

EFFECTS OF ELEVATED CO₂ ON ABOVEGROUND GROWTH IN SEEDLINGS OF FOUR DOMINANT *QUERCUS* SPECIES

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Abstract. Seedlings of four *Quercus* species dominant in Korea (*Quercus mongolica*, *Quercus serrata*, *Quercus acutissima*, and *Quercus variabilis*) were grown at different CO₂ levels (ambient; 380 ppmv and enriched; 800 ppmv) to determine growth responses under elevated CO₂. Three weeks after germination, seedlings were transplanted into chambers and grown over a period of 105 days. Aboveground plant parts were harvested at the end of the experiment to measure dry weight, leaf area, specific leaf area (SLA), leaf area ratio (LAR), leaf weight ratio (LWR), and leaf quality (carbon, nitrogen). *Q. mongolica* exhibited increased growth, *Q. serrata* and *Q. acutissima* did not respond to enrichment, and the growth of *Q. variabilis* was diminished with elevated CO₂. Total aboveground biomass of each seedling increased by 31% for *Q. mongolica*, but for *Q. variabilis*, it decreased significantly by 39% under CO₂-enriched conditions ($p < 0.05$). SLA and LAR decreased, and LWR was unchanged or decreased slightly in the elevated CO₂ treatment for all species, with the exception of *Q. acutissima*. In addition, the elevated CO₂ treatment was correlated with a decrease in total N concentrations, and an increase in the C/N ratio of the leaves of *Q. mongolica* and *Q. acutissima*. In conclusion, plant growth responses to elevated CO₂ were species-specific, and they showed large interspecific variation.

Keywords: CO₂ enrichment, *Quercus*, tree growth, nitrogen, C/N ratio

Introduction

Since the industrial revolution, anthropogenic activities, such as fossil fuel use and deforestation, have caused a dramatic increase in the atmospheric CO₂ concentration. As a result, global climate change is accelerating and is a major concern worldwide.

In the preindustrial age, atmospheric CO₂ concentrations were approximately 280 ppm, increasing over time to reach the current level of 400 ppm (IPCC, 2014). This increase in atmospheric CO₂ is likely to continue due to anthropogenic activities and is expected to reach about 700 ppm by the end of the 21st century (Houghton et al., 2001; IPCC, 2007). As a result, extreme weather, desertification expansion, melting polar ice, rising sea levels, ecosystem destruction, and reduced species diversity are rapidly progressing, and the main cause is the increasing atmospheric CO₂ concentration (IPCC, 2007). According to IPCC Fourth Assessment Report, continuous greenhouse gas emissions at or above the current rates will cause further warming and serious changes in the global climate system in the 21st century.

Natural terrestrial and ocean ecosystems are absorbing more than half of the total anthropogenic CO₂ emissions (Tans et al., 1990; Fan et al., 1998; Canadell et al., 2007; Lal, 2008). Among them, the forest ecosystem is a major C sink in terrestrial ecosystems (Ceulemans et al., 1999), stores more than 50% of total terrestrial C, and

has a high potential for sequestration of atmospheric CO₂ (Dixon et al., 1994; Lorenz and Lal, 2010). In particular, temperate forests cover only 8% of the global land surface, but are known to account for about 40% of total terrestrial C uptake and play an important role for C sequestration of atmospheric CO₂ (Martin et al., 2001; Wamelink et al., 2009; Tyrrell et al., 2012). Many studies have focused on aboveground tree responses and have shown that increasing concentrations of atmospheric CO₂ may lead to changes in forest ecosystem structure and function through the direct effects of elevated CO₂ on tree physiology, development, and growth (Bazzaz, 1990; Jarvis, 1998; Ceulemans, 1999).

Forest comprise 64% of the total land area in Korea (Korea Forest Service, 2012), and tree species in the genus *Quercus* are dominant (Yim, 1977; Yim, 1995; Yang, 2001), covering about 27% of total forested area (Sim and Han, 2003). However, the effects of elevated CO₂ on the growth of dominant tree species and, relatedly, understanding C sequestration by terrestrial forest ecosystems are still not sufficiently studied in Korea. Accordingly, this study selected dominant deciduous tree species that occupied large areas and seem to be migrating to northern latitudes in response to warming caused by elevated CO₂ on the Korean peninsula. The seeds of *Q. mongolica*, *Q. variabilis*, *Q. serrata*, and *Q. acutissima* were germinated, and the seedlings were raised in ambient (380 ppm) and elevated CO₂ conditions (800 ppm). We harvested the plant at leaf falling season and analysed plant yield, growth parameters, and C and N concentrations in growing leaves because the C/N ratio is a measure of litter quality and is correlated with decomposition rates.

Materials and Methods

Study species

Quercus tree species are common on the Korea peninsula and distributed in most areas of the country, including the foothills and mountainous areas (Yim, 1977; Kim, 1990; Yim, 1995; Yang, 2001). Yang (2001) estimated that *Q. mongolica* occupied about 10% of total forested area, and the four species of oaks, *Q. mongolica*, *Q. variabilis*, *Q. serrata*, and *Q. acutissima*, occupied 72% of total deciduous forest area in South Korea. These oaks also determine ecosystem structure and functioning in temperate deciduous forest ecosystems on the Korean peninsula, and are situated in areas impacted by global warming caused by elevated CO₂.

Experimental design and treatments

The experiment was carried out in two growth chambers (2.4 m length × 1.2 m width × 1 m height) that controlled temperature, soil moisture, and CO₂ concentration in a green house. The control chamber was maintained at ambient CO₂ levels (380 ppmv) and the elevated CO₂ chamber was treated at twice the concentration of ambient CO₂ levels (approximately 800 ppmv). The CO₂ concentration in the chambers was regulated and monitored by an infrared gas analyzer (LI-840, LI-COR), and the plants were grown from April to September. Air temperatures in the chambers were maintained near ambient temperatures at 25 ± 3.1°C during the day and 19 ± 1.6°C during night. Seeds of the study species were provided by the Korean Forest Research Institute.

Seeds of the four species were sown in plastic trays and germinated at 25°C in an incubator. Three weeks after germination, seedlings of each species were transplanted

into a pot (1.2 m length × 0.6 m width × 0.3 m height) with an artificial soil mixture of peat moss and vermiculite (2:1, v/v). Transplanted seedlings were uniform in size; those that did not meet this requirement were excluded. Thirty individual seedlings of each species were transplanted from each pot into four individual pots filled with artificial soil mixture, which were placed in the chamber (in all, 240 seedlings in eight pots). Each pot was fertilized once before transplanting seedlings (N: 330 mg L⁻¹, P: 220 mg L⁻¹, K: 400 mg L⁻¹). The seedlings were watered twice a week to prevent water stress.

