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Effects of Temperature and Light Conditions on Growth of Current-Year Seedlings of Warm-Temperate Evergreen Tree Species and Cool-Temperate Deciduous Tree Species

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1. Introduction

It is suggested that global warming affects plant distribution along latitudinal and altitudinal gradients because vegetation changes with thermal conditions. Simulation studies predicted that global warming largely affects plant distribution (e.g., Morin et al., 2008). Actually, vegetation change during several decades has been observed (Penuelas et al., 2007; Lenoir et al., 2008). By contrast, some other studies did not observe vegetation changes (Holtmeier & Broll, 2007; Harsch et al., 2009). Interpretation of results of simulation models also needs caution because simulation results are different according to modeling methods even for same species (Thuiller, 2003). Therefore, there is still uncertainty of effects of global warming on plant distribution.

Plant distribution is determined by integrated demographic processes such as seed dispersal, seed germination, growth and survival of individual plants. Since early demographic phase such as seedling establishment is more susceptible to environmental conditions than the adult phase (Kullman, 2002), it is important to clarify effects of temperature on seedling growth to predict effects of global warming on plant distribution. There are many experimental studies that examined effects of temperature on growth of tree seedlings (Danby & Hik, 2007; Hoch & Körner, 2009; Munier et al., 2010). For example, Yin et al. (2008) reported that seedling growth of *Betula albo-sinensis* increased in the warm condition with 0.51°C higher than the ambient air condition. Many experimental studies that examined effects of temperature were conducted at bright conditions (e.g. Danby & Hik, 2007; Way & Sage, 2008). However, most seedlings distribute in dark closed-canopy conditions in forests. Therefore, it is necessary to examine effects of temperature on seedling growth not only in bright conditions but also in dark conditions.

Plants plastically change morphology according to light conditions. For example, relative biomass allocation to leaves is greater in dark conditions than in bright conditions,

accompanied with reduction of leaf mass per area (LMA) (Ellsworth & Reich, 1992; Gould, 1993; Niinemets et al., 1999; Takahashi et al., 2005). These morphological changes increase light capture per plant, which is an adaptive strategy in dark conditions. Thus, plants adapt to changing environments through morphological plasticity. This study compared growth responses to temperature and light conditions among three species with different climatically distribution ranges. This comparison is important to clarify effects of global warming on distribution shift of vegetation.

Central Japan is a latitudinal vegetation ecotone between warm-temperate evergreen broad-leaved forests and cool-temperate deciduous broad-leaved forests. Ishigami et al. (2003) simulated net primary production (NPP) of forests by the modified model of BIOME3 (Haxeltine & Prentice, 1996). They predicted that NPP of warm-temperate evergreen broad-leaved forests is greater than that of cool-temperate deciduous broad-leaved forests above the current northern distribution limit of warm-temperate evergreen broad-leaved forests if air temperature is increased by global warming. According to the simulation result of NPP, Ishigami et al. (2003) suggested that the northern distribution limit of warm-temperate evergreen broad-leaved forests will move to the north. However, the northern distribution limit would not move to the north easily because of competition with existing northern vegetation (Kohyama & Shigesada, 1995). Therefore, it is important to compare growth responses of seedlings to temperature and light conditions between warm-temperate evergreen broad-leaved species and cool-temperate deciduous broad-leaved species to clarify vegetation changes due to global warming.

It is considered that warm-temperate evergreen broad-leaved species cannot distribute in the cool-temperate zone due to low winter temperature, not due to low summer temperature for the growth (Kira, 1949). Cold winter temperature decreases photochemical efficiency of leaves in warm-temperate evergreen broad-leaved species (Aranda et al., 2005; Taneda & Tatenos, 2005). Reduction of photochemical efficiency due to cold temperature is more conspicuous in bright conditions than dark conditions (Matsuki et al., 2003). Therefore, it is necessary to examine growth responses to temperature and light conditions not only during growth period but also during dormant period (winter) to clarify how temperature affects growth of warm-temperate evergreen broad-leaved species.

This study examined effects of temperature and light conditions on seedling growth of a warm-temperate evergreen broad-leaved species and two cool-temperate deciduous broad-leaved species to answer the following two questions.

- (1) Do the warm-temperate evergreen and cool-temperate deciduous broad-leaved species grow more in higher temperature and light conditions?
- (2) Do high temperature conditions mitigate reduction of photochemical efficiency in winter for the warm-temperate evergreen broad-leaved species?

