

Chapter 1

Air pollution and global change: A double challenge to forest ecosystems

D.F. Karnosky*

*School of Forest Resources and Environmental Science, Michigan Technological University,
101 U.J. Noblet Forestry Building, 1400 Townsend Drive, Houghton, MI 49931, USA
E-mail: karnosky@mtu.edu*

K.E. Percy

*Natural Resources Canada, Canadian Forest Service-Atlantic Forestry Centre, P.O. Box 4000,
Fredericton, New Brunswick, E3B 5P7 Canada*

R.C. Thakur

*School of Forest Resources and Environmental Science, Michigan Technological University,
101 U.J. Noblet Forestry Building, 1400 Townsend Drive, Houghton, MI 49931, USA*

R.E. Honrath Jr.

*Department of Civil and Environmental Engineering, Michigan Technological University,
1400 Townsend Drive, Houghton, MI 49931, USA*

Abstract

The world's forests provide a host of wood products, and non-wood resources, and they are critically important in conserving plant, animal, insect and microbial diversity, maintaining soil and water resources, and providing opportunities for employment and recreation. Only recently have we started to value forests for their ability to sequester carbon from the atmosphere. The rapidly changing atmospheric environment with its mix of increasing anthropogenic emissions means that the future world's forests will be faced with unprecedented levels of carbon dioxide and other greenhouse gases, and rising temperatures due to the trapping of radiative heating by the greenhouse gases. In addition, large expanses of these ecosystems will be concurrently exposed to elevated levels of tropospheric ozone, particulates, nitrogen oxides, and acidic rainfall or other air pollutants. Finally, increasing demand for forest products and expanding development pressures from our rapidly growing world population will mean continued land use change and forest habitat loss. Thus, it is very difficult to predict the condition or productivity of forests in this century. In this book, a number of

*Corresponding author.

forest and atmospheric scientists summarize what is known on the impacts of air pollution and climate change on forest ecosystems.

1. Introduction

Forests cover 3.87 billion ha worldwide or 30% of the Earth's land area (Fig. 1). Besides providing annually about 3.3 billion cubic meters of roundwood and nearly 3.0 billion cubic meters of fuelwood, forests are important for many non-wood forest products as well as for soil and water conservation, biological diversity conservation, support of agricultural systems, employment generation, provision of recreational opportunities, and protection of natural and cultural heritage (FAO, 2001). Nearly 70% of the water vapor passes through the stomata of forest trees and forests hold about 50% of the world's carbon stocks. It is estimated that forests sequester some 2.0 Pg annually of carbon emitted that would otherwise end up in the atmosphere, contributing to global warming (Houghton, 2001). Furthermore, forests account for ~70% of the carbon exchange between land and the atmosphere (Schlesinger, 1997).

2. How will the world's forests respond to elevated CO₂, warming climate, and increasing air pollution loading?

It is well known that atmospheric carbon dioxide (CO₂) is rising globally (Keeling et al., 1995) and that much of the increase in atmospheric CO₂ is due to elevated anthropogenic emissions (IPCC, 2001) and degradation of tropical forests that would otherwise be larger CO₂ sinks (O'Brien, 2000). Concurrently, other greenhouse gases, such as methane and nitrous oxide, are also increasing (Fig. 2). Together these greenhouse gases are trapping considerable radiant energy near the Earth's surface, resulting in the so-called "greenhouse effect" of warming climate (Fig. 3). Simultaneously, the atmospheric concentration of tropospheric ozone (O₃) is increasing (Fig. 4) downwind of major metropolitan regions around the world such that nearly 50% of the world's forests are expected to be at risk from levels of O₃ over 60 ppb by the year 2100 (Fowler et al., 1999). In addition, particularly in developing countries where industrialization and urbanization are expanding at a rapid rate, levels of acidic deposition from sulfur and nitrogen oxides emitted into the atmosphere are also increasing (Streets et al., 2000; Streets and Waldhoff, 2000). Thus, our world's forests will be exposed to a combination of air pollutant stresses and rapidly changing climate over the next century making it difficult to predict how forest ecosystems will respond.

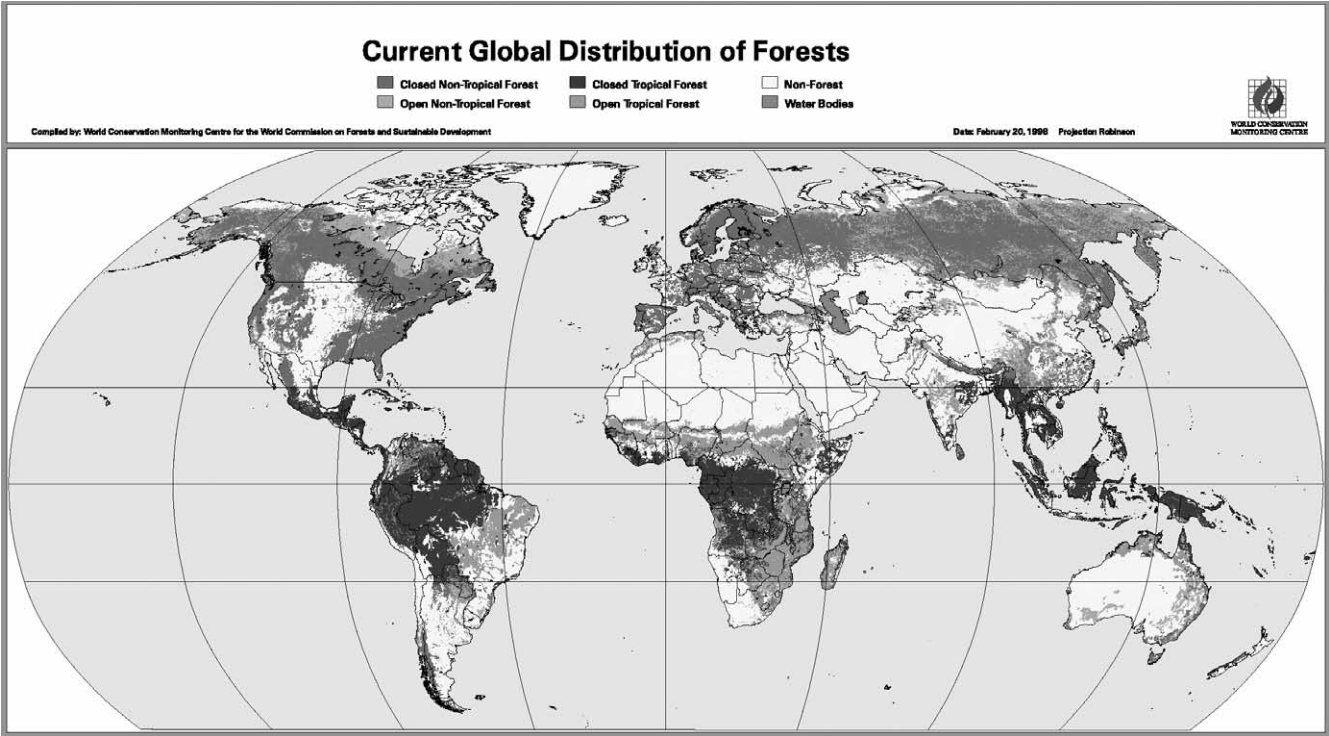
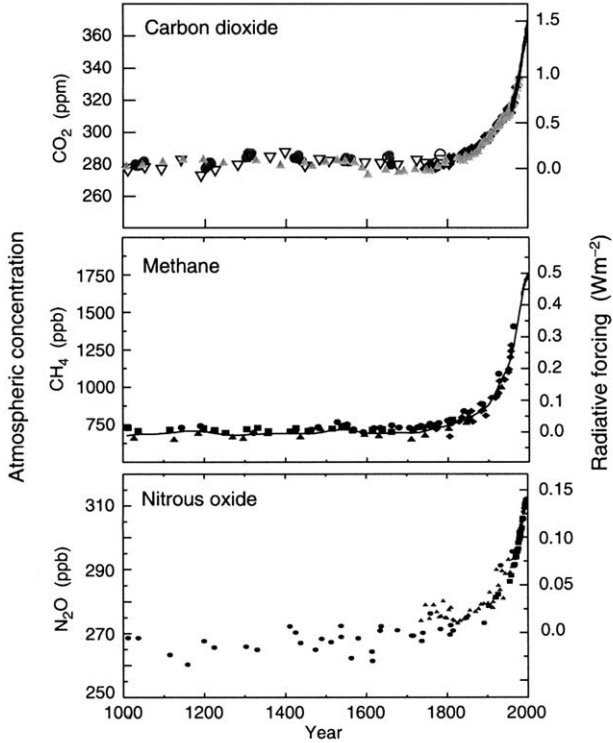


Figure 1. Global distribution of the world's forests (from FAO, 2001).

Indicators of the human influence on the atmosphere during the Industrial Era

(a) Global atmospheric concentrations of three well mixed greenhouse gases



(b) Sulphate aerosols deposited in Greenland ice

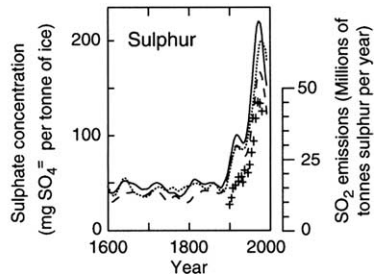
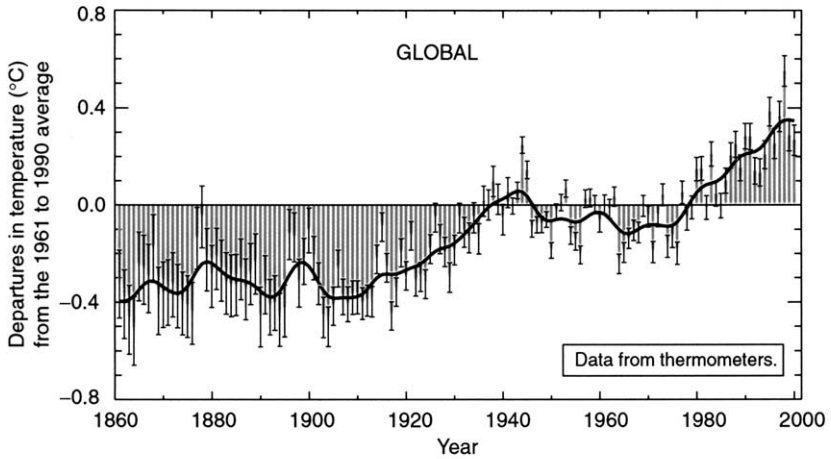


Figure 2. Historical atmospheric concentrations of carbon dioxide, methane, and nitrous oxides, and sulphate aerosols deposited in Greenland ice (from IPCC, 2001).

Variations of the Earth's surface temperature for:

(a) the past 140 years



(b) the past 1,000 years

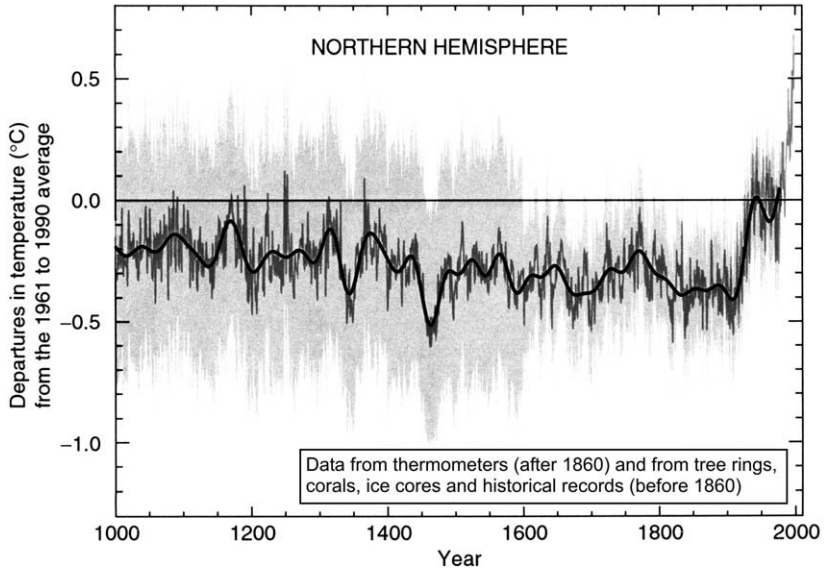


Figure 3. Variations of the Earth's surface temperature for (a) the past 140 years and (b) the past 1000 years (from IPCC, 2001).

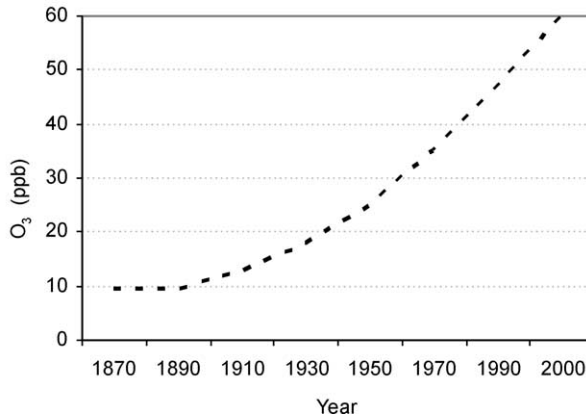


Figure 4. Historical trends in tropospheric O₃ (adapted from Marenco *et al.*, 1994).

3. CO₂

The rise in atmospheric CO₂ has been described as an “all-you-can-eat-buffet” for forest trees as CO₂ is the basic building block of photosynthesis and as it rises, trees have higher photosynthetic rates. On average, trees grown under elevated CO₂ photosynthesize at about a 60% higher rate than under background CO₂ levels (Norby *et al.*, 1999). In addition, trees growing under elevated CO₂ generally have lower stomatal conductance and improved water use efficiency.

Short-term growth responses under elevated CO₂ have predictably followed the same trends as photosynthetic enhancement with average growth enhancement being about 27% (Norby *et al.*, 1999). However, it is difficult to extrapolate the results of the growth studies to growth trends for trees over their life-times or for forest stands over their rotation as most growth studies have been conducted:

- for a relatively short time (from less than one year to a few years) considering that forest trees have life times or rotation ages from decades to centuries;
- for the most part, using small seedlings whose responses may or may not be indicative of older and larger trees;
- in laboratory growth chambers, greenhouses, or open-top chambers with trees grown in pots or with different environmental conditions (temperature, light and humidity, for example) than trees would receive in the forests;
- free of weed competition; and
- with pest control.

Table 1. Summary of growth responses for forest trees exposed to elevated CO₂ in free-air CO₂ exposure (FACE) experiments

| FACE experiment | Species | Soil nutrients | Tree age (yrs) | Growth enhancement | Growth acclimation | References |
|-----------------|-----------------|----------------|----------------|---------------------------------|--------------------|--|
| POPFACE | Hybrid poplars | Moderate | 2 | Yes (+10 to 11%) ^a | – | Gielen and Ceulemans, 2001 |
| FACTS II | Trembling aspen | Moderate | 5 | Yes (+12% to +13%) ^b | No | Isebrands et al., 2001; Percy et al., 2002 |
| | Paper birch | Moderate | 5 | Yes (+24 to +25%) ^c | No | Karnosky et al., 2003 |
| | Sugar maple | Moderate | 5 | No ^c | – | Karnosky et al., 2003 |
| Oak Ridge | Sweetgum | Low | 20 | Yes (+15 to +33%) ^d | No | Norby et al. 2001, 2002 |
| FACTS I | Loblolly pine | Low | 20 | Yes (~26%) ^d | Yes | DeLucia et al., 1999; Oren et al., 2001; Hamilton et al., 2002 |

^aHeight.^bVolume.^cHeights and diameters.^dBasal area.