Plant growth analysis

Aboveground plant parts were harvested at 105 days from transplantation in the ambient and CO₂ elevated treatment chambers. Harvested plants were separated into stems and leaves, and then stems of individual plants were measured for height, and leaves were scanned to determine leaf area. Scanned leaf images were used to determine leaf area using an image-editing program (ImageJ Version 1.48; <http://rsb.info.nih.gov/ij/>). Separated plant parts were oven-dried for 4 days at 80°C, and then weighed.

The dry weight of each plant part and leaf area were used to calculate the following parameters:

Specific leaf area (SLA): leaf area / leaf dry weight (cm² g⁻¹)

Leaf area ratio (LAR): total leaf area / total plant dry weight (cm² g⁻¹)

Leaf weight ratio (LWR): total leaf weight / total plant dry weight (g g⁻¹)

The effects of elevated CO₂ on plant growth are presented as the percent change in biomass in the elevated CO₂ treatment compared to the ambient air treatment.

C and N analysis

The fresh leaves were sampled twice, at 40 and 80 days after transplantation, in both treatments to compare the impact of elevated CO₂ on leaf quality and C/N ratio. The plant samples were oven-dried for 4 days at 80°C and ground in a ball-mill. C and N concentrations were then determined by an automatic element analyzer (Flash EA 1112 series, Thermo Fisher Scientific).

Statistical analysis

Statistically significant differences between treatments were determined using *t*-tests with SPSS (ver. 12.0.1). The *t*-tests were used to identify significant differences (*p* < 0.05) in the morphological characteristics and growth parameters of the four species, and the chemical content (carbon, nitrogen and C/N ratio) of two of these species (*Q. mongolica* and *Q. acutissima*). Principal component analysis (PCA) was performed to study the effects of elevated CO₂ on morphological characteristics and growth of the four *Quercus* species using R v.2.15.3 (R Development Core Team, 2012). Data for the PCA analysis were converted to percent change in elevated CO₂ values relative to ambient values.

Results

Plant growth

Plant growth results for each oak species in ambient and elevated CO₂ conditions for one growing season are summarized in *Table 1*.

Table 1. Comparison of morphological characteristics and growth of four species (*Q. mongolica*, *Q. variabilis*, *Q. serrata*, and *Q. acutissima*) grown in ambient and elevated CO₂ chambers

	<i>Q. moglica</i>			<i>Q. variabilis</i>			<i>Q. serrata</i>			<i>Q. acutissima</i>		
	Ambient	Elevated CO ₂	<i>p</i>	Ambient	Elevated CO ₂	<i>p</i>	Ambient	Elevated CO ₂	<i>p</i>	Ambient	Elevated CO ₂	<i>p</i>
Stem length (cm)	18.79 ±0.83	22.42 ±0.98	***	31.84 ±3.10	25.09 ±2.21	*	23.89 ±1.84	22.81 ±1.71	NS	50.57 ±1.52	48.19 ±1.81	NS
Leaf size (cm ² leaf ⁻¹)	12.59 ±0.75	14.12 ±0.82	NS	17.22 ±1.28	11.60 ±0.82	***	7.86 ±0.39	6.98 ±0.55	NS	18.77 ±0.81	18.24 ±0.80	NS
Leaf area (cm ² capita ⁻¹)	149.1 ±12.3	185.8 ±9.1	**	297.3 ±42.5	149.9 ±15.7	***	105.8 ±9.1	100.8 ±10.8	NS	461.3 ±20.7	426.2 ±27.7	NS
Leaf weight (g leaf ⁻¹)	0.068 ±0.004	0.080 ±0.005	*	0.091 ±0.008	0.077 ±0.006	NS	0.036 ±0.002	0.033 ±0.003	NS	0.091 ±0.004	0.093 ±0.004	NS
Stem biomass (g capita ⁻¹)	0.499 ±0.047	0.638 ±0.036	**	0.977 ±0.197	0.581 ±0.086	*	0.283 ±0.031	0.316 ±0.040	NS	1.720 ±0.114	1.473 ±0.125	NS
Leaves biomass (g capita ⁻¹)	0.796 ±0.066	1.058 ±0.060	***	1.625 ±0.257	0.999 ±0.115	**	0.482 ±0.042	0.472 ±0.055	NS	2.256 ±0.124	2.179 ±0.148	NS
Total aboveground biomass (g capita ⁻¹)	1.295 ±0.108	1.696 ±0.081	***	2.602 ±0.445	1.580 ±0.194	**	0.765 ±0.071	0.788 ±0.087	NS	3.976 ±0.229	3.651 ±0.263	NS

Difference of parameters within individual species has been tested by t-test. *: $p < 0.1$; **: $p < 0.05$; ***: $p < 0.01$; NS: not significant (mean ± standard deviation)

Q. acutissima showed the largest total aboveground biomass, *Q. mongolica* and *Q. variabilis* had intermediate levels, and *Q. serrata* exhibited the smallest amount of aboveground biomass at both CO₂ levels. The other growth characteristics of stems and leaves were different depending on the tree species.

Only *Q. mongolica* showed increased growth in the elevated CO₂ treatment compared with ambient (Fig. 1). Stem length and leaf area were significantly larger at elevated CO₂ compared to ambient conditions ($p < 0.05$). The mean size and weight of a single leaf showed an increase of approximately 12% and 18%, respectively, in the elevated CO₂ treatment, but this was not statistically significant. Stems, leaves, and total aboveground biomass of individual seedlings increased by 28%, 33%, and 31%, respectively relative to the ambient treatment ($p < 0.05$).

