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Ecophysiological Responses of Northern Birch Forests to the Changing Atmospheric CO₂ and O₃ Concentrations

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ABSTRACT

The effects on birch (*Betula* spp.) of elevated carbon dioxide (CO₂) and ozone (O₃), 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 CO₂ levels give rise to a net enhancement of the growth of birch trees, whereas high O₃ 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 CO₂ and O₃ 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 (CO₂) and ozone (O₃) and their effect on future terrestrial ecosystems (IPCC, 2007; Sitch *et al.*, 2007). CO₂ is the substrate in photosynthesis but O₃ is toxic to plants. In considering forest

decline in Japan, it is necessary to examine the role of O₃ (Kume *et al.*, 2009; Tamura *et al.*, 2002). The atmospheric CO₂ concentration has steadily been increasing from 300 ppm at the beginning in 20th 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 O₃ 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 O₃ 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 21st century (Vingarzan, 2004).

Reliable data on the effects of elevated CO₂ and/or O₃ 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 CO₂ reduces stomatal conductance, and this may limit O₃ uptake and consequently alleviate the effects of O₃ 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 (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 CO₂ and/or O₃ on birch trees and forests. Although sulfur dioxide and nitrogen oxide are still important issues of atmospheric environment in some region, rising CO₂ and O₃ 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 CO₂ and O₃, 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 CO₂

Increasing atmospheric CO₂ 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 CO₂ stimulates the rate of photosynthesis (the difference between the uptake and emission of CO₂) in the short-term. Over a long period, however, acclimation of plants to a higher concentration of CO₂ 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 CO₂ should make birches more susceptible to stresses such as drought or heat (Kitao *et al.*, 2007, 2005). It is obvious that elevated CO₂ affects the photosynthetic process, but over long time-scales, elevated CO₂ 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 CO₂ 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 CO₂ (Kruijt *et al.*, 1999). On the other hand, there is an exceptional case that stomatal conductance increased with CO₂ 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 CO₂ assimilation in photosynthesis in

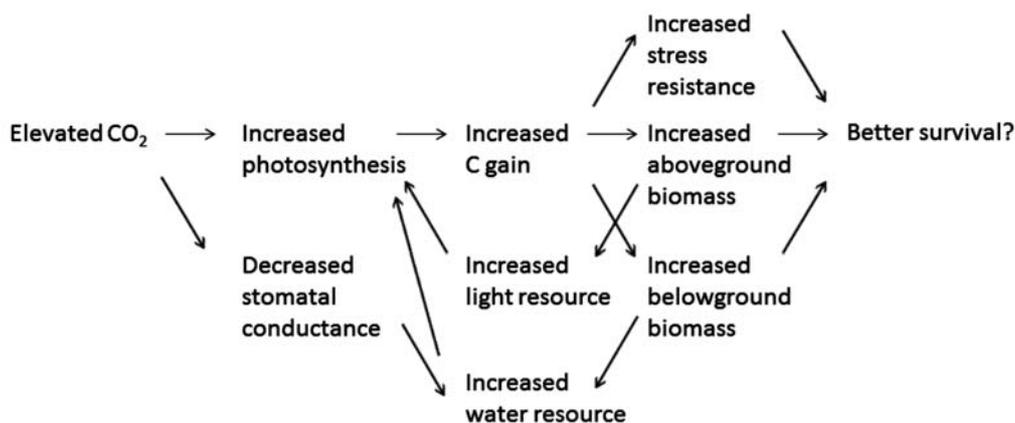


Fig. 1. Major trend in ecophysiological responses to elevated CO₂ in birch trees.

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 CO₂ 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 CO₂, 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 CO₂ 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 CO₂ enrichment; also, herbivorous insects fed with leaves from a high CO₂ environment did less well. Other studies have also found changes in foliar chemical composition due to CO₂ 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 CO₂ 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 CO₂ 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 CO₂ (Sefcik *et al.*, 2006; Kerstiens, 1998; Kubiske and Pregitzer, 1996). Shade-intolerant trees are in fact more responsive to raised CO₂ 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 CO₂ levels.

These studies show that high levels of CO₂ induce significant responses by birch trees and forests (Fig. 1). Most research set up experiments in which the ambient CO₂ concentration was set at 350 to 380 ppm, and elevated CO₂ at 500 to 720 ppm. The response of the forests is not necessarily linear with increasing CO₂, and results over short periods are of little value to long-term prediction future, so it is necessary to conduct researches at high CO₂ levels over long periods in order to estimate the future of the forests. Interactions exist between environmental stress and elevated CO₂ (Song and Cheng, 2010; Luo *et al.*, 1999). Ozone is one such stress factor.

