasts, is considered one of the most important physiological factors, especially for plants growing under poor light conditions. It has been known that ϕ differs among woody plant species growing in the same forest floor (Hashimoto 1993). However, as described above, there were no large interspecific differences in ϕ except for July. For p_{max}, on the other hand, *T. dolabrata* var. *hondai* showed values higher than or almost equal to those of *Q. mongolica* var. *grosseserrata* throughout the growing season. Accordingly, saplings of *T. dolabrata* var. *hondai* might be able to more efficiently utilize high intensity light such as sunflecks although examinations are required on the leaf photosynthetic response to transient light and the leaf photo-inhibition (Pearcy 1990; Chazdon & Pearcy 1991).

Leaf CO_2 balance

The total amount of daily gross photosynthesis of leaves (P_g) in the whole growing season was 7600 mmol CO_2 m^{-2} in *T. dolabrata* var. *hondai* and 3100 mmol CO_2 m^{-2} in *Q. mongolica* var. *grosseserrata*; the latter was only 41% of the former (Figs 4, 5). The total amount of daily dark respiration (R) was 5300 and 3200 mmol CO_2 m^{-2} in *T. dolabrata* var. *hondai* and *Q. mongolica* var. *grosseserrata*, respectively, and so the surplus production was 2300 mmol CO_2 m^{-2} in the former while it was − 100 mmol CO_2 m^{-2}, slightly negative, in the latter (Fig. 6). These results support the high survivability in *T. dolabrata* var. *hondai* sap-

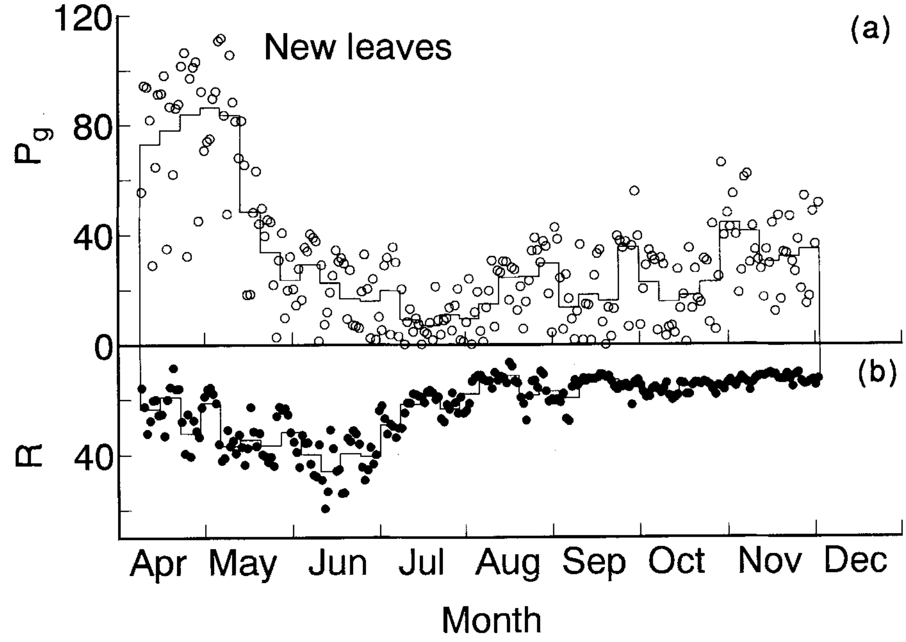

Fig. 4. Seasonal courses of (a) daily gross photosynthesis (P_g) and (b) daily respiration (R) in leaves of *T. dolabrata* var. *hondai* saplings. Horizontal bars show weekly means. Measurements are in mmol CO_2 m^{-2} day^{-1}.