2. Materials and methods

2.1 Study site

This study was conducted at the two sites in Nagano Prefecture, central Japan: the campus of Shinshu University (N36°15'04'', E137°58'41'', 630 m above sea level) in Matsumoto, and the Yatsugatake experimental forest (N35°56'40'', E138°28'11'', 1350 m a.s.l.) of Tsukuba University in Nobeyama (Fig. 1). The mean annual precipitation of Matsumoto was 1035.7 mm during 2000–2009. The mean annual temperature was 12.2°C. The mean monthly



Fig. 1. Distributions (areas surrounded by red lines) of *Quercus myrsinaefolia*, *Q. crispula* and *Betula platyphylla* var. *japonica* in Japan. Distributions of the two *Quercus* species and *B. platyphylla* var. *japonica* were redrawn from Horikawa (1972) and Okuyama (1982), respectively. Blue and green dots indicate locations of two study sites, Matsumoto and Nobeyama, respectively.

temperatures in January and in August were -0.3 and 24.8°C , respectively. The mean annual precipitation of Nobeyama was 1435.3 mm during 2000–2009. The mean annual temperature was 7.2°C . The mean monthly temperatures in January and in August were -5.4 and 19.2°C , respectively.

2.2 Study species

This study examined a warm-temperate evergreen broad-leaved species (*Quercus myrsinaefolia* Blume) and two cool-temperate deciduous broad-leaved species (*Betula platyphylla* var. *japonica* Hara and *Quercus crispula* Blume) (Fig. 1). *Q. myrsinaefolia* is a shade-tolerant tall tree species that distributes in the northern part of warm-temperate zone (Horikawa, 1972). *B. platyphylla* var. *japonica* and *Q. crispula* are shade-intolerant and mid-shade-tolerant tall tree species, respectively (Samejima, 1979; Koike, 1988; Masaki et al., 1992). *B. platyphylla* var. *japonica* and *Q. crispula* often form pure stands after disturbances such as strong wind, forest fire and clear cutting (Samejima, 1979; Kamitani, 1993; Namikawa et al., 1997).

Q. myrsinaefolia distributes below 700 m a.s.l. in the warm-temperate zone, and the northern distribution limit is about $\text{N}38^{\circ}$ (Horikawa, 1972). Distribution of *Q. myrsinaefolia* is limited to below 500 m a.s.l. in the north of $\text{N}36^{\circ}$. Although the southern part of Nagano Prefecture was the northern distribution limit of *Q. myrsinaefolia* (Horikawa, 1972), the distribution of *Q. myrsinaefolia* is recently observed in central part (Matsumoto area) of Nagano Prefecture probably because of escapes of seeds from planted *Q. myrsinaefolia* trees (Otsuka & Ozeki, 2008). *B. platyphylla* var. *japonica* distributes in central and northern Japan (Okuyama, 1981). *B. platyphylla* var. *japonica* distributes mainly at about 1000 m and 1300 m a.s.l. in Matsumoto and Nobeyama, respectively (Editorial Board of Flora of Nagano Prefecture, 1997). *Q. crispula* is one of the dominant species in cool-temperate deciduous broad-leaved forests, and widely distributes in the cool-temperate zone of Japan (Horikawa, 1972). *Q. crispula* distributes mainly at about 1000 m and 1300 m a.s.l. in Matsumoto and Nobeyama, respectively, like *B. platyphylla* var. *japonica*. Therefore, Matsumoto is the northern distribution limit for the warm-temperate evergreen species *Q. myrsinaefolia*, and Nobeyama is optimal thermal conditions for the two cool-temperate deciduous species *B. platyphylla* var. *japonica* and *Q. crispula*.

2.3 Seedling growth experiments

Growth experiments were conducted at Matsumoto and Nobeyama to examine effects of temperature and light conditions on the current-year seedling growth of *Q. myrsinaefolia*, *B. platyphylla* var. *japonica* and *Q. crispula*. A greenhouse experiment was also conducted at Matsumoto to make optimal temperature conditions for the warm-temperate evergreen *Q. myrsinaefolia* because Matsumoto is the northern distribution limit of this species. Windows of the greenhouse were opened in summer to avoid extreme rising of air temperature inside the greenhouse. Increase of air temperature in the greenhouse was 3°C on the average. Therefore, air temperature increased in the order of Nobeyama, Matsumoto and the greenhouse at Matsumoto. Nobeyama, Matsumoto and the greenhouse at Matsumoto are referred to T1, T2 and T3, respectively, in this study. Two light conditions (20% and 54% light) were set at each temperature condition by using shade cloth. 20% and 54% light conditions are referred to L1 and L2, respectively.

Species	Variables	T	L	T × L	n
Qm	Stem height	56.1***	< 0.1	0.3	99
	Stem diameter	16.1***	12.5***	0.2	46
	Dry mass	24.2***	15.1***	1.5	46
	LMA	3.5*	7.0*	1.2	47
Qc	Stem height	46.2***	3.1	1.3	94
	Stem diameter	18.0***	36.2***	1.6	94
	Dry mass	11.6***	14.2***	0.6	94
	LMA	32.4***	67.4***	0.4	93
Bp	Stem height	517.5***	0.4	1.0	120
	Stem diameter	768.0***	11.5***	1.3	120
	Dry mass	595.9***	49.5***	8.3***	117
	LMA	2.3	52.9***	2.3	109

*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

Table 1. ANOVA results of stem height, stem diameter, seedling dry mass and leaf mass per area (LMA) for *Quercus myrsinaefolia* (Qm), *Quercus crispula* (Qc) and *Betula platyphylla* var. *japonica* (Bp) to test three temperature conditions (T), two light conditions (L) and the interaction (T × L) on the four variables. F-values and the number of samples (n) are shown.