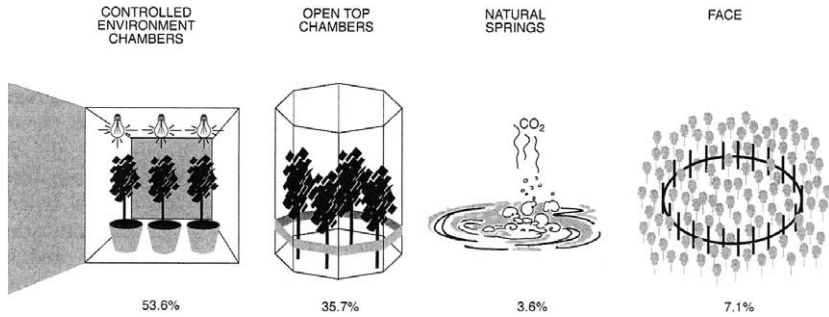


Figure 5. The most common types of facilities used in CO₂-enrichment studies (from Gielen and Ceulemans, 2001). In addition, branch chambers have been useful for examining gas exchange parameters of large trees in-situ (Teskey *et al.*, 1991; Vann and Johnson, 1995).

Research on forest trees has evolved from controlled environment chambers to open-top chambers and then on to studies utilizing natural CO₂ springs or free-air CO₂ exposure (FACE) facilities (Fig. 5). Long-term growth studies around CO₂ vents and two of the former FACE experiments (the FACTS I loblolly pine study and the Oak Ridge sweetgum study) (Table 1) suggest that growth enhancement under elevated CO₂ may be rather limited and that nutrient status of the soils may drive the response. The two poplar experiments are being conducted on soils higher in nutrients and growth enhancement has not diminished through two years (POPFACE) or 5 years (FACTS II).

The effects of elevated CO₂ on forest ecosystems are still being actively studied. However, from the standpoint of individual trees, we know that elevated CO₂ stimulates photosynthesis (Tjoelker *et al.*, 1998; Noormets *et al.* 2001a, 2001b), impacts foliar senescence in autumn (Karnosky *et al.*, 2003), and stimulates aboveground (Norby *et al.* 1999, 2002) and belowground (King *et al.*, 2001; Kubiske and Godbold, 2001) growth. Trees grown under elevated CO₂ generally have lower nitrogen concentrations in their foliage, lower Rubisco concentrations (Moore *et al.*, 1999), and altered defense compounds (Lindroth *et al.* 1993, 1997) and altered levels of antioxidants (Polle *et al.* 1993, 1997; Wustman *et al.*, 2001). See Chapter 3 for more information on CO₂ effects on forest ecosystems.

4. O₃

Evidence indicates that our emissions of nitrogen oxides (NO_x = NO + NO₂) and volatile organic compounds (VOCs) have significantly increased levels of O₃ over large regions of the globe (e.g., Crutzen, 1988; Marengo *et al.*, 1994;

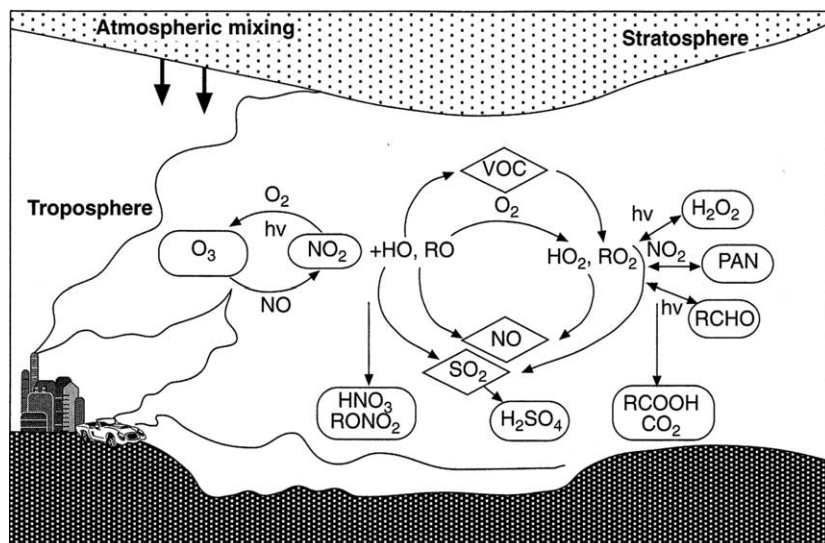


Figure 6. Schematic representation of gas-phase chemistry resulting in the generation of ozone and other by-products in polluted air. Primary pollutants, emitted from anthropogenic sources, are shown in diamond-shaped boxes; secondary pollutants, formed as a result of atmospheric reactions, are shown in circular boxes. PAN, peroxyacyl nitrate; VOC, volatile organic compounds (from Barnes and Wellburn, 1998).

Yienger et al., 2000). Anthropogenically driven increases in tropospheric O₃ form a large fraction (~20%) of the estimated greenhouse effect (Hauglustaine et al., 1994; Marenco et al., 1994; Kiehl et al., 1999; Berntsen et al., 2000). In addition, increasing levels of “background” O₃ are expected to affect strategies for attainment of air quality standards in urban areas in the future (see below) and increase the size of regions over which crop production is reduced due to O₃ damage (Chameides et al., 1994; Fowler et al., 1999). Finally, O₃ is a primary determinant of the oxidizing strength of the troposphere, through its photolysis in the presence of water vapor to form HO radicals, and changing tropospheric O₃ levels result in alteration of HO concentrations, impacting the lifetimes of most potential pollutants in the troposphere (Thompson, 1992) (Fig. 6).

Impacts on the tropospheric O₃ budget on a global scale occur through two mechanisms: (1) the production of O₃ over regions of O₃ precursor emissions followed by export to the global atmosphere of a fraction of the O₃ so produced, and (2) the export of O₃ precursors followed by production of O₃ in regions remote from sources. Ozone production efficiency is non-linear with respect to NO_x concentration (Liu et al., 1987) and is NO_x-limited in

most of the non-urban troposphere (Crutzen, 1988). As a result, in-situ production of O_3 in remote regions as the result of exported nitrogen oxides is expected to be more efficient than is production in source regions followed by export of O_3 . Global model simulations indicate a significant impact of long-range transport of peroxyacetyl nitrate (PAN) and its analogs upon NO_x levels in remote regions (Moxim et al., 1996; Horowitz and Jacob, 1999; Levy II et al., 1999), and calculate that photochemical production is by far the dominant source term in the O_3 budget throughout the troposphere (Wang et al., 1998). Impacts of precursor emissions from North America, Europe, and Asia upon air quality in Europe, Asia, and North America, respectively, are sufficient to potentially affect the ability of nations in the downwind regions to attain air quality standards for O_3 , currently or in the future (Jacob et al., 1999; Berntsen et al., 1999; Lin et al., 2000; Yienger et al., 2000; Lelieveld et al., 2002). Impacts of long-range transport from Asia upon O_3 in air reaching North America have been observed (e.g., at the Cheeka Peak site (Jaffe et al., 1999)) and in northern California (Parrish et al., 1992), as has transport from North America carrying elevated O_3 to Europe (e.g., Stohl and Trickl, 1999). Indeed, modeling analyses indicate that 20% of the violations of the European Council O_3 standard that occurred in the summer of 1997 would not have occurred in the absence of North American emissions (Li et al., 2003). However, emissions of nitrogen oxides worldwide are changing rapidly. Globally, emissions increases are expected to significantly enhance export, particularly from Asia; in contrast, it is likely that an increasing emphasis upon NO_x reductions to decrease O_3 standard violations in the United States and Europe will result in declining nitrogen oxides export from North America in the future (e.g., Jacob et al., 1999; Jonson et al., 2001).

4.1. Worldwide O_3 trends

While peak values of O_3 around major metropolitan areas in the US have generally decreased over the past 20 years (Lin et al., 2001), background base levels continue to increase worldwide (Fowler et al., 1998; Collins et al., 2000; Derwent et al., 2002). Particularly noteworthy is the rapid increase in O_3 levels near major cities in developing countries in Asia (Aunan et al., 2000; Cheung and Wang, 2001; Gupta et al., 2002), Central America (Raga and Raga, 2000; Skiba and Davydova-Belitskaya, 2002), and South America (Romero et al., 1999). Probably the highest O_3 concentrations in the world now occur in the vicinity of Mexico City which is faced with ideal conditions for photochemical oxidant production (high elevation, high incident radiation that does not vary significantly during the year, high daily temperatures, and high VOC and NO_x

emissions by mobile and fixed sources in the rapidly growing city (Raga and Raga, 2000)).

4.2. Ozone and forests

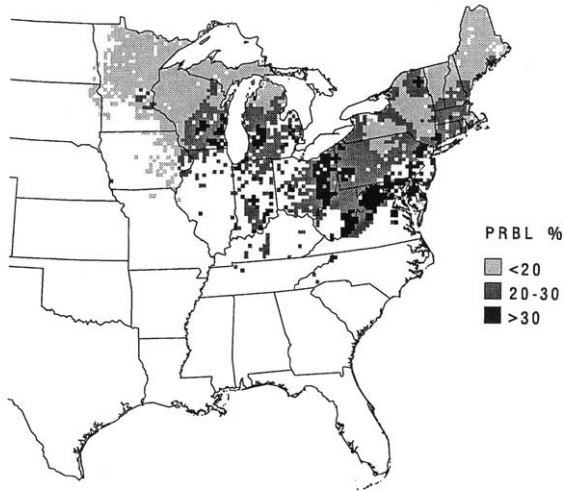
Ozone is a highly reactive oxidative stressor that enters the plant through the stomates and is highly reactive with cell walls and membranes in the cells surrounding the stomatal cavity. Ozone causes degradation of chlorophyll (Keller, 1988) and rubisco, adversely affecting the important machinery for photosynthesis (Coleman et al., 1995a). Ozone also induces premature leaf abscission (Keller, 1988; Karnosky et al., 1996) and can affect leaf size (Oksanen et al., 2001) and carbon allocation to roots (Coleman et al., 1995b; Coleman et al., 1996). Ozone has also been implicated in weakening trees such that they succumb to insect (Cobb and Stark, 1970; Percy et al., 2002) or disease (Karnosky et al., 2002) attacks. For agricultural crops in the US, it is estimated that 90% of the crop loss caused by air pollution is the result of O₃, either alone or in combination with other pollutants (Heck et al., 1982). We suspect a similar statement could be made for O₃ and forest trees in North America (McLaughlin and Percy, 1999).

The impacts of O₃ on forest tree populations have been studied in considerable detail. One of the first such problems to be diagnosed was the oxidant damage to ponderosa pine (*Pinus ponderosa*) over large areas of the San Bernardino Mountains in southern California (Miller et al., 1963). Community changes related to natural succession caused by interspecific variability in response to oxidants were initially described in this region by Miller (1973). He noted that mixed forests of ponderosa pine, sugar pine (*Pinus lambertiana*) and white fir (*Abies concolor*) were changing to predominantly fir because of the greater sensitivity of the pines to oxidants. Similar results have been described for Jeffrey pine (*Pinus jeffreyi*) and ponderosa pine at several locations along the western slope of the Sierra Nevadas (Peterson et al., 1989; Miller et al., 1996; Kurpius et al., 2002).

More recently, similar O₃-induced population impacts have been noted in the mountain pine forests surrounding Mexico City where O₃ remains at exceedingly high levels (100–200 ppb peaks or more) throughout the year (Miller, 1993; Miller and Tejeda, 1994). In this area, *Pinus hartwegii* appears to be the most highly sensitive to O₃ and has been severely impacted since the 1970s (Hall et al., 1996) with widespread dieback and decline resulting in its replacement in an extensive forest area surrounding Mexico City.

In the eastern United States, O₃ has been linked to visible foliar injury and growth decrease (Dochinger and Seliskar, 1970), decreased reproduction (Benoit et al., 1983), and increased mortality rates (Karnosky, 1981) for eastern white pine (*Pinus strobus*). Since the responses of eastern white pine appear

A. Aspen (1988)



B. Aspen (1989)

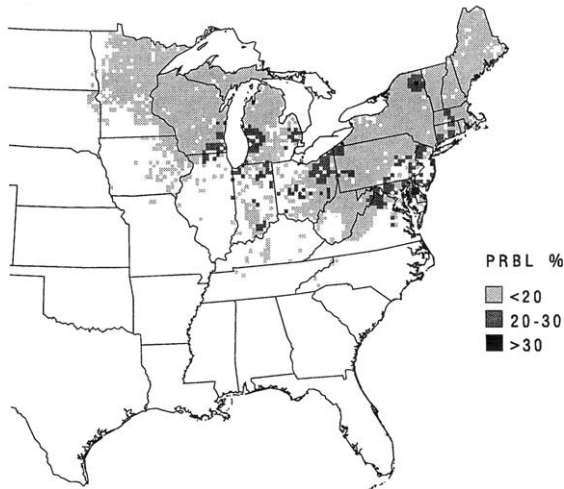


Figure 7. Variation in aspen seedling biomass loss with year-to-year exposure variation: 1988 (A) and 1989 (B) estimated exposures. PRBL calculated for each 20-km cell based on estimated ozone exposure value (three-month SUM06) and Weibull parameters for each species' response function (from Hogsett et al., 1997).

to be highly heritable, the components are in place for Phase I of natural selection, that is the elimination of sensitive genotypes. Since O_3 sensitive genotypes make up a relatively small portion of natural eastern white pine stands and the selection pressure conveyed by O_3 is rather low (Taylor and Pitelka,

1991), the question has been raised: “Does it really matter if we lose these sensitive genotypes?” Surely, this remains an openly debated and important research topic.

Similar responses to O₃ for sensitive genotypes of trembling aspen are expected. Evidence for population changes induced by O₃ in trembling aspen (*Populus tremuloides*) in the eastern United States are the studies by Berrang et al. (1986, 1989, 1991) which have shown a strong positive correlation between O₃ concentration at the population origin and the mean O₃ tolerance of the population. Populations from more heavily polluted areas tended to be more tolerant of O₃ than did populations from relatively pristine areas. As in eastern white pine, O₃ responses in aspen are highly heritable (Karnosky, 1977). Ozone has been shown to decrease aboveground biomass accumulation by 20 to 40% or more for sensitive genotypes (Wang et al., 1986; Karnosky et al., 1996) (Fig. 7) and 10 to 20% for more tolerant genotypes of aspen (Karnosky et al., 1996; Isebrands et al., 2001).

Ozone can also affect the relative abundance of understory vegetation in forests. Barbo et al. (1998) showed that O₃ exposures can cause shifts in the competitive interactions between plant species, thereby altering community structure. These understory plant interactions could also influence the ability of forest trees to naturally regenerate, grow and reproduce.

