

# Ecophysiological Responses of Northern Birch Forests to the Changing Atmospheric CO<sub>2</sub> and O<sub>3</sub> Concentrations

Korin Kawaguchi<sup>1)</sup>, Yasutomo Hoshika<sup>2)</sup>, Makoto Watanabe<sup>2)</sup> and Takayoshi Koike<sup>2)</sup>.\*

<sup>1)</sup>Graduate School of Agriculture, Hokkaido University, Sapporo, Hokkaido 060-8589, Japan

<sup>2)</sup>Research Faculty of Agriculture, Hokkaido University, Sapporo, Hokkaido 060-8589, Japan

\*Corresponding author. Tel: +81-11-706-3854, E-mail: [tkoike@for.agr.hokudai.ac.jp](mailto:tkoike@for.agr.hokudai.ac.jp)

## ABSTRACT

The effects on birch (*Betula* spp.) of elevated carbon dioxide (CO<sub>2</sub>) and ozone (O<sub>3</sub>), which are both increasing in the troposphere, are surveyed in detail based on the literature. Birches establish themselves in the open field after disturbances, and then become dominant trees in temperate or boreal forests. Ecophysiological approaches include the measurement of photosynthesis, biomass, growth, and survival of seedlings and trees. Elevated CO<sub>2</sub> levels give rise to a net enhancement of the growth of birch trees, whereas high O<sub>3</sub> generally reduces growth. Although the effects of the two are opposed, there is also an interactive effect. Basic physiological responses of the single genus *Betula* to CO<sub>2</sub> and O<sub>3</sub> are set out, and some data are summarized regarding ecological interactions between trees, or between trees and other organisms.

**Key words:** *Betula*, Elevated carbon dioxide, Ozone, Tree physiology, Forest ecology

## 1. INTRODUCTION

Recent changes in atmospheric composition are likely to have a large influence on forest ecosystems (Lorenz and Lal, 2010; Karnosky *et al.*, 2003a). In particular, in East Asia, the effects are likely to be serious because of rapid industrialization with emission of greenhouse gases. Interactions between the atmosphere and biosphere have been studied for an extended period (Quillet *et al.*, 2010; Fowler *et al.*, 2009; Räisänen and Tuomenvirta, 2009; Smith, 1990); the principal concerns are the increasing tropospheric concentrations of carbon dioxide (CO<sub>2</sub>) and ozone (O<sub>3</sub>) and their effect on future terrestrial ecosystems (IPCC, 2007; Sitch *et al.*, 2007). CO<sub>2</sub> is the substrate in photosynthesis but O<sub>3</sub> is toxic to plants. In considering forest

decline in Japan, it is necessary to examine the role of O<sub>3</sub> (Kume *et al.*, 2009; Tamura *et al.*, 2002). The atmospheric CO<sub>2</sub> concentration has steadily been increasing from 300 ppm at the beginning in 20<sup>th</sup> century to more than 390 ppm in 2011 (NOAA, 2012; IPCC, 2007), and it will reach 400 to 700 ppm at the year 2100 (IPCC, 2007). Tropospheric O<sub>3</sub> concentration also has increased by 0.5 to 2% per year at many monitoring stations around the world (Naja and Akimoto, 2004; Vingarzan, 2004), and in most areas of East Asia the O<sub>3</sub> concentration exceeded 40 ppb on yearly average (Nagashima *et al.*, 2010) and reached 60 ppb in spring-time (Nagashima *et al.*, 2010; Yamaji *et al.*, 2008). Ozone concentration in East Asia may reach 60 ppb on yearly average in 2020 (Yamaji *et al.*, 2008) or during the 21<sup>st</sup> century (Vingarzan, 2004).

Reliable data on the effects of elevated CO<sub>2</sub> and/or O<sub>3</sub> on forest health and vitality have come from open-top chambers (OTCs) or free-air concentration enrichment systems (FACEs), which are semi-closed and open gas-treatment systems respectively, in which plants are grown in the atmospheric conditions believed to be likely in the future (Karnosky *et al.*, 2007). In general, elevated CO<sub>2</sub> reduces stomatal conductance, and this may limit O<sub>3</sub> uptake and consequently alleviate the effects of O<sub>3</sub> on plants (Volin *et al.*, 1998).

Birch is the collective name for deciduous broad-leaved tree species in the genus *Betula*. There are more than 100 birch species (Govaerts and Frodin, 1998), and natural birch forests are broadly distributed across continents in the northern hemisphere: Eurasia (Hynynen *et al.*, 2010; Mao *et al.*, 2010; Zyryanova *et al.*, 2010; Alexeyev *et al.*, 2000), North America (Chapin *et al.*, 2006; Erdmann, 1990; Grelen, 1990; Lamson, 1990; Safford *et al.*, 1990), and Japan (Mao *et al.*, 2010).

Birches are commercially important species, as well as ecologically important. Following disturbances such as forest fires or clear cutting of forests, many birch trees establish themselves in the early stage of forest succession, because birch has light demanding traits

**Table 1.** Major tree genera in Hokkaido and their timber stocks and air-dried wood density.

Common name	Coniferous			Broadleaved		
	Fir	Larch	Spruce	Birch	Oak	Linden
Stock ( $\times 10^6 \text{ m}^3$ )	203 (28%)	93 (13%)	66 (9%)	81 (11%)	52 (7%)	39 (5%)
Density ( $\text{g/cm}^3$ )	0.40	0.50	0.43	0.67	0.68	0.50

Note: Values in parentheses express the proportion of total timber stock. Data on timber stock are from Hokkaido Prefecture (2011). Data on air-dried wood density are from FFPRI (2004) and refer to the following species: Fir: *Abies sachalinensis*, Larch: *Larix kaempferi*, Spruce: *Picea jezoensis*, Birch: *Betula maximowicziana*, Oak: *Quercus mongolica* var. *crispula*, Linden: *Tilia japonica*.

and high growth rate (Koike, 1988). As a result, birches play a key role in forest ecosystems, especially in boreal forests where the number of tree species is small. In Hokkaido, the northerly island in Japan, birch trees occupy about 11% of the total forest timber stock (Table 1), surpassing other genera in broadleaved forests (Hokkaido Prefecture, 2011). Moreover, birch has a high photosynthetic rate and responds rapidly to the environment (Koike, 1995a, 1988). Furthermore, birch wood is denser than that of almost all other dominant tree species in northern regions such as Hokkaido (FFPRI, 2004) and Alaska (Packee *et al.*, 1992). The birch tree therefore has good carbon (C) accumulation capacity as well as its C assimilation capacity. The birch is regarded as an important tree in forest dynamics as well as commercial point.

In this review we describe the effects of elevated concentrations of CO<sub>2</sub> and/or O<sub>3</sub> on birch trees and forests. Although sulfur dioxide and nitrogen oxide are still important issues of atmospheric environment in some region, rising CO<sub>2</sub> and O<sub>3</sub> concentrations have recently become more major concerns (Paoletti *et al.*, 2010). These gases have effects on forest ecosystems including birch forest all around the world. Additionally, we focus on the similarity and difference for the traits of CO<sub>2</sub> and O<sub>3</sub>, both gases are absorbed through stomata on leaves but they bring opposite effects on tree. Different species of birch are all regarded as 'birches' and there are differences in characteristics within a genus, and even among individuals in a single species, in response to environmental changes (Vapaavuori *et al.*, 2009).

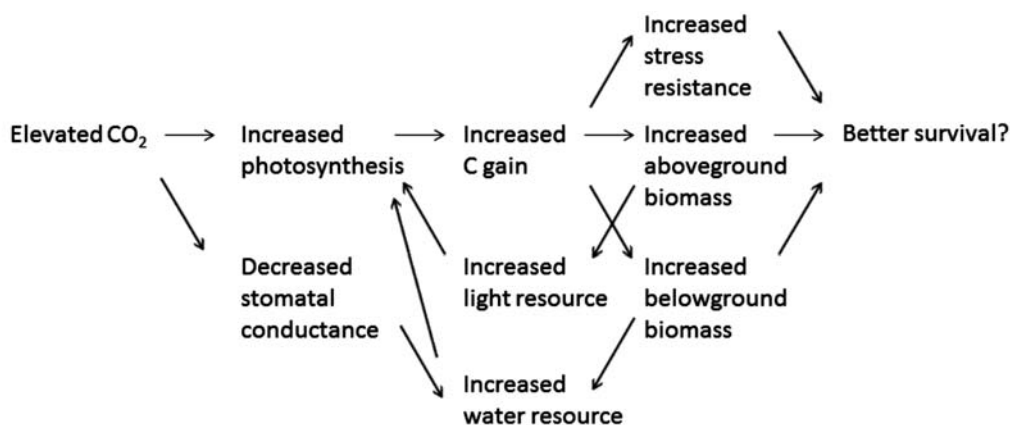
## 2. EFFECTS OF CO<sub>2</sub>

Increasing atmospheric CO<sub>2</sub> is a critical problem (IPCC, 2007), which can affect several physiological aspects of plants and biotic interactions between plants and insects (Körner *et al.*, 2007). Because a forest ecosystem consists of many trees, which contain various organs, we can detect the responses of whole tree through those organs: leaves, branches, stems and roots.

At leaf level, elevated CO<sub>2</sub> stimulates the rate of photosynthesis (the difference between the uptake and emission of CO<sub>2</sub>) in the short-term. Over a long period, however, acclimation of plants to a higher concentration of CO<sub>2</sub> takes place; this process finally induces downward- or down-regulation of photosynthesis, observed in the decrease of photosynthetic parameters such as the maximum rate of carboxylation and the maximum rate of electron transport (Eguchi *et al.*, 2008a; Cao *et al.*, 2007; Zhang and Dang, 2006; Kitao *et al.*, 2005; Rey and Jarvis, 1998; Tjoelker *et al.*, 1998; Koike *et al.*, 1996). The parameters specifying chlorophyll fluorescence, which indicates the stress condition of the photosynthetic pathway, suggests that elevated CO<sub>2</sub> should make birches more susceptible to stresses such as drought or heat (Kitao *et al.*, 2007, 2005). It is obvious that elevated CO<sub>2</sub> affects the photosynthetic process, but over long time-scales, elevated CO<sub>2</sub> may not increase C gain in birches very much.

Stomatal conductance is an important parameter, because it indicates gas exchange capacity such as photosynthesis and transpiration of a leaf. In most cases, elevated CO<sub>2</sub> decreases the stomatal conductance (Eguchi *et al.*, 2008b; Zhang *et al.*, 2008; Cao *et al.*, 2007), implying that leaves can prevent water loss by narrowing their stomata. The decrease in stomatal conductance can also be explained as a consequence of the decrease in stomatal density of leaves (Kürschner *et al.*, 1997; Rey and Jarvis, 1997). For individual trees, the reduced stomatal conductance of leaves does not always prevent water loss to the atmosphere, because of the higher total leaf area under elevated CO<sub>2</sub> (Kruijt *et al.*, 1999). On the other hand, there is an exceptional case that stomatal conductance increased with CO<sub>2</sub> enrichment (Kubiske and Pregitzer, 1997) and this may be due to increased root volume for water gain (Wang *et al.*, 1998; Berntson *et al.*, 1997).