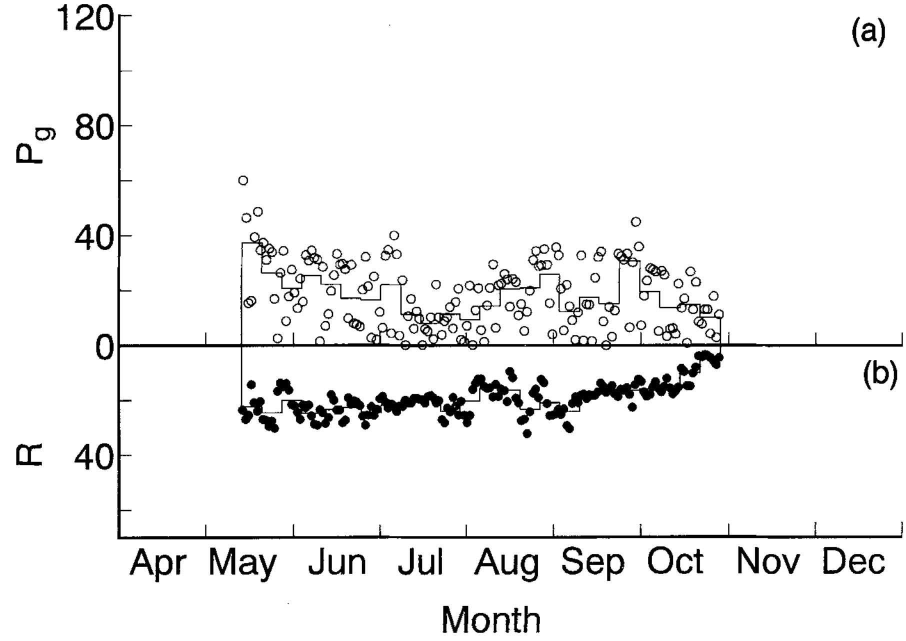

Fig. 5. Seasonal courses of (a) daily gross photosynthesis (P_g) and (b) daily respiration (R) in leaves of *Q. mongolica* var. *grosseserrata* saplings. Horizontal bars show weekly means. Measurements are in mmol CO_2 m^{-2} day^{-1}.

lings and the high mortality in *Q. mongolica* var. *grosseserrata* saplings (Table 1).

The saplings of *T. dolabrata* var. *hondai*, because of the attached evergreen leaves, perform photosynthetic production actively under the bright light environment in the two periods, from the time of the snow cover disappearance to the foliage emergence of the overstory deciduous trees and from the defoliation of those trees to the snow fall (Fig. 6; Lassoie *et al.* 1983). Leaf expansion and leaf fall seasons of the saplings, however, almost coincided with that of the overstory trees in *Q. mongolica* var. *grosseserrata*. The saplings were thus shaded by the overstory trees in the whole growing season. It would appear difficult for *Q. mongolica* var. *grosseserrata* to survive for long periods under closed canopies (Imada 1974; Kanazawa 1982; Sakurai & Saito 1983). As is shown in Fig. 6, negative values of P_n were prominent in the rainy season from the end of June till the end of July when PPFD