Not all tree species are susceptible to current levels of O₃. For example, Taylor (1994) has suggested that growth reductions for loblolly pine (*Pinus taeda*) in the southeastern US are not occurring at current O₃ levels. At the other extreme of O₃ effects is the Mexico City area where hundreds of thousands of pine (*Pinus* spp.) trees are dying due to prolonged exposures to very high levels of O₃ (Hall et al., 1996). For the eastern United States, Chappelka and Samuelson (1998) estimate that growth losses average about 0 to 10%. Worldwide, Fowler et al. (1999) estimate that some 24% of the world’s forests are currently exposed to damaging concentrations and that this number will increase to 50% of the world’s forests by the year 2100.

There remain many unanswered questions about the effects of O₃ on forest trees. The reader is referred to Chapters 4–13, 22 and 23 in this book for additional research findings on O₃ effects on forest trees.

5. Global warming

The global average surface temperature has increased since 1861. Over the 20th century the increase has been 0.6 ± 0.2 °C (Fig. 3). The 1990s was the warmest decade and 1998 was the warmest year on record (IPCC, 2001). Furthermore, the average nighttime temperature is increasing about 0.2 °C per decade, twice as fast as daytime temperature increases.

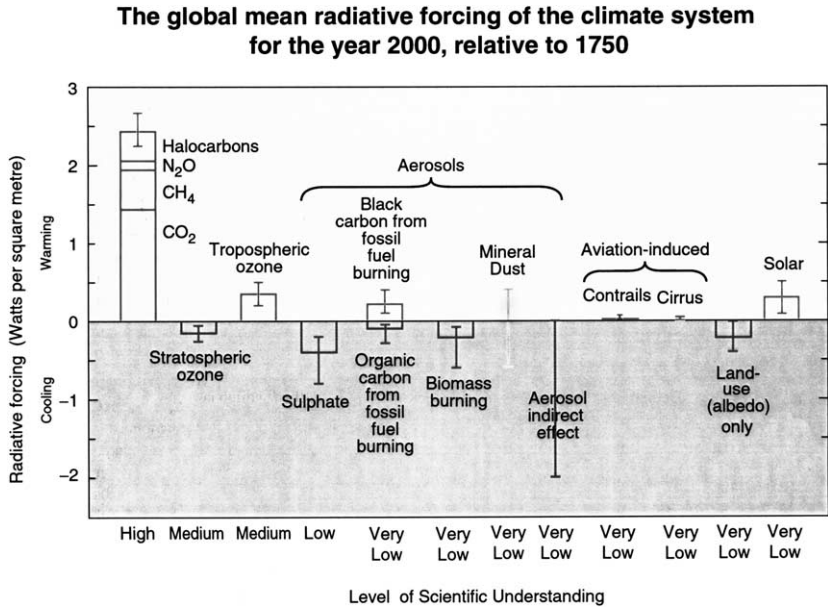


Figure 8. The global mean radiative forcing of the climate system for the year 2000, relative to 1750 (from IPCC, 2001).

While there is considerable debate as to the cause of the global warming, the bulk of the scientific community has concluded that the causes of increasing warming trends are dominated by anthropogenic forcing of the global energy balance, with a smaller contribution due to natural variability. Analysis of the global mean radiative forcing of the climate system (Fig. 8) suggests that anthropogenic greenhouse gases (CO₂, CH₄, N₂O, halocarbons, and O₃) are largely responsible for global warming by trapping radiative heat near the Earth's surface (IPCC, 2001).

5.1. Future trends

Emissions of CO₂ due to fossil fuel burning are virtually certain to be the dominant influence in increasing atmospheric CO₂ during the 21st century (Stott et al., 2000; IPCC, 2001). Despite the Kyoto protocol in which countries have pledged to cut back CO₂ emissions, CO₂ emissions continue to rise worldwide. Efforts to reduce CO₂ from the atmosphere have included strategies for tree planting to sequester carbon (Sedjo, 1989; Sampson, 1992). While little is known about how effectively trees will sequester carbon under elevated temperatures and with increasing CO₂ (Karnosky et al., 2001), the process of set-

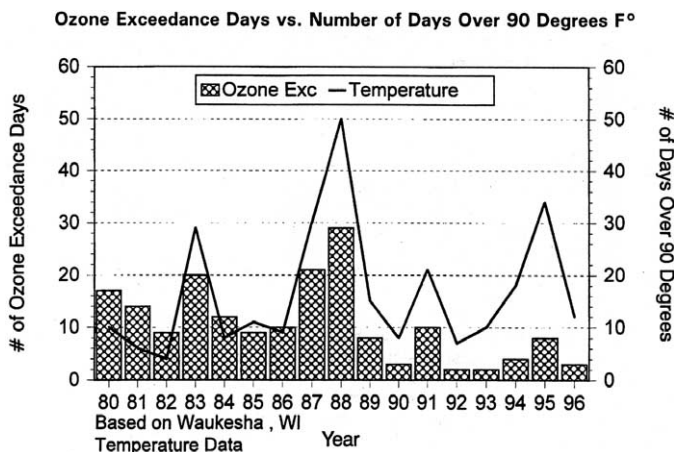


Figure 9. Dependence of ozone exceedance days on temperature from 1980 to 1996 for Waukesha, Wisconsin (from Wisconsin Department of Natural Resources, 1997).

ting up methods to monitor, evaluate, report, verify and certify forestry projects for climate change mitigation is moving forward (Vine et al., 2001) and tree planting is being counted on as one of the key methods to stabilize atmospheric CO₂ concentrations (Swart et al., 2002).

Increases in tropospheric O₃ are believed to have caused a warming effect which is about 15 to 20% of that due to CO₂ and other greenhouse gases (Hauglustaine et al., 1994; Kiehl et al., 1999; Berntsen et al., 2000; Shine, 2001). Tropospheric ozone is also expected to continue to increase through the 21st century (Stevenson et al., 1998; Brasseur et al., 1998; IPCC, 2001). The complicated interrelatedness of increasing global temperature and ozone suggests that tropospheric ozone will increase under global warming for two reasons. First, the reactions in tropospheric O₃ formation (Fig. 6) are enhanced as temperatures increase and there is a well known link of elevated tropospheric O₃ and high temperatures (Fig. 9). Second, as temperatures increase, trees and other plants emit larger amounts of volatile organic compounds (VOC) (Monson et al., 1995) which rapidly react with hydroxyl radical (OH), O₃, and nitrate (NO_x). Such reactions can, among other things, enhance O₃ (Fuentes et al., 2001). Currently, estimated global VOC emissions total 1150 Tg yr⁻¹, or about an order of magnitude greater than VOC emissions from anthropogenic sources (Guenther et al., 1995; Komenda et al., 2001). Modelled estimates of VOC emission increases in the next century under warming temperatures suggest VOC emissions could double (Constable et al., 1999), although research is needed to more accurately

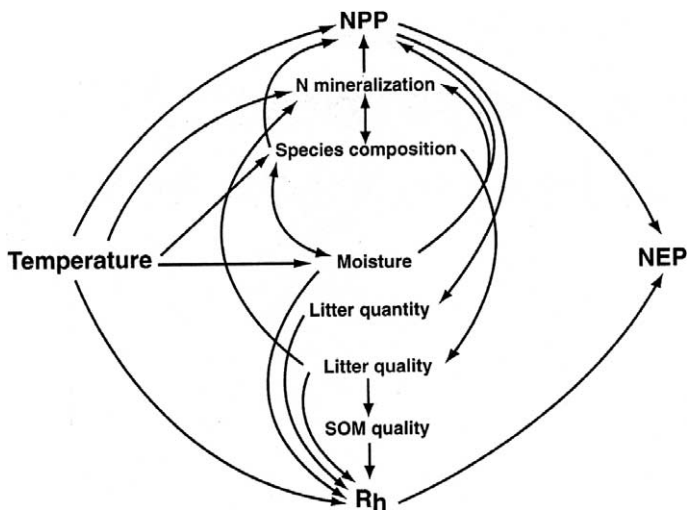


Figure 10. Direct and indirect effects of temperature on net primary production (NPP), heterotrophic respiration (R_h), and net ecosystem production (NEP). Soil organic matter is labeled as SOM (from Shaver et al., 2000).

ascertain how environmental changes will affect VOC emissions (Fuentes et al., 2001).

5.2. Global warming and forests

Temperature affects virtually all chemical and biological processes in plants so it is likely the effects of global warming will be dramatic and complex for forest ecosystems (Melillo et al., 1993; Shaver et al., 2000). For example, the complexity of temperature effects can be seen in an examination of the carbon budget under elevated temperature (Fig. 10) where temperature is seen affecting rates of N mineralization, soil moisture content and precipitation, and measures of growth (NPP) and heterotrophic respiration (R_h). The balance between these two processes determines net ecosystem production (NEP) which is yet difficult to accurately predict (McNulty et al., 1996; Nabuurs et al., 2002) resulting in model projections suggesting that global forests could be carbon sinks or sources in the future (Dixon et al., 1994).

While we know very little about net ecosystem production under global warming, it is generally believed that soil respiration increases exponentially with an increase in soil temperature (Raich and Schlesinger, 1992; Atkin et al., 2000). This is particularly significant as we realize that the 3 m of soil are estimated to contain 2344 Pg of organic carbon (C), which is known

The Global Carbon Cycle

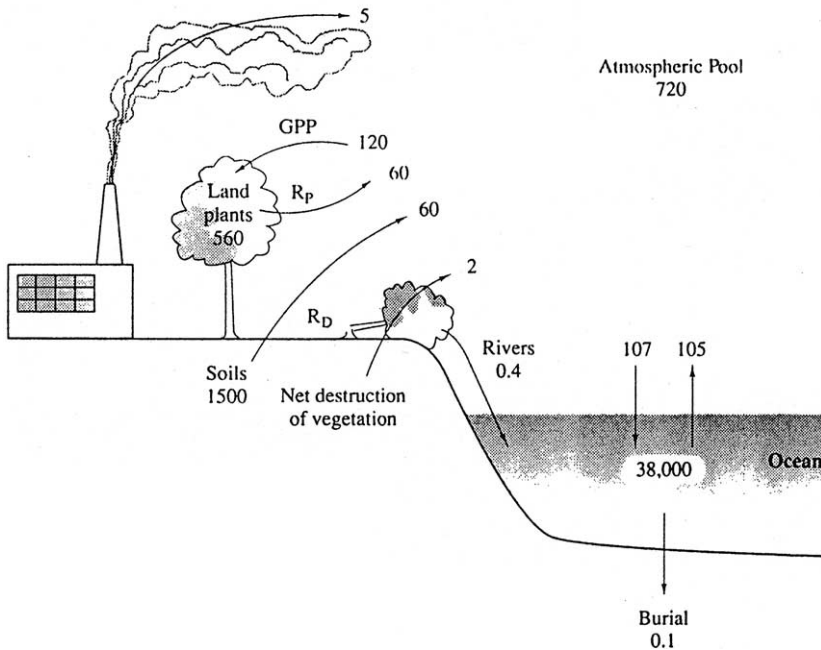


Figure 11. The global carbon cycle. All pools are expressed in units of 10^{15} gC and all fluxes in units of 10^{15} gC/yr (from Schlesinger, 1997).

to interact with the atmosphere (Jobbagy and Jackson, 2000). Considering the importance of forest soils in storing C (Fig. 11), the potential for soil carbon to be respired at unprecedented rates into the atmosphere presents another potential very large source of CO_2 in the atmosphere. Particularly vulnerable to increased soil warming are the forest soils in boreal and arctic regions which represent 20 to 60% of the global soil carbon pool and where low temperatures and permafrost currently limit decomposition (Hobbie et al., 2000). Rates of fine root turnover are also strongly temperature dependent so that there is a great deal of uncertainty as to how root systems will respond to global warming (Pregitzer et al., 2000).

Among the most certain changes predicted to occur under global warming in forest ecosystems are for species composition and ranges to be altered (Pitelka, 1997; Iverson and Prasad, 1998; Bakkenes et al., 2002). Examination of past range changes provides insights into the potential for range changes to occur under the rapid global warming (Davis et al., 1986; Fig. 12). While trees have considerable genetic diversity and capacity to evolve in the face

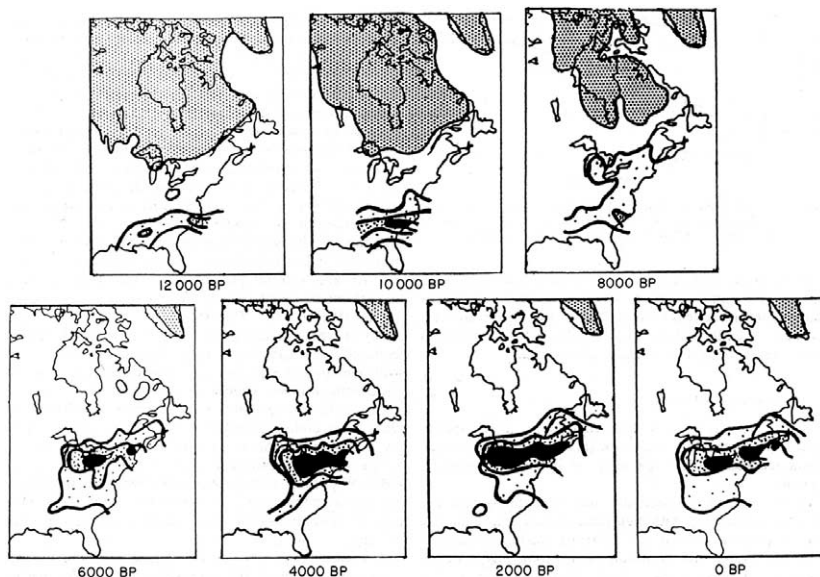


Figure 12. Isopoll maps of American beech (*Fagus grandifolia*) in the eastern USA from 12000 BP to the present day (isopolls at 1, 5, and 10%) (from Davis et al., 1986).

of changing climate (Bradshaw and McNeilly, 1991), it is likely that major changes in ranges will take place (Pitelka, 1997). Particularly pronounced changes will likely occur in boreal regions and boreal treeline species that may be among the most vulnerable (MacDonald et al., 1993; Makinen et al., 2000; Lloyd and Fastie, 2002) where trees are currently growing at the cold margins of the forest. In addition to direct responses to temperature changes, climate change can affect forests by altering the frequency, intensity, duration and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, wind storms, ice storms, frost occurrence and landslides (Dale et al., 2001). The rapid nature of today's climate change challenges trees adaptive capability to migrate (Davis and Shaw, 2001). This rapid rate of climate change, coupled with land use changes such as habitat fragmentation by human development that impede gene flow, can be expected to disrupt the interplay of adaptation and migration, likely affecting forest productivity and threatening the persistence of many species (Davis and Shaw, 2001; Rehfeldt et al., 2002).

Another major change related to global warming is the noticeable change of the phenology of bud break and bud set. Earlier dates of average spring bud break and later dates of fall bud set have been detected resulting in a longer growing season in forest trees around the world (Menzel and Fabian, 1999;

Menzel, 2000; Penuelas and Filella, 2001; Parmesan and Yohe, 2003). This lengthening of the growing season may have already contributed to increased biomass accumulation (Menzel and Fabian, 1999) and is likely affecting insect and animal phenology and bird migration patterns (Penuelas and Filella, 2001).

