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

In this review we describe the effects of elevated concentrations of CO$_2$ and/or O$_3$ on birch trees and forests. Although sulfur dioxide and nitrogen oxide are still important issues of atmospheric environment in some region, rising CO$_2$ and O$_3$ concentrations have recently become more major concerns (PaOLETTI et al., 2010). These gases have effects on forest ecosystems including birch forest all around the world. Additionally, we focus on the similarity and difference for the traits of CO$_2$ and O$_3$, both gases are absorbed through stomata on leaves but they bring opposite effects on tree. Different species of birch are all regarded as ‘birches’ and there are differences in characteristics within a genus, and even among individuals in a single species, in response to environmental changes (VAPAavuori et al., 2009).

### 2. Effects of CO$_2$

Increasing atmospheric CO$_2$ is a critical problem (IPCC, 2007), which can affect several physiological aspects of plants and biotic interactions between plants and insects (KÖRNER et al., 2007). Because a forest ecosystem consists of many trees, which contain various organs, we can detect the responses of whole tree through those organs: leaves, branches, stems and roots. At leaf level, elevated CO$_2$ stimulates the rate of photosynthesis (the difference between the uptake and emission of CO$_2$) in the short-term. Over a long period, however, acclimation of plants to a higher concentration of CO$_2$ 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 carbon fixation and the maximum rate of electron transport (EGUCHI et al., 2008a; CAO et al., 2007; ZHANG and DANG, 2006; KITAO et al., 2005; REY and Jarvis, 1998; TJOELKER et al., 1998; KOIKE et al., 1996). The parameters specifying chlorophyll fluorescence, which indicates the stress condition of the photosynthetic pathway, suggests that elevated CO$_2$ should make birches more susceptible to stresses such as drought or heat (KITAO et al., 2007, 2005). It is obvious that elevated CO$_2$ affects the photosynthetic process, but over long timescales, elevated CO$_2$ may not increase C gain in birches very much.

Stomatal conductance is an important parameter, because it indicates gas exchange capacity such as photosynthesis and transpiration of a leaf. In most cases, elevated CO$_2$ decreases the stomatal conductance (EGUCHI et al., 2008b; ZHANG et al., 2008; CAO et al., 2007), implying that leaves can prevent water loss by narrowing their stomata. The decrease in stomatal conductance can also be explained as a consequence of the decrease in stomatal density of leaves (KÜRSCHNER et al., 1997; REY and Jarvis, 1997). For individual trees, the reduced stomatal conductance of leaves does not always prevent water loss to the atmosphere, because of the higher total leaf area under elevated CO$_2$ (KRIJUIT et al., 1999). On the other hand, there is an exceptional case that stomatal conductance increased with CO$_2$ enrichment (KUBISKE and PREGitzer, 1997) and this may be due to increased root volume for water gain (WANG et al., 1998; BERNTSON et al., 1997).

Nitrogen (N) is a component of proteins, including the enzyme Ribulose-1,5-biphosphate-carboxylase/oxygenase (Rubisco) which catalyzes the primary reaction involved in CO$_2$ assimilation in photosynthesis in

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

| Common name | Coniferous | | | Broadleaved | | |
|-------------|------------|------------|-----------|-------------|----------|
| Stock ($\times 10^6$ m$^3$) | Fir | Larch | Spruce | Birch | Oak | Linden |
| 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.
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 (NOₓ), 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 Aki-moto, 2004), tropospheric O₃ pollution is a global problem (Sitch et al., 2007; Vingarzan, 2004; Aki-moto, 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 (UNEC, 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; Paolletti 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 (Paolletti 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...
by O3 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 O3 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 O3 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 O3 treatment. Antioxidants such as ascorbates are believed to be stimulated in leaves by O3, but this is not certain (Riikonen et al., 2009). These reports above indicate stimulated C metabolism by O3. As well as N, the allocation pattern of C also changes so that trees can cope with O3 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 O3 (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 O3 stress.

Although such biomass reductions have been observed in most cases, O3-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, O3 has a negative impact on the growth of birch trees, in contrast to the effect of CO2 (Fig. 2). However, it is not easy to estimate interactions between O3 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-
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 Perez-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: Kostiainen 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 (Kostiainen 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 lowest 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 CO$_2$/O$_3$ 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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