Nitrogen (N) is a component of proteins, including the enzyme Ribulose-1,5-biphosphate-carboxylase/oxygenase (Rubisco) which catalyzes the primary reaction involved in CO<sub>2</sub> assimilation in photosynthesis in



**Fig. 1.** Major trend in ecophysiological responses to elevated CO<sub>2</sub> in birch trees.

many plants; N concentrations in leaves tend to correlate positively with the photosynthetic rate (Lambers *et al.*, 2008; Cao *et al.*, 2007). In a high CO<sub>2</sub> environment, the leaf N concentration ordinarily decreases (Zhang *et al.*, 2008; Cao *et al.*, 2007; Mattson *et al.*, 2005; Juurola, 2003; Kuokkanen *et al.*, 2003; McDonald *et al.*, 1999; Tjoelker *et al.*, 1998; Kubiske and Pregitzer, 1996). The reduction in leaf N is partly explained by dilution of leaf N with more assimilates from photosynthesis under elevated CO<sub>2</sub>, consistent with increased starch accumulation (Zhang *et al.*, 2008; Mattson *et al.*, 2005; Rey and Jarvis, 1998; Tjoelker *et al.*, 1998), which is believed to be a factor in the down-regulation of photosynthesis (Peterson *et al.*, 1999; Rey and Jarvis, 1998).

The C/N ratio (i.e. the ratio of C to N amount in plant tissue) is known to be a good indicator of leaf chemical characteristics. According to the results mentioned above, it is reasonable to suppose that the leaf C/N ratio increases with increasing CO<sub>2</sub> concentration (Koike *et al.*, 2006; Mattson *et al.*, 2005; Juurola, 2003). The increase in the C/N ratio brings changes in the photosynthetic capacity and also in defense capability against herbivores such as insects, which employs phenolic compounds accumulated in leaves. With some exceptions, Koike *et al.* (2006) and Wang *et al.* (2009) found a greater amount of tannin in leaves and an increased C/N ratio with CO<sub>2</sub> enrichment; also, herbivorous insects fed with leaves from a high CO<sub>2</sub> environment did less well. Other studies have also found changes in foliar chemical composition due to CO<sub>2</sub> enrichment (Ji *et al.*, 2011; Mattson *et al.*, 2005; Kuokkanen *et al.*, 2003; McDonald *et al.*, 1999). Because herbivory is an important component in C balance of trees, interactions between insect-herbivore and trees should also be taken into account in considering the effect on trees of atmospheric changes (Fig. 1).

An increase in leaf-level C due to CO<sub>2</sub> enrichment implies better growth of the whole tree, leading in turn to greater biomass of the tree (Kitao *et al.*, 2005; Castovsky and Bazzaz, 1999; Wang *et al.*, 1998; Berntson *et al.*, 1997; Rey and Jarvis, 1997; Wayne and Bazzaz, 1997; Poorter *et al.*, 1996) with much more available resources (Fig. 1).

A rise in CO<sub>2</sub> will also induce changes at broader ecological levels (Potvin *et al.*, 2007), inducing changes not only in individual trees but in the overall tree population, tree community and the whole forest. Depending on the growth characteristics of tree species, and in the low-light conditions at the forest floor, shade-tolerant trees (e.g. oak and maple) may grow better than shade-intolerant trees such as birch under elevated CO<sub>2</sub> (Sefcik *et al.*, 2006; Kerstiens, 1998; Kubiske and Pregitzer, 1996). Shade-intolerant trees are in fact more responsive to raised CO<sub>2</sub> than shade-tolerant trees in high-light environments such as open fields (Kubiske and Pregitzer, 1996). It is reasonable to consider that birch forests should expand into harsh fields by improving drought tolerance (Castovsky and Bazzaz, 1999) or nutrient acquisition with mycorrhiza (Berntson *et al.*, 1997) at elevated CO<sub>2</sub> levels.

These studies show that high levels of CO<sub>2</sub> induce significant responses by birch trees and forests (Fig. 1). Most research set up experiments in which the ambient CO<sub>2</sub> concentration was set at 350 to 380 ppm, and elevated CO<sub>2</sub> at 500 to 720 ppm. The response of the forests is not necessarily linear with increasing CO<sub>2</sub>, and results over short periods are of little value to long-term prediction future, so it is necessary to conduct researches at high CO<sub>2</sub> levels over long periods in order to estimate the future of the forests. Interactions exist between environmental stress and elevated CO<sub>2</sub> (Song and Cheng, 2010; Luo *et al.*, 1999). Ozone is one such stress factor.

### 3. EFFECTS OF O<sub>3</sub>

Ozone is formed in the troposphere by a photochemical reaction between hydrocarbons and nitrogen oxides (NO<sub>x</sub>), and human activity is responsible for a proportion of these (Stockwell *et al.*, 1997). Since there is significant inter-continental transport of these O<sub>3</sub> precursors (Nagashima *et al.*, 2010; Naja and Akimoto, 2004), tropospheric O<sub>3</sub> pollution is a global problem (Sitch *et al.*, 2007; Vingarzan, 2004; Akimoto, 2003). Ozone has very high oxidative capacity, and high O<sub>3</sub> concentrations cause injury to plants (Pellinen *et al.*, 2002), although low concentrations of O<sub>3</sub> may stimulate plant growth (Jäger and Krupa, 2009; Yamaji *et al.*, 2003). High O<sub>3</sub> levels eventually lead to significant reduction in whole-plant biomass, and perhaps increased susceptibility to other stresses such as insects or pathogens. Compared to preindustrial levels, the present O<sub>3</sub> level is likely to have reduced tree biomass by 7% in global terrestrial ecosystems (Wittig *et al.*, 2009). The wood chemistry of pines (Smith, 1990) and the leaf surface characteristics of aspen (Percy *et al.*, 2003, 2002) are affected by O<sub>3</sub>, which renders trees susceptible to insect attack or pathogen infestation.

The impact of O<sub>3</sub> has been suggested by field observations such as tree-ring analysis in pine forests (Miller *et al.*, 1997), and recent experiments now use OTCs or FACEs (Matyssek *et al.*, 2010) in which trees are grown under gas treatments. Such kinds of researches revealed that damage or growth reduction of birch was observed even after O<sub>3</sub> treatment at low concentrations, meaning high sensitivity to O<sub>3</sub> (*Betula pendula* and *Betula pubescens*: Oksanen *et al.*, 2009), but the O<sub>3</sub> sensitivity of birch may be less (*Betula platyphylla*: Yamaguchi *et al.*, 2011; Kohno *et al.*, 2005). Ozone sensitivity is variable among the genus *Betula* (Manninen *et al.*, 2009; Oksanen and Rousi, 2001), and even among clones (genotypes) within the same species (Manninen *et al.*, 2009; Oksanen, 2003) and this prevents us from generalizing unified O<sub>3</sub> effects on a single species.

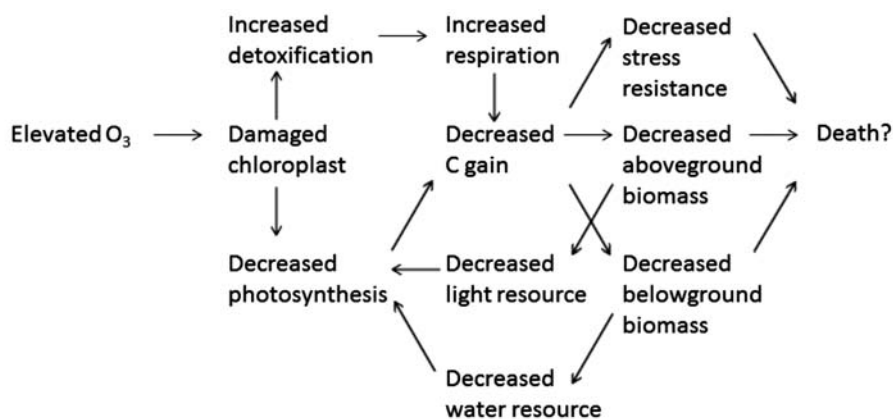
Ozone is taken up mainly through leaf stomata, and exerts its toxicity upon foliar internal tissue (Tausz *et al.*, 2007). Stomatal O<sub>3</sub> uptake is largely responsible for the impact of O<sub>3</sub> on leaves and trees (Wittmann *et al.*, 2007). To explain the reduction in biomass of trees caused by O<sub>3</sub>, a leaf-level stomatal flux-based model has been proposed in which non-stomatal O<sub>3</sub> deposition was taken into account (UNECE, 2004), improving on the conventional “accumulated exposure over a threshold” (AOT) model, which involves only the O<sub>3</sub> concentration. This novel flux-based model assumes

that the leaves which are strongly irradiated by sunlight at the top of the canopy are responsible for the O<sub>3</sub> uptake of the tree. The flux-based model has been applied to several species (Emberson *et al.*, 2007) and its validity has been verified (Karlsson *et al.*, 2007; Uddling *et al.*, 2004). Hoshika *et al.* (2011a, b) used it to examine the spatial difference in maps created by flux-based and AOT modeling of forests in East Asia. Estimation of O<sub>3</sub> uptake by birch forests in China differed depending on the model, suggesting the importance of stomatal closure induced by water-stress in dry regions (Hoshika *et al.*, 2011a).

Here we shall review the responses of birches to O<sub>3</sub> stress. High O<sub>3</sub> damages chloroplasts (Prozherina *et al.*, 2003; Pääkkönen *et al.*, 1998) and reduces the photosynthetic rate (Mäenpää *et al.*, 2011; Shimizu and Feng, 2007; Uddling *et al.*, 2005; Shavnin *et al.*, 1999). This can be reflected in changes in chlorophyll fluorescence that reveals O<sub>3</sub> stress in photosynthetic pathways (Mao *et al.*, 2012; Wittmann *et al.*, 2007; Shavnin *et al.*, 1999). These negative effects of O<sub>3</sub> give rise to visible symptoms on leaves (Mao *et al.*, 2012; Vahala *et al.*, 2003).

It is generally believed that the stomatal conductance of birch is not significantly affected by O<sub>3</sub> (Matyssek *et al.*, 2010; Wittig *et al.*, 2007). Although Oksanen (2003) exceptionally reported that O<sub>3</sub> treatment had increased stomatal conductance, this could be attributed to increased stomatal density, which is common response to O<sub>3</sub> (Oksanen, 2005; Paoletti and Grulke, 2005; Pääkkönen *et al.*, 1998; Maurer *et al.*, 1997). Increase in stomatal density may be reflected in smaller leaf size under elevated O<sub>3</sub> (Oksanen, 2003, 2001; Oksanen and Saleem, 2001; Pääkkönen *et al.*, 1998), for the ratio of guard cells (equal to stomata) to epidermal cells on leaf is unaffected by O<sub>3</sub> (Prozherina *et al.*, 2003). In terms of the reason why stomatal conductance does not increase despite increased density of stomata under elevated O<sub>3</sub>, the effectiveness of low stomatal aperture against O<sub>3</sub> stress, or impaired photosynthetic pathway by O<sub>3</sub> seems to be a good answer (Paoletti and Grulke, 2005). There are cases where stomatal conductance decreased by O<sub>3</sub> (Shimizu and Feng, 2007; Oksanen *et al.*, 2005a; Maurer *et al.*, 1997). Above-mentioned inhibition of photosynthesis caused by O<sub>3</sub>, or exacerbation by other stresses (Oksanen *et al.*, 2005a; Maurer *et al.*, 1997) might cause the decrease in stomatal conductance. Altogether, responses of stomatal conductance to O<sub>3</sub> can be variable even in a single species (*Betula pendula*: Oksanen, 2005), and stomatal conductance alone should not be an indicator of O<sub>3</sub> stress.