3. EFFECTS OF O₃

Ozone is formed in the troposphere by a photochemical reaction between hydrocarbons and nitrogen oxides (NO_x), and human activity is responsible for a proportion of these (Stockwell *et al.*, 1997). Since there is significant inter-continental transport of these O₃ precursors (Nagashima *et al.*, 2010; Naja and Akimoto, 2004), tropospheric O₃ pollution is a global problem (Sitch *et al.*, 2007; Vingarzan, 2004; Akimoto, 2003). Ozone has very high oxidative capacity, and high O₃ concentrations cause injury to plants (Pellinen *et al.*, 2002), although low concentrations of O₃ may stimulate plant growth (Jäger and Krupa, 2009; Yamaji *et al.*, 2003). High O₃ 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 O₃ 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 O₃, which renders trees susceptible to insect attack or pathogen infestation.

The impact of O₃ 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 O₃ treatment at low concentrations, meaning high sensitivity to O₃ (*Betula pendula* and *Betula pubescens*: Oksanen *et al.*, 2009), but the O₃ 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 O₃ 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 O₃ uptake is largely responsible for the impact of O₃ on leaves and trees (Wittmann *et al.*, 2007). To explain the reduction in biomass of trees caused by O₃, a leaf-level stomatal flux-based model has been proposed in which non-stomatal O₃ deposition was taken into account (UNECE, 2004), improving on the conventional “accumulated exposure over a threshold” (AOT) model, which involves only the O₃ 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 O₃ 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 O₃ 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 O₃ stress. High O₃ 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 O₃ stress in photosynthetic pathways (Mao *et al.*, 2012; Wittmann *et al.*, 2007; Shavnin *et al.*, 1999). These negative effects of O₃ 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 O₃ (Matyssek *et al.*, 2010; Wittig *et al.*, 2007). Although Oksanen (2003) exceptionally reported that O₃ treatment had increased stomatal conductance, this could be attributed to increased stomatal density, which is common response to O₃ (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 O₃ (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 O₃ (Prozherina *et al.*, 2003). In terms of the reason why stomatal conductance does not increase despite increased density of stomata under elevated O₃, the effectiveness of low stomatal aperture against O₃ stress, or impaired photosynthetic pathway by O₃ seems to be a good answer (Paoletti and Grulke, 2005). There are cases where stomatal conductance decreased by O₃ (Shimizu and Feng, 2007; Oksanen *et al.*, 2005a; Maurer *et al.*, 1997). Above-mentioned inhibition of photosynthesis caused by O₃, 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 O₃ can be variable even in a single species (*Betula pendula*: Oksanen, 2005), and stomatal conductance alone should not be an indicator of O₃ stress.

Chemical compounds in leaf can be altered by O₃. Although N concentration in green leaf is not affected

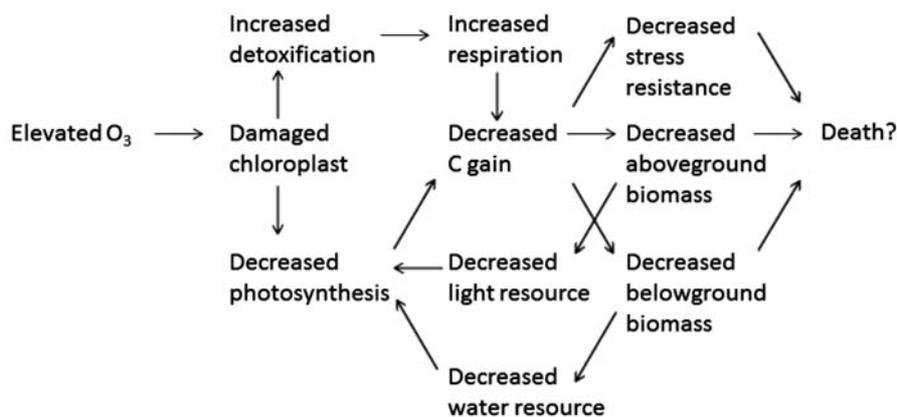


Fig. 2. Major trend in ecophysiological responses to elevated O_3 in birch trees.