Seeds of *Q. myrsinaefolia*, *B. platyphylla* var. *japonica* and *Q. crispula* were collected in 2008. Seeds were sown in plastic pots (diameter 15 cm × height 13 cm) filled with horticulture soil and leaf mold. The number of pots was 20 for each light condition (L1 and L2) at each temperature condition (T1, T2 and T3) for each species. Seed sowing was conducted between late March and early April in 2009. However, seeds of *B. platyphylla* var. *japonica* were sown again at T1 in early June because seeds did not germinate. Pots were watered once a week or according to the need during the experiment period. All pots were randomly moved within each treatment once a week to minimize effects of pot position on seedling growth.

Seedlings of the three species were excavated and washed carefully in early October in 2009 after the cease of the current-year growth. In terms of *Q. myrsinaefolia*, only the half number of seedlings was excavated at each light and temperature condition, and the other seedlings were remained for the measurement of photochemical efficiency (see next paragraph). Stem diameter at the base and stem height were measured at the harvest for the three species. Seedlings were divided into stem, root and leaf, and then all leaves were scanned by using the free graphic software ImageJ (<http://rsbweb.nih.gov/ij/>) to measure total leaf area per seedling. Each organ was oven-dried at 80°C for two days, and was weighed.

The ratio of light-induced variable to maximum fluorescence of chlorophyll (Fv/Fm) of *Q. myrsinaefolia* was measured as a surrogate for photochemical efficiency of PSII (Demmig-Adams et al., 1989). Photochemical efficiency was measured around the noon once a month from summer of 2009 to the next summer by using a chlorophyll fluorometer OS-30p (Opti-Science, NH, USA). The measurement was conducted after 30 min of dark acclimation.

Two-way ANOVA was done to examine effects of temperature and light conditions on stem height, stem diameter, LMA and seedling dry mass (including root) for the three species (*Q. myrsinaefolia*, *B. platyphylla* var. *japonica* and *Q. crispula*).

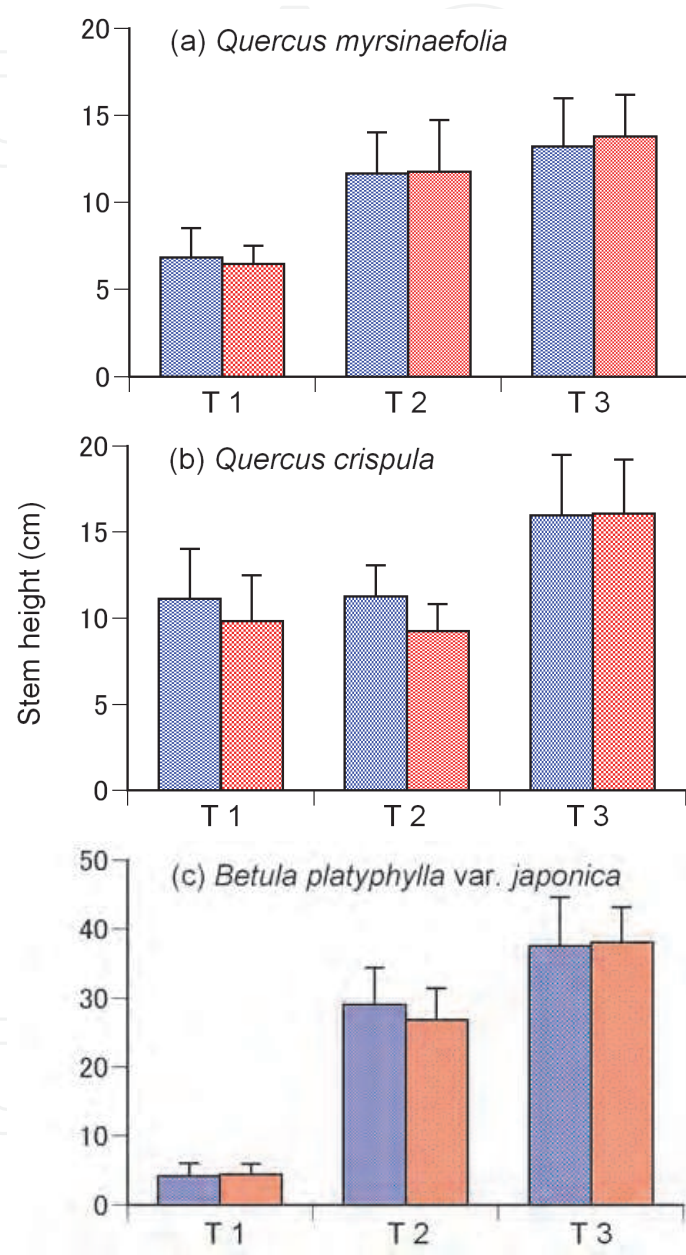


Fig. 2. Stem height for the three species at the three temperature and two light conditions. Blue and red bars indicate L1 and L2 light conditions, respectively. Mean values with positive standard deviations are shown.