Chemical compounds in leaf can be altered by O<sub>3</sub>. Although N concentration in green leaf is not affected



**Fig. 2.** Major trend in ecophysiological responses to elevated  $O_3$  in birch trees.

by  $O_3$  so much (Manninen *et al.*, 2009; Shimizu and Feng, 2007; Karlsson *et al.*, 2003; Oksanen and Rousi, 2001; Saleem *et al.*, 2001; Oksanen and Saleem, 1999; Pääkkönen *et al.*, 1998), N concentration in leaf litter (fallen leaves) increased by  $O_3$  treatment, suggesting the impaired capacity of trans-locating N from senescent leaves to tree body (Uddling *et al.*, 2005). This may lead increased N loss at the whole tree level. On the other hand, ozone reduces the Rubisco concentration (Oksanen, 2005; Yamaji *et al.*, 2003; Oksanen and Rousi, 2001) and the concentration of chlorophyll (Wittmann *et al.*, 2007; Oksanen *et al.*, 2005a; Oksanen and Saleem, 1999; Shavnin *et al.*, 1999) in leaves, which is involved in photosynthesis and consists of N as well as Rubisco. We believe that the allocation pattern of N in a leaf changes and much N is needed for repair of damaged tissue, resulting in impaired photosynthesis. Some other researchers did not observe decreases in chlorophyll or Rubisco (Shimizu and Feng, 2007; Saleem *et al.*, 2001) despite decreases in the photosynthetic rate (Shimizu and Feng, 2007). It is possible that the slower photosynthetic rate is due to a decrease in stomatal conductance as a result from exclusion of  $O_3$  from leaves (Shimizu and Feng, 2007).

In the tree, ozone stimulates detoxification substances such as phenolic compounds (Oksanen, 2005; Yamaji *et al.*, 2003; Saleem *et al.*, 2001; Pääkkönen *et al.*, 1998). Sugars for the formation of these substances in leaves may be increased (Landolt *et al.*, 1997) whereas starch may decrease (Oksanen, 2003; Oksanen, 2001; Saleem *et al.*, 2001) under  $O_3$  treatment. Antioxidants such as ascorbates are believed to be stimulated in leaves by  $O_3$ , but this is not certain (Riikonen *et al.*, 2009). These reports above indicate stimulated C metabolism by  $O_3$ . As well as N, the allocation pattern of C also changes so that trees can cope with  $O_3$  stress rather than invest C in their growth (Fig. 2).

Moreover, ozone stress also reduces the chance of C acquisition, with shorter leaf longevity (Oksanen, 2005; Uddling *et al.*, 2005; Prozherina *et al.*, 2003; Maurer *et al.*, 1997), or with decreased leaf biomass (Manninen *et al.*, 2009; Shimizu and Feng, 2007; Oksanen, 2001; Oksanen and Rousi, 2001), leaf area (Oksanen, 2001; Saleem *et al.*, 2001; Oksanen and Saleem, 1999; Pääkkönen *et al.*, 1998), and leaf number (Oksanen and Rousi, 2001; Pääkkönen *et al.*, 1998) per tree, in addition to impaired photosynthesis. Such C deficiency may lead to the reduction in tree growth at elevated  $O_3$  (Manninen *et al.*, 2009; Shimizu and Feng, 2007; Karlsson *et al.*, 2003; Oksanen, 2001; Maurer and Matyssek, 1997), which in turn reflects in the growth of tree organ. Decreased stem growth (Matyssek *et al.*, 2002) implies increased risk of stem breakage by disturbances such as wind and snow, and decreased root growth (Shimizu and Feng, 2007; Karlsson *et al.*, 2003; Matsumura, 2001; Oksanen, 2001; Oksanen and Rousi, 2001) means water- and nutrient deficiency in birch trees under  $O_3$  stress.

Although such biomass reductions have been observed in most cases,  $O_3$ -induced compensatory responses have been reported, yielding either greater leaf biomass (Wittmann *et al.*, 2007; Karlsson *et al.*, 2003) or greater stem height (Oksanen and Rousi, 2001) or both (Yamaji *et al.*, 2003). Perhaps the annual growth patterns of trees (Kolb and Matyssek, 2003) or hormesis, i.e., growth stimulation by toxins at low concentrations (Jäger and Krupa, 2009) are related to this process.

In the way described,  $O_3$  has a negative impact on the growth of birch trees, in contrast to the effect of  $CO_2$  (Fig. 2). However, it is not easy to estimate interactions between  $O_3$  and other stresses, and there are difficulties in scaling from results of individual- or population level experiments to a mature community (Matyssek and Sandermann, 2003). Drought (or water-

ing) or application of fertilizer has been used in combination with O<sub>3</sub> (drought: Shimizu and Feng, 2007; Pääkkönen *et al.*, 1998; fertilization: Shavnin *et al.*, 1999; Landolt *et al.*, 1997; Maurer and Matyssek, 1997; Maurer *et al.*, 1997). Since these environmental factors and high CO<sub>2</sub> can influence and even negate the effect of O<sub>3</sub> (Yamaguchi *et al.*, 2011), sensitivity to O<sub>3</sub> of every tree species must be evaluated according to the physical environment around trees (i.e., soil moisture or soil nutrient).

#### 4. COMBINED EFFECTS OF CO<sub>2</sub> AND O<sub>3</sub>

Of several types of environmental stress, O<sub>3</sub> was the strongest interactive factor with the atmospheric CO<sub>2</sub> concentration, because high CO<sub>2</sub> greatly mitigated the effect of O<sub>3</sub> on trees (Poorter and Pérez-Soba, 2001). It is important to assess the impacts of these gases on forests, because the gases are first absorbed through stomata into the leaf and may largely counteract the effects of each other. Mortensen (1995) first looked at the combined effects of CO<sub>2</sub> and O<sub>3</sub> on birch. The experimental period was relatively short, about one month, but the concentrations of the gases were about 560 ppm for (elevated) CO<sub>2</sub> and about 60 ppb for (elevated) O<sub>3</sub>, which are realistic values. The Aspen FACE in the north-central USA is the only site that enables a free-air enrichment system of CO<sub>2</sub> and O<sub>3</sub> to forest stands, and many data gathered there have been published on the effect of elevated CO<sub>2</sub> and O<sub>3</sub> on birch forests (Karnosky *et al.*, 2005, 2003b). King *et al.* (2005) reported a 5-year study at the Aspen FACE, revealing larger differences between treatments at the longer timescale. In many cases the increases in the biomass of birch trees due to elevated CO<sub>2</sub> were weakened in the presence of high O<sub>3</sub> (*Betula papyrifera*: Kostianen *et al.*, 2008; King *et al.*, 2005; *Betula pubescens*: Mortensen, 1995), but Riikonen *et al.* (2004: *Betula pendula*) and Matsumura *et al.* (2005: *Betula platyphylla*) found compensation, namely that combined treatment with both elevated CO<sub>2</sub> and O<sub>3</sub> resulted in no growth reduction compared to the trees under elevated CO<sub>2</sub> alone. There seems to be species difference in responses to the treatments among birch trees.

The compensated biomass under higher CO<sub>2</sub> and O<sub>3</sub> regimes is reflected in the difference in growth increment of trees (Kostianen *et al.*, 2006; Riikonen *et al.*, 2004), which is further mediated by leaf processes. Responses of trees in the amount of foliage (Talhelm *et al.*, 2012; King *et al.*, 2005; Riikonen *et al.*, 2004) and also in the total leaf area (Uddling *et al.*, 2008; Kull *et al.*, 2005; Riikonen *et al.*, 2004) are

significant, as elevated CO<sub>2</sub> alleviated the negative effects of O<sub>3</sub>. These parameters may be affected by the treatments through changes in spatial leaf distribution within trees (Kull *et al.*, 2003), leaf size (Riikonen *et al.*, 2010, 2008a; Peltonen *et al.*, 2005; Mortensen, 1995), and leaf thickness (Riikonen *et al.*, 2010, 2008a, 2004; Oksanen *et al.*, 2005b; Eichelmann *et al.*, 2004).

Negative effects of O<sub>3</sub> on many photosynthetic parameters were alleviated by high CO<sub>2</sub> (Riikonen *et al.*, 2008a, 2005; Eichelmann *et al.*, 2004; Karnosky *et al.*, 2003b). Analyses of chlorophyll fluorescence indicated that the stress condition of the photosynthetic system caused by O<sub>3</sub> alone was relieved in a mixture of elevated CO<sub>2</sub> and O<sub>3</sub> (Kontunen-Soppela *et al.*, 2010; Riikonen *et al.*, 2005). For down-regulation of photosynthesis, which is typically triggered by high CO<sub>2</sub> concentrations, Riikonen *et al.* (2005) found little effect of O<sub>3</sub> alone or in combination with elevated CO<sub>2</sub>.

Ozone uptake to leaves was limited under elevated CO<sub>2</sub>+O<sub>3</sub> conditions, as a result of lower stomatal conductance than in the ambient CO<sub>2</sub> environment (Uddling *et al.*, 2009; Riikonen *et al.*, 2008a, b, 2005; Padu *et al.*, 2005). Based on these works, we understand that the O<sub>3</sub>-induced depression of photosynthesis is slightly improved by high CO<sub>2</sub> at the leaf level. However, Uddling *et al.* (2010) stated that high CO<sub>2</sub> reduced stomatal conductance in only a single piece of FACE experiments. Canopy conductance is believed to increase, largely because of increased foliage and root biomass under elevated CO<sub>2</sub>+O<sub>3</sub> conditions (Uddling *et al.*, 2009). Stomata act to exclude O<sub>3</sub> from leaves, but some defense functions within a leaf, such as accumulation of antioxidants, may be more effective than stomatal closure in reducing damage due to O<sub>3</sub> (Padu *et al.*, 2005; Peltonen *et al.*, 2005). There is no clear trend in the response of stomatal density to changes in elevated CO<sub>2</sub>/O<sub>3</sub> (Riikonen *et al.*, 2010, 2008b; Oksanen *et al.*, 2005b; Vanhatalo *et al.*, 2001). More studies on stomatal density should be conducted, because sample number in each study is very low.