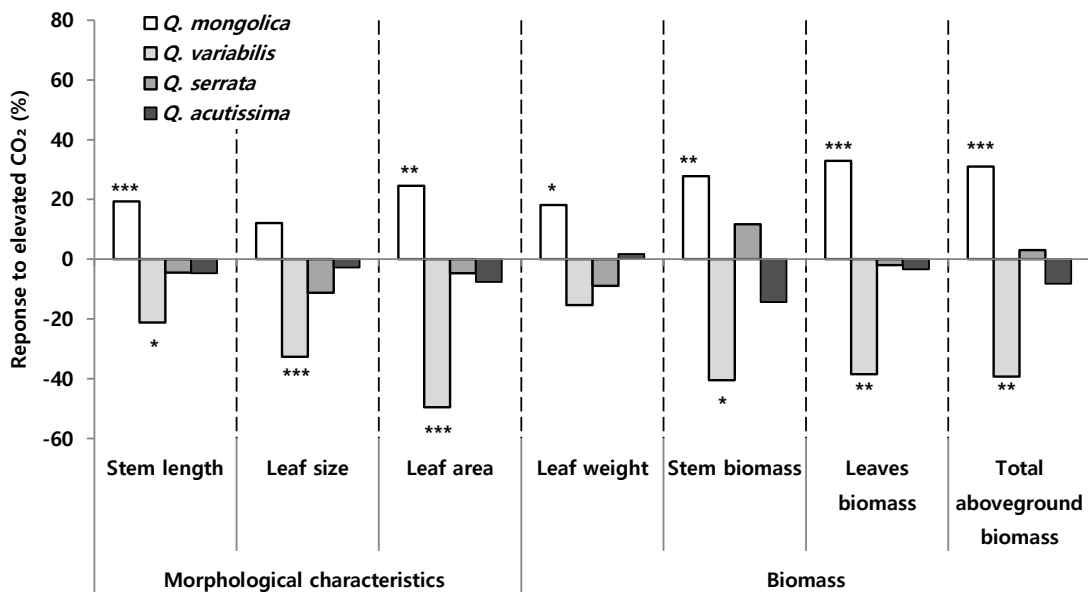


Figure 1. Percent response of morphological characteristics and growth of four species (*Q. mongolica*, *Q. variabilis*, *Q. serrata*, and *Q. acutissima*) to elevated CO₂. Species differences were determined by t-tests. *: $p < 0.1$; **: $p < 0.05$; ***: $p < 0.01$

Seedlings of *Q. serrata* and *Q. acutissima* did not respond to the elevated CO₂ treatment, and the growth responses were not statistically significant. However, there were patterns of decreases in morphological traits and growth in the elevated CO₂ treatment. Stem height and total aboveground biomass of *Q. serrata* increased by 11.7% and 3.1%, respectively, and leaf weight of *Q. acutissima* increased by 1.7% relative to ambient, which was not statistically significant.

On the other hand, the growth of *Q. variabilis* seedlings significantly decreased in the elevated CO₂ treatment (Fig. 1 and Table 1). Plant height and single leaf size significantly decreased by 21% and 33%, respectively, in the CO₂ enriched conditions ($p < 0.05$). Leaf area per capita decreased to 50% and the leaf weight of a single leaf also decreased, but there was no statistical significance. Stems, leaves, and aboveground biomass significantly decreased by 41%, 39%, and 39%, respectively, under CO₂ enriched conditions relative to ambient ($p < 0.05$; except for stem biomass: $p = 0.071$).

Biomass allocation patterns

The SLA of all species decreased in the elevated CO₂ treatment, and *Q. mongolica*, *Q. serrata*, and *Q. variabilis* showed significant differences between ambient and CO₂ enrichment conditions (Fig. 2). The LAR of all species also decreased in the elevated CO₂ treatment, and *Q. variabilis* and *Q. serrata* showed significant differences between ambient and elevated CO₂ treatments ($p < 0.05$). In addition, the LWR was also unchanged or decreased slightly in all species with no significant differences between the two CO₂ treatments, except for *Q. acutissima*, which showed increased LWR ($p < 0.05$). These results indicate that elevated CO₂ reduced the leaf area. However, there were trends of increased weight or mass of leaves by CO₂ enrichment.

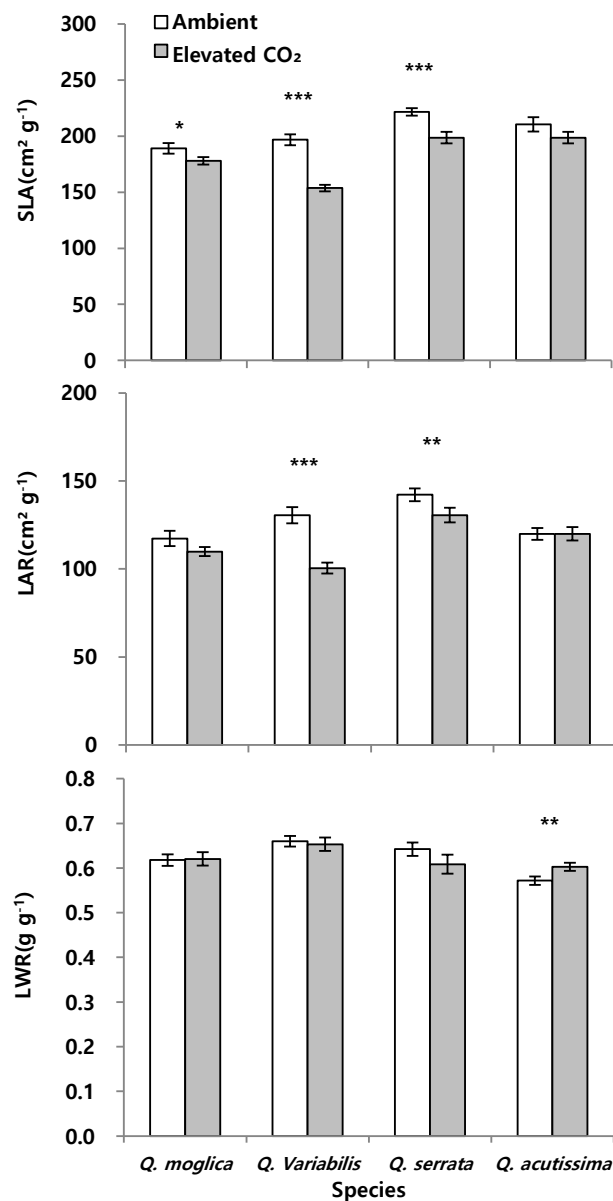


Figure 2. Specific leaf area (SLA), leaf area ratio (LAR), and leaf weight ratio (LWR) for four species (*Q. mongolica*, *Q. variabilis*, *Q. serrata*, and *Q. acutissima*) grown in ambient and elevated CO₂ chambers. Species differences were determined by *t*-tests. *: $p < 0.1$; **: $p < 0.05$; ***: $p < 0.01$

C and N concentrations

The changes in leaf C and N concentrations during plant growth are shown in Table 2. There were no significant differences in the C concentrations in all leaves between ambient and elevated CO₂, and ranged between 44% and 45% during the growing period. The total N concentration of *Q. mongolica* was 2.42% and 2.49% in the ambient, and 2.35% and 2.26% in the elevated CO₂ conditions at 40 days and 80 days, respectively. In *Q. mongolica*, the elevated CO₂ treatment reduced total N concentrations and increased the C/N ratio, however this was not statistically significant.