Forest insect and disease pests are likely to be also changing as a result of global warming (Cannon, 1998; Harrington et al., 1999; Chakraborty et al., 2000; Volney and Fleming, 2000; Bale et al., 2002). For example, the change in forest tree phenology described above must be met with changes in insect phenology or they will hatch out at a time when there is no foliage at a proper stage for feeding. The effects of asynchrony of insect egg hatch and budbreak was seen over large parts of the northern Great Lakes region in the spring of 2002 as a late spring due to cold temperatures resulted in delayed aspen bud break, after the majority of forest tent caterpillars had hatched. This resulted in a high mortality rate in the otherwise peak cycle forest tent caterpillars (Mattson, personal communication).

The occurrence and abundance of various insects and disease pests are generally predicted to increase under global warming (Chakraborty et al., 2000; Bale et al., 2002). Especially worrisome is the possibility of major forest pests moving northward into temperate forests that were growing in areas with winter temperatures limiting southern forest pests. For example, the pine wood nematode has generally been a major nuisance only in subtropical or southern temperature forests (Suzuki, 1999). This serious pest of pines will likely become a major pest problem in the prime northern pine species such as loblolly pine in the US and Scots pine in Europe. Furthermore, non-indigenous species are likely to be particularly opportunistic under global warming (Cannon, 1998).

The availability of water resources of forests under global warming is likely to become an ever-increasing concern as droughts are predicted to be more common in many parts of the world where forests are already facing common moisture stress problems (Hanson and Weltzin, 2000). This could be a critically important factor, more important than temperature changes, for arid and semi-arid tropical forests that are just marginally alive (Desanker and Justice, 2001; Hulme et al., 2001). See Chapter 3 for more on global warming.

6. Sulfur and nitrogen oxides and acidic deposition

The burning of fossil fuels, particularly coal, has been responsible for deposition of sulfur and nitrogen to forest ecosystems around the world. These pollutants can be transported long distances from tall smokestacks and they can be deposited either in precipitation or in particulate form. The principal forms of impact are acidification, caused by both sulfur and nitrogen, and eutrophication of lakes and streams, caused by nitrogen (Hirst et al., 2000).

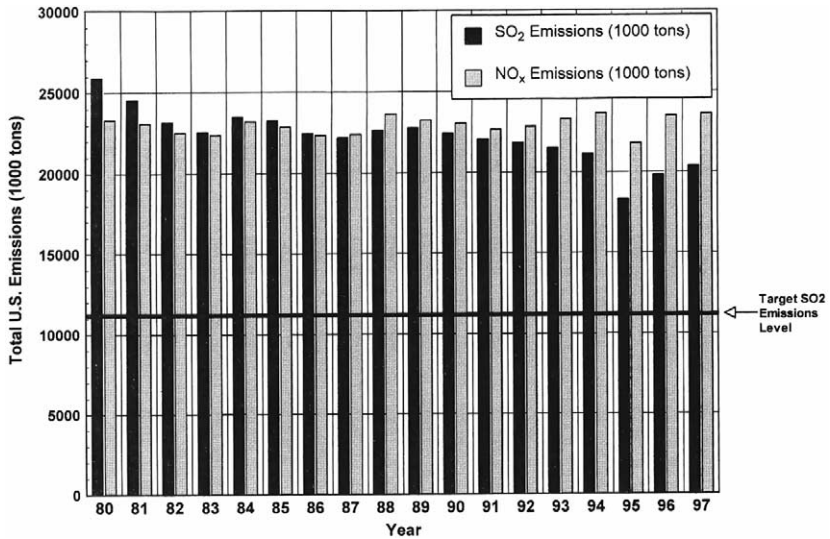


Figure 13. SO₂ and NO_x emissions in the United States from 1980 through 1997. The target SO₂ emissions were based on the 1980 emission levels (from Lynch et al., 2000).

Forest dieback due primarily to the burning of soft coal, which is particularly high in sulfur content, has occurred over some 2.8 million ha in Europe, primarily in the region of the “Black Triangle” near the common borders of the Czech Republic, Germany, and Poland (Percy, 2002). The International Cooperative Programme on Assessment and Monitoring of Air Pollutant Effects on Forests (ICP Forests) has identified defoliation rates of 39.7% in Poland and 71.9% in the Czech Republic (EC/PHARE, 1999).

While pollution control legislation in the United States (Furiness et al., 1998; Lynch et al., 2000) and Europe (Erisman et al., 1998; Alewell et al., 2000) have produced reductions in sulfur emissions (Figs. 13 and 14) and deposition (Fig. 15), nitrogen emissions have continued to rise (Fowler et al., 1999; Lynch et al., 2000; Galloway and Cowling, 2002; Galloway et al., 2002). Considerable areas of forests in Europe still have nitrogen and sulfur deposition above levels referred to as critical loads (the deposition a natural area can stand without damage) (Hirst et al., 2000). The impacts of acidification on forests are numerous including: soil acidification, leaching of nutrients from foliage and soils, volatilization of ammonia from the soil, mobilization of toxic minerals such as Al from soils, and alteration of fine root turnover, frost hardiness, mycorrhizal fungi associations and foliage retention (Aber et al., 1989; Jeffries and Maron, 1997). Calcium nitration resulting in membrane destabilization has also been associated with decline of spruce trees due to acid rain

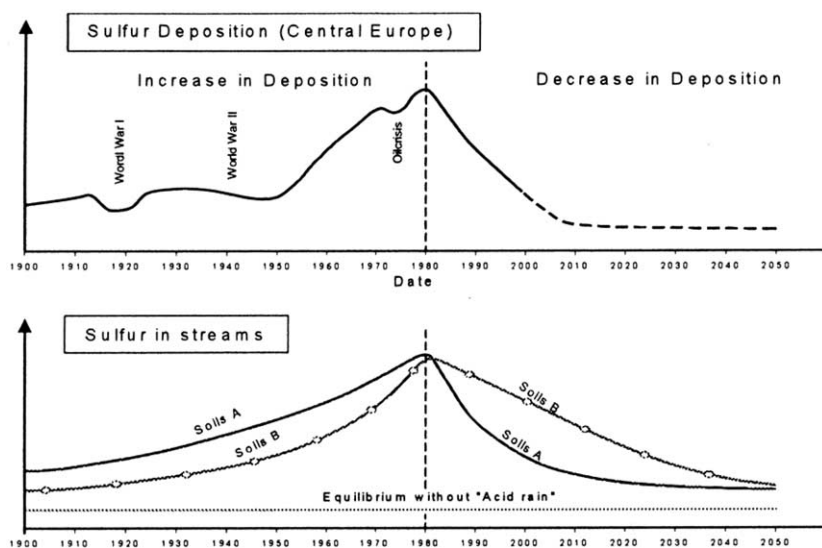


Figure 14. Trends in sulfur deposition (top) and sulfur in streams (bottom) in Europe from 1900 to 2050 (from Alewell, 2001).

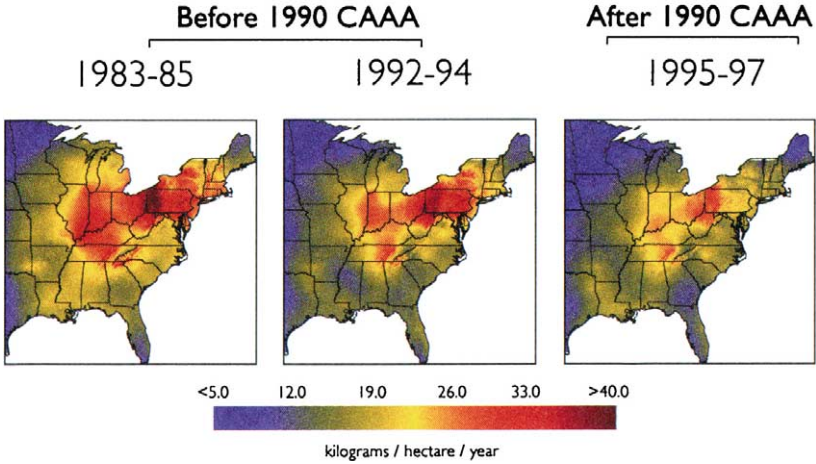
(DeHayes et al., 1999). Forests in which nitrogen deposition is no longer providing a net fertilization effect are referred to as nitrogen saturated. The classic example of this continues to be the forests in the San Bernardino Mountains in the Los Angeles air basin which have received high impacts of nitrogen deposition for the past 60 years or more (Bytnerowicz and Fenn, 1996; Bytnerowicz et al. 2002a, 2002b).

Fowler et al. (1999) predicts a six-fold increase in the area of global forest at risk from acidification between 1985 and 2050, with the majority of the increase being from subtropical and tropical forest regions. The majority of these increases will come from developing countries in Asia (Figs. 16 and 17) (Arndt et al., 1997; Lefohn et al., 1999; Streets et al., 2000). Huge increases in both nitrogen and sulfur emissions are predicted for the rapidly industrializing countries of China (Streets and Waldhoff, 2000; Vallack et al., 2001) and India (Parshar et al., 1998). See Chapters 14–18 for more on these pollutants.

7. Other air pollutants

In this short review, we have not attempted to comprehensively describe all air pollutants that impact forests. While the largest acreages worldwide impacted by air pollution are those affected by O_3 and acidic deposition, there

SULFATE WET DEPOSITION



NITRATE WET DEPOSITION

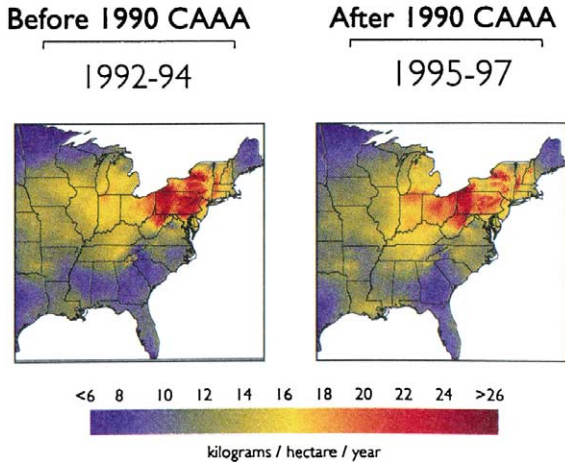


Figure 15. Recent patterns of wet deposition before and after the implementation of the 1990 Clean Air Act Amendments (CAAA) (from Driscoll et al., 2001).

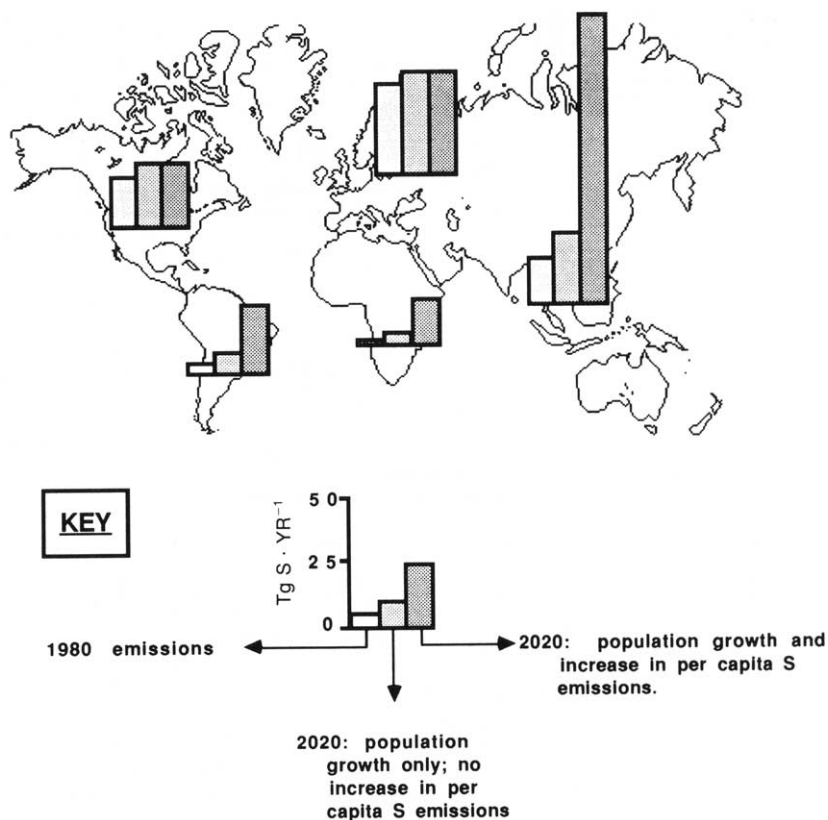


Figure 16. The emission of sulfur(s) to the atmosphere in 1980 compared to 2020 with no change and with a change in per capita energy consumption (from Galloway, 1989).

are large areas of forests worldwide that are impacted by particulate pollution (Kretschmar, 1994; Edgerton et al., 1999), heavy metals (Mankovska, 1997a, 1997b; Straszewski et al., 2001), gaseous sulfur dioxide (Arndt et al., 1997; Streets et al., 2000; Vallack et al., 2001) and various other photochemical oxidants (Parshar et al., 1998; Streets and Waldhoff, 2000; Vallack et al., 2001; Derwent et al., 2002). With the exception of the regional photochemical oxidant problems, these are generally point-source pollutants around major factories or power plants. While these were very common in the early industrialization periods of western countries, they have largely been cleaned up. However, they are still significant problems in developing countries (Arndt et al., 1997; Vallack et al., 2001; Gupta et al., 2002; Skiba and Davydova-Belitskaya, 2002)

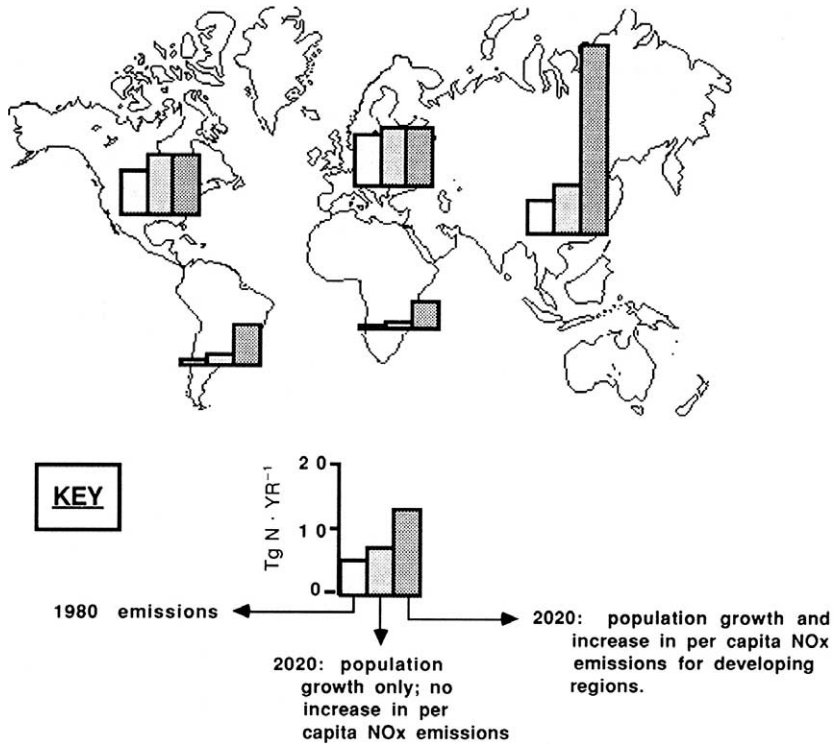


Figure 17. The emission of nitrogen (N) to the atmosphere in 1980 compared to 2020 with no change and with a change in per capita energy consumption (from Galloway, 1989).

and in countries in transition from the communist influence (Mankovska, 1997a, 1997b; Straszewski et al., 2001).