The amount and the activity of Rubisco were decreased by elevated CO<sub>2</sub> or O<sub>3</sub> treatment; Rubisco also decreased under the combination treatment (Kontunen-Soppela *et al.*, 2010; Riikonen *et al.*, 2005; Eichelmann *et al.*, 2004). Elevated CO<sub>2</sub> induced a decrease in the leaf N concentration whether or not O<sub>3</sub> was elevated (Riikonen *et al.*, 2005), and the combination of the gases reduces leaf N more than treatments with either high CO<sub>2</sub> or high O<sub>3</sub> (Agrell *et al.*, 2005; Kopper *et al.*, 2001; Lindroth *et al.*, 2001). Also, the starch concentration in leaves tends to increase under a combination of elevated CO<sub>2</sub>+O<sub>3</sub> more than in high concen-

trations of CO<sub>2</sub> or O<sub>3</sub> alone (Riikonen *et al.*, 2008a; Agrell *et al.*, 2005; Lindroth *et al.*, 2001; Kopper *et al.*, 2001). Consequently, we can say that the photosynthetic down-regulation in birch can be exacerbated under higher CO<sub>2</sub> and O<sub>3</sub> regime.

Birch leaves are relatively undesirable as food for insects when the concentrations of CO<sub>2</sub> and O<sub>3</sub> are both high because phenolic compounds increases more under CO<sub>2</sub>+O<sub>3</sub> enrichment than with CO<sub>2</sub> alone (Peltonen *et al.*, 2010; Karonen *et al.*, 2006; Agrell *et al.*, 2005; Kopper *et al.*, 2001; Lindroth *et al.*, 2001). Besides aboveground C dynamics, atmospheric changes can alter belowground C dynamics through changes in foliar chemistry. Fallen leaves decompose on forest soil. Much work has focused on changes in decomposition rate of leaf litter (Parsons *et al.*, 2008; Kasurinen *et al.*, 2007, 2006). Elevated O<sub>3</sub> accelerated, and elevated CO<sub>2</sub> delayed, the decomposition of leaves. There was an interactive effect, such that the decomposition rate was slowest under the combined treatment (Parsons *et al.*, 2008). The decomposition of leaves by soil microbes and living roots of trees involves respiration, and has been investigated. Only CO<sub>2</sub> treatment causes difference in soil respiration in general (Kasurinen *et al.*, 2004; King *et al.*, 2001), but the combination treatments yielded the highest respiration rates (Pregitzer *et al.*, 2006; Kasurinen *et al.*, 2004). These interactive results might be due to changes in soil temperature which is affected by leaf area (Pregitzer *et al.*, 2006). Therefore, under elevated CO<sub>2</sub> and O<sub>3</sub> regime, CO<sub>2</sub> emission from forest soil may offset increased C sequestration capacity of the soil.

Nutrient dynamics in forest soil is similarly affected. Elevated CO<sub>2</sub> increased, and elevated O<sub>3</sub> decreased, the input of many nutrients to soil (Talhelm *et al.*, 2012; Liu *et al.*, 2007). This is due to litter amount, and O<sub>3</sub> has also detrimental effects on soil microbes controlling soil N dynamics, with which mineralization, nitrification, and immobilization processes are all involved (Holmes *et al.*, 2003), and on mycorrhizae (Kasurinen *et al.*, 2005). In this way, belowground changes in soil nutrient, in mycorrhiza association, and in root volume are considered to cause aboveground responses to atmospheric changes (Zak *et al.*, 2007a; Kasurinen *et al.*, 2005; Holmes *et al.*, 2003). In addition, since the responses in N acquisition of birch and aspen trees to changing CO<sub>2</sub>/O<sub>3</sub> regimes clearly differ (Zak *et al.*, 2007b), the better survival of birch than aspen when they grow together (Kubiske *et al.*, 2007) implies changes in the community composition of birch forests in the future. Changes in nutrient concentration of plant bodies might therefore have a large effect on future ecosystem dynamics through complex processes (Lindroth, 2010), and we do not have any unified trends

especially in interactive effects of elevated CO<sub>2</sub> and O<sub>3</sub> on belowground processes.

Darbah *et al.* (2008) found that O<sub>3</sub> stimulated flowering of the birch trees, and CO<sub>2</sub> improved the seed quality. It is possible that allergy due to birch pollen will increase in the future. As the greatest amount of catkins under combined CO<sub>2</sub>+O<sub>3</sub> treatment indicated (Vanhatalo *et al.*, 2003), O<sub>3</sub> may accelerate aging of birch trees; the trees come into bloom at a younger age, and a greater C amount under elevated CO<sub>2</sub> gives rise to higher seed biomass (Riikonen *et al.*, 2004). Interactions of these gases in the future may lead to changes in propagation process of birch trees.

Overall, negative effects of O<sub>3</sub> are alleviated under elevated CO<sub>2</sub>. It is easy to overestimate or underestimate the structure and function of birch forests when either of elevated CO<sub>2</sub> or O<sub>3</sub> alone is considered. Although there are many publications, most derive from researches in the Aspen FACE or in Finland, not Asian birch forests. Because uncertainties still exist about photosynthesis, especially regarding stomatal response (Onandia *et al.*, 2011) and down-regulation, and C/N allocation for repair of leaves, it is particularly important to determine how CO<sub>2</sub> and O<sub>3</sub>, independently and together, influence photosynthetic and metabolic pathways.

## 5. CONCLUSIONS

Changes in tree biomass caused by rising atmospheric CO<sub>2</sub> and O<sub>3</sub> have been confirmed. Because of enriched CO<sub>2</sub>, birch forests are likely to accumulate much C in the future, particularly if tropospheric O<sub>3</sub> is low. Where the O<sub>3</sub> level is high, the fertilization effect of CO<sub>2</sub> will be reduced. For photosynthesis and for within-tree allocation of C and N, the responses to changing CO<sub>2</sub> and O<sub>3</sub> have not yet been quantified adequately because the researchers have been reported variable results. There are not size-dependent, or species-specific differences in response to the gas treatments in most cases. The number of birch species used in the experiments is about 10. The ages and/or sizes of the trees in the experiments are comparable. Although the degree of compensation in biomass under elevated CO<sub>2</sub> plus O<sub>3</sub> regimes tends to differ depending on the species, other responses under the condition may vary rather than have general trends. This is considered to be results from experimental condition such as soil environment or short-term responses to other stresses. Furthermore, scaling presents further difficulties (Kolb and Matyssek, 2003; Matyssek and Sandermann, 2003). Responses to O<sub>3</sub> may differ between juvenile and mature trees, due to differences in the amount of

living tissue which involves respiratory costs, stomatal aperture, C allocation and the light conditions in the tree canopy (Kolb and Matyssek, 2003). Responses of mature birch trees have not been elucidated experimentally. On the other hand, high CO<sub>2</sub>/O<sub>3</sub> treatment for short periods could cause long-term carry-over effects (Oksanen and Saleem, 2001; Rey and Jarvis, 1997), so that it is reasonable to consider the effects of atmospheric change by seedling experiments. Field surveys of trees and their environmental conditions, and comparison of the resulting data, should make it possible to find a new factor currently missing but evidently needed to determine responses to environmental stresses.

## ACKNOWLEDGEMENT

We are grateful for financial support in part by the Environment Research and Technology Development Fund (B-1105) of the Ministry of the Environment of Japan and by the Grant-in-aid from JSPS (Type B: 23380078).

## REFERENCES

- Agrell, J., Kopper, B., McDonald, E.P., Lindroth, R.L. (2005) CO<sub>2</sub> and O<sub>3</sub> effects on host plant preferences of the forest tent caterpillar (*Malacosoma disstria*). *Global Change Biology* 11, 588-599.
- Akimoto, H. (2003) Global air quality and pollution. *Science* 302, 1716-1719.
- Alexeyev, V.A., Birdsey, R.A., Stakanov, V.D., Korotkov, I.A. (2000) Carbon storage in the Asian boreal forests of Russia. In *Fire, Climate Change, and Carbon Cycling of the Boreal Forest* (Kasischke, E.S. and Stocks, B.J. Eds), *Ecological Studies* 138, Springer, New York, pp. 239-257.
- Berntson, G.M., Wayne, P.M., Bazzaz, F.A. (1997) Below-ground architectural and mycorrhizal responses to elevated CO<sub>2</sub> in *Betula alleghaniensis* populations. *Functional Ecology* 11, 684-695.
- Cao, B., Dang, Q.L., Zhang, S. (2007) Relationship between photosynthesis and leaf nitrogen concentration in ambient and elevated [CO<sub>2</sub>] in white birch seedlings. *Tree Physiology* 27, 891-899.
- Castovsky, S., Bazzaz, F.A. (1999) Elevated CO<sub>2</sub> influences the responses of two birch species to soil moisture: implications for forest community structure. *Global Change Biology* 5, 507-518.
- Chapin, F.S., Hollingsworth, T., Murray, D.F., Viereck, L.A., Walker, M.D. (2006) Floristic diversity and vegetation distribution in the Alaskan Boreal Forest. In *Alaska's Changing Boreal Forest* (Chapin, F.S., Oswood, M.W., Van Cleve, K., Viereck, L.A. and Verbyla, D.L. Eds), Oxford Univ Press, New York, pp. 81-99.
- Darbaj, J.N.T., Kubiske, M.E., Nelson, N., Oksanen, E., Vapaavuori, E., Karnosky, D.F. (2008) Effects of decadal exposure to interacting elevated CO<sub>2</sub> and/or O<sub>3</sub> on paper birch (*Betula papyrifera*) reproduction. *Environmental Pollution* 155, 446-452.
- Eguchi, N., Karatsu, K., Ueda, T., Funada, R., Takagi, K., Hiura, T., Sasa, K., Koike, T. (2008a) Photosynthetic responses of birch and alder saplings grown in a free air CO<sub>2</sub> enrichment system in northern Japan. *Trees* 22, 437-447.
- Eguchi, N., Morii, N., Ueda, T., Funada, R., Takagi, K., Hiura, T., Sasa, K., Koike, T. (2008b) Changes in petiole hydraulic properties and leaf water flow in birch and oak saplings in a CO<sub>2</sub>-enriched atmosphere. *Tree Physiology* 28, 287-295.
- Eichelmann, H., Oja, V., Rasulov, B., Padu, E., Bichele, I., Pettai, H., Möls, T., Kasparova, I., Vapaavuori, E., Laisk, A. (2004) Photosynthetic parameters of birch (*Betula pendula* Roth) leaves growing in normal and in CO<sub>2</sub>- and O<sub>3</sub>-enriched atmospheres. *Plant, Cell and Environment* 27, 479-495.
- Emberson, L.D., Büker, P., Ashmore, M.R. (2007) Assessing the risk caused by ground level ozone to European forest trees: a case study in pine, beech, and oak across different climate regions. *Environmental Pollution* 147, 454-466.
- Erdmann, G.G. (1990) Yellow birch. *Betula alleghaniensis* Britton. In *Silvics of North America*, vol.2, *Hardwoods* (Burns, R.M. and Honkala, B.H. Eds), USDA Agriculture Handbook 654, [http://www.na.fs.fed.us/pubs/silvics\\_manual/volume\\_2/betula/alleganiensis%20.htm](http://www.na.fs.fed.us/pubs/silvics_manual/volume_2/betula/alleganiensis%20.htm), retrieved on 10th Jan. 2012.
- FFPRI (2004) *The Handbook of Wood Industry*. (4th Ed.), Maruzen, Tokyo, pp. 192-193. (In Japanese)
- Fowler, D., Pilegaard, K., Sutton, M.A., Ambus, P., Rai-vonen, M., Duyzer, J., Simpson, D., Fagerli, H., Fuzzi, S., Schjoerring, J.K., Granier, C., Neftel, A., Isaksen, I.S.A., Laj, P., Maione, M., Monks, P.S., Burkhardt, J., Daemmgen, U., Neirynek, J., Personne, E., Wichink-Kruit, R., Butterbach-Bahl, K., Flechard, C., Tuovinen, J.P., Coyle, M., Gerosa, G., Loubet, B., Altimir, N., Gruenhage, L., Ammann, C., Cieslik, S., Paoletti, E., Mikkelsen, T.N., Ro-Poulsen, H., Cellier, P., Cape, J.N., Horváth, L., Loreto, F., Niinemets, Ü., Palmer, P.I., Rinne, J., Misztal, P., Nemitz, E., Nilsson, D., Pryor, S., Gallagher, M.W., Vesala, T., Skiba, U., Brüggemann, N., Zechmeister-Boltenstern, S., Williams, J., O'Dowd, C., Facchini, M.C., de Leeuw, G., Flossman, A., Chaumerliac, N., Erisman, J.W. (2009) Atmospheric composition change: ecosystems-atmosphere interaction. *Atmospheric Environment* 43, 5193-5267.
- Govaerts, R., Frodin, D. (1998) World checklist and bibliography of Fagales (Betulaceae, Corylaceae, Fagaceae, and Ticodendraceae). The Royal Botanic Gardens.
- Grelen, H.E. (1990) River birch. *Betula nigra* L. In *Silvics of North America*, vol.2, *Hardwoods* (Burns, R.M. and Honkala, B.H. Eds), USDA Agriculture Handbook