Table 2. C and N concentrations and C/N ratio of *Q. mongolica* and *Q. acutissima* leaves at 40 and 80 days during growth periods

	40 day			80 day		
	Ambient	Elevated CO ₂	<i>p</i>	Ambient	Elevated CO ₂	<i>p</i>
<i>Q. mongolica</i>						
C (%)	44.92±0.62	45.48±0.80	NS	44.62±0.30	44.32±0.68	NS
N (%)	2.42±0.20	2.35±0.43	NS	2.49±0.33	2.26±0.49	NS
C/N	18.60±1.42	19.87±4.00	NS	18.17±2.55	20.26±3.96	NS
<i>Q. acutissima</i>						
C (%)	45.85±0.23	45.66±0.81	NS	45.90±0.31	45.66±0.88	NS
N (%)	2.72±0.39	2.24±0.23	*	3.04±0.19	1.85±0.29	***
C/N	17.10±2.46	20.59±2.10	*	15.17±0.96	25.18±3.80	***

Difference of parameters within individual species has been tested by t-test. *: $p < 0.1$; **: $p < 0.05$; ***: $p < 0.01$; NS: not significant (mean ± standard deviation)

In *Q. acutissima*, total N concentrations were 2.72% and 3.04% in ambient, and 2.24% and 1.85% in elevated CO₂ at 40 days and 80 days, respectively, and the elevated CO₂ treatment significantly reduced total N concentrations in leaves. Therefore, the C/N ratio was increased by elevated CO₂ ($p < 0.01$), and the difference in the C/N ratio between the ambient and elevated CO₂ treatments increased with time.

PCA analysis

The results of the PCA to identify the relative effects of elevated CO₂ on each aboveground part and the morphological parameters of the four *Quercus* species are shown in Fig. 3. The horizontal PC1 axis elucidated 56.8% of the variation in all the factors, including factors related to growth in seedling height, growth in the mass of each plant part, and leaf area and weight. The vertical PC2 axis explained 21.9% of the variation in all the factors, and leaf area and leaf weight parameters (SLA, LAR, and LWR) are shown.

Q. mongolica formed a cluster to right side of the PC1 axis, which demonstrates that all aboveground growth components positively responded to elevated CO₂ conditions.

However, *Q. variabilis* clustered on the left side of the PC1 axis, and the growth components responded negatively to elevated CO₂ treatment. *Q. serrata* and *Q. acutissima* were widely distributed in each quadrant of the central axis, and growth was not affected by elevated CO₂. In particular, these patterns show very different responses to elevated CO₂ between each species studied.

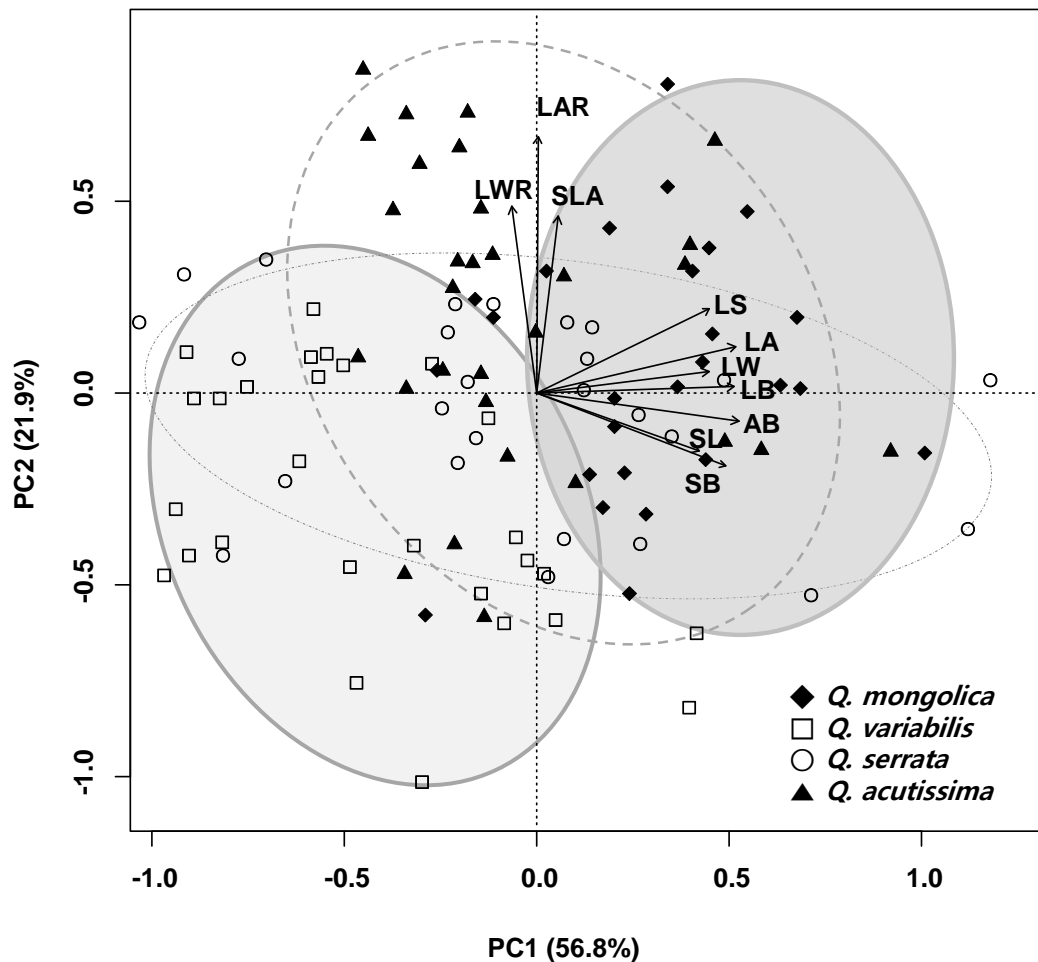


Figure 3. Principal component analysis on morphological characteristics and growth parameters of the four species (*Q. mongolica*, *Q. variabilis*, *Q. serrata*, and *Q. acutissima*) grown in the ambient and elevated CO₂ chambers. AB: aboveground biomass; LA: leaf area; LB: leaf biomass; LS: leaf size; LW: leaf weight; SB: stem biomass; SL: stem length

Discussion

Climate change due to increased atmospheric CO₂ is the biggest environmental issue facing humanity. Several problems are associated with this issue, including changes in primary production and C dynamics of natural ecosystems. To understand and recognize the changes in production and C dynamics, it is necessary to examine whether and how changes in growth and the chemical composition of plant species affect biogeochemical cycling caused by CO₂ elevation and climate change.