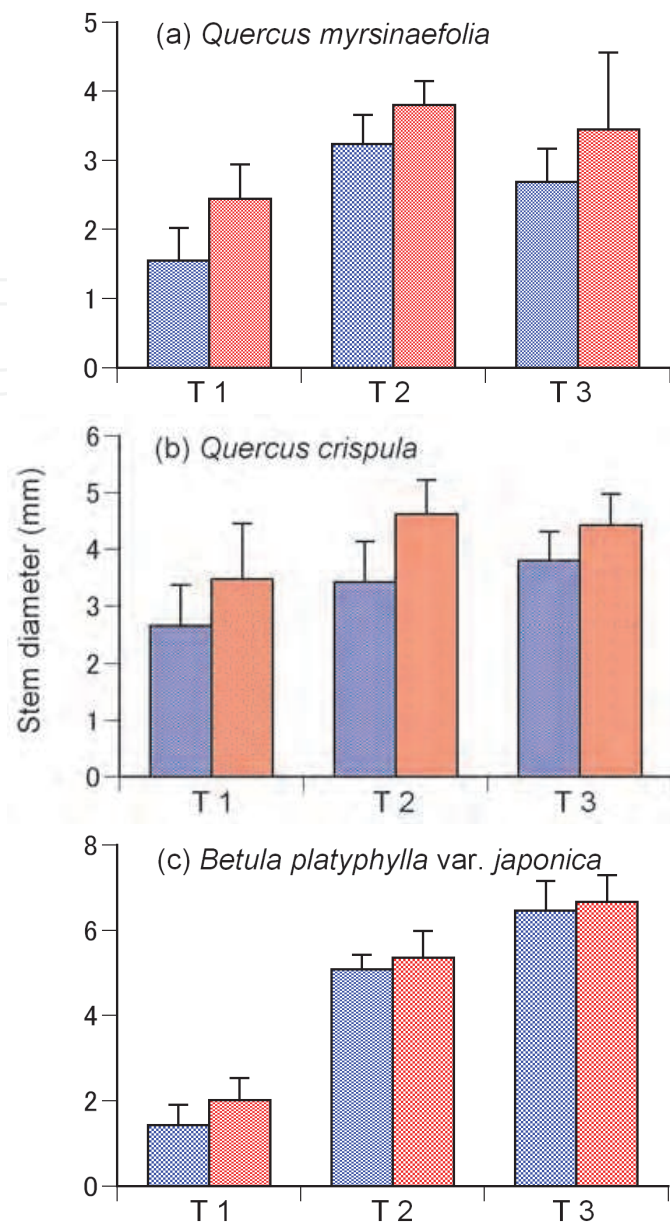


Fig. 3. Stem diameter for the three species at the three temperature and two light conditions. Blue and red bars indicate L1 and L2 light conditions, respectively. Mean values with positive standard deviations are shown.

3. Results

3.1 Growth of the three species

Effect of temperature on stem height was significant for the three species (Table 1), i.e., stem height was greater in higher temperature conditions, irrespective of light conditions (Fig. 2). However, stem height of *Q. crispula* was not different between T1 and T2 because of the shoot re-growth from the base after the shoot die-back in late May at T2. The difference in stem height of *Q. myrsinaeolia* between T2 and T3 was also not large (Fig. 2). Light conditions did not affect stem height for the three species (Table 1). By contrast, stem diameter of the three species was different not only among the three temperature conditions

but also between the two light conditions (Table 1). Stem diameter of the three species was greater at L2 than L1 for each temperature condition (Fig. 3). Stem diameter was greater at T2 and T3 than T1 for *Q. crispula*. Stem diameter of *B. platyphylla* var. *japonica* increased in the order of T1, T2 and T3. However, stem diameter of *Q. myrsinaefolia* was slightly smaller at T3 than T2 for the two light conditions.