8. Pollutant interactions

Although we have discussed the various air pollutants individually, they seldom occur as individual pollutants (Fig. 6). More often, forests are faced with interacting pollutants which may counteract or exacerbate one another (Krupa and Kickert, 1989; Kickert and Krupa, 1990; Isebrands et al., 2000; Karnosky et al., 2001). For example, both elevated CO₂ and low levels of nitrogen deposition generally have stimulatory effects on forest tree growth and reproduction while excess nitrogen, sulfur oxides, O₃ and other air pollutants generally negatively impact forest ecosystems. Thus, predicting outcomes of multiple pollutant interactions for forest ecosystems is difficult, es-

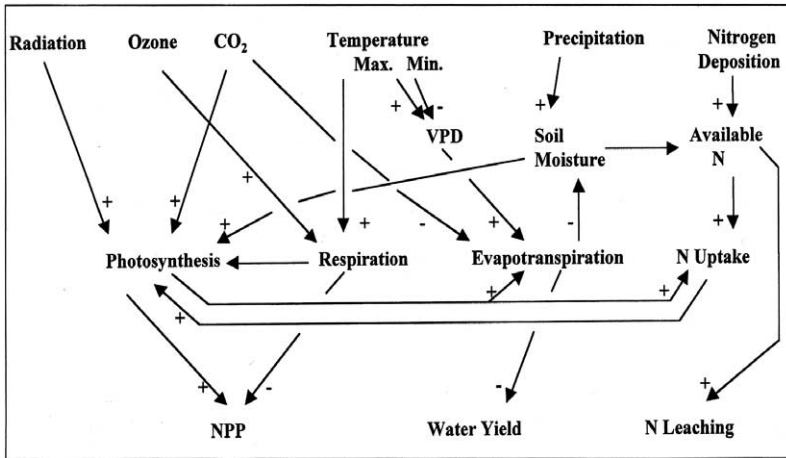


Figure 18. Interactions among environmental factors that are subject to change through human activities, and major processes affecting carbon, water, and nitrogen dynamics in forest ecosystem. (+) Indicates an enhancement, and (-) a suppression, of the receptor process (from Aber et al., 2001).

pecially since these interactions are also affected by other environmental variables such as temperature, relative humidity, and soil moisture (Fig. 18), land-use (Caspersen et al., 2000), and they can also be affected by competitive environment of the forest (Fig. 19). Also, far less research has been done on interacting pollutants than on single pollutants.

In what turned out to be a classic pollutant interaction, many eastern white pine trees in the Ohio River Valley began showing symptoms such as tip-burned and shortened needles, poor needle retention, and stunted growth in the 1960s. The cause was later found to be a synergistic interaction of moderately elevated levels of O_3 and SO_2 (Dochinger et al., 1970; Costonis, 1970).

Probably the most studied interaction with forest trees is that of elevated CO_2 and O_3 . Since these two pollutants are increasing in the troposphere at about the same rate (IPCC, 2001), this interaction will impact large areas of future forests. Fowler et al. (1999) estimate nearly 50% of the world's forests will be exposed to O_3 concentrations greater than 60 ppb by the year 2100. Atmospheric CO_2 levels are expected to be doubled over current levels by then (Stott et al., 2000; IPCC, 2001).

This is a complex interaction that is affected by concentrations of the two interacting pollutants, the species and genotypes involved as considerable genetic variation in responses to both of these pollutants occurs, and it can also be affected by other stresses such as competition (McDonald et al., 2002), drought stress or nitrogen additions (Karnosky et al., 1992). Thus, it is not surprising

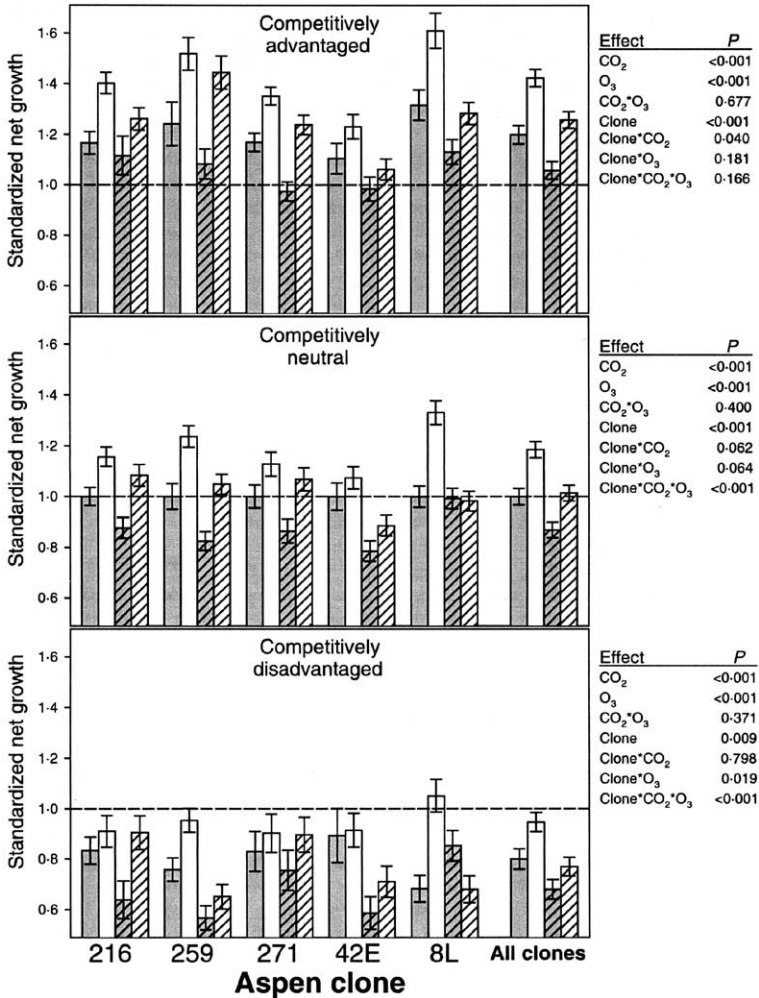


Figure 19. Standardized net growth (SNG) responses averaged during the 1998–2001 period for mixed-clone aspen stands exposed to combinations of ambient and elevated CO₂ and O₃. Bars represent least-squares mean estimates (LS means) ± 1 SE for individual clones, with the average response across clones identified as ‘All clones’. Shaded bars, ambient CO₂ treatments; unshaded bars, elevated CO₂ treatments; open bars, ambient O₃ treatments; hatched bars, elevated O₃ treatments. The competition status indices (CSI) for this analysis were means of annual CSI values during the 4-year period, with competitively advantaged (+) and disadvantaged (–) LS means calculated at ±90 cm values of the CSI covariate. The dashed horizontal lines denote SNG response in competitively ‘neutral’ (CSI = 0), ambient conditions, for reference. Analysis of covariance (ANCOVA) results for fixed effects of atmospheric treatments, clone and their interactions under competitively advantaged, neutral and disadvantaged conditions are reported next to each panel (from McDonald et al., 2002).

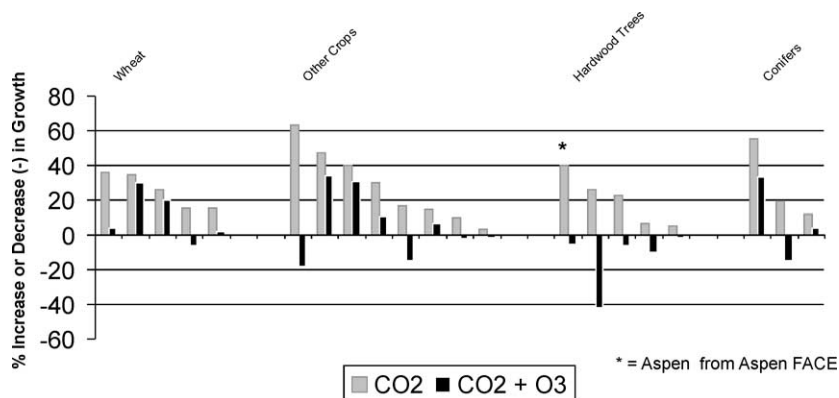


Figure 20. Relative effects of controlled exposure to elevated CO₂ on normalized plant growth under CO₂ alone (striped bars; 500–713 $\mu\text{mol mol}^{-1}$ CO₂) and elevated CO₂ plus ozone (dotted bars) (Modified and expanded from Barnes and Wellburn, 1998). Data presented for wheat (*Triticum aestivum*) taken from Barnes et al. (1995); Rudorff et al. (1996); McKee et al. (1997); Bender et al. (1999) and Hudak et al. (1999); other crops including soybean (*Glycine max*) taken from Heagle et al. (1998) and Miller et al. (1998), tomato (*Lycopersicon esculentum*) taken from Olszyk and Wise (1997) and Hao et al. (2000), rice (*Oryza sativa*) taken from Olszyk and Wise (1997), potato (*Solanum tuberosum*) taken from Donnelly et al. (2001) and Lawson et al. (2001), and corn (*Zea mays*) taken from Rudorff et al. (1996); hardwood trees including hybrid poplars (*Populus hybrids*) taken from Dickson et al. (1998), trembling aspen (*Populus tremuloides*) taken from Volin and Reich (1996), Volin et al. (1998), and Isebrands et al. (2001), and oak (*Quercus pe-trea*) taken from Broadmeadow and Jackson (2000); and conifers including ponderosa pine taken from David Olszyk (personal communication) and Scots pine (*Pinus sylvestris*) taken from Broadmeadow and Jackson (2000) and Utriainen et al. (2000). Each pair of bars represents one species (Karnosky et al., 2003).

that some conflicting results have been found. For example, with trembling aspen, Volin and Reich (1996) and Volin et al. (1998) suggest that elevated CO₂ ameliorates the effects of O₃ on photosynthesis and growth while Kull et al. (1996), Isebrands et al. (2001), Wustman et al. (2001), McDonald et al. (2002), and Mankovska et al. (2003) suggest that CO₂ does not ameliorate and in some cases it exacerbates the negative effects of O₃. The results of numerous CO₂/O₃ interaction studies that have examined growth or biomass production are shown in Fig. 20. See Chapters 19–23 for more on pollutant interactions.

9. Management of genetic resources for future forests

While there has been a great deal of research on the impacts of air pollution and climate change, there has not yet been much research on the possible consequences of these effects on managed forests (Lindner, 2000). One area par-

ticularly important in future managed forests is the genetic makeup of these forests.

Tree breeding and genetic selection has generally involved either plus tree selection followed by progeny testing or provenance testing followed by progeny testing of superior phenotypes. Then, seed orchards have been established and rogued to provide the seed for the next generation. This process has continued with advanced generation selection and breeding in a few commercially important tree species. In all facets of these programs, selection is done based on the conditions prior to selection and for the most part these selections are not done on the basis of predicted pollution and climate scenarios that will be in place during the rotation of the commercial forest. Screening and selection of genotypes suitable for future pollution and climate scenarios is generally thought to be nearly impossible because of the complexity and cost of such programs. Thus, an alternative strategy in which a wider genetic base is maintained in our breeding population is essential for developing future forests (Namkoong, 1991). Maintaining large amounts of genetic diversity will increase the probability that adequate adaptability is maintained to meet rapidly changing environmental conditions (Gregorius, 1986; Müller-Starck, 1989; Koski, 1996; Rehfeldt et al., 1999). Planting a diverse array of species, seed sources, or families, is a hedge against the uncertainty inherent in current projections of warming (Ledig and Kitzmiller, 1992).

Alternative strategies are also needed to insure that gene banks, clone banks, seed zones, seed collection areas and other in-situ conservation strategies are maintained in multiplicative manner such that the changing pollution and/or climate scenarios will not result in the loss of such collections from single vulnerable test sites (Martin, 1996; Hannah et al., 2002). Given the past several decades of “laissez-faire” attitude towards traditional genetic field trials and field conservation efforts, this need to conserve forest genetic resources in multiple amounts may help genetics regain prominence amongst the forestry community.

10. Conclusions and knowledge gaps

10.1. Air monitoring

- The global distribution of air pollution is just being elucidated. An important research need is to develop ways to sort out the relative global versus national contributions to important air pollutants such as NO_x and O_3 .
- The actual concentrations of important pollutants, such as NO_x , SO_2 , and O_3 , in forested areas of the world continue to be largely unknown. Devel-

opment and strategic deployment of relatively inexpensive passive monitors offer many opportunities to address these questions in forested areas.

10.2. Increasing CO₂ and global warming

- CO₂ continues to increase in the atmosphere. The effects of elevated CO₂ on long-term forest productivity, ecosystem stability, and genetic diversity of forests are largely unknown.
- Global warming is now indisputedly taking place at unprecedented rates. The rate of change in species composition and function is largely speculation at best and needs solid research attention. The possible expansion of insect and disease pests under warming climates and less harsh winters has important forest ecosystem implications and is critically important to study. Finally, the usefulness of tree planting and improved forest management for increasing C sequestration in forest ecosystems is largely unknown. Thus, research on carbon budgets and CO₂ mitigation potential of various forestry practices are important research areas to address.

10.3. S and N oxides and acidification

- While great improvements in acidic deposition have been made in several western countries, S and N deposition are increasing in many developing countries and the effects of these problems are not well understood.

10.4. Other air pollutants (particulates, heavy metals, etc.)

- The forests of many of the former Eastern Bloc countries suffered from deposition as particulates and heavy metals, as well as from acidic deposition. The restoration of forest ecosystem degraded by air pollution, particularly in countries in transition from a Communist government, remains a very high priority for much of Eastern Europe.

10.5. Pollutant interactions

- While local large-scale deposition of single pollutants can often cause local damage to forest ecosystems around pollution point sources, most modern air pollution problems are more regional in distribution. Thus, complex air pollution interactions with other air pollutants, with environmental variables such as temperature, relative humidity, light, and soil moisture, and with other stresses such as drought, low fertility, or insect or disease pests often occur. Without exception, pollutant interactions have not been studied to the same detail as have single pollutants. Furthermore, modellers have largely

ignored pollutant interactions in their global projections of net ecosystem carbon budgets.

10.6. *Managing future forests*

- Our future forests will continue to be exposed to unprecedented global environmental changes. Thus, it is critically important that the case for reforestation programs include high genetic diversity. Studies comparing the effects of global change on genetically diverse versus genetically disparate communities are critically needed. Deployment strategies for maximizing forest productivity, while optimizing genetic diversity, are needed for the forest products industry as well as for forests designed to sequester carbon.

