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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

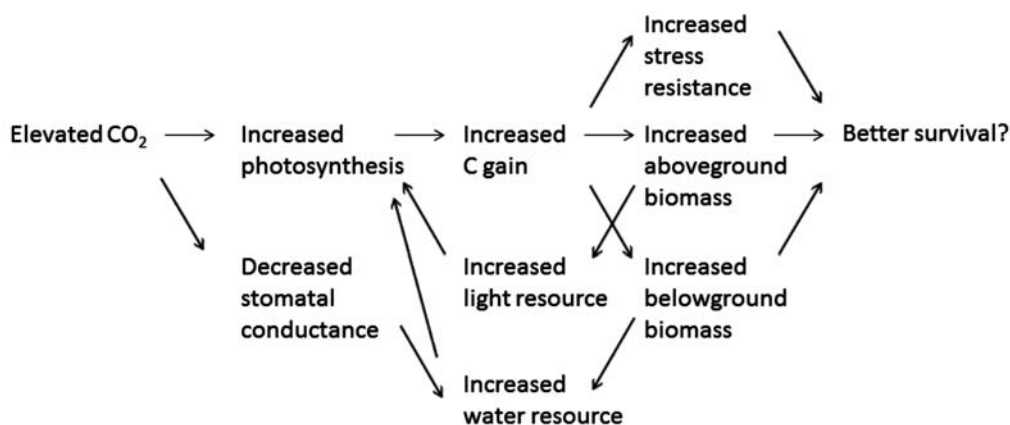


Fig. 1. Major trend in ecophysiological responses to elevated CO_2 in birch trees.

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_2 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_2 , 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_2 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_2 enrichment; also, herbivorous insects fed with leaves from a high CO_2 environment did less well. Other studies have also found changes in foliar chemical composition due to CO_2 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_2 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_2 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_2 (Sefcik *et al.*, 2006; Kerstiens, 1998; Kubiske and Pregitzer, 1996). Shade-intolerant trees are in fact more responsive to raised CO_2 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_2 levels.

These studies show that high levels of CO_2 induce significant responses by birch trees and forests (Fig. 1). Most research set up experiments in which the ambient CO_2 concentration was set at 350 to 380 ppm, and elevated CO_2 at 500 to 720 ppm. The response of the forests is not necessarily linear with increasing CO_2 , and results over short periods are of little value to long-term prediction future, so it is necessary to conduct researches at high CO_2 levels over long periods in order to estimate the future of the forests. Interactions exist between environmental stress and elevated CO_2 (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

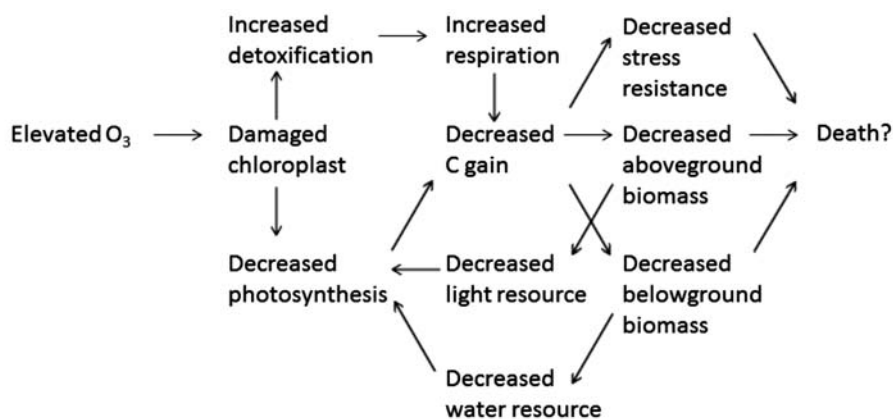


Fig. 2. Major trend in ecophysiological responses to elevated O_3 in birch trees.

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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