

Review

Perspectives regarding 50 years of research on effects of
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Received 23 August 2006; accepted 27 August 2006

*Elevated tropospheric ozone remains an important phytotoxic air pollutant over large areas of US forests.***Abstract**

Tropospheric ozone (O₃) was first determined to be phytotoxic to grapes in southern California in the 1950s. Investigations followed that showed O₃ to be the cause of foliar symptoms on tobacco and eastern white pine. In the 1960s, “X” disease of ponderosa pines within the San Bernardino Mountains was likewise determined to be due to O₃. Nearly 50 years of research have followed. Foliar O₃ symptoms have been verified under controlled chamber conditions. Studies have demonstrated negative growth effects on forest tree seedlings due to season-long O₃ exposures, but due to complex interactions within forest stands, evidence of similar losses within mature tree canopies remains elusive. Investigations on tree growth, O₃ flux, and stand productivity are being conducted along natural O₃ gradients and in open-air exposure systems to better understand O₃ effects on forest ecosystems. Given projected trends in demographics, economic output and climate, O₃ impacts on US forests will continue and are likely to increase.

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Keywords: O₃; Interacting multiple stresses; Forest ecosystems; Black cherry; Eastern white pine; Aspen; Ponderosa pine**1. Introduction**

Tropospheric ozone background concentrations have increased 36% since pre-industrial times (IPCC, 2001). These increases are driven by rising emissions of oxidized nitrogen (NO_x) and volatile organic compounds from fossil fuel combustion (Finlayson-Pitts and Pitts, 1997; Fowler et al., 1998; Ryerson et al., 2001) as these compounds act as precursors to O₃ formation.

Ozone is known to impact forest trees in many ways including inducing visible foliar symptoms (Chappelka et al., 1999a; Schaub et al., 2005), decreasing foliar chlorophyll content

(Reich, 1983), accelerating leaf senescence (Reich and Lassoie, 1985; Stow et al., 1992; Pell et al., 1999), decreasing photosynthesis (Barnes, 1972; Reich, 1983; Coleman et al., 1995a), increasing respiration (Reich, 1983; Noormets et al., 2001), altering carbon allocation (Friend and Tomlinson, 1992; Coleman et al., 1995b), water balance (Panek, 2004), and epicuticular wax composition and structure (Mankovska et al., 1998, 2005; Percy et al., 2002), affecting canopy architecture (Dickson et al., 2001), predisposing trees to attack by pests (Stark et al., 1968; Karnosky et al., 2002), and decreasing growth and productivity (Wang et al., 1986a,b; Karnosky et al., 1996) and fitness (Berrang et al., 1986, 1989; Karnosky et al., 2003b). Responses to O₃ vary tremendously by species (Davis et al., 1981), genotype (Steiner and Davis, 1979; Karnosky and Steiner, 1981; Lee et al., 2002), leaf age (Davis and Wood, 1973) and leaf position in canopy (Schaub et al.,

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2005). Responses can also be altered by environmental factors such as soil moisture (Grulke et al., 2003), temperature (Davis and Wood, 1972; Chappelka et al., 1990), light intensity (Fredricksen et al., 1996), and nutrient availability (Tjoelker and Luxmoore, 1991).

Over the past 50 years, a large volume of literature has documented O₃ impacts on forest trees (see reviews by Kickert and Krupa, 1990; Miller, 1993; Skelly et al., 1997; Chappelka and Samuelson, 1998; McLaughlin and Percy, 1999; Krupa et al., 2000; Bytnerowicz et al., 2003; Percy et al., 2003). In this review, we examine O₃ effects on a number of ecologically and commercially important North American tree species that have been thoroughly studied over the past five decades, and we discuss remaining research needs.

2. Early history

Two mysterious diseases of conifers, “X” disease of ponderosa pine (*Pinus ponderosa*) in southern California and eastern white pine (*Pinus strobus*) needle blight (Linzon, 1960; Hepting and Berry, 1961) were linked to O₃ in the 1960s (Miller et al., 1963; Linzon, 1966; Richards et al., 1968; Dochinger and Heck, 1969; Costonis and Sinclair, 1969). A flurry of research triggered by this pioneering research confirmed early results linking O₃ to these two diseases for western conifers (Miller and Millecan, 1971; Evans and Miller, 1972a,b) and eastern white pine (Dochinger and Seliskar, 1970; Dochinger et al., 1970; Costonis, 1970; Houston, 1974).