In the present study, oak species from the same genus exhibited different growth responses to elevated CO₂ (Fig. 1 and 3). Total aboveground biomass for *Q. mongolica*

increased by 31% relative to ambient CO₂ in response to elevated CO₂. However, the growth of aboveground biomass of *Q. variabilis* markedly decreased, and *Q. serrata* and *Q. acutissima* exhibited no significant response to elevated CO₂. Joel et al. (2001) suggested that the stimulation of plant growth by elevated CO₂ depends in part on the growth potential of individual plants or species. Each species responds very differently to elevated CO₂ for unknown reasons (Norby, 1996; Tanglely, 2001; Craine et al., 2003; Körner, 2005), including aboveground growth responses (Smith et al., 2013). The responses of plants to elevated CO₂ vary greatly depending on other environmental factors such as light, water, nutrients, and resource availability (Bazzaz and Carlson, 1984; Field et al., 1992; Hungate et al., 1997a, b). Moreover, elevated CO₂ has consistently shown positive effects on plants with mild temperature increases, but plant growth responses to elevated CO₂ vary under different temperature regimes, and can diminish with heat stress (Wang et al., 2012).

Although root responses to elevated CO₂ were not investigated in this study, many studies have reported that elevated CO₂ stimulates root growth (El Kohen and Mousseau, 1994; Crookshanks et al., 1998; De Graaff et al., 2006), and that the root/shoot ratio is significantly higher under elevated CO₂ than under ambient treatments (Luo et al., 2006; Nie et al., 2013). In a meta-analysis, root biomass exhibited larger increases than shoot biomass with elevated CO₂; therefore increasing root biomass with elevated CO₂ may enhance the potential to store C (De Graaff et al., 2006; Luo et al., 2006; Nie et al., 2013). In addition, these effects are expected to cause increased amounts of C input into the soil (De Graaff et al., 2006).

In addition, the increased atmospheric CO₂ concentrations caused significant leaf morphology changes (*Fig. 1* and *Table 1*). In the total area of leaves per capita and single leaf size, leaf biomass and dry weight showed variable responses to elevated CO₂ depending on the species. The results for *Q. mongolica*, which exhibited increased leaf area with elevated CO₂, were consistent with the findings of many studies (El Kohen and Mousseau, 1994; Ceulemans et al., 1995; Oksanen et al., 2001), and Gielen et al. (2001) even found that *Phyllostachys nigra* had a 225% increase in leaf area index. In contrast, *Q. serrata* and *Q. acutissima* exhibited no response to elevated CO₂, which is comparable to the findings of other studies (El Kohen and Mousseau, 1994; Gielen et al., 2001). Moreover, leaf area was found to be either reduced or unchanged with elevated CO₂ in a few studies (Mousseau and Enoch, 1989a, b), which is analogous to the negative response of *Q. variabilis*.

However, different patterns were observed with leaf growth and morphological characteristics. SLA and LAR decreased, and LWR was unchanged by elevated CO₂ in the present study (*Fig. 2*), which is consistent with the findings of other studies, although the effects are not always significant. In a meta-analysis of previous studies, plants exposed to elevated CO₂ exhibited a decrease in SLA of 6% (Ainsworth and Long, 2005) or 13% (Poorter and Navas, 2003), although this trend varied with plant functional group and species. Moreover, LAR decreased by an average of 13% in a meta-analysis of 130 studies (Poorter and Navas, 2003). In many C₃ plants, LWR remained unchanged (Poorter et al., 1996; Poorter and Navas, 2003) or decreased under elevated CO₂ conditions (Ishikawa, 2008). The reduction in SLA by elevated CO₂ is due to increases in leaf mass rather than leaf size (Yin, 2002), resulting in increased leaf density (Roumet et al., 1999). These results suggest that increases in leaf thickness and decreases in leaf size are consistent responses to elevated CO₂. Therefore, plants will potentially produce a smaller and thicker leaf owing to elevated CO₂.

Generally, plants, including trees, respond to elevated atmospheric CO₂ by enhanced net photosynthesis, growth, and dry mass production (Lemon, 1983; Strain and Cure, 1985; Jarvis et al., 1989), because CO₂ is used as a source for photosynthesis. Moreover, elevated CO₂ enhances growth rates to a greater extent in young seedlings than in mature trees (Tolley and Strain, 1985; Bazzaz et al., 1989). However, in our study, plant responses to elevated CO₂ were species-specific, and in some cases, there was no impact, or even a negative impact on growth. Therefore, the response of plants to elevated CO₂ is not consistent among species. The response of plants to elevated CO₂ depends largely on the spatial and temporal availability of other resources, in particular water and nutrients (Field et al., 1992).

The genus *Quercus* is distributed throughout South Korea, existing in different microclimates and has locally different distribution depending on species. In other studies, *Q. mongolica*, which exhibits increased growth with elevated CO₂, is the most shade-tolerant species among the oak species (Sim and Han, 2003). The growth of *Q. serrata* and *Q. acutissima* are unaffected by elevated CO₂ and grow well in higher light and moisture conditions than other *Quercus* species (Jeong et al., 2009; Lim et al., 2012). A meta-analysis of literature data revealed a greater growth response to elevated CO₂ in shade-tolerant species than in shade-intolerant species (Kerstiens, 2001). In contrast, *Q. variabilis*, which exhibited a negative response to elevated CO₂, reduced in growth rate with high levels of moisture, and preferred dry environmental conditions (Jeong et al., 2009). Cho et al. (2013) found that with elevated CO₂ levels, *Q. variabilis* has a reduced ability to cope with environmental changes. In this view, the negative response of *Q. variabilis* appears to be due to the reduction in the tolerance to environmental changes caused by elevated CO₂. The response to CO₂ enrichment might depend strongly on the response of specific species under varying patterns of environmental factors, such as precipitation and warming (Xu et al., 2014). Additionally, individual species and multifactor dependencies must be considered in a projection of terrestrial ecosystem response to climatic change (Xu et al., 2014).

On the other hand, increased CO₂ resulted in significantly lower N concentrations in leaf tissue, which led to high C/N ratios, whereas there was no effect of CO₂ on C concentrations (Billings et al., 2003). In a meta-analysis, leaf N concentrations decreased to 5.2–16.5% with elevated CO₂, regardless of temperature treatments (Curtis and Wang, 1998; Norby et al., 1999; Billings et al., 2003; Wang et al., 2012), and Cotrufo et al. (1998) found a 14% reduction in N concentrations in plant tissue with elevated CO₂. Reductions in litter N concentrations are expected to result in decreased litter decomposition rates (Cotrufo et al., 1995). In addition, the increased C/N ratio was strongly influenced by decreased N concentrations, because C concentration was unchanged with elevated CO₂ (Table 2). In many studies, increased C/N ratios have been observed in elevated CO₂ experiments (Johnson et al., 1997; Norby et al., 2001; Billings et al., 2003). Consequently, these leaf chemical changes, such as N concentrations and C/N ratio, are considered highly important factors because they are good predictors of decomposition rates (Melillo et al., 1982; Berg and Ekbohm, 1991; Gallardo and Merino, 1993; Bargali, 1996; Ganjegunte et al., 2004; Ge et al., 2013).