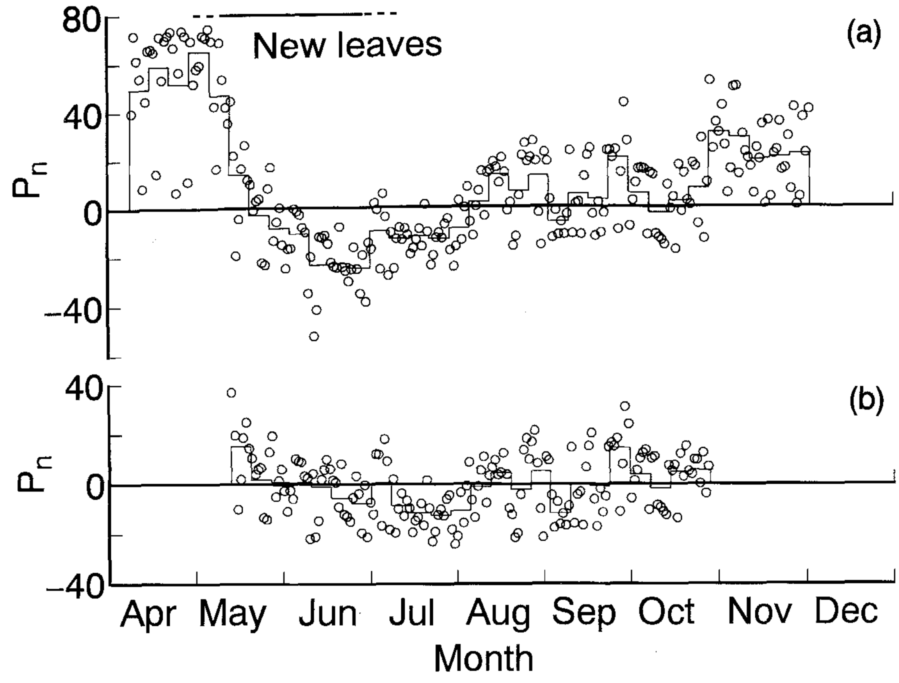

Fig. 6. Seasonal courses of daily surplus production (P_n) in leaves of (a) *T. dolabrata* var. *hondai* and (b) *Q. mongolica* var. *grosseserrata* saplings. Horizontal bars show weekly means. Measurements are in mmol CO_2 m^{-2} day^{-1}.

apparently decreased. Therefore, there is a possibility that the low PPFD in the rainy season works fatally on the survivorship of *Q. mongolica* var. *grosseserrata* saplings through the deterioration of CO_2 balance.

Carbon balance in individual level

The *T. dolabrata* var. *hondai* saplings tended to show active lateral elongation, rather than height growth, in some primary branches attached at the lower part of the stem axis (Hashimoto & Ishii 1990). This sort of branch takes a creeping form of growth, which is reinforced by the effect of snow pressure in the winter time, and occasionally generates roots from the grounding part to produce a new individual. This is the so called creeping branch propagation method (Yamanouchi 1936; Satoo 1955). According to a previous study (Hashimoto & Ishii 1990), more than 80% of the saplings had no underground connection to the other individuals: besides, the decay of the underground connection part was observed for most individuals originating from creeping branches. It is therefore considered that most of the saplings dealt with here were independent with respect to the material balance at an individual level.

Most of the *T. dolabrata* var. *hondai* saplings sampled here (15–30 cm in height) had stem lengths of 30–50 cm (Table 6). The respiration of branches and stems for these saplings is equivalent to about 22% of that of the leaves on average from

Table 6. Dry weights and mean respiration rates of above ground parts of *T. dolabrata* var. *hondai*.

Stem length (cm)	Sample size	Weight (g) Stem	Branch	Leaf	C/F ratio	Data size	Respiration rate C (nmol CO_2 g^{-1} s^{-1}) June	Sept.	F June	Sept.
0–30	12	7.2 (2.5)	5.6 (1.6)	26.0 (4.4)	0.46 (0.10)	–				
30–50	41	8.5 (3.2)	6.8 (2.8)	27.7 (7.0)	0.59 (0.23)	4	0.65 (0.06)	0.38 (0.06)	1.86 (0.29)	0.88 (0.11)
50–	11	13.9 (8.5)	8.8 (5.6)	32.2 (9.4)	0.76 (0.39)	–				

The figures in parentheses represent the SD.
F and C represent the photosynthetic (leaf) and non-photosynthetic (branch and stem) parts, respectively.

data of the weights and respiration rates per unit weight for those parts. Assuming that the respiration of the underground part is about one-third of stems and branches (Hagihara & Hozumi 1981), about 77% of the whole respiration of the individual level is ascribed to leaves. As the total amounts of daily gross photosynthesis (P_g) and dark respiration (R) in leaves in the whole growing season are estimated to be 7600 and 5300 mmol CO_2 m^{-2}, respectively, the CO_2 balance on individual level is expressed as $7600L - 5300L/0.77 = 717L$ (mmol CO_2), where L represents the total leaf area per individual. Assuming that the respiratory consumption is negligible in the winter time (Negisi 1966), it follows that about 10% of the gross photosynthetic production is accumulated as growth or storage material.