The link of adverse effects of O₃ beyond visible symptoms and reduced growth to whole ecosystem change was made by Stark et al. (1968) who demonstrated that O₃ predisposed trees to mortality-causing insects and by Dr Paul Miller and his colleagues (Miller, 1973; Taylor and Miller, 1973) who showed that O₃ differentially affected the survival of various tree species, thus resulting in community change. This early research paved the way for the next 50 years of research on O₃ effects on the forests of southern California (summarized in Miller and McBride, 1999), led by the USFS Pacific Southwest Research Station (Dr Paul Miller) and Statewide Air Pollution Research Center at University of California, Riverside (Dr O.C. Taylor).

Simultaneously, in the eastern US major research programs to examine the impacts of O₃ on forest trees were begun at The Pennsylvania State University (Dr Al Wood), the Boyce Thompson Institute (Dr Len Weinstein and Dr Jay Jacobson), and the USFS Northeastern Forest Experiment Station in Delaware (Dr Leon Dochinger). Smaller programs were initiated at universities and state and federal agencies throughout the eastern United States. These programs flourished in the 1970s during the early EPA research mandate to establish air quality guidelines for O₃ and again in the 1980s during the NAPAP Program where researchers examined possible links between acid rain and O₃ impacts. Beginning in the 1990s, the Forest Response Program of the US Forest Service also provided a boost to O₃ research on forest trees across the US. This program later became part of the current US Forest

Service Global Change Program, which is part of the US National Global Change Initiative.

3. Case studies

3.1. Eastern white pine

Eastern white pine, a commercially important tree species for lumber, pulp, and Christmas trees, is distributed across southern Canada and the northeastern US from Maine to Minnesota south to Georgia. Throughout the range, reports of foliar symptoms attributable to O₃, or to mixtures of O₃ and SO₂, were reported over two decades starting in the early 1960s (Berry and Ripperton, 1963; Hepting, 1968; Costonis and Sinclair, 1969; Dochinger et al., 1970; Berry, 1973; Duchelle et al., 1983).

Symptomatic eastern white pine trees were referred to in a number of ways in the early literature including having foliage with needle blight (Costonis and Sinclair, 1969), emergence tipburn (Fig. 1C,D, Berry and Ripperton, 1963), semi-mature needle blight (Linzon, 1967), and chlorotic dwarf (Fig. 1A,B; Dochinger et al., 1970). While some authors argued that factors other than O₃ may have been involved in symptom induction, including foliar pathogens (Linzon, 1967; Dreisbach and Merrill, 1989), the consensus in the literature was that O₃ was likely involved in causing the widespread symptoms.

3.1.1. Symptomatology

Early symptoms on eastern white pine needles included collapse of palisade cells adjacent to stomata, forming light colored flecks that radiate from the stomata (Costonis and Sinclair, 1969; Costonis, 1970). Following the injury to the palisade cells, chlorophyll destruction occurs leading to larger, more visible chlorotic flecks characteristic of O₃-induced symptoms.

Symptoms are initiated on young, developing needles in early to mid-summer. Depending on the sensitivity of individual trees, symptoms sometimes advance from the chlorotic fleck into pink lesions, and then to brown necrotic bands on the needle followed by a spreading orange or red necrosis to the needle tip (Fig. 1). Tolerant trees are generally asymptomatic. Affected needles tend to senesce prematurely after only one or two growing seasons while needles on tolerant trees often remain on the trees for 3–5 years (Costonis, 1970). The most sensitive genotypes tend to have short, stunted needles, poor needle retention, and only minimal height and diameter growth each year (Dochinger et al., 1970).

3.1.2. Physiological effects

Eastern white pine varies in its O₃ sensitivity (Houston and Stairs, 1973; Houston, 1974; Hayes and Skelly, 1977; Thor and Gall, 1978; Fig. 1). For O₃-sensitive genotypes, it has been documented that O₃ at relatively low levels decreases the capacity of these trees to photosynthesize (Botkin et al., 1972; Mann et al., 1980; McLaughlin et al., 1982). In addition, increased dark respiration, decreased translocation, and



Fig. 1. Examples of emergence tipburn (A) and chlorotic dwarf (B) on eastern white pine in southern Ohio. Tipburn symptoms of O_3 exposure on eastern white pine from ambient air in southern Wisconsin (C) and verified on grafted O_3 -sensitive clones (left in D) following fumigation with 100 ppb O_3 for 6 h. (Photo credits: A,B,C: David Karnosky; D: Daniel Houston.)

reduced amounts and longevity of foliar biomass contribute to altering the carbon economy of O_3 -sensitive eastern white pine trees (McLaughlin et al., 1982). Reduced mean annual radial increment growth has also been documented for O_3 -sensitive trees exposed to ambient O_3 (Benoit et al., 1982). The reduced growth of O_3 -sensitive genotypes exposed to long-term O_3 exposure results in decreased competitive ability of the O_3 -sensitive genotypes, leading to increased mortality (Karnosky, 1980), especially when these trees are competing against more tolerant trees.