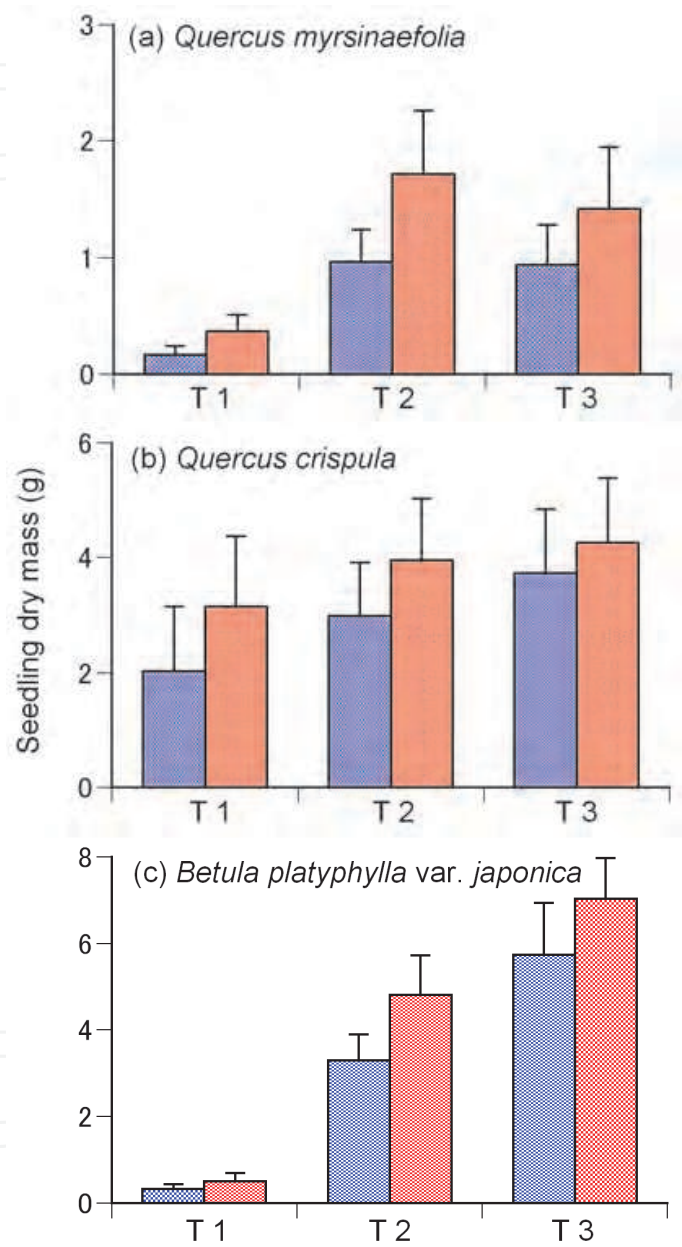


Fig. 4. Seedling dry mass for the three species at the three temperature and two light conditions. Blue and red bars indicate L1 and L2 light conditions, respectively. Mean values with positive standard deviations are shown.

Effects of temperature and light conditions on seedling dry mass were significant for the three species (Table 1), i.e., seedling dry mass was greater at higher temperature and brighter light conditions (Fig. 4). However, seedling dry masses of *Q. myrsinaefolia* at T3 were similar to and smaller than those at T2 for L1 and L2, respectively.

LMA was greater at L2 than L1 for the three species (Fig. 5, Table 1). LMA of *Q. myrsinaefolia* and *Q. crispula* was significantly different among the three temperature conditions (Table 1). Although LMA of the two species was greater at T2 than T1 and T3, the difference was not large (Fig. 5).