The ratio of surplus production to gross production on an annual basis seems to range from 40 to 60% in some coniferous seedlings in the open (Negisi 1966) or *Abies veitchii* Lindl. seedlings in relatively bright forest floors (Matsumoto 1985). Accordingly the figure estimated here is never so high, but it explains the high survivability of *T. dolabrata* var. *hondai* saplings under deciduous trees. Considering that the density of the saplings was increasing (Table 1), via the creeping branch propagation method, their positive carbon balance not merely enabled them to survive but also contributed to the population.

Seedling mortality is extremely high in the early developmental stage of *F. crenata* (Nakashizuka 1988) and *Q. mongolica* var. *grosseserrata* (Kanazawa 1982). In contrast, the new individuals of *T. dolabrata* var. *hondai* produced by creeping branch propagation are considered to have extremely low mortality due to inheriting a matured photosynthetic system from the parent individual.

However, the C/F ratio, one of the key factors strongly affecting the CO_2 balance at the individual level, tends to rise with an increase in the size (Table 6). Therefore, the larger-sized individuals would suffer relatively larger carbon loss by respiratory consumption of non-photosynthetic parts.

Effects of phenology of overstory trees

The leaf expansion season differs between *Q. mongolica* var. *grosseserrata* and *F. crenata* (Maruyama 1978; Maruyama & Sato 1990); about 2 weeks later in *Q. mongolica* var. *grosseserrata* than in *F. crenata* in this study area. Assuming that the leaf expansion of the overstory trees starts 2 weeks earlier, similar to *F. crenata*, the annual surplus production of leaves is estimated to decrease 1600 mmol CO_2 m^{-2}, 70% of the original value. This reduction has a serious effect on the carbon balance at an individual level: the ratio of surplus production to gross production is lowered to a scarcely positive value. Therefore, the difference in starting time of leaf expansion of the overstory trees would appreciably affect the survival and abundance of *T. dolabrata* var. *hondai* saplings in cool temperate deciduous forests.

REFERENCES

Boardman N. K. (1977) Comparative photosynthesis of sun and shade plants. *Annual Review of Plant Physiology and Plant Molecular Biology* **28**: 355–377.

Causton D. R. & Dale M. P. (1990) The monomolecular and rectangular hyperbola as empirical models of the response of photosynthetic rate to photon flux density, with applications to three *Veronica* species. *Annals of Botany* 65: 389–394.

Chazdon R. L. & Pearcy R. W. (1991) The importance of sunflecks for forest understory plants. *Bioscience* 41: 760–766.

Fujishima S. (1948) *Lecture of Silviculture*. Yokendou, Tokyo (in Japanese).

Hagihara A. & Hozumi K. (1981) Respiration consumption by woody organs in a *Chamaecyparis obtusa* plantation. *Journal of the Japanese Forestry Society* 63: 156–164.

Hashimoto R. (1991) Analysis of light compensation point for CO_2 gas exchange of *Thujopsis dolabrata* var. *hondai* young growths growing on the forest floor. *Environment Control in Biology* 29: 167–177.

Hashimoto R. (1993) Photosynthetic responses to light intensity for saplings of some tree species growing in the shaded undergrowth of a *Quercus serrata* forest. *Environment Control in Biology* 31: 139–146.

Hashimoto R. & Ishii K. (1990) Growth and development of hiba (*Thujopsis dolabrata* var. *hondai*) young growths in a gap of mizunara oak–hiba forest. *Transactions of the 101st Annual Meeting of the Japanese Forestry Society*: 365–366 (in Japanese).

Hashizume H. (1991) Species ecology of buna. In: *Natural Environment and its Conservation on Buna (Fagus crenata) forest* (eds H. Murai, K. Yamaya, H.

Kataoka & M. Yui) pp. 53–64. Soft Science Inc., Tokyo (in Japanese).

Hinckley T. M., Teskey R. O., Duhme F. & Richter H. (1981) The water relations of the hardwood forest. In: *Water Deficits and Plant Growth* (ed. T. T. Kozlowski) pp. 153–208. Academic Press, New York.

Imada M. (1974) Study of the high forest system of mizunara (*Quercus crispula* Blume). *Bulletin of Kyushu University Forests* **45**: 81–226 (in Japanese with English summary).