3.1.3. Genetic implications

While white pine mortality linked to O_3 stress is not large in terms of the species total growing stock (as O_3 sensitive genotypes do not make up a large proportion of all eastern white pine genotypes), consequences of the loss of O_3 -sensitive genotypes may still be significant. In fact, hypersensitive individuals may no longer be observed in much of the eastern US (Bennett et al., 1994). Certainly, this represents Stage I of natural selection: the elimination of sensitive genotypes (Bradshaw and McNeilly, 1989). However, it is not known if these trees carried any useful rare alleles that would be beneficial in the future that would not be retained in O_3 -tolerant genotypes (Karnosky et al., 1989).

3.2. Ponderosa pine

Ponderosa pine, a widely distributed western conifer ranging from northern Mexico, northward to the Canadian Rocky Mountains, and east to the Black Hills of South Dakota and western Oklahoma, is also sensitive to O_3 . The first detection of O_3 -induced foliar symptoms on ponderosa pine was made in southern California (Miller et al., 1963; Miller, 1969; Miller and Millecan, 1971). Ponderosa pines growing in the San Bernardino Mountains, which are downwind of the Los Angeles Air Basin, were particularly affected.

3.2.1. Symptomatology

Chlorotic mottle, but not tip burn, dominates the symptoms of O_3 exposure to ponderosa pine (Evans and Miller, 1972a; Miller et al., 1996; Fig. 2). The mottle frequently appears in the one-third of the needle surface nearest the tip on 1-year-old or older needles, and progresses basipetally until the entire needle is affected (Miller et al., 1963). Shortened needles and premature needle loss resulting in thin canopies (Fig. 2) also characterize O_3 -induced injury on sensitive ponderosa pine trees (Miller et al., 1996). In contrast to the rather widely scattered occurrence of O_3 -caused symptoms on eastern white pine, the extreme nature of the O_3 events in the San

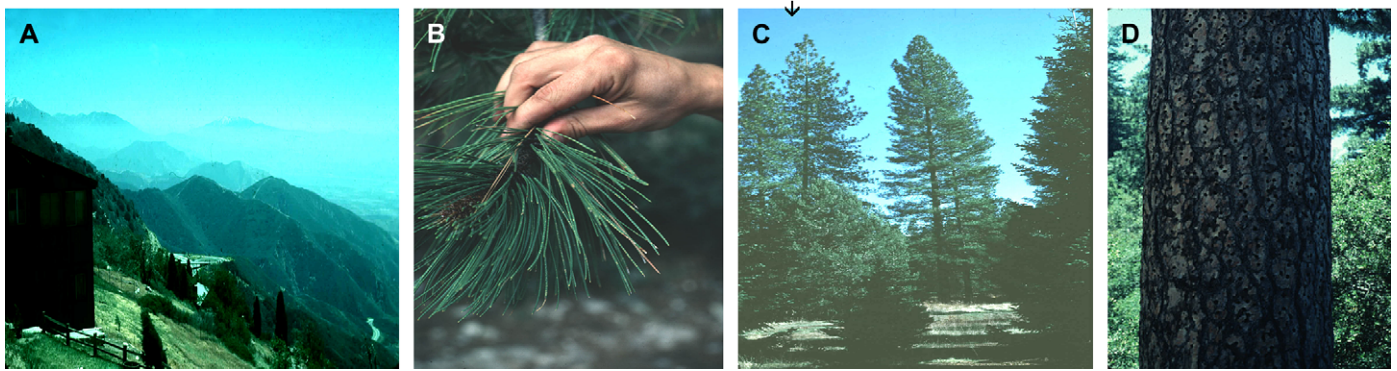


Fig. 2. (A) Photochemical oxidant haze over the San Bernardino Mountains. Visible symptoms of O_3 injury to ponderosa pine foliage is dominated by chlorotic mottle (B) and premature needle loss leading to thin canopies ($\downarrow$) in (C). O_3 -stressed trees are attacked and killed by bark beetles whose exit holes are shown in (D). (Photo credits: David Karnosky.)