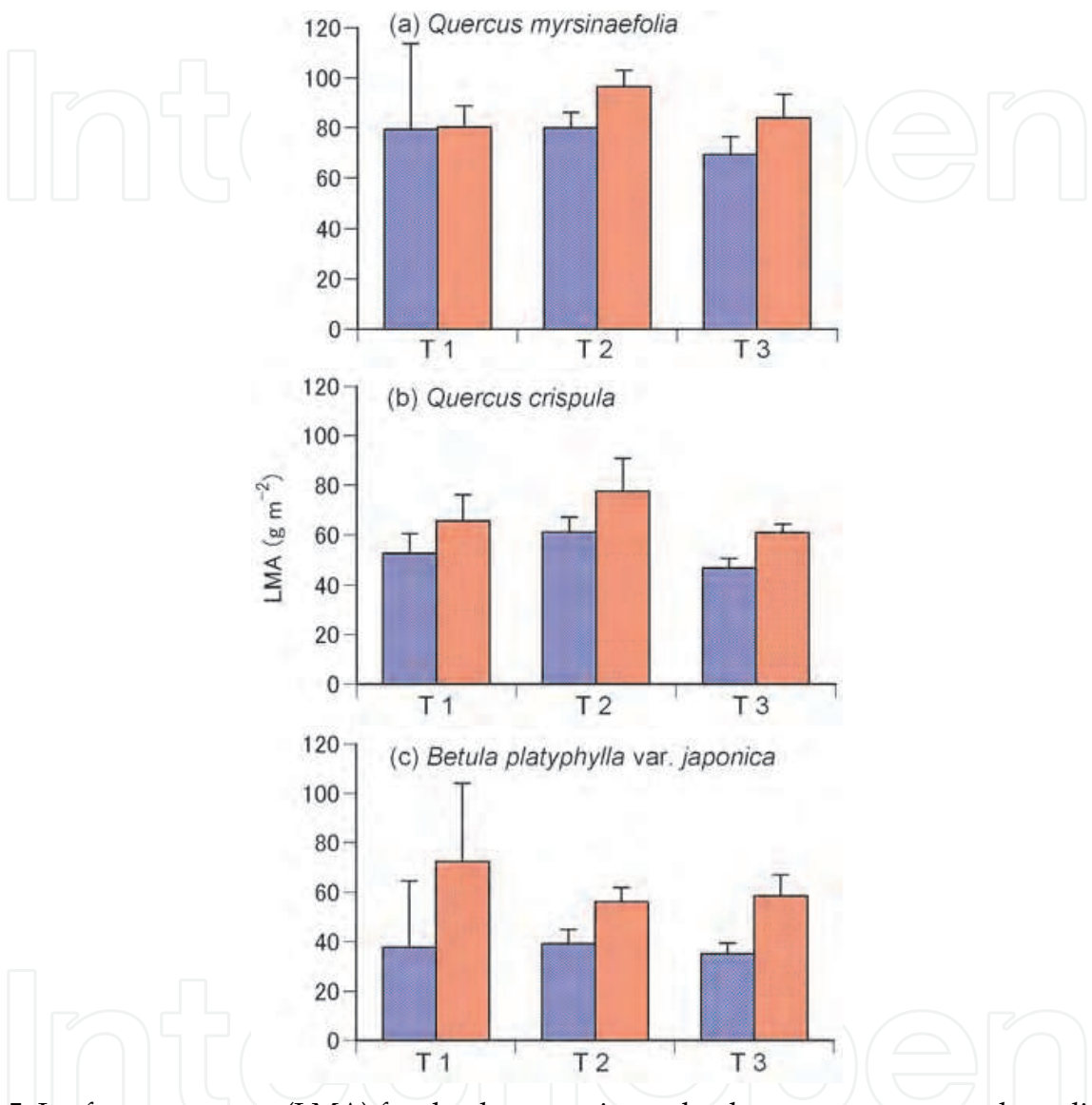


Fig. 5. Leaf mass per area (LMA) for the three species at the three temperature and two light conditions. Blue and red bars indicate L1 and L2 light conditions, respectively. Mean values with positive standard deviations are shown.

3.2 Photochemical efficiency of *Q. myrsinaefolia*

Values of photochemical efficiency (F_v/F_m) differed, according to temperature and light conditions and season (Fig. 6). In August of 2009, F_v/F_m values were similar between the two light conditions for the three temperature conditions. Although F_v/F_m value was about 0.8 at T3 in August, F_v/F_m values slightly decreased as temperature decreased from T3 to T1. F_v/F_m value was about 0.7 at T1 in August of 2009. F_v/F_m value decreased from autumn to winter in each temperature condition. This tendency was more conspicuous at L2

than L1 in each temperature condition. In addition, Fv/Fm value decreased to almost zero in February at T1, and all seedlings died by March (Fig. 7). By contrast, although Fv/Fm values decreased in winter at T2 and T3, these values increased again from spring to summer (Fig. 6) and the seedlings grew well by autumn (Fig. 8).