These results might indicate an increase in annual litter fall (Finzi and Schlesinger, 2002; Norby et al., 2002) and a decrease in decomposition on the forest floor caused by lower initial litter N concentrations with elevated CO₂ (Cotrufo et al., 2005) in temperate deciduous forests. Thus, elevated CO₂ levels in the atmosphere might increase the leaf litter layer, because leaves are not easily decomposed on the forest

floor (Cotrufo et al., 2005). These mechanisms might lead to a reduction in atmospheric CO₂ concentrations by the accumulation of C on the forest floor (Schlesinger and Lichter, 2001). Moreover, Norby and Cotrufo (1998) suggested that there is a potential for increased C sequestration in the terrestrial biosphere. However, Norby and Zak (2011) demonstrated that increased net primary production with elevated CO₂ does not necessarily increase ecosystem C storage. Therefore, future studies should focus on reductions in atmospheric CO₂ by organic matter accumulation on the forest floor in temperate deciduous oak trees, which are the dominant species on the Korean peninsula. To this end, well-thought-out research on the C balance between soil organic matter and decomposition of organic matter under the various environmental conditions of elevated atmospheric CO₂ is required.

Conclusions

The present study demonstrated that *Q. mongolica* exhibited a pattern of increasing growth under elevated CO₂ conditions, whereas *Q. serrata* and *Q. acutissima* did not exhibit a distinct pattern of change in growth with elevated CO₂, owing to great variation in responses to CO₂ enrichment. However, *Q. variabilis* exhibited a dramatic reduction in aboveground biomass to 40% in enriched CO₂ as compared to that in ambient CO₂. These results suggest a potential for future changes in the distribution areas of dominant species caused by climate change on the Korean peninsula. Consequently, there is a requirement for more research, particularly long-term research, on the effects of elevated CO₂ levels and other environmental changes on oaks, as this study was conducted in limited conditions with respect to elevated CO₂.

REFERENCES

- [1] Ainsworth, E.A., Long, S.P. (2005): What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. - *New Phytologist* 165: 351-372.
- [2] Bargali, S.S. (1996): Weight loss and N release in decomposing wood litter in a eucalypt plantation age series. - *Soil Biology and Biochemistry* 28: 699-702.
- [3] Bazzaz, F.A. (1990): The response of natural ecosystems to the rising global CO₂ levels. - *Annual Review of Ecology and Systematics* 21: 167-196.
- [4] Bazzaz, F.A., Carlson, R.W. (1984): The response of plants to elevated CO₂. - *Oecologia* 62: 196-198.
- [5] Bazzaz, F.A., Garbutt, K., Reekie, E.G., Williams, W.E. (1989): Using growth analysis to interpret competition between a C₃ and a C₄ annual under ambient and elevated CO₂. - *Oecologia* 79: 223-235.
- [6] Berg, B., Ekbohm, G. (1991): Litter mass-loss rates and decomposition patterns in some needle and leaf litter types. Long-term decomposition in a Scots pine forest. VII. - *Canadian Journal of Botany* 69: 1449-1456.
- [7] Billings, S.A., Zitzer, S.F., Weatherly, H., Schaeffer, S.M., Charlet, T., Arnone, J.A., Evans, R.D. (2003): Effects of elevated carbon dioxide on green leaf tissue and leaf litter quality in an intact Mojave Desert ecosystem. - *Global Change Biology* 9: 729-735.
- [8] Canadell, J.G., Le Quéré, C., Raupach, M.R., Field, C.B., Buitenhuis, E.T., Ciais, P., Conway, T.J., Gillett, N.P., Houghton, R.A., Marland, G. (2007): Contributions to accelerating atmospheric CO₂ growth from economic activity, carbon intensity, and

- efficiency of natural sinks. - Proceedings of the national academy of sciences 104: 18866-18870.
- [9] Ceulemans, R., Janssens, I.A., Jach, M.E. (1999): Effects of CO₂ enrichment on trees and forests: Lessons to be learned in view of future ecosystem studies. - Annals of Botany 84: 577-590.
- [10] Ceulemans, R., Jiang, X.N., Shao, B.Y. (1995): Growth and physiology of one-year old poplar (*Populus*) under elevated atmospheric CO₂ levels. - Annals of Botany 75: 609-617.
- [11] Cho, K.T., Jang, R.H., Lee, S.H., Han, Y.S., You, Y.H. (2013): Effects of global warming and environmental factors of light, soil moisture, and nutrient level on ecological niche of *Quercus acutissima* and *Quercus variabilis*. - Korean Journal of Ecology and Environment 46(3): 429-439.
- [12] Cotrufo, M.F., de Angelis, P., Polle, A. (2005): Leaf litter production and decomposition in a poplar short-rotation coppice exposed to free air CO₂ enrichment (POPFACE). - Global Change Biology 11: 971-982.
- [13] Cotrufo, M.F., Ineson, P., Roberts, J.D. (1995): Decomposition of birch leaf litters with varying C-to-N ratios. - Soil Biology and Biochemistry 27: 1219-1221.
- [14] Cotrufo, M.F., Ineson, P., Scott, A. (1998): Elevated CO₂ reduces the nitrogen concentration of plant tissues. - Global Change Biology 4: 43-54.
- [15] Craine, J.M., Reich, P.B., Tilman, G.D., Ellsworth, D., Fargione, J., Knops, J., Naeem, S. (2003): The role of plant species in biomass production and response to elevated CO₂ and N. - Ecology Letters 6: 623-625.
- [16] Crookshanks, M., Taylor, G., Broadmeadow, M. (1998): Elevated CO₂ and tree root growth: contrasting responses in *Fraxinus excelsior*, *Quercus petraea* and *Pinus sylvestris*. - New Phytologist 138: 241-250.
- [17] Curtis, P.S., Wang, X. (1998): A meta-analysis of elevated CO₂ effects on woody plant mass, form, and physiology. - Oecologia 113: 299-313.
- [18] De Graaff, M.A., Van Groenigen, K.J., Six, J., Hungate, B., Van Kessel, C. (2006): Interactions between plant growth and soil nutrient cycling under elevated CO₂: a meta-analysis. - Global Change Biology 12: 2077-2091.
- [19] Dixon, R.K., Solomon, A.M., Brown, S., Houghton, R.A., Trexler, M.C., Wisniewski, J. (1994): Carbon pools and flux of global forest ecosystems. - Science 263: 185-190.
- [20] El Kohen, A., Mousseau, M. (1994): Interactive effects of elevated CO₂ and mineral nutrition on growth and CO₂ exchange of sweet chestnut seedlings (*Castanea sativa*). - Tree Physiology 14: 679-690.
- [21] Fan, S., Gloor, M., Mahlman, J., Pacala, S., Sarmiento, J., Takahashi, T., Tans, P. (1998): A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. - Science 282: 442-446.
- [22] Field, C.B., Chapin, F.S., Matson, P.A., Mooney, H.A. (1992): Responses of terrestrial ecosystems to the changing atmosphere: a resource-based approach. - Annual Review of Ecology and Systematics 23: 201-235.
- [23] Finzi, A.C., Schlesinger, W.H. (2002): Species control variation in litter decomposition in a pine forest exposed to elevated CO₂. - Global Change Biology 8: 1217-1229.
- [24] Gallardo, A., Merino, J. (1993): Leaf decomposition in two Mediterranean ecosystems of southwest Spain: Influence of substrate quality. - Ecology 74: 152-161.
- [25] Ganjgunte, G.K., Condron, L.M., Clinton, P.W., Davis, M.R., Mahieu, N. (2004): Decomposition and nutrient release from radiata pine (*Pinus radiata*) coarse woody debris. - Forest Ecology and Management 187: 197-211.
- [26] Ge, X., Zeng, L., Xiao, W., Huang, Z., Geng, X., Tan, B. (2013): Effect of litter substrate quality and soil nutrients on forest litter decomposition: A review. - Acta Ecologica Sinica 33: 102-108.
- [27] Gielen, B., Calfapietra, C., Sabatti, M., Ceulemans, R. (2001): Leaf area dynamics in a closed poplar plantation under free-air carbon dioxide enrichment. - Tree Physiology 21: 1245-1255.