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References

- Aber, J.D., Nadelhoffer, K.J., Steudler, P., Melillo, J.M., 1989. Nitrogen saturation in northern forest ecosystems. *Bioscience* 39, 378–386.
- Aber, J., Neilson, R.P., McNulty, S., Lenihan, J.M., Bachelet, D., Drapek, R.J., 2001. Forest processes and global environmental change: Predicting the effects of individual and multiple stressors. *Bioscience* 51, 735–751.
- Alewell, C., 2001. Predicting reversibility of acidification: The European sulfur story. *Water Air Soil Pollut.* 130, 1271–1276.
- Alewell, C., Manderscheid, B., Gerstberger, P., Matzner, E., 2000. Effects of reduced atmospheric deposition on soil solution chemistry and elemental contents of spruce needles in NE-Bavaria, Germany. *J. Plant Nutr. Soil Sci.* 163, 509–516.
- Arndt, R.L., Carmichael, G.R., Streets, D.G., Bhatti, N., 1997. Sulfur dioxide emissions and sectorial contributions to sulfur deposition in Asia. *Atmos. Environ.* 31, 1553–1572.
- Atkin, O.K., Edwards, E.J., Loveys, B.R., 2000. Response of root respiration to changes in temperature and to relevance to global warming. *New Phytol.* 147, 141–154.
- Aunan, K., Bernsten, T.K., Seip, H.M., 2000. Surface ozone in China and its possible impact on agricultural crop yields. *Ambio* 29, 294–301.
- Bakkenes, M., Alkemade, J.R.M., Ihle, F., Leemans, R., LaTour, J.B., 2002. Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biol.* 8, 390–407.

- Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symnioudis, I., Watt, A.D., Whittaker, J.B., 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biol.* 8, 1–16.
- Barbo, D.N., Chappelka, A.H., Somers, G.L., Miller-Goodman, M.S., Stolte, K., 1998. Diversity of an early successional plant community as influenced by ozone. *New Phytol.* 138, 653–662.
- Barnes, J.D., Wellburn, A.R., 1998. Air pollutant combinations. In: DeKok, L.J., Stulen, I. (Eds.), *Responses of plant metabolism to air pollution and global change*. Backhuys Publishers, Leiden, The Netherlands, pp. 147–164.
- Barnes, J.D., Ollerenshaw, J.H., Whitfield, C.P., 1995. Effects of elevated CO₂ and/or O₃ on growth, development and physiology of wheat (*Triticum aestivum* L.). *Global Change Biol.* 1, 129–142.
- Bender, J., Herstein, U., Black, C.R., 1999. Growth and yield responses of spring wheat to increasing carbon dioxide, ozone and physiological stresses: A statistical analysis of 'ESPACE-wheat' results. *Eur. J. Agron.* 10, 185–195.
- Benoit, L.F., Skelly, J.M., Moore, L.D., Dochinger, L.S., 1983. The influence of ozone on *Pinus strobus* L. pollen germination. *Can. J. Forest Res.* 13, 184–187.
- Berntsen, T.K., Karlsdóttir, S., Jaffe, D.A., 1999. Influence of Asian emissions on the composition of air reaching the North Western United States. *Geophys. Res. Lett.* 26, 2171–2174.
- Berntsen, T.K., Myhre, G., Stordal, F., Isaksen, I.S.A., 2000. Time evolution of tropospheric ozone and its radiative forcing. *J. Geophys. Res.* 105, 8915–8930.
- Berrang, P.C., Karnosky, D.F., Bennett, J.P., 1989. Natural selection for ozone tolerance in *Populus tremuloides* II. Field verification. *Can. J. Forest Res.* 19, 519–522.
- Berrang, P.C., Karnosky, D.F., Bennett, J.P., 1991. Natural selection for ozone tolerance in *Populus tremuloides*: An evaluation of nationwide trends. *Can. J. Forest Res.* 21, 1091–1097.
- Berrang, P.C., Karnosky, D.F., Mickler, R.A., Bennett, J.P., 1986. Natural selection for ozone tolerance in *Populus tremuloides*. *Can. J. Forest Res.* 16, 1214–1216.
- Bradshaw, A.D., McNeilly, T., 1991. Evolutionary response to global climatic change. *Ann. Bot.* 67, 5–14.
- Brasseur, G.P., Kiehl, J.T., Muller, J.-F., Schneider, T., Granier, C., Tie, X., Hauglustaine, D., 1998. Past and future changes in global tropospheric ozone: Impact on radiative forcing. *Geophys. Res. Lett.* 25, 3807–3810.
- Broadmeadow, M.S., Jackson, S.B., 2000. Growth responses of *Quercus petraea*, *Fraxinus excelsior* and *Pinus sylvestris* to elevated carbon dioxide, ozone, and water supply. *New Phytol.* 146, 437–451.
- Bytnerowicz, A., Fenn, M.E., 1996. Nitrogen deposition in California forests: A review. *Environ. Pollut.* 92, 127–146.
- Bytnerowicz, A., Godzik, B., Fraczek, W., Grodzinska, K., Krywult, M., Badea, O., Barancok, P., Blum, O., Cerny, M., Godzik, S., Mankovska, B., Manning, W., Moravcik, P., Musselman, R., Oszlanyi, J., Postelnicu, D., Szduj, J., Varsavova, M., Zota, M., 2002a. Distribution of ozone and other air pollutants in forests of the Carpathian Mountains in central Europe. *Environ. Pollut.* 116, 3–25.
- Bytnerowicz, A., Tausz, M., Alonso, R., Jones, D., Johnson, R., Grulke, N., 2002b. Summer-time distribution of air pollutants in Sequoia National Park, California. *Environ. Pollut.* 188, 187–203.
- Cannon, R.J.C., 1998. The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. *Forestry* 72, 237–247.

- Caspersen, J.P., Pacala, S.W., Jenkins, J.C., Hurtt, G.C., Moorcroft, P.R., Birdsey, R.A., 2000. Contributions of land-use history to carbon accumulation in US forests. *Science* 290, 1148–1151.
- Chakraborty, S., Tiedemann, A.V., Teng, P.S., 2000. Climate change: Potential impact on plant diseases. *Environ. Pollut.* 108, 317–326.
- Chameides, W., Kasibhatla, P., Yienger, J., Levy II, H., 1994. Continental-scale metro-ago-plexes, regional ozone pollution, and world food production. *Science* 264, 74–77.
- Chappelka, A.H., Samuelson, L.J., 1998. Ambient ozone effects on forest trees of the eastern United States: A review. *New Phytol.* 139, 91–108.
- Cheung, V.T.F., Wang, T., 2001. Observational study of ozone pollution at a rural site in the Yangtze Delta of China. *Atmos. Environ.* 35, 4947–4958.
- Cobb Jr., F.W., Stark, R.W., 1970. Decline and mortality of smog-injured ponderosa pine. *J. For.* 68, 147–149.
- Coleman, M.D., Dickson, R.E., Isebrands, J.G., Karnosky, D.F., 1995a. Photosynthetic productivity of aspen clones varying in sensitivity to tropospheric ozone. *Tree Physiol.* 15, 585–592.
- Coleman, M.D., Dickson, R.E., Isebrands, J.G., Karnosky, D.F., 1995b. Carbon allocation and partitioning in aspen clones varying in sensitivity to tropospheric ozone. *Tree Physiol.* 15, 593–604.
- Coleman, M.D., Dickson, R.E., Isebrands, J.G., Karnosky, D.F., 1996. Root growth and physiology of potted and field-grown trembling aspen exposed to tropospheric ozone. *Tree Physiol.* 16, 145–152.
- Collins, W.J., Stevenson, D.S., Johnson, C.E., Derwent, D., 2000. The European regional ozone distribution and its link with the global scale for the years 1992 and 2015. *Atmos. Environ.* 34, 255–267.
- Constable, J.V.H., Guentner, A.B., Schimel, D.S., Monson, R.K., 1999. Modelling changes in VOC emissions in response to climate change in the continental United States. *Global Change Biol.* 5, 791–806.
- Costonis, A.C., 1970. Acute foliar injury of eastern white pine induced by sulfur dioxide and ozone. *Phytopathology* 69, 994–999.
- Crutzen, P.J., 1988. Tropospheric ozone: An overview. In: Isaksen, I.S.A. (Ed.), *Tropospheric Ozone*. Reidel, Norwell, MA, pp. 3–32.
- Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, I.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., Wotton, B.M., 2001. Climate change and forest disturbances. *Bioscience* 51, 723–734.
- Davis, M.B., Woods, K., Webb, S.L., Futuyama, R.P., 1986. Dispersal versus climate: Expansion of *Fagus* and *Tsuga* into the Upper Great Lakes region. *Vegetatio* 67, 93–103.
- Davis, M.B., Shaw, R.G., 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* 292, 673–679.
- DeHayes, D.H., Schaberg, P.G., Hawley, G.J., Strimbeck, G.R., 1999. Acid rain impacts on calcium nutrition and forest health. *Bioscience* 49, 789–800.
- DeLucia, E.H., Hamilton, J.G., Naidu, S.L., Thomas, R.B., Andrews, J.A., Finzi, A., Lavine, M., Matamala, R., Mohan, J.E., Hendrey, G.R., Schlesinger, W.H., 1999. Net primary production of a forest ecosystem with experimental CO₂ enrichment. *Science* 284, 1177–1179.
- Derwent, R., Collins, W., Johnson, C., Stevenson, D., 2002. Global ozone concentration and regional air quality. *Environ. Sci. Technol.* 36, 379–382.
- Desanker, P.V., Justice, C.O., 2001. Africa and global climate change: Critical issues and suggestions for further research and integrated assessment modelling. *Clim. Res.* 17, 93–103.
- Dickson, R.E., Coleman, M.D., Riemenschneider, D.E., Isebrands, J.G., Hogan, G.D., Karnosky, D.F., 1998. Growth of five hybrid poplar genotypes exposed to interacting elevated CO₂ and O₃. *Can. J. Forest Res.* 28, 1706–1716.

- Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., Wisniewski, J., 1994. Carbon pools and flux of global forest ecosystems. *Science* 263, 185–190.
- Dochinger, L.S., Bender, F.W., Fox, F.L., Heck, W.W., 1970. Chlorotic dwarf of eastern white pine caused by an ozone and sulphur dioxide interaction. *Nature* 225, 476.
- Dochinger, L.S., Seliskar, C.E., 1970. Air pollution and the chlorotic dwarf disease of eastern white pine. *Forest Sci.* 16, 46–55.
- Donnelly, A., Craigan, J., Black, C.R., Colls, J.J., Landon, G., 2001. Elevated CO₂ increases biomass and tuber yield in potato even at high ozone concentrations. *New Phytol.* 149, 265–274.
- Driscoll, C.T., Lawrence, G.B., Bulger, A.J., Butler, T.J., Cronan, C.S., Egar, C., Lambert, K.F., Likens, G.E., Stoddard, J.L., Weathers, K.C., 2001. *Acid Rain Revisited: Advances in Scientific Understanding Since the Passage of the 1970 and 1990 Clean Air Act Amendments*. Hubbard Brook Research Foundation. Science Links Publication.
- EC/PHARE, 1999. Conservation and sustainable management of forests in Central and Eastern European countries. PHARE Environmental Consortium.
- Edgerton, S.A., Bian, X., Doran, J.C., Fast, J.D., Hubbe, J.M., Malone, E.L., Shaw, W.J., Whiteman, C.D., Zhong, S., Arriaga, J.L., Ortiz, E., Ruiz, M., Sosa, G., Vega, E., Limon, T., Guzman, F., Archuleta, J., Bossert, J.E., Elliot, S.M., Lee, J.T., McNair, L.A., Chow, J.C., Watson, J.G., Coulter, R.L., Doskey, P.V., Gaffney, J.S., Marley, N.A., Neff, W., Petty, R., 1999. Particulate air pollution in Mexico City: A collaborative research project. *J. Air Waste Manag. Assoc.* 49, 1221–1229.
- Erisman, J.W., Mennen, M.G., Fowler, D., Flechard, C.R., Spindler, G., Gruner, A., Duyzer, J.H., Ruigrok, W., Wyers, G.P., 1998. Deposition monitoring in Europe. *Environ. Monit. Assess.* 53, 279–295.
- FAO, 2001. *State of the World's Forests 2001*. The FAO Forestry Department, Rome, Italy.
- Fowler, D., Flechard, C., Skiba, U., Coyle, M., Cape, J.N., 1998. The atmospheric budget of oxidized nitrogen and its role in ozone formation and deposition. *New Phytol.* 139, 11–23.
- Fowler, D., Cape, J.N., Coyle, M., Flechard, C., Kuylenstierna, J., Hicks, K., Derwent, D., Johnson, C., Stevenson, D., 1999. The global exposure of forests to air pollutants. *Water Air Soil Pollut.* 116, 5–32.
- Fuentes, J.D., Hayden, B.P., Garstang, M., Lerdau, M., Fitzjarrald, D., Baldocchi, D.D., Monson, R., Lamb, B., Geron, C., 2001. New directions: VOCs and biosphere–atmosphere feedbacks. *Atmos. Environ.* 35, 189–191.
- Furiness, C., Smith, L., Ran, L., Cowling, E., 1998. Comparison of emissions of nitrogen and sulfur oxides to deposition of nitrate and sulfate in the USA by state in 1990. *Environ. Pollut.* 102 (S1), 313–320.
- Galloway, J.N., 1989. Atmospheric acidification projections for the future. *Ambio* 18, 161–166.
- Galloway, J.N., Cowling, E.B., 2002. Reactive nitrogen and the world: 200 years of change. *Ambio* 31, 64–71.
- Galloway, J.N., Cowling, E.B., Seitzinger, S.P., Socolon, R.H., 2002. Reactive nitrogen: Too much of a good thing? *Ambio* 31, 60–63.
- Gielen, B., Ceulemans, R., 2001. The likely impact of rising atmospheric CO₂ on natural and managed *Populus*: A literature review. *Environ. Pollut.* 115, 335–358.
- Gregorius, H.-R., 1986. The importance of genetic multiplicity for tolerance of atmospheric pollution. In: *Proceedings of 18th IUFRO World Congress*. Ljubljana, Yugoslavia, pp. 195–305.
- Guenther, A., Hewitt, C.N., Eickson, D., Fall, R., Geron, C., Graedel, T., Harley, P., Klinger, L., Lerdau, M., McKay, W.A., Pierce, T., Scholes, B., Steinbrecher, R., Tallamraju, R., Taylor, J., Zimmerman, P., 1995. A global model of natural volatile organic compound emissions. *J. Geophysiol. Res.* 100, 8873–8892.