Bernardino Mountains in the 1960s and 1970s resulted in widespread damage to a large portion of the ponderosa pine trees in the San Bernardino National Forest.

3.2.2. Physiological effects

Studies of O_3 -induced effects on ponderosa pine seedlings suggest that long-term O_3 exposure can have significant effects on photosynthetic capacity (Beyers et al., 1992). Negative carry-over effects of O_3 on root growth and carbohydrate concentrations of ponderosa pine seedlings have been found in subsequent growing seasons (Andersen et al., 1997). Furthermore, it is well documented that O_3 -stressed ponderosa pines in the San Bernardino Mountains suffer from subsequent attack by bark beetles (Stark and Cobb, 1969; Jones et al., 2004), leading to mortality. This long-term case study has provided compelling evidence for the important role of O_3 in predisposing trees to other biotic or abiotic stressors.

3.2.3. Ecosystem effects and long-term trends

McLaughlin and Percy (1999) concluded that changes in depth and vigor of root systems, shifts in C pool sizes and C allocation patterns, and changes in supply rates of N and Ca, caused by O_3 and acidic deposition (singly or in combination), represent key shifts in ecological function in diverse forest types across large geographic areas in North America. Differential mortality of O_3 -sensitive species, such as ponderosa pine and Jeffrey pine, has been implicated as one of the mechanisms leading to shifts in species composition and community structure in O_3 -stressed western pine forests (McBride et al., 1985). As with eastern white pine, there may be selection occurring for O_3 tolerance within these two western conifers, although it has not been proven that actual changes in gene frequency have occurred (Patterson and Rundel, 1995). Decreasing maximum hourly O_3 concentrations in the San Bernardino Mountains during 1963 to 1999 suggest that the rigorous air quality standards of southern California are having a positive impact on O_3 maxima in the region. However, these areas still receive relatively high concentrations of O_3 ; in addition, they also are subjected to high amounts of N deposition

(Fenn and Bytnerowicz, 1993; Bytnerowicz, 2002), which may confound the O_3 responses.

3.3. Trembling aspen

Trembling aspen (*Populus tremuloides*) is the most widely distributed tree species in North America, ranging from across Canada and Alaska south throughout the mountainous regions and east through the midwestern and northeastern US. First shown to be sensitive to O_3 by Karnosky (1976, 1977), this species has been the subject of extensive study by many research groups over the past 30 years (Wang et al., 1986a; Greitner et al., 1994; Karnosky et al., 1996; Clark et al., 1996; Yun and Laurence, 1999; Percy et al., 2002).

3.3.1. Symptomatology

Unlike many broad leaf tree species for which O_3 -caused symptoms are generally upper leaf surface black or red stipple (Skelly et al., 1979), the first O_3 -induced symptoms to appear on trembling aspen leaves are generally moderate to large black necrotic areas which extend across the veins and are bifacial in nature (Karnosky, 1976; Fig. 3). As with most trees, physiological maturity and senescence of foliage are accelerated by O_3 (Greitner et al., 1994).

3.3.2. Physiological effects

There is considerable genetic variation in aspen in response to elevated O_3 (Karnosky, 1976, 1977; Wang et al., 1986a; Karnosky et al., 1996, 2005; Yun and Laurence, 1999). For sensitive genotypes, O_3 adversely affects carbon gain by decreasing photosynthesis (Coleman et al., 1995a; Clark et al., 1996), degrading chlorophyll (Gagnon et al., 1992), reducing Rubisco (Noormets et al., 2001), increasing respiration (Noormets et al., 2001), and altering carbon allocation (Coleman et al., 1995b). Ozone causes adverse effects on most components of growth of aspen (Wang et al., 1986a; Karnosky et al., 1996, 2003a, 2005), but root growth appears to be most severely impacted (Coleman et al., 1996; Karnosky et al., 1996). Aspen trees stressed by O_3 are subject to more severe attack by foliar pathogens such as rust caused by