- [28] Houghton, J.T., Ding, Y., Griggs, D.J., Nogue, M., van der Linden, P.J., Dai, X., Maskell, K., Johnson, C.A. (2001): Climate change 2001: the scientific basis. - Cambridge University Press, Cambridge, UK
- [29] Hungate, B., Chapin III, F., Zhong, H., Holland, E., Field, C. (1997a): Stimulation of grassland nitrogen cycling under carbon dioxide enrichment. - *Oecologia* 109: 149-153.
- [30] Hungate, B.A., Lund, C.P., Pearson, H.L., CHAPIN III, F.S. (1997b): Elevated CO₂ and nutrient addition after soil N cycling and N trace gas fluxes with early season wet-up in a California annual grassland. - *Biogeochemistry* 37: 89-109.
- [31] IPCC (2007): Climate change 2007-the physical science basis - In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (ed.) Working group I contribution to the fourth assessment report of the IPCC. Cambridge University Press, Cambridge, UK,
- [32] IPCC. (2014): Climate change 2014-Impacts, adaptation, and vulnerability. Part A: Global and sectoral aspect - In: Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R., White, L.L. (ed.) Contribution of Working Group II to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, UK,
- [33] Ishikawa, S.I. (2008): Growth and Photosynthetic Responses of One C₃ and Two C₄ Chenopodiaceae Plants to Three CO₂ Concentration Conditions. - *Journal of Ecology and Environment* 31: 261-267.
- [34] Jarvis, P.G. (1998): European forests and global change: the likely impacts of rising CO₂ and temperature. - Cambridge University Press, Cambridge, UK
- [35] Jarvis, P.G., Morison, J.I.L., Chaloner, W.G., Cannell, M.G.R., Roberts, J., Jones, H.G., Amtmann, R. (1989): Atmospheric carbon dioxide and forests. - *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 324: 369-392.
- [36] Jeong, H.M., Kim, H.R., You, Y.H. (2009): Growth difference among saplings of *Quercus acutissima*, *Q. variabilis* and *Q. mongolica* under the environmental gradients treatment. - *Korean Journal of Environment and Ecology* 27(1): 82-87.
- [37] Joel, G., Chapin, F.S., Chiariello, N.R., Thayer, S.S., Field, C.B. (2001): Species-specific responses of plant communities to altered carbon and nutrient availability. - *Global Change Biology* 7: 435-450.
- [38] Johnson, D.W., Ball, J., T, Walker, R.F. (1997): Effects of CO₂ and nitrogen fertilization on vegetation and soil nutrient content in juvenile ponderosa pine. - *Plant and Soil* 190: 29-40.
- [39] Kerstiens, G. (2001): Meta-analysis of the interaction between shade-tolerance, light environment and growth response of woody species to elevated CO₂. - *Acta Oecologica* 22(1): 61-69.
- [40] Kim, J.W. (1990): A syntaxonomic scheme for the deciduous oak forests of South Korea. - *Abstracta Botanica* 14: 51-81.
- [41] Korea Forest Service (2012): Forestry statistics at a glance. - Korea Forest Service, Daejeon, Korea
- [42] Körner, C. (2005): An Introduction to the Functional Diversity of Temperate Forest Trees - In: Scherer-Lorenzen, M., Körner, C., Schulze, E.D. (ed.) *Forest Diversity and Function: Temperate and Boreal systems*. Springer, Berlin, Germany, 13-37
- [43] Lal, R. (2008): Carbon sequestration. - *Philosophical Transactions of the Royal Society B: Biological Sciences* 363: 815-830.
- [44] Lemon, E.R. (1983): CO₂ and plants. The response of plants to rising levels of atmospheric carbon dioxide. - Westview Press, Inc., Boulder, Colorado, USA
- [45] Lim, H., Kim, H.R., You, Y.H. (2012): Growth difference between the seedlings of *Quercus serrata* and *Q. aliena* under light, moisture and nutrient gradients. - *Journal of Wetlands Research* 14(2): 237-242.