- Gupta, H.K., Gupta, V.B., Rao, C.V.C., Gajghate, D.G., Hasan, M.Z., 2002. Urban ambient air quality and its management strategy for a metropolitan city in India. *Environ. Contam. Toxicol.* 68, 347–354.
- Hall, J.P., Magasi, L., Carlson, L., Stolte, K., Niebla, E., Bauer, M.L., Gonzalez-Vicente, C.E., Hernades-Tejeda, T., 1996. Health of North American forests. North American Forestry Commission Report. Natural Resources Canada, Ottawa.
- Hamilton, J.G., DeLucia, E.H., George, K., Naidu, S.L., Finzi, A.C., Schlesinger, W.H., 2002. Forest carbon balance under elevated CO₂. *Oecologia* 131, 250–260.
- Hannah, L., Midgley, G.F., Lovejoy, T., Bond, W.J., Bush, M., Lovett, J.C., Scott, D., Woodward, F.I., 2002. Conservation of biodiversity in a changing climate. *Cons. Biol.* 16, 264–268.
- Hanson, P.J., Weltzin, J.F., 2000. Drought disturbance from climate change: response of United States forests. *Sci. Total Environ.* 262, 205–220.
- Hao, X., Hale, B.A., Ormrod, D.P., Papadopoulos, A.P., 2000. Effects of pre-exposure to ultraviolet-B radiation on responses of ambient and elevated carbon dioxide. *Environ. Pollut.* 110, 217–224.
- Harrington, R., Woiwod, I., Sparks, T., 1999. Climate change and trophic interactions. *Trees* 14, 146–150.
- Hauglustaine, D.A., Granier, C., Brasseur, G.P., Megie, G., 1994. The importance of atmospheric chemistry in the calculation of radiative forcing on the climate system. *J. Geophysiol. Res.* 99, 1173–1186.
- Heagle, A.S., Miller, J.E., Pursley, W.A., 1998. Influence of ozone stress on soybean response to carbon dioxide enrichment: III. Yield and seed quality. *Crop Sci.* 38, 128–134.
- Heck, W.W., Taylor, O.C., Adams, R., Bingham, G., Miller, J., Preston, E., 1982. Assessment of crop loss from ozone. *J. Air Pollut. Control Assoc.* 32, 353–361.
- Hirst, D., Karesen, K., Host, G., Posch, M., 2000. Estimating the exceedance of critical loads in Europe by considering local variability in deposition. *Atmos. Environ.* 34, 3789–3800.
- Hobbie, S.E., Schimel, J.P., Trumbore, S.E., Randerson, J.R., 2000. Controls over carbon storage and turnover in high-latitude soils. *Global Change Biol.* 6 (S1), 196–210.
- Hogsett, W.E., Weber, J.E., Tingey, D., Herstrom, A., Lee, E.H., Laurence, J.A., 1997. Environmental auditing: An approach for characterizing tropospheric ozone risk to forests. *Environ. Manag.* 21, 105–120.
- Horowitz, L.W., Jacob, D.J., 1999. Global impact of fossil fuel combustion on atmospheric NO_x. *J. Geophysiol. Res.* 104, 23 823–23 850.
- Houghton, R.A., 2001. Counting terrestrial sources and sinks of carbon. *Clim. Change* 48, 525–534.
- Hudak, C., Bender, J., Weigel, H.-J., Miller, J., 1999. Interactive effects of elevated CO₂, O₃, and soil water deficient on spring wheat (*Triticum aestivum* L. cv. Nandu). *Agronomie* 19, 677–687.
- Hulme, M., Doherty, R., Ngara, T., New, M., Lister, D., 2001. African climate change: 1900–2100. *Clim. Res.* 17, 145–168.
- IPCC, 2001. Climate change 2001: Impacts, adaptation and vulnerability. Summary for policymakers. Intergovernmental Panel on Climate Change, Geneva.
- Isebrands, J.G., Dickson, R.E., Rebbeck, J., Karnosky, D.F., 2000. Interacting effects of multiple stresses on growth and physiological processes in northern forest trees. In: Mickler, R.A., Birdsey, R.A., Hom, J. (Eds.), *Responses of Northern U.S. Forests to Environmental Change*. Springer-Verlag, New York, pp. 149–180.
- Isebrands, J.G., McDonald, E.P., Kruger, E., Hendrey, G., Pregitzer, K., Percy, K., Sober, J., Karnosky, D.F., 2001. Growth responses of *Populus tremuloides* clones to interacting carbon dioxide and tropospheric ozone. *Environ. Pollut.* 115, 359–371.
- Iverson, L.R., Prasad, A.M., 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecol. Monogr.* 68, 465–485.

- Jacob, D.J., Logan, J.A., Murti, P.P., 1999. Effect of rising Asian emissions on surface ozone in the United States. *Geophysiol. Res. Lett.* 26, 2175–2178.
- Jaffe, D., Anderson, T., Covert, D., Kotchenruther, R., Trost, B., Danielson, J., Simpson, W., Bernsten, T., Karlsdotir, S., Blake, D., Harris, J., Carmichael, G., Uno, I., 1999. Transport of Asian air pollution to North America. *Geophysiol. Res. Lett.* 26, 711–714.
- Jeffries, R.L., Maron, J.L., 1997. The embarrassment of riches: Atmospheric deposition of nitrogen and community and ecosystem processes. *Trends Ecol. Evolut.* 12, 74–77.
- Jobbagy, E.G., Jackson, R.B., 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol. Applic.* 10, 423–436.
- Jonson, J.E., Sundet, J.K., Tarrasón, L., 2001. Model calculations of present and future levels of ozone and ozone precursors with a global and a regional model. *Atmos. Environ.* 35, 525–537.
- Karnosky, D.F., 1977. Evidence for genetic control of response to sulfur dioxide and ozone in *Populus tremuloides* Michx. *Can. J. Forest Res.* 7, 435–436.
- Karnosky, D.F., 1981. Changes in eastern white pine stands related to air pollution stress. *Mitteilungen der Forstlichen Bundesversuchsanstalt Wien* 137, 41–45.
- Karnosky, D.F., Gagnon, Z.E., Reed, D.D., Witter, J.A., 1992. Effects of genotype on the response of *Populus tremuloides* Michx. to ozone and nitrogen deposition. *Water Air Soil Pollut.* 62, 189–199.
- Karnosky, D.F., Gagnon, Z.E., Dickson, R.E., Coleman, M.D., Lee, E.H., Isebrands, J.G., 1996. Changes in growth, leaf abscission, and biomass associated with seasonable tropospheric ozone exposures of *Populus tremuloides* clones and seedlings. *Can. J. Forest Res.* 16, 23–27.
- Karnosky, D.F., Oksanen, E., Dickson, R.E., Isebrands, J.G., 2001. Impacts of interacting greenhouse gases on forest ecosystems. In: Karnosky, D.F., Scarascia-Mugnozza, G., Ceulemans, R., Innes, J. (Eds.), *The Impact of Carbon Dioxide and Other Greenhouse Gases on Forest Ecosystems*. CABI Publishing, New York, pp. 253–267.
- Karnosky, D.F., Percy, K.E., Xiang, B., Callan, B., Noormets, A., Mankovska, B., Hopkin, A., Sober, J., Jones, W., Dickson, R.E., Isebrands, J.G., 2002. Interacting CO₂-tropospheric O₃ and predisposition of aspen (*Populus tremuloides* Michx.) to infection by *Melampsora medusae* rust. *Global Change Biol.* 8, 329–338.
- 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.C., Sober, A., Sober, J., Jones, W.S., Anttonen, S., Vapaavuori, E., Mankovska, B., Heilman, W.E., Isebrands, J.G., 2003. Tropospheric O₃ moderates responses of temperate hardwood forests to elevated CO₂: A synthesis of molecular to ecosystem results from the Aspen FACE project. *Funct. Ecol.* 17, 289–304.
- Keeling, C.M., Whort, T.P., Wahlen, M., Vander Pliet, J., 1995. International extremes in the rate of rise of atmospheric carbon dioxide since 1980. *Nature* 375, 666–670.
- Keller, T., 1988. Growth and premature leaf fall in American aspen as bioindications for ozone. *Environ. Pollut.* 52, 183–192.
- Kiehl, J.T., Schneider, T.L., Portmann, R.W., Solomon, S., 1999. Climate forcing due to tropospheric and stratospheric ozone. *J. Geophysiol. Res.* 104, 31 239–31 254.
- Kickert, R.N., Krupa, S.V., 1990. Forest responses to tropospheric ozone and global climate change: An analysis. *Environ. Pollut.* 68, 29–65.
- King, J.S., Pregitzer, K.S., Zak, D.R., Karnosky, D.F., Isebrands, J.G., Dickson, R.E., Hendrey, G.R., Sober, J., 2001. Fine root biomass and fluxes of soil carbon in young stands of paper birch and trembling aspen is affected by elevated CO₂ and tropospheric O₃. *Oecologia* 128, 237–250.
- Komenda, M., Parusel, E., Wedel, A., Koppman, R., 2001. Measurements of biogenic VOC emissions: Sampling, analysis and calibrating. *Atmos. Environ.* 35, 2069–2080.

- Koski, V., 1996. Breeding plans in case of global warming. *Euphatica* 92, 235–239.
- Kretzschmar, J.G., 1994. Particulate matter levels and trends in Mexico City, Sao Paulo, Buenos Aires, and Rio De Janeiro. *Atmos. Environ.* 28, 3181–3191.
- Krupa, S.V., Kickert, R.N., 1989. The greenhouse effect: Impacts of ultraviolet (UV)-B radiation, carbon dioxide (CO₂) and ozone (O₃) on vegetation. *Environ. Pollut.* 61, 263–392.
- Kubiske, M.E., Godbold, D.L., 2001. Growth and function of roots and root systems. In: Karnosky, D., Scarascia-Mugnozza, G., Ceulemans, R., Innes, J. (Eds.), *The Impact of Carbon Dioxide and Other Greenhouse Gasses on Forest Ecosystems*. CABI Publishing, New York, pp. 325–340.
- Kull, O., Sober, A., Coleman, M.D., Dickson, R.E., Isebrands, J.G., Gagnon, Z., Karnosky, D.F., 1996. Photosynthetic response of aspen clones to simultaneous exposures of ozone and CO₂. *Can. J. Forest Res.* 16, 639–648.
- Kurpius, M.R., McKay, M., Goldstein, A.H., 2002. Annual ozone deposition to a Sierra Nevada ponderosa pine plantation. *Atmos. Environ.* 36, 4503–4515.
- Lawson, T., Craigon, J., Black, C.R., Colls, J.J., Tulloch, A.-M., Landon, G., 2001. Effects of elevated carbon dioxide and ozone on the growth and yield of potatoes (*Solanum tuberosum*) grown in open-top chambers. *Environ. Pollut.* 111, 479–491.
- Ledig, F.T., Kitzmiller, J.H., 1992. Genetic strategies for reforestation in the face of global climate change. *Forest Ecol. Manag.* 50, 153–169.
- Lefohn, A.S., Husar, J.D., Husar, R.B., 1999. Estimating historical anthropogenic global sulfur emission patterns for the period 1850–1990. *Atmos. Environ.* 33, 3435–3444.
- Lelieveld, J., Berresheim, H., Borrmann, S., Crutzen, P.J., Dentener, F.J., Fischer, H., Feichter, J., Flatau, P.J., Heland, J., Holzinger, R., Korrmann, R., Lawrence, M.G., Levin, Z., Markowicz, K.M., Mihalopoulos, N., Minikin, A., Ramanathan, V., de Reus, M., Roelofs, G.J., Scheeren, H.A., Sciare, J., Schlager, H., Schultz, M., Slegmund, P., Steil, B., Stephanou, E.G., Steir, P., Traub, M., Warneke, C., Williams, J., Ziereis, H., 2002. Global air pollution crossroads over the Mediterranean. *Science* 298, 794–799.
- Levy II, H., Moxim, W.J., Klonecki, A.A., Kasibhatla, P.S., 1999. Simulated tropospheric NO_x: Its evaluation, global distribution and individual source contributions. *J. Geophysiol. Res.* 104, 26 279–26 306.
- Li, Q., Jacob, D.J., Bey, I., Palmer, P.I., Duncan, B.N., Field, B.D., Martin, R.V., Fiore, A.M., Yantosca, R.M., Parrish, D.D., Simmonds, P.G., Oltmans, S.J., 2003. Transatlantic transport of pollution and its effects on surface ozone in Europe and North America. *J. Geophysiol. Res.* (In press).
- Lin, C.-Y.C., Jacob, D.J., Munger, J.W., Fiore, A.M., 2000. Increasing background ozone in surface air over the United States. *Geophysiol. Res. Lett.* 27, 3465–3468.
- Lin, C.-Y.C., Jacob, D.J., Fiore, A.M., 2001. Trends in exceedances of the ozone air quality standard in the continental United States, 1980–1998. *Atmos. Environ.* 35, 3217–3228.
- Lindner, M., 2000. Developing adaptive forest management strategies to cope with climate change. *Tree Physiol.* 20, 299–307.
- Lindroth, R.L., Kinney, K.K., Platz, C.L., 1993. Responses of deciduous trees to elevated atmospheric CO₂: productivity, phytochemistry and insect performance. *Ecology* 74, 763–777.
- Lindroth, R.L., Roth, S., Kruger, E.L., Volin, J.C., Koss, P.A., 1997. CO₂-mediated changes in aspen chemistry: Effects on gypsy moth performance and susceptibility to virus. *Global Change Biol.* 3, 279–289.
- Liu, S.C., Trainer, M., Fehsenfeld, F.C., Parrish, D.D., Williams, E.J., Fahey, D.W., Hübler, G., Murphy, P.C., 1987. Ozone production in the rural troposphere and the implications for regional and global ozone distributions. *J. Geophysiol. Res.* 92, 4191–4207.
- Lloyd, A.H., Fastie, C.L., 2002. Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Clim. Change* 52, 481–509.

- Lynch, J.A., Bowersox, V.C., Grimm, J.W., 2000. Changes in sulfate deposition in eastern USA following implementation of Phase I of Title IV of the Clear Air Act Amendments of 1990. *Atmos. Environ.* 34, 1665–1680.
- MacDonald, G.M., Edwards, T.W.D., Moser, K.A., Pienitz, R., Smol, J.P., 1993. Rapid response of tree-line vegetation and lakes to post climate warming. *Nature* 361, 243–246.
- Makinen, H., Nojd, P., Mielikainen, K., 2000. Climatic signal in annual growth variation of Norway spruce (*Picea abies*) along a transect from central Finland to the Arctic timberline. *Can. J. Forest Res.* 30, 769–777.
- Mankovska, B., 1997a. Deposition of heavy metals in Slovakia—Assessment on the basis of moss and humus analyses. *Ekologia* 16, 433–442.
- Mankovska, B., 1997b. Geochemical mapping of environmental stress by selected elements through foliar analysis. *Slovak Geol. Mag.* 3, 53–66.
- Mankovska, B., Percy, K., Karnosky, D.F., 2003. Impact of greenhouse gases on epicuticular waxes of *Populus tremuloides* Michx: Results from an open-air exposure and a natural O₃ gradient. *Ekologia* (in press).
- Marenco, A., Gouget, H., Nédélec, P., Pagés, J.-P., Karchner, F., 1994. Evidence of a long-term increase in tropospheric ozone from the Pic du Midi data series; Consequences: Positive radiative forcing. *J. Geophysiol. Res.* 99, 16 617–16 632.
- Martin, P.H., 1996. Will forest preserves protect temperate and boreal biodiversity from climate change? *Forest Ecol. Manag.* 85, 335–341.
- McDonald, E.P., Kruger, E.L., Riemenschneider, D.E., Isebrands, J.G., 2002. Competitive status influences tree-growth responses to elevated CO₂ and O₃ in aggrading aspen stands. *Funct. Ecol.* 16, 792–801.
- McKee, I.F., Bullimore, J.F., Long, S.P., 1997. Will elevated CO₂ concentrations protect the yield of wheat from O₃ damage? *Plant Cell Environ.* 20, 77–84.
- McLaughlin, S., Percy, K., 1999. Forest health in North America: Some perspectives on actual and potential roles of climate and air pollution. *Water Air Soil Pollut.* 116, 151–197.
- McNulty, S.G., Vose, J.M., Swank, W.T., 1996. Potential climate change effects on loblolly pine forest productivity and drainage across the southern United States. *Ambio* 25, 449–453.
- Melillo, J.M., McGuire, D., Kicklighter, D.W., Moore III, B., Vorosmarty, C.J., Schloss, A.L., 1993. Global climate change and terrestrial net primary production. *Nature* 363, 234–240.
- Menzel, A., Fabian, P., 1999. Growing season extended in Europe. *Nature* 397, 659.
- Menzel, A., 2000. Trends in phenological phases in Europe between 1951 and 1996. *Int. J. Biometeorol.* 44, 76–81.
- Miller, J.E., Heagle, A.S., Pursley, W.A., 1998. Influence of ozone stress on soybean response to carbon dioxide enrichment: II. Biomass and development. *Crop Sci.* 38, 122–128.
- Miller, P.R., 1973. Oxidant-induced community change in a mixed conifer forest. *Adv. Chem.* 122, 101–117.
- Miller, P.R., 1993. Response of forests to ozone in a changing atmospheric environment. *Angew. Bot.* 67, 42–46.
- Miller, P.R., Tejada, T.H., 1994. Comparison of ozone exposure characteristics in forested regions near Mexico City and Los Angeles. *Atmos. Environ.* 28, 141–148.
- Miller, P.R., Parmeter, J.R., Taylor, O.C., Cardiff, E.A., 1963. Ozone injury to the foliage of ponderosa pine. *Phytopathology* 53, 1072–1076.
- Miller, P.R., Stolte, K.W., Duriscoe, D.M., Pronos, J., 1996. Evaluating ozone air pollution effects on pines in the western United States. USDA Forest Service Pacific Southwest Research Station, General Technical Report PSW-GTR-155.
- Monson, R.K., Lerdau, M.T., Sharkey, T.D., Schimel, D.S., 1995. Biological aspects of constructing volatile organic compound emission inventories. *Atmos. Environ.* 29, 2989–3002.