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 O₃ (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 CO₂ can influence and even negate the effect of O₃ (Yamaguchi *et al.*, 2011), sensitivity to O₃ 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 CO₂ AND O₃

Of several types of environmental stress, O₃ was the strongest interactive factor with the atmospheric CO₂ concentration, because high CO₂ greatly mitigated the effect of O₃ 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 CO₂ and O₃ on birch. The experimental period was relatively short, about one month, but the concentrations of the gases were about 560 ppm for (elevated) CO₂ and about 60 ppb for (elevated) O₃, which are realistic values. The Aspen FACE in the north-central USA is the only site that enables a free-air enrichment system of CO₂ and O₃ to forest stands, and many data gathered there have been published on the effect of elevated CO₂ and O₃ 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 CO₂ were weakened in the presence of high O₃ (*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 CO₂ and O₃ resulted in no growth reduction compared to the trees under elevated CO₂ alone. There seems to be species difference in responses to the treatments among birch trees.

The compensated biomass under higher CO₂ and O₃ 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 CO₂ alleviated the negative effects of O₃. 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 O₃ on many photosynthetic parameters were alleviated by high CO₂ (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 O₃ alone was relieved in a mixture of elevated CO₂ and O₃ (Kontunen-Soppela *et al.*, 2010; Riikonen *et al.*, 2005). For down-regulation of photosynthesis, which is typically triggered by high CO₂ concentrations, Riikonen *et al.* (2005) found little effect of O₃ alone or in combination with elevated CO₂.

Ozone uptake to leaves was limited under elevated CO₂+O₃ conditions, as a result of lower stomatal conductance than in the ambient CO₂ environment (Uddling *et al.*, 2009; Riikonen *et al.*, 2008a, b, 2005; Padu *et al.*, 2005). Based on these works, we understand that the O₃-induced depression of photosynthesis is slightly improved by high CO₂ at the leaf level. However, Uddling *et al.* (2010) stated that high CO₂ 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 CO₂+O₃ conditions (Uddling *et al.*, 2009). Stomata act to exclude O₃ 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 O₃ (Padu *et al.*, 2005; Peltonen *et al.*, 2005). There is no clear trend in the response of stomatal density to changes in elevated CO₂/O₃ (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 CO₂ or O₃ treatment; Rubisco also decreased under the combination treatment (Kontunen-Soppela *et al.*, 2010; Riikonen *et al.*, 2005; Eichelmann *et al.*, 2004). Elevated CO₂ induced a decrease in the leaf N concentration whether or not O₃ was elevated (Riikonen *et al.*, 2005), and the combination of the gases reduces leaf N more than treatments with either high CO₂ or high O₃ (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 CO₂+O₃ more than in high concen-

trations of CO₂ or O₃ 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 CO₂ and O₃ regime.

Birch leaves are relatively undesirable as food for insects when the concentrations of CO₂ and O₃ are both high because phenolic compounds increases more under CO₂+O₃ enrichment than with CO₂ 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 O₃ accelerated, and elevated CO₂ 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 CO₂ 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 CO₂ and O₃ regime, CO₂ emission from forest soil may offset increased C sequestration capacity of the soil.

Nutrient dynamics in forest soil is similarly affected. Elevated CO₂ increased, and elevated O₃ decreased, the input of many nutrients to soil (Talhelm *et al.*, 2012; Liu *et al.*, 2007). This is due to litter amount, and O₃ 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 CO₂/O₃ 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 CO₂ and O₃ on belowground processes.

Darbah *et al.* (2008) found that O₃ stimulated flowering of the birch trees, and CO₂ 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 CO₂+O₃ treatment indicated (Vanhatalo *et al.*, 2003), O₃ may accelerate aging of birch trees; the trees come into bloom at a younger age, and a greater C amount under elevated CO₂ 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 O₃ are alleviated under elevated CO₂. It is easy to overestimate or underestimate the structure and function of birch forests when either of elevated CO₂ or O₃ 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 CO₂ and O₃, independently and together, influence photosynthetic and metabolic pathways.

5. CONCLUSIONS

Changes in tree biomass caused by rising atmospheric CO₂ and O₃ have been confirmed. Because of enriched CO₂, birch forests are likely to accumulate much C in the future, particularly if tropospheric O₃ is low. Where the O₃ level is high, the fertilization effect of CO₂ will be reduced. For photosynthesis and for within-tree allocation of C and N, the responses to changing CO₂ and O₃ 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 CO₂ plus O₃ 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 O₃ 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 CO₂/O₃ 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.