- 654, [http://www.na.fs.fed.us/pubs/silvics\\_manual/volume\\_2/betula/nigra.htm](http://www.na.fs.fed.us/pubs/silvics_manual/volume_2/betula/nigra.htm), retrieved on 10th Jan. 2012.
- Hokkaido Prefecture (2011) Forestry statistics of Hokkaido in the fiscal year 2010. <http://www.pref.hokkaido.lg.jp/sr/sum/kcs/rin-toukei/22rtk.htm>, retrieved on 10th Jan. 2012. (In Japanese)
- Holmes, W.E., Zak, D.R., Pregitzer, K.S., King, J.S. (2003) Soil nitrogen transformations under *Populus tremuloides*, *Betula papyrifera* and *Acer saccharum* following 3 years exposure to elevated CO<sub>2</sub> and O<sub>3</sub>. *Global Change Biology* 9, 1743-1750.
- Hoshika, Y., Hajima, T., Shimizu, Y., Takigawa, M., Omasa, K. (2011a) Estimation of stomatal ozone uptake of deciduous trees in East Asia. *Annals of Forest Science* 68, 607-616.
- Hoshika, Y., Shimizu, Y., Omasa, K. (2011b) A comparison between stomatal ozone uptake and AOT40 of deciduous trees in Japan. *iForest* 4, 128-135.
- Hynynen, J., Niemistö, P., Viherä-Aarnio, A., Brunner, A., Hein, S. (2010) Silviculture of birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.) in northern Europe. *Forestry* 83, 103-119.
- IPCC (2007) Technical summary. In *Climate Change 2007: The Physical Science Basis* (Solomon, S., Qin, D., Manning, M., Marquis, M., Averyt, K., Tingor, M.M.B., Miller, H.L. and Chen, Z. Eds), Cambridge University Press, New York, pp. 19-940.
- Jäger, H.J., Krupa, S.V. (2009) Hormesis-its relevance in phytotoxicology. In *Air Quality and Ecological Impacts* (Legge, A.H. Ed), *Developments in Environmental Science* vol.9, Elsevier, pp. 137-152.
- Ji, L.Z., An, L.L., Wang, X.W. (2011) Growth responses of gypsy moth larvae to elevated CO<sub>2</sub>: the influence of methods of insect rearing. *Insect Science* 18, 409-418.
- Jurola, E. (2003) Biochemical acclimation patterns of *Betula pendula* and *Pinus sylvestris* seedlings to elevated carbon dioxide concentrations. *Tree Physiology* 23, 85-95.
- Karlsson, P.E., Braun, S., Broadmeadow, M., Elcira, S., Emberson, L., Gimeno, B.S., Le Thiec, D., Novak, K., Oksanen, E., Schaub, M., Uddling, J., Wilkinson, M. (2007) Risk assessments for forest trees: the performance of the ozone flux versus the AOT concepts. *Environmental Pollution* 146, 608-616.
- Karlsson, P.E., Uddling, J., Skärby, L., Wallin, G., Sellén, G. (2003) Impact of ozone on the growth of birch (*Betula pendula*) saplings. *Environmental Pollution* 124, 485-495.
- Karnosky, D.F., Percy, K.E., Thakur, R.C., Honrath, R.E. Jr. (2003a) Air pollution and global change: a double challenge to forest ecosystems. In *Air Pollution, Global Change and Forests in the New Millennium* (Karnosky, D.F., Percy, K.E., Chappelka, A.H., Simpson, C. and Pikkarainen, J. Eds), *Developments in Environmental Science* vol.3. Elsevier, Oxford, pp. 1-42.
- Karnosky, D.F., Pregitzer, K.S., Zak, D.R., Kubiske, M.E., Hendrey, G.R., Weinstein, D., Nosal, M., Percy, K.E. (2005) Scaling ozone responses of forest trees to the ecosystem level in a changing climate. *Plant, Cell and Environment* 28, 965-981.
- Karnosky, D.F., Skelly, J.M., Percy, K.E., Chappelka, A.H. (2007) Perspectives regarding 50 years of research on effects of tropospheric ozone air pollution on US forests. *Environmental Pollution* 147, 489-506.
- Karnosky, D.F., Zak, D.R., Pregitzer, K.S., Awmack, C.S., Bockheim, J.G., Dickson, R.E., Hendrey, G.R., Host, G.E., King, J.S., Kopper, B.J., Kruger, E.L., Kubiske, M.E., Lindroth, R.L., Mattson, W.J., McDonald, E.P., Noormets, A., Oksanen, E., Parsons, W.F.J., Percy, K.E., Podila, G.K., Riemenschneider, D.E., Sharma, P., Thakur, R., Söber, A., Söber, J., Jones, W.S., Anttonen, S., Vapaavuori, E., Mankovska, B., Heilman, W., Isebrands, J.G. (2003b) Tropospheric O<sub>3</sub> moderates responses of temperate hardwood forests to elevated CO<sub>2</sub>: a synthesis of molecular to ecosystem results from the Aspen FACE project. *Functional Ecology* 17, 289-304.
- Karonen, M., Ossipov, V., Ossipova, S., Kapari, L., Loponen, J., Matsumura, H., Kohno, Y., Mikami, C., Sakai, Y., Izuta, T., Pihlaja, K. (2006) Effects of elevated carbon dioxide and ozone on foliar proanthocyanidins in *Betula platyphylla*, *Betula ermanii*, and *Fagus crenata* seedlings. *Journal of Chemical Ecology* 32, 1445-1458.
- Kasurinen, A., Keinänen, M.M., Kaipainen, S., Nilsson, L.O., Vapaavuori, E., Kontro, M.H., Holopainen, T. (2005) Below-ground responses of silver birch trees exposed to elevated CO<sub>2</sub> and O<sub>3</sub> levels during three growing seasons. *Global Change Biology* 11, 1167-1179.
- Kasurinen, A., Kokko-Gonzales, P., Riikonen, J., Vapaavuori, E., Holopainen, T. (2004) Soil CO<sub>2</sub> efflux of two silver birch clones exposed to elevated CO<sub>2</sub> and O<sub>3</sub> levels during three growing seasons. *Global Change Biology* 10, 1654-1665.
- Kasurinen, A., Peltonen, P.A., Julkunen-Tiitto, R., Vapaavuori, E., Nuutinen, V., Holopainen, T., Holopainen, J.K. (2007) Effects of elevated CO<sub>2</sub> and O<sub>3</sub> on leaf litter phenolics and subsequent performance of litter-feeding soil macrofauna. *Plant and Soil* 292, 25-43.
- Kasurinen, A., Riikonen, J., Oksanen, E., Vapaavuori, E., Holopainen, T. (2006) Chemical composition and decomposition of silver birch leaf litter produced under elevated CO<sub>2</sub> and O<sub>3</sub>. *Plant and Soil* 282, 261-280.
- Kerstiens, G. (1998) Shade-tolerance as a predictor of responses to elevated CO<sub>2</sub>. *Physiologia Plantarum* 102, 472-488.
- King, J.S., Kubiske, M.E., Pregitzer, K.S., Hendrey, G.R., McDonald, E.P., Giardina, C.P., Quinn, V.S., Karnosky, D.F. (2005) Tropospheric O<sub>3</sub> compromises net primary production in young stands of trembling aspen, paper birch and sugar maple in response to elevated atmospheric CO<sub>2</sub>. *New Phytologist* 168, 623-636.
- King, J.S., Pregitzer, K.S., Zak, D.R., Sober, J., Isebrands, J.G., Dickson, R.E., Hendrey, G.R., Karnosky, D.F. (2001) Fine-root biomass and fluxes of soil carbon in young stands of paper birch and trembling aspen as affected by elevated atmospheric CO<sub>2</sub> and tropospheric