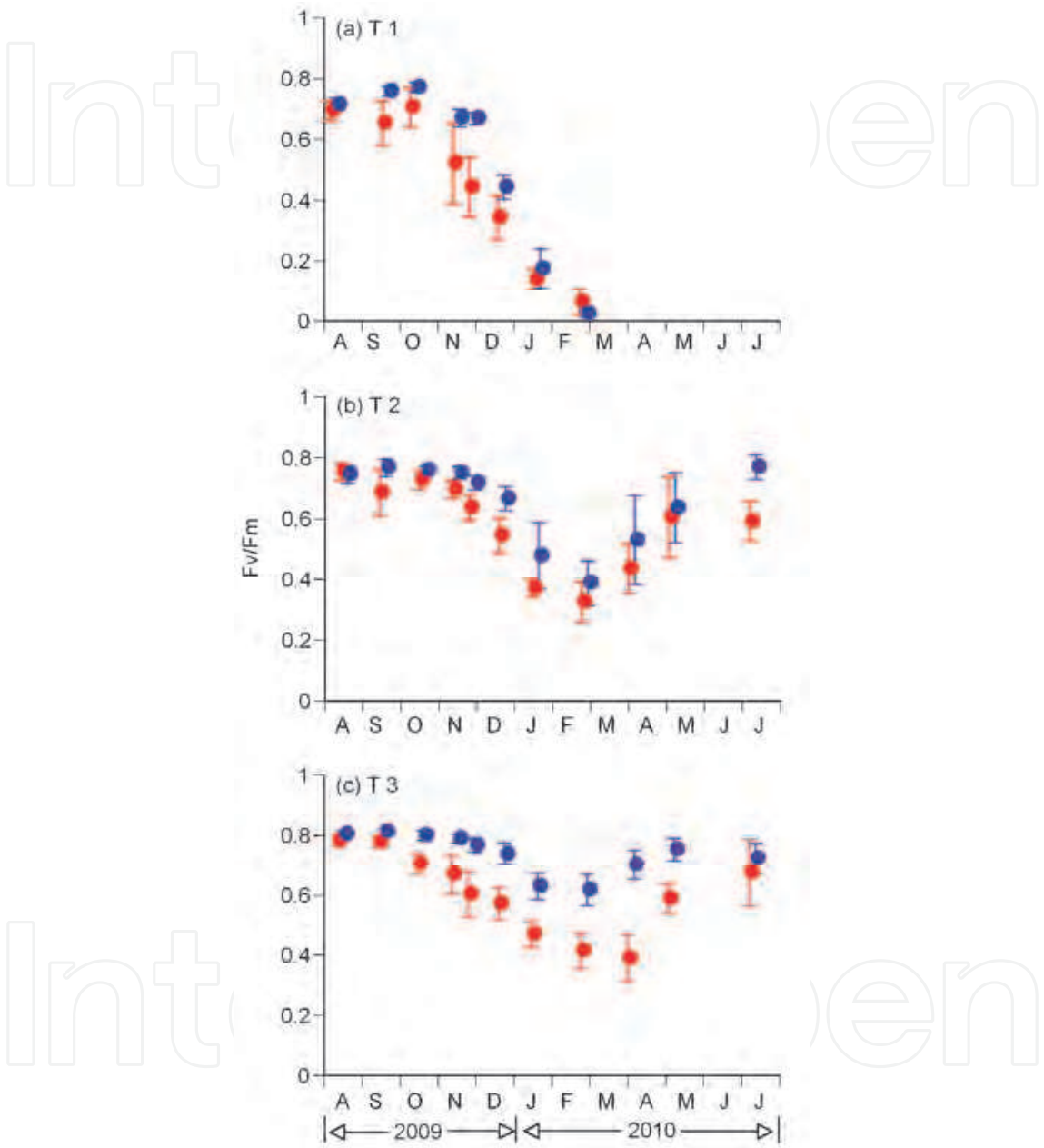


Fig. 6. Seasonal change of Fv/Fm of *Quercus myrsinaefolia* at three temperature and two light conditions. Blue and red circles indicate L1 and L2 light conditions, respectively. Mean values with standard deviations are shown.

4. Discussion

This study showed (1) that high temperature and light conditions increased the current-year seedling growth of the warm-temperate evergreen and the two cool-temperate deciduous

species, except for the effect of light on stem height, and (2) that high temperature mitigated reduction of photochemical efficiency (F_v/F_m) of *Q. myrsinaefolia* in winter. Furthermore, winter temperature was so cold at T1 for *Q. myrsinaefolia* that all seedlings of this species died in winter. Therefore, this study showed that high temperature and light conditions increased the seedling growth of the three species and survival of *Q. myrsinaefolia* in winter.

February 16



March 11



Fig. 7. A current-year seedling of *Quercus myrsinaefolia* at T1 with L1 light condition on February 16 and March 11, 2010. These photos were taken for a same seedling. Die-back was observed on March 11.

Light conditions did not affect stem height of the three species. Seiwa & Kikuzawa (1989) also reported that stem height of current-year seedlings was not different between bright and dark conditions for deciduous broad-leaved species with small seeds, while stem height was smaller in bright conditions than dark conditions for those of large seeds. Thus, stem height is not always taller in brighter conditions for current-year seedlings. This may reflect a survival strategy in forests. Litter accumulation on forest floor is a factor reducing seed germination and seedling survival (Goldberg & Werner, 1983). Therefore, the current-year seedlings germinated below litter layer have to grow over the litter layer. Furthermore, high growth of stem height is also advantageous for survival because of competition with other plants. Therefore, seedlings of the three species would preferentially grow stem height more than stem diameter in dark conditions as compared with bright conditions.

LMA was smaller at darker conditions for the three species at the three temperature conditions, which is advantageous for light capture efficiency per unit leaf mass. LMA of *Q. myrsinaefolia* and *Q. crispula* was also affected by temperature. Although LMA of the two

species tended to be greater at T2 than T1 and T3, these differences were not large. By contrast, Woodward (1979) observed that low temperature increased LMA of *Phleum bertolonii* and *P. alpinum* because of increase of cell diameter. Unfortunately, this study did not examine cell diameter of leaves at the three temperature conditions. However, it is possible that light dominates the control of LMA of the current-year seedlings of the three species, compared with temperature.



Fig. 8. A 1-year old seedling of *Quercus myrsinaefolia* at T3 with L1 light condition on October 14, 2010.

Many previous studies about effects of temperatures on plant growth have been conducted so far in cold environments such as alpine region and tundra (Chapin & Shaver, 1985; Molau, 1997; Arft et al., 1999; Hollister & Webber, 2000). It is often reported that high temperature increases plant growth in such cold environments (Chapin & Shaver, 1996; Takahashi, 2005), meaning that cold temperature limits plant growth. Increase of temperature enhances photosynthetic rates in cold environments because of temperature dependency of photosynthetic rates (DeLucia & Smith, 1987). Furthermore, high temperature throughout a year expands the growth period of plants (Chmielewski & Rotzer, 2001). Nevertheless, seedling dry mass, stem height and diameter of *Q. myrsinaefolia* at T3 were similar to or smaller than those at T2 (the temperature conditions of the northern distribution limit). This suggests that temperature during the growth period is not a major factor limiting the growth of *Q. myrsinaefolia*. Northern distribution limits of warm-

temperate evergreen broad-leaved forests tend to be determined by coldness in winter, not by warmth during the growth period (Kira, 1991). Thus, winter temperature may be important for the distribution of *Q. myrsinaefolia* along latitudinal gradients.