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REFERENCES

- Agrell, J., Kopper, B., McDonald, E.P., Lindroth, R.L. (2005) CO₂ and O₃ 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 CO₂ 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 [CO₂] in white birch seedlings. *Tree Physiology* 27, 891-899.
- Castovsky, S., Bazzaz, F.A. (1999) Elevated CO₂ 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 CO₂ and/or O₃ 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 CO₂ 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 CO₂-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 CO₂- and O₃-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, 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, 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 CO₂ and O₃. *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 CO₂: 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 O₃ moderates responses of temperate hardwood forests to elevated CO₂: 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., Lopenen, 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 CO₂ and O₃ levels during three growing seasons. *Global Change Biology* 11, 1167-1179.
- Kasurinen, A., Kokko-Gonzales, P., Riikonen, J., Vapaavuori, E., Holopainen, T. (2004) Soil CO₂ efflux of two silver birch clones exposed to elevated CO₂ and O₃ 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 CO₂ and O₃ 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 CO₂ and O₃. *Plant and Soil* 282, 261-280.
- Kerstiens, G. (1998) Shade-tolerance as a predictor of responses to elevated CO₂. *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 O₃ compromises net primary production in young stands of trembling aspen, paper birch and sugar maple in response to elevated atmospheric CO₂. *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 CO₂ and tropospheric

- O₃. *Oecologia* 128, 237-250.
- Kitao, M., Koike, T., Tobita, H., Maruyama, Y. (2005) Elevated CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ and tropospheric ozone. *Plant, Cell and Environment* 33, 1016-1028.
- Kopper, B.J., Lindroth, R.L., Nordheim, E.V. (2001) CO₂ and O₃ 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) CO₂ 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 CO₂ and O₃. *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 CO₂ and O₃. *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 CO₂ concentration and climate. *Hydrology and Earth System Sciences* 3, 55-59.
- Kubiske, M.E., Pregitzer, K.S. (1996) Effects of elevated CO₂ 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 CO₂. *Functional Ecology* 11, 24-32.
- Kubiske, M.E., Quinn, V.S., Marquardt, P.E., Karnosky, D.F. (2007) Effects of elevated atmospheric CO₂ and/or O₃ on intra- and interspecific competitive ability of aspen. *Plant Biology* 9, 342-355.
- Kull, O., Tulva, I., Vapaavuori, E. (2003) Influence of elevated CO₂ and O₃ 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 CO₂ 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 CO₂-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, 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 CO₂ and O₃ 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 CO₂ and tropospheric O₃ 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 O₃ and/or CO₂ 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) CO₂ 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) CO₂ 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 CO₂ 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 CO₂ and/or O₃ 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 CO₂ and O₃ enrichment. *New Phytologist* 165, 131-142.
- Paoletti, E., Grulke, N.E. (2005) Does living in elevated CO₂ 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 CO₂ and O₃ 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 CO₂ and O₃ 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 CO₂ and O₃. *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 CO₂ enrichment. *Plant, Cell and Environment* 22, 1109-1119.
- Poorter, H., Pérez-Soba, M. (2001) The growth response of plants to elevated CO₂ 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 CO₂: 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 CO₂ exposure. *Annals of Botany* 80, 809-816.
- Rey, A., Jarvis, P.G. (1998) Long-term photosynthetic acclimation to increased atmospheric CO₂ 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 CO₂ and O₃ 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 CO₂ and O₃. *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 O₃ 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 CO₂ and O₃. *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 CO₂ and O₃. *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, 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 CO₂ 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 O₃ in aspen and aspen-birch forests under free-air CO₂ and O₃ 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 (CO₂) and O₃ exposure on growth of northern conifer and deciduous tree species. *Trees* 17, 211-220.
- Vanhatalo, M., Huttunen, S., Bäck, J. (2001) Effects of elevated [CO₂] and O₃ 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 CO₂ concentration partially masks the negative effects of elevated O₃ 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 CO₂ 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 CO₂ concentrations. *Global Change Biology* 4, 797-807.
- Wayne, P.M., Bazzaz, F.A. (1997) Light acquisition and growth by competing individuals in CO₂-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 CO₂ and O₃ alter the flow of ¹⁵N 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 CO₂ and O₃. *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 CO₂ 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.

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