- Moore, B.D., Cheng, S.H., Sims, D., Seemann, J.R., 1999. The biochemical and molecular basis for photosynthetic acclimation of elevated atmospheric CO₂. *Plant Cell Environ.* 22, 567–582.
- Moxim, W.J., Levy, H., Kasibhatla, P.S., 1996. Simulated global tropospheric PAN: Its transport and impact. *J. Geophysiol. Res.* 101, 12 621–12 638.
- Müller-Starck, G., 1989. Genetic implications of environmental stress in adult forest stands of *Fagus sylvatica* L. In: Scholz, F., Gregorius, H.-R., Rudin, D. (Eds.), *Genetic Effects of Air Pollutants in Forest Tree Populations*. Springer-Verlag, pp. 127–142.
- Nabuurs, G.-J., Pussinen, A., Karjalainen, T., Erhard, M., Kramer, K., 2002. Stemwood volume increment changes in European forests due to climate change—a simulation study with the EFISCEM model. *Global Change Biol.* 8, 304–316.
- Namkoong, G., 1991. Maintaining diversity in breeding for resistance in forest trees. *Annu. Rev. Phytopathol.* 29, 325–342.
- Noormets, A., Söber, A., Pell, E.J., Dickson, R.E., Podila, G.K., Söber, J., Isebrands, J.G., Karnosky, D.F., 2001a. Stomatal and nonstomatal control of photosynthesis in trembling aspen (*Populus tremuloides* Mich.) exposed to elevated CO₂ and O₃. *Plant Cell Environ.* 24, 327–336.
- Noormets, A., McDonald, E.P., Kruger, E.L., Isebrands, J.G., Dickson, R.E., Karnosky, D.F., 2001b. The effect of elevated CO₂ and/or O₃ on potential plant level carbon gain in aspen. *Trees* 15, 262–270.
- Norby, R.J., Wullschleger, S.D., Gunderson, C.A., Johnson, D.W., Ceulemans, R., 1999. Tree responses to rising CO₂ in field experiments: implications for the future forest. *Plant Cell Environ.* 22, 683–714.
- Norby, R.J., Todd, D.E., Fults, J., Johnson, D.W., 2001. Allometric determination of tree growth in a CO₂-enriched sweetgum stand. *New Phytol.* 150, 477–487.
- Norby, R.J., Hanson, P.J., O'Neill, E.G., Tschaplinski, T.J., Weltzin, J.F., Hansen, R.A., Cheng, W., Wullschleger, S.D., Gunderson, C.A., Edwards, N.T., Johnson, D.W., 2002. Net primary productivity of a CO₂-enriched deciduous forest and the implications for carbon storage. *Ecol. Applic.* 12, 1261–1266.
- O'Brien, K.L., 2000. Upscaling tropical deforestation: implications for climate change. *Clim. Change* 44, 311–329.
- Oren, R., Ellsworth, D.S., Johnson, K.H., Phillips, N., Ewers, B.E., Maier, C., Schafer, K.V.R., McCarthy, H., Hendrey, G., McNulty, S.G., Katul, G., 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere. *Nature* 411, 469–472.
- Oksanen, E., Söber, J., Karnosky, D.F., 2001. Interactions of elevated CO₂ and ozone in leaf morphology of aspen (*Populus tremuloides*) and birch (*Betula papyrifera*) in aspen FACE experiment. *Environ. Pollut.* 115, 437–446.
- Olszyk, D.M., Wise, C., 1997. Interactive effects of elevated CO₂ and O₃ on rice and flacca tomato. *Agric. Ecosyst. Environ.* 66, 1–10.
- Parnesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42.
- Parrish, D.D., Hahn, C.J., Williams, E.J., Norton, R.B., Fehsenfeld, F.C., Singh, H.B., Shetter, J.D., Gandrud, B.W., Ridley, B.A., 1992. Indications of photochemical histories of Pacific air masses from measurements of atmospheric trace species at Point Arena, California. *J. Geophysiol. Res.* 97, 15 883–15 901.
- Parshar, D.C., Kulshrestha, U.C., Sharma, C., 1998. Anthropogenic emissions of NO_x, NH₃ and N₂O in India. *Nutr. Cycling Agroecosyst.* 52, 255–259.
- Penuelas, J., Filella, I., 2001. Responses to a warming world. *Science* 294, 793–795.
- Percy, K.E., 2002. Is air pollution an important factor in forest health? Szaro, R.C., Bytnerowicz, A., Oszlanyi, J. (Eds.), *Effects of Air Pollution on Forest Health and Biodiversity in Forests of the Carpathian Mountains*. IOS Press, Amsterdam, pp. 23–42.

- 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 CO₂- and O₃-enriched atmospheres. *Nature* 420, 403–407.
- Peterson, D.L., Arbaugh, M.J., Robinson, L., 1989. Ozone injury and growth trends of ponderosa pine in the Sierra Nevada. In: Olson, R.K., Lefohn, A.S. (Eds.). In: *Effects of Pollution on Western Forests*. Transaction Series, Vol. 16. Air and Waste Manag. Association, Pittsburgh, PA, pp. 293–308.
- Pitelka, L.F., 1997. Plant migration and climate change. *American Scientist* 85, 464–473.
- Polle, A., Pfirrmann, T., Chakrabarti, S., Rennenberg, H., 1993. The effects of enhanced ozone and enhanced carbon dioxide concentrations on biomass, pigments, and antioxidative enzymes in spruce needles (*Picea abies* L.). *Plant Cell Environ.* 16, 311–316.
- Polle, A., Eiblmeier, M., Sheppard, L., Murray, M., 1997. Responses of antioxidative enzymes to elevated CO₂ in leaves of beech (*Fagus sylvatica* L.) seedlings grown under a range of nutrient regimes. *Plant Cell Environ.* 20, 1317–1321.
- Pregitzer, K.S., King, J.S., Burton, A., Brown, S.E., 2000. Responses of tree fine roots to temperature. *New Phytol.* 147, 105–115.
- Raga, G.B., Raga, A.C., 2000. On the formation of an elevated ozone peak in Mexico City. *Atmos. Environ.* 34, 4097–4102.
- Raich, J.W., Schlesinger, W.H., 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B, 81–99.
- Rehfeldt, G.E., Ying, C.C., Spittlehouse, D.L., Hamilton Jr., D.A., 1999. Genetic responses to climate in *Pinus contorta*: Niche breadth, climate change, and reforestation. *Ecol. Monogr.* 69, 375–407.
- Rehfeldt, G.E., Tchebakova, N.M., Parfenova, Y.I., Wykoff, W.R., Kuzmina, N.A., Milyutin, L.I., 2002. Intraspecific responses to climate in *Pinus sylvestris*. *Global Change Biol.* 8, 912–929.
- Romero, H., Ihl, M., Rivera, A., Zalazar, P., Azocar, P., 1999. Rapid urban growth, land-use change and air pollution in Santiago, Chile. *Atmos. Environ.* 33, 4039–4047.
- Rudorff, B.F.T., Mulchi, C.L., Lee, E.H., Rowland, R., Pausch, R., 1996. Effects of enhanced O₃ and CO₂ enrichment on plant characteristics in wheat and corn. *Environ. Pollut.* 94, 53–60.
- Sampson, R.N., 1992. Forestry opportunities in the United States to mitigate the effects of global warming. *Water Air Soil Pollut.* 64, 157–180.
- Schlesinger, W.H., 1997. *Biogeochemistry: An Analysis of Global Change*. Academic Press, San Diego, CA.
- Sedjo, R.A., 1989. Forests to offset the greenhouse effect. *J. For.* 87, 12–15.
- Shaver, G.R., Canadell, J., Chapin III, F.S., Gurevitch, J., Harte, J., Henry, G., Ineson, P., Jonasson, S., Melillo, J., Pitelka, L., Rustad, L., 2000. Global warming and terrestrial ecosystems: A conceptual framework for analysis. *Bioscience* 50, 871–882.
- Shine, K.P., 2001. Atmospheric ozone and climate change. *Ozone Sci. Eng.* 23, 429–435.
- Skiba, Y.N., Davydova-Belitskaya, V., 2002. Air pollution estimates in Guadalajara City. *Environ. Mod. Assess.* 7, 153–162.
- Stevenson, D.S., Johnson, C.E., Collins, W.J., Derwent, R.G., Shine, K.P., Edwards, J.M., 1998. Evolution of tropospheric ozone radiative forcing. *Geophysiol. Res. Lett.* 25, 3819–3822.
- Stohl, A., Trickl, T., 1999. A textbook example of long-range transport: simultaneous observation of ozone maxima of stratospheric and North American origin in the free troposphere over Europe. *J. Geophysiol. Res.* 104, 30445–30462.
- Stott, P.A., Tett, S.F.B., Jones, G.S., Allen, M.R., Mitchell, J.F.B., Jenkins, G.J., 2000. External control of 20th century temperature by natural and anthropogenic forcing. *Science* 290, 2133–2137.

- Straszewski, T., Szduj, J., Kubiesa, P., Godzik, S., 2001. Hazard of spruce stands in the Pieniny National Park due to regional and transboundary air pollution. *Ecologia* 20 (S4), 249–256.
- Streets, D.G., Waldhoff, S.T., 2000. Present and future emissions of air pollutants in China: SO₂, NO_x, and CO. *Atmos. Environ.* 34, 363–374.
- Streets, D.G., Tsai, N.Y., Akimoto, H., Oka, K., 2000. Sulfur dioxide emissions in Asia in the period 1985–1997. *Atmos. Environ.* 34, 4413–4424.
- Suzuki, K., 1999. Sustainability of pine forests in relation to pine wilt and decline. In: *Proceedings of International Symposium*. Tokyo, Japan.
- Swart, R., Mitchell, J., Morita, T., Raper, S., 2002. Stabilization scenarios for climate impact assessment. *Global Environ. Change* 12, 155–165.
- Taylor Jr., G.E., Pitelka, L.F., 1991. Genetic diversity of plant populations and the role of air pollution. In: Barker, J.R., Tingey, D.T. (Eds.), *Air Pollution Effects on Biodiversity*. Van Nostrand Reinhold, New York, pp. 111–130.
- Taylor Jr., G.E., 1994. Role of genotype in the response of loblolly pine to tropospheric ozone: Effects at the whole-tree, stand, and regional level. *J. Environ. Qual.* 23, 63–82.
- Teskey, R.O., Dougherty, P., Wiselogel, A.E., 1991. The design and performance of branch chambers suitable for long-term ozone fumigation of foliage in large trees. *J. Environ. Qual.* 20, 591–595.
- Thompson, A.M., 1992. The oxidizing capacity of the Earth's atmosphere: Probable past and future changes. *Science* 256, 1157–1165.
- 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 Physiol.* 18, 715–726.
- Utriainen, J., Janhunen, S., Helmisaari, H.-S., Holopainen, T., 2000. Biomass allocation, needle structural characteristics and nutrient composition in Scots pine seedlings exposed to elevated CO₂ and O₃ concentrations. *Trees* 14, 475–484.
- Vallack, H.W., Cinderby, S., Kuylenstierna, J.C.I., Heaps, C., 2001. Emission inventories for SO₂ and NO_x in developing country regions in 1995 with projected emissions for 2025 according to two scenarios. *Water Air Soil Pollut.* 130, 217–222.
- Vann, D.R., Johnson, A.H., 1995. Design and field operation of an in-situ environmental enclosure for tree branches. *Environ. Pollut.* 89, 37–46.
- Vine, E.L., Sathage, J.A., Makundi, W.R., 2001. An overview of guidelines and issues for the monitoring, evaluation, reporting, verification, and certification of forestry projects for climate change mitigation. *Global Environ. Change* 11, 203–216.
- Volin, J.C., Reich, P.B., 1996. The interaction of elevated CO₂ and O₃ on growth, photosynthesis and respiration of three perennial species grown in low and high nitrogen. *Physiol. Plant.* 96, 674–684.
- Volin, J.C., Reich, P.B., Givnish, T.J., 1998. Elevated carbon dioxide ameliorates the effects of ozone on photosynthesis and growth: species respond similarly regardless of photosynthetic pathway or plant functional group. *New Phytol.* 138, 315–325.
- Volney, W.J.A., Fleming, R.A., 2000. Climate change and impacts of boreal forest insects. *Agric. Ecosyst. Environ.* 82, 283–294.
- Wang, D., Karnosky, D.F., Bormann, F.H., 1986. Effects of ambient ozone on the productivity of *Populus tremuloides* Michx. grown under field conditions. *J. Geophysiol. Res.* 16, 47–55.
- Wang, Y., Jacob, D.J., Logan, J.A., 1998. Global simulation of tropospheric O₃–NO_x–hydrocarbon chemistry 3. Origin of tropospheric ozone and effects of nonmethane hydrocarbons. *J. Geophysiol. Res.* 103, 10757–10767.
- Wisconsin Department of Natural Resources. 1997. Wisconsin 1996 Air Quality Report. State of Wisconsin Department of Natural Resources. Bureau of Air Management PUBL-AM-221-97.

- Wustman, B.A., Oksanen, E., Karnosky, D.F., Sober, J., Isebrands, J.G., Hendrey, G.R., Pregitzer, K.S., Podila, G.K., 2001. Effects of elevated CO₂ and O₃ on aspen clones varying in O₃ sensitivity: Can CO₂ ameliorate the harmful effects of O₃? *Environ. Pollut.* 115, 473–481.
- Yienger, J.J., Galanter, M., Holloway, T.A., Phadnis, M.J., Guttikunda, S.K., Carmichael, G.R., Moxim, W.J., Levy II, H., 2000. The episodic nature of air pollution transport from Asia to North America. *J. Geophysiol. Res.* 105, 26 931–26 945.