- O<sub>3</sub>. *Oecologia* 128, 237-250.
- Kitao, M., Koike, T., Tobita, H., Maruyama, Y. (2005) Elevated CO<sub>2</sub> and limited nitrogen nutrition can restrict excitation energy dissipation in photosystem II of Japanese white birch (*Betula platyphylla* var. *japonica*) leaves. *Physiologia Plantarum* 125, 64-73.
- Kitao, M., Lei, T.T., Koike, T., Kayama, M., Tobita, H., Maruyama, Y. (2007) Interaction of drought and elevated CO<sub>2</sub> concentration on photosynthetic down-regulation and susceptibility to photoinhibition in Japanese white birch seedlings grown with limited N availability. *Tree Physiology* 27, 727-735.
- Kohno, Y., Matsumura, H., Ishii, T., Izuta, T. (2005) Establishing critical levels of air pollutants for protecting East Asian vegetation-A challenge. In *Plant Responses to Air Pollution and Global Change* (Omasa, K., Nouchi, I. and De Kok, L.J. Eds), Springer, pp. 243-250.
- Koike, T. (1988) Leaf structure and photosynthetic performance as related to the forest succession of deciduous broad-leaved trees. *Plant Species Biology* 3, 77-87.
- Koike, T. (1995a) Physiological ecology of the growth characteristics of Japanese mountain birch in northern Japan: a comparison with Japanese mountain white birch. In *Vegetation Science in Forestry* (Box, E.O., Peet, R.K., Miyazawa, T., Yamada, I., Fujiwara, K. and Maycock, P.F. Eds), Kluwer Academic Publishers, The Netherlands, pp. 409-422.
- Koike, T. (1995b) Effects of CO<sub>2</sub> in interaction with temperature and soil fertility on the foliar phenology of alder, birch, and maple seedlings. *Canadian Journal of Botany* 73, 149-157.
- Koike, T., Lei, T.T., Maximov, T.C., Tabuchi, R., Takahashi, K., Ivanov, B.I. (1996) Comparison of the photosynthetic capacity of Siberian and Japanese birch seedlings grown in elevated CO<sub>2</sub> and temperature. *Tree Physiology* 16, 381-385.
- Koike, T., Tobita, H., Shibata, T., Matsuki, S., Konno, K., Kitao, M., Yamashita, N., Maruyama, Y. (2006) Defense characteristics of seral deciduous broad-leaved tree seedlings grown under differing levels of CO<sub>2</sub> and nitrogen. *Population Ecology* 48, 23-29.
- Kolb, T.E., Matyssek, R. (2003) Limitations and perspectives about scaling ozone impacts in trees. In *Air Pollution, Global Change and Forests in the New Millennium* (Karnosky, D.F., Percy, K.E., Chappelka, A.H., Simpson, C. and Pikkariainen, J. Eds), *Developments in Environmental Science* vol.3., Elsevier, Oxford, pp. 141-174.
- Kontunen-Soppela, S., Ossipov, V., Ossipova, S., Oksanen, E. (2007) Shift in birch leaf metabolome and carbon allocation during long-term open-field ozone exposure. *Global Change Biology* 13, 1053-1067.
- Kontunen-Soppela, S., Riikonen, J., Ruhanen, H., Brosché, M., Somervuo, P., Peltonen, P., Kangasjärvi, J., Auvinen, P., Paulin, L., Keinänen, M., Oksanen, E., Vapaavuori, E. (2010) Differential gene expression in senescing leaves of two silver birch genotypes in response to elevated CO<sub>2</sub> and tropospheric ozone. *Plant, Cell and Environment* 33, 1016-1028.
- Kopper, B.J., Lindroth, R.L., Nordheim, E.V. (2001) CO<sub>2</sub> and O<sub>3</sub> effects on paper birch (Betulaceae: *Betula papyrifera*) phytochemistry and whitemarked tussock moth (Lymantriidae: *Orgyia leucostigma*) performance. *Environmental Entomology* 30, 1119-1126.
- Körner, C., Morgan, J., Norby, R. (2007) CO<sub>2</sub> fertilization: when, where, how much? In *Terrestrial Ecosystems in a Changing World* (Canadell, J.G., Pataki, D.E. and Pitelka, L.F. Eds), Springer, Berlin, pp. 9-22.
- Kostiainen, K., Jalkanen, H., Kaakinen, S., Saranpää, P. (2006) Wood properties of two silver birch clones exposed to elevated CO<sub>2</sub> and O<sub>3</sub>. *Global Change Biology* 12, 1230-1240.
- Kostiainen, K., Kaakinen, S., Warsta, E., Kubiske, M.E., Nelson, N.D., Sober, J., Karnosky, D.F., Saranpää, P., Vapaavuori, E. (2008) Wood properties of trembling aspen and paper birch after 5 years of exposure to elevated concentrations of CO<sub>2</sub> and O<sub>3</sub>. *Tree Physiology* 28, 805-813.
- Kruijt, B., Barton, C., Rey, A., Jarvis, P.G. (1999) The sensitivity of stand-scale photosynthesis and transpiration to changes in atmospheric CO<sub>2</sub> concentration and climate. *Hydrology and Earth System Sciences* 3, 55-59.
- Kubiske, M.E., Pregitzer, K.S. (1996) Effects of elevated CO<sub>2</sub> and light availability on the photosynthetic light response of trees of contrasting shade tolerance. *Tree Physiology* 16, 351-358.
- Kubiske, M.E., Pregitzer, K.S. (1997) Ecophysiological responses to simulated canopy gaps of two tree species of contrasting shade tolerance in elevated CO<sub>2</sub>. *Functional Ecology* 11, 24-32.
- Kubiske, M.E., Quinn, V.S., Marquardt, P.E., Karnosky, D.F. (2007) Effects of elevated atmospheric CO<sub>2</sub> and/or O<sub>3</sub> on intra- and interspecific competitive ability of aspen. *Plant Biology* 9, 342-355.
- Kull, O., Tulva, I., Vapaavuori, E. (2003) Influence of elevated CO<sub>2</sub> and O<sub>3</sub> on *Betula pendula* Roth crown structure. *Annals Botany* 91, 559-569.
- Kume, A., Numata, S., Watanabe, K., Honoki, H., Nakajima, H., Ishida, M. (2009) Influence of air pollution on the mountain forests along the Tateyama-Kurobe Alpine route. *Ecological Research* 24, 821-830.
- Kuokkanen, K., Yan, S., Niemelä, P. (2003) Effects of elevated CO<sub>2</sub> and temperature on the leaf chemistry of birch *Betula pendula* (Roth) and the feeding behaviour of the weevil *Phyllobius maculicornis*. *Agriculture and Forest Entomology* 5, 209-217.
- Kürschner, W.M., Wagner, F., Visscher, E.H., Visscher, H. (1997) Predicting the response of leaf stomatal frequency to a future CO<sub>2</sub>-enriched atmosphere: constraints from historical observations. *Geologische Rundschau* 86, 512-517.
- Lambers, H., Chapin, F.S., Pons, T.L. (2008) *Plant Physiological Ecology*. (2nd Ed.), Springer, pp. 58-59.
- Lamson, N.I. (1990) Sweet birch. *Betula lenta* L. In *Silvics of North America*, vol.2, *Hardwoods* (Burns, R.M. and

- Honkala, B.H. Eds), USDA Agriculture Handbook 654, [http://www.na.fs.fed.us/pubs/silvics\\_manual/volume\\_2/betula/lenta.htm](http://www.na.fs.fed.us/pubs/silvics_manual/volume_2/betula/lenta.htm), retrieved on 10th Jan. 2012.
- Landolt, W., Günthardt-Goerg, M.S., Pfenninger, I., Einig, W., Hampp, R., Maurer, S., Matyssek, R. (1997) Effect of fertilization on ozone-induced changes in the metabolism of birch (*Betula pendula*) leaves. *New Phytologist* 137, 389-397.
- Lindroth, R.L. (2010) Impacts of elevated atmospheric CO<sub>2</sub> and O<sub>3</sub> on forests: phytochemistry, trophic interactions, and ecosystem dynamics. *Journal of Chemical Ecology* 36, 2-21.
- Lindroth, R.L., Kopper, B.J., Parsons, W.F.J., Bockheim, J.G., Karnosky, D.F., Hendrey, G.R., Pregitzer, K.S., Isebrands, J.G., Sober, J. (2001) Consequences of elevated carbon dioxide and ozone for foliar chemical composition and dynamics in trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). *Environmental Pollution* 115, 395-404.
- Liu, L., King, J.S., Giardina, C.P. (2007) Effects of elevated atmospheric CO<sub>2</sub> and tropospheric O<sub>3</sub> on nutrient dynamics: decomposition of leaf litter in trembling aspen and paper birch communities. *Plant and Soil* 299, 65-82.
- Lorenz, K., Lal, R. (2010) Carbon Sequestration in Forest Ecosystems. Springer, pp. 5-11.
- Luo, Y., Canadell, J., Mooney, H.A. (1999) Interactive effects of carbon dioxide and environmental stress on plants and ecosystems. In *Carbon Dioxide and Environmental Stress* (Luo, Y. and Mooney, H.A. Eds), Academic Press, San Diego, pp. 393-408.
- Mäenpää, M., Riikonen, J., Kontunen-Soppela, S., Rousi, M., Oksanen, E. (2011) Vertical profiles reveal impact of ozone and temperature on carbon assimilation of *Betula pendula* and *Populus tremula*. *Tree Physiology* 31, 808-818.
- Manninen, S., Huttunen, S., Vanhatalo, M., Pakonen, T., Hämäläinen, A. (2009) Inter- and intra-specific responses to elevated ozone and chamber climate in northern birches. *Environmental Pollution* 157, 1679-1688.
- Mao, Q., Hoshika, Y., Watanabe, M., Koike, T. (2012) Symptom of ozone injured leaves in 3 kinds of birch species in Hokkaido. *Boreal Forest Research*. (In press)
- Mao, Q.Z., Watanabe, M., Koike, T. (2010) Growth characteristics of two promising tree species for afforestation, birch and larch in the northeastern part of Asia. *Eurasian Journal of Forest Research* 13, 69-76.
- Matsumura, H. (2001) Impacts of ambient ozone and/or acid mist on the growth of 14 tree species: an open-top chamber study conducted in Japan. *Water, Air, and Soil Pollution* 130, 959-964.
- Matsumura, H., Mikami, C., Sakai, Y., Murayama, K., Izuta, T., Yonekura, T., Miwa, M., Kohno, Y. (2005) Impacts of elevated O<sub>3</sub> and/or CO<sub>2</sub> on growth of *Betula platyphylla*, *Betula ermanii*, *Fagus crenata*, *Pinus densiflora*, and *Cryptomeria japonica* seedlings. *Journal of Agricultural Meteorology* 60, 1121-1124.
- Mattson, M.J., Julkunen-Tiitto, R., Herms, D.A. (2005) CO<sub>2</sub> enrichment and carbon partitioning to phenolics: do plant responses accord better with the protein competition or the growth-differentiation balance models? *Oikos* 111, 337-347.
- Matyssek, R., Günthardt-Goerg, M.S., Maurer, S., Christ, R. (2002) Tissue structure and respiration of stems of *Betula pendula* under contrasting ozone exposure and nutrition. *Trees* 16, 375-385.
- Matyssek, R., Karnosky, D.F., Wieser, G., Percy, K., Oksanen, E., Grams, T.E.E., Kubiske, M., Hanke, D., Pretzsch, H. (2010) Advances in understanding ozone impacts on forest trees: messages from novel phytotron and free-air fumigation studies. *Environmental Pollution* 158, 1990-2006.
- Matyssek, R., Sandermann, H. Jr. (2003) Impact of ozone on trees: an ecophysiological perspective. *Progress in Botany* 64, 349-404.
- Maurer, S., Matyssek, R. (1997) Nutrition and the ozone sensitivity of birch (*Betula pendula*). II. Carbon balance, water-use efficiency and nutritional status of the whole plant. *Trees* 12, 11-20.
- Maurer, S., Matyssek, R., Günthardt-Goerg, M.S., Landolt, W., Einig, W. (1997) Nutrition and the ozone sensitivity of birch (*Betula pendula*). I. Responses at the leaf level. *Trees* 12, 1-10.
- McDonald, E.P., Agrell, J., Lindroth, R.L. (1999) CO<sub>2</sub> and light effects on deciduous trees: growth, foliar chemistry, and insect performance. *Oecologia* 119, 389-399.
- Miller, P.R., Arbaugh, M.J., Temple, P.J. (1997) Ozone and its known and potential effects on forests in Western United States. In *Forest Decline and Ozone* (Sandermann, H., Wellburn, A.R. and Heath, R.L. Eds), Ecological Studies vol.127. Springer, Berlin, pp. 39-68.
- Mortensen, L.M. (1995) Effect of carbon dioxide concentration on biomass production and partitioning in *Betula pubescens* Ehrh. seedlings at different ozone and temperature regimes. *Environmental Pollution* 87, 337-343.
- Nagashima, T., Ohara, T., Sudo, K., Akimoto, H. (2010) The relative importance of various source regions on East Asia surface ozone. *Atmospheric Chemistry and Physics* 10, 11305-11322.
- Naja, M., Akimoto, H. (2004) Contribution of regional pollution and long-range transport to the Asia-Pacific region: analysis of long-term ozonesonde data over Japan. *Journal of Geophysical Research* 109, D21306.
- NOAA (2012) Trends in atmospheric carbon dioxide. <http://www.esrl.noaa.gov/gmd/ccgg/trends/global.html>, retrieved on 7th Aug. 2012.
- Oksanen, E. (2001) Increasing tropospheric ozone level reduced birch (*Betula pendula*) dry mass within a five years period. *Water, Air, and Soil Pollution* 130, 947-952.
- Oksanen, E. (2003) Responses of selected birch (*Betula pendula* Roth) clones to ozone change over time. *Plant, Cell and Environment* 26, 875-886.
- Oksanen, E. (2005) Northern conditions enhance the susceptibility of birch (*Betula pendula* Roth) to oxidative stress caused by ozone. In *Plant Responses to Air Pol-*