- [46] Lorenz, K., Lal, R. (2010): Carbon sequestration in forest ecosystems. - Springer, New York
- [47] Luo, Y., Hui, D., Zhang, D. (2006): Elevated CO₂ stimulates net accumulations of carbon and nitrogen in land ecosystems: a meta-analysis. - *Ecology* 87: 53-63.
- [48] Martin, P.H., Nabuurs, G.J., Aubinet, M., Karjalainen, T., Vine, E.L., Kinsman, J., Heath, L.S. (2001): Carbon Sinks in Temperate Forests 1. - *Annual Review of Energy and the Environment* 26: 435-465.
- [49] Melillo, J.M., Aber, J.D., Muratore, J.F. (1982): Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. - *Ecology* 63: 621-626.
- [50] Mousseau, M. (1993): Effects of elevated CO₂ on growth, photosynthesis and respiration of sweet chestnut (*Castanea sativa* Mill.). - *Vegetatio* 104/105: 413-419.
- [51] Mousseau, M., Enoch, H.Z. (1989a): Carbon dioxide enrichment reduces shoot growth in sweet chestnut seedlings (*Castanea sativa* Mill.). - *Plant, Cell and Environment* 12: 927-934.
- [52] Mousseau, M., Enoch, H.Z. (1989b): Effect of doubling atmospheric CO₂ concentration on growth, dry matter distribution and CO₂ exchange of 2 yr old sweet chestnut trees (*Castanea sativa* Mill.). - *Annals of forest Science* 46: 506-508.
- [53] Nie, M., Lu, M., Bell, J., Raut, S., Pendall, E. (2013): Altered root traits due to elevated CO₂: a meta-analysis. - *Global Ecology and Biogeography* 22: 1095-1105.
- [54] Norby, R.J. (1996): Oaks in a high-CO₂ world. - *Annales des sciences forestieres* 53: 413-429.
- [55] Norby, R.J., Cotrufo, M.F. (1998): Global change: a question of litter quality. - *Nature* 396: 17-18.
- [56] Norby, R.J., Cotrufo, M.F., Ineson, P., O'Neill, E.G., Canadell, J.G. (2001): Elevated CO₂, litter chemistry, and decomposition: a synthesis. - *Oecologia* 127: 153-165.
- [57] Norby, R.J., Hanson, P.J., O'Neill, E.G., Tschaplinski, T.J., Weltzin, J.F., Hansen, R.A., Cheng, W., Wullschleger, S.D., Gunderson, C.A., Edwards, N.T. (2002): Net primary productivity of a CO₂-enriched deciduous forest and the implications for carbon storage. - *Ecological Applications* 12: 1261-1266.
- [58] Norby, R.J., Wullschleger, S.D., Gunderson, C.A., Johnson, D.W., Ceulemans, R. (1999): Tree responses to rising CO₂ in field experiments: implications for the future forest. - *Plant, Cell & Environment* 22: 683-714.
- [59] Norby, R.J., Zak, D.R. (2011): Ecological lessons from free-air CO₂ enrichment (FACE) experiments. - *Annual review of ecology, evolution, and systematics* 42: 181-203.
- [60] Oksanen, E., Sober, J., Karnosky, D.F. (2001): Impacts of elevated CO₂ and/or O₃ on leaf ultrastructure of aspen (*Populus tremuloides*) and birch (*Betula papyrifera*) in the Aspen FACE experiment. - *Environmental Pollution* 115: 437-446.
- [61] Poorter, H., Navas, M.L. (2003): Plant growth and competition at elevated CO₂: on winners, losers and functional groups. - *New Phytologist* 157: 175-198.
- [62] Poorter, H., Roumet, C., Campbell, B.D. (1996): Interspecific variation in the growth response of plants to elevated CO₂: a search for functional types - In: Körner, C., Bazzaz, F.A. (ed.) *Carbon dioxide, Populations and Communities*. Academic Press, New York, 375-412
- [63] Roumet, C., Laurent, G., Roy, J. (1999): Leaf structure and chemical composition as affected by elevated CO₂: genotypic responses of two perennial grasses. - *New Phytologist* 143: 73-81.
- [64] Schlesinger, W.H., Lichter, J. (2001): Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO₂. - *Nature* 411: 466-469.
- [65] Sim, J.S., Han, S.S. (2003): Ecophysiological characteristics of deciduous oak species (III) - Photosynthetic responses of leaves to change of light intensity. - *Journal of Korean Forestry Society* 93: 208-204.

- [66] Smith, A.R., Lukac, M., Hood, R., Healey, J.R., Miglietta, F., Godbold, D.L. (2013): Elevated CO₂ enrichment induces a differential biomass response in a mixed species temperate forest plantation. - *New Phytologist* 198: 156-168.
- [67] Strain, B.R., Cure, J.D. (1985): Direct effects of increasing carbon dioxide on vegetation. - United States Department of Energy, National Technical Information Service, Springfield, Virginia, USA
- [68] Tanglely, L. (2001): High CO₂ Levels May Give Fast-Growing Trees an Edge. - *Science* 292: 36-37.
- [69] Tans, P.P., Fung, I.Y., Takahashi, T. (1990): Observational constraints on the global atmospheric CO₂ budget. - *Science* 247: 1431-1438.
- [70] Tolley, L.C., Strain, B.R. (1985): Effects of CO₂ enrichment and water stress on gas exchange of *Liquidambar styraciflua* and *Pinus taeda* seedlings grown under different irradiance levels. - *Oecologia* 65: 166-172.
- [71] Tyrrell, M.L., Ross, J., Kelty, M. (2012): Carbon dynamics in the temperate forest - In: Ashton, M.S., Tyrrell, M.L., Spalding, D., Gentry, B. (ed.) *Managing Forest Carbon in a Changing Climate*. Springer, New York, 77-107
- [72] Wamelink, G.W.W., Wieggers, H.J.J., Reinds, G.J., Kros, J., Mol-Dijkstra, J.P., Van Oijen, M., De Vries, W. (2009): Modelling impacts of changes in carbon dioxide concentration, climate and nitrogen deposition on carbon sequestration by European forests and forest soils. - *Forest Ecology and Management* 258: 1794-1805.
- [73] Wang, D., Heckathorn, S.A., Wang, X., Philpott, S.M. (2012): A meta-analysis of plant physiological and growth responses to temperature and elevated CO₂. - *Oecologia* 169: 1-13.
- [74] Xu, Z., Shimizu, H., Ito, S., Yagasaki, Y., Zou, C., Zhou, G., Zheng, Y. (2014): Effects of elevated CO₂, warming and precipitation change on plant growth, photosynthesis and peroxidation in dominant species from North China grassland. - *Planta* 239(2): 421-435.
- [75] Yang, K.C. (2001): Classification of major habitats based on the climate conditions and topographic features in Korea. - Chung-Ang University, Seoul, Korea
- [76] Yim, Y.J. (1977): Distribution of forest vegetation and climate in the Korean peninsula. IV: Zonal distribution of forest vegetation in relation to thermal climate. - *Japanese Journal of Ecology* 27: 269-278.
- [77] Yim, Y.J. (1995): Composition and distribution of deciduous broad-leaved forests in Korea - In: Box, E.O., Peet, R.K., Masuzawa, T., Yamada, I., Fujiwara, K., Maycock, P.F. (ed.) *Vegetation Science in Forestry*. Kluwer Academic Publishers, Dordrecht, Netherlands, 273-298
- [78] Yin, X. (2002): Responses of leaf nitrogen concentration and specific leaf area to atmospheric CO₂ enrichment: a retrospective synthesis across 62 species. - *Global Change Biology* 8: 631-642.