Increase of temperature clearly mitigated reduction of photochemical efficiency (F_v/F_m) of *Q. myrsinaefolia* during winter. This tendency was more conspicuous at brighter conditions. In forests, seedlings hardly grow in understory dark conditions, and grow vigorously in canopy gaps (Takahashi et al., 2001; Takahashi & Rustandi, 2006). Therefore, it is suggested that increase of photochemical efficiency of *Q. myrsinaefolia* by increase of temperature would enhance the growth in bright conditions. This effect may be large in the northern distribution limit of *Q. myrsinaefolia* because *Q. myrsinaefolia* co-dominates with many deciduous broad-leaved species there (Otsuka et al., 2004). Much light penetrates into forest floor in winter because of leaf fall of deciduous broad-leaved species. Understory seedlings and saplings of *Q. myrsinaefolia* can assimilate during winter after leaf fall of deciduous broad-leaved species, and the photosynthetic production during winter increases the growth and survival of *Q. myrsinaefolia* in the understory (Takenaka, 1986). Therefore, increase of winter temperature would enhance the growth and photochemical efficiency of *Q. myrsinaefolia* in the northern distribution limit.

The growth of the two cool-temperate deciduous broad-leaved species (*Q. crispula* and *B. platyphylla* var. *japonica*) was greater at T2 and T3 conditions than T1 (the optimal temperature conditions). Many studies showed that tree growth is greater nearer the southern and lower distribution limits along latitudinal and altitudinal gradients, respectively (Persson, 1998; Mäkinen et al., 2000; Li et al., 2003; Takahashi & Yoshida, 2009). Although the results of the previous studies were conducted in natural distribution ranges, the result of this study showed that tree growth increases in the temperature conditions warmer than the natural distribution range. Drought stress increases near southern and lower distribution limits (Buckley et al., 1997; Takahashi et al., 2003a; Adams & Kolb, 2005; Hart et al., 2010; Lebourgeois et al., 2010). On the contrary, increase of temperature prolongs the growth period (Sparks et al., 2000; Chmielewski & Rotzer, 2001; Fujimoto, 2008). Although increase of temperature induces drought stress to some extent, it would increase annual growth of plants by increasing annual carbon gain through increase of growth period.

The high growth of *Q. crispula* and *B. platyphylla* var. *japonica* at the two temperature conditions (T2 and T3) warmer than the current distribution range suggests that the natural distribution ranges of the two species are not determined by optimal temperature conditions alone (i.e., the concept of ecological niche). Although *Q. crispula* is a common species in old-growth deciduous broad-leaved forests (Masaki et al., 1992; Takahashi et al., 2003b), *Q. crispula* is recognized as a gap-dependent species (Yamamoto, 1989). It is reported that saplings of deciduous broad-leaved species distributed mainly in canopy gaps in an evergreen broad-leaved forest (Miura et al., 2001). In deciduous broad-leaved forests, understory saplings increase carbon gain by leafing before leaf expansion of canopy trees (Seiwa & Kikuzawa, 1996). However, understory of evergreen broad-leaved forests is dark conditions throughout a year, which have restricted saplings of deciduous broad-leaved species into canopy gaps. Therefore, actual distribution ranges are largely affected not only by temperature conditions but also by competition with other species (Takahashi, 2003).

5. Conclusion

This study predicted that high winter temperature mitigates the reduction of photochemical efficiency and reduces winter mortality of *Q. myrsinaefolia*. Furthermore, this study showed that increase of temperature enhances the growth of not only *Q. myrsinaefolia* but also *Q. crispula* and *B. platyphylla* var. *japonica*. It is possible that global warming intensifies competition between warm-temperate and cool-temperate broad-leaved species at their latitudinal ecotones. Therefore, it is unclear whether *Q. myrsinaefolia* will gain parts of the habitat now covered by *B. platyphylla* var. *japonica* and *Q. crispula* under global warming. This study examined only one warm-temperate broad-leaved species and two cool-temperate broad-leaved species, and the results of this study are not enough to show general responses of the two life forms to temperature and light conditions because of large variations in responses to temperature and light conditions within a life form (Parsons et al., 1994; Takahashi et al., 2003a; van der Werf et al., 2007). Therefore, it is necessary to analyze many species for each life form to clarify general growth responses to temperature and light conditions.

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This book addresses the theme of the impacts of global warming on different specific fields, ranging from the regional and global economy, to agriculture, human health, urban areas, land vegetation, marine areas and mangroves. Despite the volume of scientific work that has been undertaken in relation to each of these issues, the study of the impacts of global warming upon them is a relatively recent and unexplored topic. The chapters of this book offer a broad overview of potential applications of global warming science. As this science continues to evolve, confirm and reject study hypotheses, it is hoped that this book will stimulate further developments in relation to the impacts of changes in the global climate.

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