- lution and Global Change (Omasa, K., Nouchi, I. and De Kok, L.J. Eds), Springer, pp. 29-36.
- Oksanen, E., Freiwald, V., Prozherina, N., Rousi, M. (2005a) Photosynthesis of birch (*Betula pendula*) is sensitive to springtime frost and ozone. *Canadian Journal of Forest Research* 35, 703-712.
- Oksanen, E., Manninen, S., Vapaavuori, E., Holopainen, T. (2009) Near-ambient ozone concentrations reduce the vigor of *Betula* and *Populus* species in Finland. *Ambio* 38, 413-417.
- Oksanen, E., Riikonen, J., Kaakinen, S., Holopainen, T., Vapaavuori, E. (2005b) Structural characteristics and chemical composition of birch (*Betula pendula*) leaves are modified by increasing CO<sub>2</sub> and ozone. *Global Change Biology* 11, 732-748.
- Oksanen, E., Rousi, M. (2001) Differences of *Betula* origins in ozone sensitivity based on open-field experiment over two growing seasons. *Canadian Journal of Forest Research* 31, 804-811.
- Oksanen, E., Saleem, A. (1999) Ozone exposure results in various carry-over effects and prolonged reduction in biomass in birch (*Betula pendula* Roth). *Plant, Cell and Environment* 22, 1401-1411.
- Oksanen, E., Sober, J., Karnosky, D.F. (2001) Impacts of elevated CO<sub>2</sub> and/or O<sub>3</sub> on leaf ultrastructure of aspen (*Populus tremuloides*) and birch (*Betula papyrifera*) in the Aspen FACE experiment. *Environment Pollution* 115, 437-446.
- Onandia, G., Olsson, A.K., Barth, S., King, J.S., Uddling, J. (2011) Exposure to moderate concentrations of tropospheric ozone impairs tree stomatal response to carbon dioxide. *Environmental Pollution* 159, 2350-2354.
- Pääkkönen, E., Günthardt-Goerg, M.S., Holopainen, T. (1998) Responses of leaf processes in a sensitive birch (*Betula pendula* Roth) clone to ozone combined with drought. *Annals of Botany* 82, 49-59.
- Packee, E.C., Quang, P.X., Smith, R.R. (1992) Bolewood specific gravity of Alaskan northern forest trees. *Forest Products Journal* 42, 29-34.
- Padu, E., Kollist, H., Tulva, I., Oksanen, E., Moldau, H. (2005) Components of apoplastic ascorbate use in *Betula pendula* leaves exposed to CO<sub>2</sub> and O<sub>3</sub> enrichment. *New Phytologist* 165, 131-142.
- Paoletti, E., Grulke, N.E. (2005) Does living in elevated CO<sub>2</sub> ameliorate tree response to ozone?-A review on stomatal responses. *Environmental Pollution* 137, 483-493.
- Paoletti, E., Schaub, M., Matyssek, R., Wieser, G., Augustaitis, A., Bastrup-Birk, A.M., Bytnerowicz, A., Günthardt-Goerg, M.S., Müller-Starck, G., Serengil, Y. (2010) Advances in air pollution science: from forest decline to multiple-stress effects on forest ecosystem services. *Environmental Pollution* 158, 1986-1989.
- Parsons, W.F.J., Bockheim, J.G., Lindroth, R.L. (2008) Independent, interactive, and species-specific responses of leaf litter decomposition to elevated CO<sub>2</sub> and O<sub>3</sub> in a northern hardwood forest. *Ecosystems* 11, 505-519.
- Pellinen, R.I., Korhonen, M.S., Tauriainen, A.A., Palva, E.T., Kangasjärvi, J. (2002) Hydrogen peroxide activates cell death and defense gene expression in birch. *Plant Physiology* 130, 549-560.
- Peltonen, P.A., Vapaavuori, E., Heinonen, J., Julkunen-Tiitto, R., Holopainen, J.K. (2010) Do elevated atmospheric CO<sub>2</sub> and O<sub>3</sub> affect food quality and performance of folivorous insects on silver birch? *Global Change Biology* 16, 918-935.
- Peltonen, P.A., Vapaavuori, E., Julkunen-Tiitto, R. (2005) Accumulation of phenolic compounds in birch leaves is changed by elevated carbon dioxide and ozone. *Global Change Biology* 11, 1305-1324.
- Percy, K.E., Awmack, C.S., Lindroth, R.L., Kubiske, M.E., Kopper, B.J., Isebrands, J.G., Pregitzer, K.S., Hendrey, G.R., Dickson, R.E., Zak, D.R., Oksanen, E., Sober, J., Harrington, R., Karnosky, D.F. (2002) Altered performance of forest pests under atmospheres enriched by CO<sub>2</sub> and O<sub>3</sub>. *Nature* 420, 403-407.
- Percy, K.E., Mankovska, B., Hopkin, A., Callan, B., Karnosky, D.F. (2003) Ozone affects leaf surface-pest interactions. In *Air Pollution, Global Change and Forests in the New Millennium* (Karnosky, D.F., Percy, K.E., Chappelka, A.H., Simpson, C. and Pikkarainen, J. Eds), *Developments in Environmental Science* vol.3, Elsevier, Oxford, pp. 247-258.
- Peterson, A.G., Ball, J.T., Luo, Y., Field, C.B., Curtis, P.S., Griffin, K.L., Gunderson, C.A., Norby, R.J., Tissue, D.T., Forstreuter, M., Rey, A., Vogel, C.S., Participants, C. (1999) Quantifying the response of photosynthesis to changes in leaf nitrogen content and leaf mass per area in plants grown under atmospheric CO<sub>2</sub> enrichment. *Plant, Cell and Environment* 22, 1109-1119.
- Poorter, H., Pérez-Soba, M. (2001) The growth response of plants to elevated CO<sub>2</sub> under non-optimal environment conditions. *Oecologia* 129, 1-20.
- Poorter, H., Roumet, C., Campbell, B.D. (1996) Interspecific variation in the growth response of plants to elevated CO<sub>2</sub>: a search for functional types. In *Carbon Dioxide, Populations, and Communities* (Körner, C. and Bazzaz, F.A. Eds), Academic Press, San Diego, pp. 375-412.
- Potvin, C., Chapin, F.S., Gonzalez, A., Leadley, P., Reich, P., Roy, J. (2007) Plant biodiversity and responses to elevated carbon dioxide. In *Terrestrial Ecosystems in a Changing World* (Canadell, J.G., Pataki, D.E. and Pitelka, L.F. Eds), Springer, Berlin, pp. 103-112.
- Pregitzer, K., Loya, W., Kubiske, M., Zak, D. (2006) Soil respiration in northern forests exposed to elevated atmospheric carbon dioxide and ozone. *Oecologia* 148, 503-516.
- Prozherina, N., Freiwald, V., Rousi, M., Oksanen, E. (2003) Interactive effect of springtime frost and elevated ozone on early growth, foliar injuries and leaf structure of birch (*Betula pendula*). *New Phytologist* 159, 623-636.
- Quillet, A., Peng, C., Garneau, M. (2010) Toward dynamic global vegetation models for simulating vegetation-