Kanazawa Y. (1982) Some analyses of the reproduction process of a *Quercus crispula* Blume population in Nikko. I. A record of acorn dispersal and seedling establishment for several years at three natural stands. *Japanese Journal of Ecology* **32**: 325–331.

Koike T. (1986) Photosynthetic responses to light intensity of deciduous broad-leaved tree seedlings raised under various artificial shade. *Environment Control in Biology* **24**: 51–58.

Kozlowski T. T., Kramer P. J. & Pallardy S. G. (1991) *The Physiological Ecology of Woody Plants*. Academic Press Inc., San Diego.

Larcher W. (1983) *Physiological Plant Ecology*, 2nd edn. Springer-Verlag, Berlin.

Lassoie J. P., Dougherty P. M., Reich P. B., Hinckley T. M., Metcalf C. M. & Dina S. J. (1983) Ecophysiological investigations of understory eastern red cedar in Central Missouri. *Ecology* **64**: 1355–1366.

Lorimer C. G. (1989) Relative effect of small and large disturbances on temperate hard forest structure. *Ecology* **70**: 565–567.

Maruyama K. (1978) Ecological studies on natural beech forests. 32. Shoot elongation characteristics and phenological behavior of forest trees in natural beech forest. *Bulletin of Niigata University Forests* **11**: 1–30 (in Japanese with English summary).

Maruyama K. & Sato T. (1990) Ecological studies on natural beech forests. 38. Annual life histories of some woody species in summer-green forest at Nukumidaira (Preliminary report). *Bulletin of Niigata University Forests* **23**: 49–84 (in Japanese with English summary).

Matsuda K. (1985) Studies on the early phase of the regeneration of a Konara oak (*Quercus serrata* Thunb.) secondary forest. II. The establishment of current-year seedlings on the forest floor. *Japanese Journal of Ecology* **35**: 145–152.

Matsumoto Y. (1985) Photosynthetic production in *Abies veitchii* advance growths growing under different light environmental conditions. IV. Computed CO_2-balance based on simulation model and adaptation in photosynthetic production to different light condition. *Bulletin of Tokyo University Forests* **74**: 97–132 (in Japanese with English summary).

Murai S. (1951) Outline of forest vegetation in the Forest Management Department of Aomori. *Aomori Rinyu* **29**: 1–13 (in Japanese).

Nakashizuka T. (1988) Regeneration of beech (*Fagus crenata*) after the simultaneous death of undergrowing dwarf bamboo (*Sasa kurilensis*). *Ecological Research* **3**: 21–35.

Negisi K. (1966) Photosynthesis, respiration and growth in 1-year-old seedlings of *Pinus densiflora, Cryptomeria japonica* and *Chamaecyparis obtusa*. *Bulletin of Tokyo University Forests* **62**: 1–115.

Pearcy R. W. (1990) Sunflecks and photosynthesis in plant canopies. *Annual Review of Plant Physiology and Plant Molecular Biology* **41**: 421–453.

Sakurai S. & Saito K. (1983) Regeneration process of *Quercus mongolica* var. *grosseserrata*. II. Emergence and disappearance of the seedlings. *Transactions of the 94th Annual Meeting of the Japanese Forestry Society*: 365–366 (in Japanese).

Satoo S. (1955) Origin and development of adventitious roots in layered branches of 4 species of conifers. *Journal of the Japanese Forestry Society* **37**: 314–317.

Schaedle M. (1975) Tree photosynthesis. *Annual Review of Plant Physiology* **26**: 101–115.

Spies T. A. & Franklin J. F. (1989) Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. *Ecology* **7**: 543–545.

Tamiya H. (1951) Some theoretical notes on the kinetics of algal growth. *The Botanical Magazine, Tokyo* **64**: 167–173.

Washitani I. & Tang Y. (1991) Microsite variation in light availability and seedling growth of *Quercus serrata* in a temperate pine forest. *Ecological Research* **6**: 305–316.

Yamanouchi S. (1936) Experiments on the establishment of layer of Hiba. *Journal of the Japanese Forestry Society* **18**: 81–105 (in Japanese).