- climate interactions and feedbacks: recent developments, limitations, and future challenges. *Environmental Reviews* 18, 333-353.
- Räisänen, J., Tuomenvirta, H. (2009) Interactions between boreal forests and climate change. In *Boreal Forest and Climate Change* (Hari, P. and Kulmala, L. Eds), *Advances in Global Change Research* vol. 34. Springer, pp. 479-528.
- Rey, A., Jarvis, P.G. (1997) Growth response of young birch trees (*Betula pendula* Roth.) after four and a half years of CO<sub>2</sub> exposure. *Annals of Botany* 80, 809-816.
- Rey, A., Jarvis, P.G. (1998) Long-term photosynthetic acclimation to increased atmospheric CO<sub>2</sub> concentration in young birch (*Betula pendula*) trees. *Tree Physiology* 18, 441-450.
- Riikonen, J., Holopainen, T., Oksanen, E., Vapaavuori, E. (2005) Leaf photosynthetic characteristics of silver birch during three years of exposure to elevated concentrations of CO<sub>2</sub> and O<sub>3</sub> in the field. *Tree Physiology* 25, 621-632.
- Riikonen, J., Kets, K., Darbah, J., Oksanen, E., Sober, A., Vapaavuori, E., Kubiske, M.E., Nelson, N., Karnosky, D.F. (2008a) Carbon gain and bud physiology in *Populus tremuloides* and *Betula papyrifera* grown under long-term exposure to elevated concentrations of CO<sub>2</sub> and O<sub>3</sub>. *Tree Physiology* 28, 243-254.
- Riikonen, J., Lindsberg, M.M., Holopainen, T., Oksanen, E., Lappi, J., Peltonen, P., Vapaavuori, E. (2004) Silver birch and climate change: variable growth and carbon allocation responses to elevated concentrations of carbon dioxide and ozone. *Tree Physiology* 24, 1227-1237.
- Riikonen, J., Mäenpää, M., Alavilamo, M., Silfver, T., Oksanen, E. (2009) Interactive effect of elevated temperature and O<sub>3</sub> on antioxidant capacity and gas exchange in *Betula pendula* saplings. *Planta* 230, 419-427.
- Riikonen, J., Percy, K.E., Kivimäenpää, M., Kubiske, M.E., Nelson, N.D., Vapaavuori, E., Karnosky, D.F. (2010) Leaf size and surface characteristics of *Betula papyrifera* exposed to elevated CO<sub>2</sub> and O<sub>3</sub>. *Environmental Pollution* 158, 1029-1035.
- Riikonen, J., Syrjä, L., Tulva, I., Mänd, P., Oksanen, E., Poteri, M., Vapaavuori, E. (2008b) Stomatal characteristics and infection biology of *Pyrenopeziza betulicola* in *Betula pendula* trees grown under elevated CO<sub>2</sub> and O<sub>3</sub>. *Environmental Pollution* 156, 536-543.
- Safford, L.O., Bjorkbom, J.C., Zasada, J.C. (1990) Paper birch. *Betula papyrifera* Marsh. In *Silvics of North America*, vol.2, *Hardwoods* (Burns, R.M. and Honkala, B.H. Eds), *USDA Agriculture Handbook* 654, [http://www.na.fs.fed.us/pubs/silvics\\_manual/volume\\_2/betula/papyrifera.htm](http://www.na.fs.fed.us/pubs/silvics_manual/volume_2/betula/papyrifera.htm), retrieved on 10th Jan. 2012.
- Saleem, A., Loponen, J., Pihlaja, K., Oksanen, E. (2001) Effects of long-term open-field ozone exposure on leaf phenolics of European silver birch (*Betula pendula* ROTH). *Journal of Chemical Ecology* 27, 1049-1062.
- Sefcik, L.K., Zak, D.R., Ellisworth, D.S. (2006) Photo-synthetic responses to understory shade and elevated carbon dioxide concentration in four northern hardwood tree species. *Tree Physiology* 26, 1589-1599.
- Shavnin, S., Maurer, S., Matyssek, R., Bilger, W., Scheidegger, C. (1999) The impact of ozone fumigation and fertilization on chlorophyll fluorescence of birch leaves (*Betula pendula*). *Trees* 14, 10-16.
- Shimizu, H., Feng, Y.W. (2007) Ozone and/or water stress could have influenced the *Betula ermanii* Cham. Forest decline observed at Oku-Nikko, Japan. *Environment Monitoring and Assessment* 128, 109-119.
- Sitch, S., Cox, P.M., Collins, W.J., Huntingford, C. (2007) Indirect radiative forcing of climate change through ozone effects on the land-carbon sink. *Nature* 448, 791-795.
- Smith, W.H. (1990) *Air Pollution and Forests*. (2nd Ed.), Springer-Verlag, New York, pp. 1-610.
- Song, H.T., Cheng, S. (2010) Various growth strategies of yellow birch seedlings in multiple-abiotic factor changing environments. *Plant, Soil and Environment* 56, 235-243.
- Stockwell, W.R., Kramm, G., Scheel, H.E., Mohnen, V.A., Seiler, W. (1997) Ozone formation, destruction and exposure in Europe and the United States. In *Forest Decline and Ozone* (Sandermann, H., Wellburn, A.R. and Heath, R.L. Eds), *Ecological Studies* vol.127, Springer, Berlin, pp. 1-38.
- Talhelm, A.F., Pregitzer, K.S., Giardina, C.P. (2012) Long-term leaf production response to elevated atmospheric carbon dioxide and tropospheric ozone. *Ecosystems* 15, 71-82.
- Tamura, T., Yonekura, T., Nakaji, T., Feng, Y., Shimizu, H., Izuta, T. (2002) Field survey on phenological characteristics and leaf components of *Betula ermanii* Cham. and soil chemical property around Mt. Mae-Shirane, Oku-Nikko, Japan. *Journal of Japan Society for Atmospheric Environment* 37, 320-330. (In Japanese with English abstract)
- Tausz, M., Grulke, N.E., Wieser, G. (2007) Defense and avoidance of ozone under global change. *Environmental Pollution* 147, 525-531.
- Tjoelker, M.G., Oleksyn, J., Reich, P.B. (1998) Seedlings of five boreal tree species differ in acclimation of net photosynthesis to elevated CO<sub>2</sub> and temperature. *Tree Physiology* 18, 715-726.
- Uddling, J., Günthardt-Goerg, M.S., Matyssek, R., Oksanen, E., Pleijel, H., Selldén, G., Karlsson, P.E. (2004) Biomass reduction of juvenile birch is more strongly related to stomatal uptake of ozone than to indices based on external exposure. *Atmospheric Environment* 38, 4709-4719.
- Uddling, J., Hogg, A.J., Teclaw, R.M., Carroll, M.A., Ellsworth, D.S. (2010) Stomatal uptake of O<sub>3</sub> in aspen and aspen-birch forests under free-air CO<sub>2</sub> and O<sub>3</sub> enrichment. *Environmental Pollution* 158, 2023-2031.
- Uddling, J., Karlsson, P.E., Glorvigen, A., Selldén, G. (2005) Ozone impairs autumnal resorption of nitrogen from birch (*Betula pendula*) leaves, causing an increase

- in whole-tree nitrogen loss through litter fall. *Tree Physiology* 26, 113-120.
- Uddling, J., Teclaw, R.M., Kubiske, M.E., Pregitzer, K.S., Ellsworth, D.S. (2008) Sap flux in pure aspen and mixed aspen-birch forests exposed to elevated concentrations of carbon dioxide and ozone. *Tree Physiology* 28, 1231-1243.
- Uddling, J., Teclaw, R.M., Pregitzer, K.S., Ellsworth, D.S. (2009) Leaf and canopy conductance in aspen and aspen-birch forests under free-air enrichment of carbon dioxide and ozone. *Tree Physiology* 29, 1367-1380.
- UNECE (2004) Manual on methodologies and criteria for modelling and mapping critical loads & levels and air pollution effects, risks and trends. <http://www.rivm.nl/en/themasites/icpmm/manual-and-downloads/index.html>, retrieved on 10th Jan. 2012.
- Vahala, J., Ruonala, R., Keinänen, M., Tuominen, H., Kangasjärvi, J. (2003) Ethylene insensitivity modulates ozone-induced cell death in birch. *Plant Physiology* 132, 185-195.
- Vanhatalo, M., Bäck, J., Huttunen, S. (2003) Differential impacts of long-term (CO<sub>2</sub>) and O<sub>3</sub> exposure on growth of northern conifer and deciduous tree species. *Trees* 17, 211-220.
- Vanhatalo, M., Huttunen, S., Bäck, J. (2001) Effects of elevated [CO<sub>2</sub>] and O<sub>3</sub> on stomatal and surface wax characteristics in leaves of pubescent birch grown under field conditions. *Trees* 15, 304-313.
- Vapaavuori, E., Holopainen, J.K., Holopainen, T., Julkunen-Tiitto, R., Kaakinen, S., Kasurinen, A., Kontunen-Soppela, S., Kostianen, K., Oksanen, E., Peltonen, P., Riikonen, J., Tulva, I. (2009) Rising atmospheric CO<sub>2</sub> concentration partially masks the negative effects of elevated O<sub>3</sub> in silver birch (*Betula pendula* Roth). *Ambio* 38, 418-424.
- Vingarzan, R. (2004) A review of surface ozone background levels and trends. *Atmospheric Environment* 38, 3431-3442.
- Volin, J.C., Reich, P.B., Givnish, T.J. (1998) Elevated carbon dioxide ameliorates the negative effect of ozone on photosynthesis and growth: species respond similarly regardless of photosynthetic pathway or plant functional group. *New Phytologist* 138, 315-325.
- Wang, X.W., Ji, L.Z., Zhang, Q.H., Liu, Y., Wang, G.Q. (2009) Effects of elevated CO<sub>2</sub> on feeding preference and performance of the gypsy moth (*Lymantria dispar*) larvae. *Journal of Applied Entomology* 133, 47-57.
- Wang, Y.P., Rey, A., Jarvis, P.G. (1998) Carbon balance of young birch trees grown in ambient and elevated atmospheric CO<sub>2</sub> concentrations. *Global Change Biology* 4, 797-807.
- Wayne, P.M., Bazzaz, F.A. (1997) Light acquisition and growth by competing individuals in CO<sub>2</sub>-enriched atmospheres: consequences for size structure in regenerating birch seedlings. *Journal of Ecology* 85, 29-42.
- Wittig, V.E., Ainsworth, E.A., Long, S.P. (2007) To what extent do current and projected increases in surface ozone affect photosynthesis and stomatal conductance of trees? A meta-analytic review of the last 3 decades of experiments. *Plant, Cell and Environment* 30, 1150-1162.
- Wittig, V.E., Ainsworth, E.A., Naidu, S.L., Karnosky, D.F., Long, S.P. (2009) Quantifying the impact of current and future tropospheric ozone on biomass, growth, physiology and biochemistry: a quantitative meta-analysis. *Global Change Biology* 15, 396-424.
- Wittmann, C., Matyssek, R., Pfanz, H., Humar, M. (2007) Effects of ozone impact on the gas exchange and chlorophyll fluorescence of juvenile birch stems (*Betula pendula* Roth.). *Environmental Pollution* 150, 258-266.
- Yamaguchi, M., Watanabe, M., Matsumura, H., Kohno, Y., Izuta, T. (2011) Experimental studies on the effects of ozone on growth and photosynthetic activity of Japanese forest tree species. *Asian Journal of Atmospheric Environment* 5, 65-78.
- Yamaji, K., Julkunen-Tiitto, R., Rousi, M., Freiwald, V., Oksanen, E. (2003) Ozone exposure over two growing seasons alters root-to-shoot ratio and chemical composition of birch (*Betula pendula* Roth). *Global Change Biology* 9, 1363-1377.
- Yamaji, K., Ohara, T., Uno, I., Kurokawa, J., Pochanart, P., Akimoto, H. (2008) Future prediction of surface ozone over east Asia using models-3 community multiscale air quality modeling system and regional emission inventory in Asia. *Journal of Geophysical Research* 113, D08306.
- Zak, D.R., Holmes, W.E., Pregitzer, K.S. (2007a) Atmospheric CO<sub>2</sub> and O<sub>3</sub> alter the flow of <sup>15</sup>N in developing forest ecosystems. *Ecology* 88, 2630-2639.
- Zak, D.R., Holmes, W.E., Pregitzer, K.S., King, J.S., Ellsworth, D.S., Kubiske, M.E. (2007b) Belowground competition and the response of developing forest communities to atmospheric CO<sub>2</sub> and O<sub>3</sub>. *Global Change Biology* 13, 2230-2238.
- Zhang, Y., Duan, B., Qiao, Y., Wang, K., Korpelainen, H., Li, C. (2008) Leaf photosynthesis of *Betula albosinensis* seedlings as affected by elevated CO<sub>2</sub> and planting density. *Forest Ecology and Management* 255, 1937-1944.
- Zyryanova, O.A., Terazawa, M., Koike, T., Zyryanov, V.I. (2010) White birch trees as resource species of Russia: their distribution, ecophysiological features, multiple utilizations. *Eurasian Journal of Forest Research* 13, 25-40.

(Received 6 February 2012, revised 12 August 2012, accepted 15 August 2012)