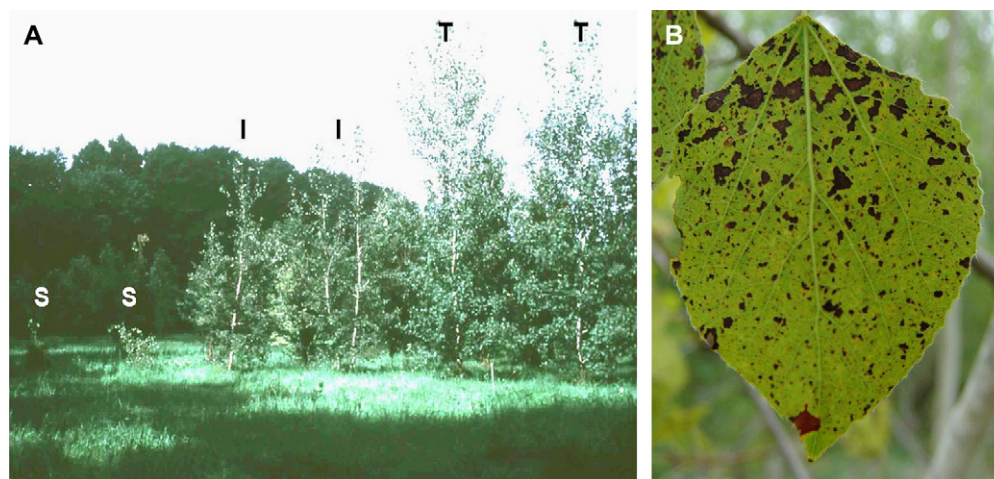


Fig. 3. (A) The differential effects of ambient O_3 on aspen tree growth can be seen in these three southern Wisconsin clones growing in southern New York where O_3 levels are quite high. The two tree plots represent 10-year-old sensitive (left), intermediate (middle) and tolerant (right) genotypes that grew at similar rates under low O_3 exposure in southern Wisconsin (from Karnosky and Thakur, 2004). (B) Typical O_3 -induced symptoms including bifacial necrosis on an O_3 -sensitive genotype grown in southern Wisconsin. (Photo credits: David Karnosky.)

Melampsora medusae (Karnosky et al., 2002). This predisposition is most likely because O_3 also negatively impacts leaf surface waxes (Mankovska et al., 1998, 2003, 2005; Percy et al., 2002) making the leaves more wettable and, therefore, creating a more conducive microenvironment for spore germination and subsequent infection by fungi.

3.3.3. Genetic implications

Because O_3 differentially impacts aspen growth (Karnosky et al., 1996, 2003a; Percy et al., 2002; Fig. 3), competitive ability (McDonald et al., 2002), and fitness (Karnosky et al., 2003b), it is not surprising then that O_3 -induced natural selection may have already impacted aspen populations in areas that have had relatively high O_3 exposures (Berrang et al., 1986, 1989, 1991). Again, rare alleles or useful genetic information may have been lost.

3.4. Black cherry

Black cherry (*Prunus serotina*), highly valued for its red heartwood that makes attractive lumber for furniture, paneling, and many other uses, is widely distributed in the eastern one-half of the US from Florida through the northern Lake States to Maine. Black cherry is also found in scattered populations in a large region of the southwestern US through Mexico. Long known to be relatively sensitive to O_3 (Davis et al., 1981), black cherry is highly variable in its response to O_3 (Lee et al., 2002), but it has a significant portion of individuals that have been reported to show visible foliar symptoms from O_3 (Simini et al., 1992; Hildebrand et al., 1996; Chappelka et al., 1997, 1999a).

3.4.1. Symptomatology

Ozone-induced symptoms on black cherry are classic adaxial reddish-purple, black, or purple-black pigmentation expressed as stipple and premature leaf drop (Davis et al.,

1981; Skelly, 2000; Fig. 4). These symptoms can be initiated by O_3 exposures consisting of 4–8 h of 100 ppb or 2 h of 190 ppb in chambers (Davis et al., 1981), but generally trees need greater exposures in the field as evidenced by the first visible symptoms being observed in mid to late August after SUM00 O_3 doses of 37.3–39.7 ppmh (Schaub et al., 2005).

3.4.2. Physiological effects

The uptake of O_3 affects black cherry photosynthesis and conductance, generally decreasing both, especially late in the growing season (Schaub et al., 2005). Light environment (Fredericksen et al., 1996), seed source (Lee et al., 2002), and leaf age (Fredericksen et al., 1995) all affect the magnitude of O_3 -induced responses in black cherry. Season-long exposures to lower O_3 concentrations have been shown to have significant adverse effects on black cherry seedling growth and biomass production (Davis and Skelly, 1992; Neufeld et al., 1995; Rebbeck, 1996; Lee et al., 2002). Significant growth decline related to O_3 visible symptoms in mature trees remains more elusive to demonstrate (Somers et al., 1998).

3.5. Eastern hardwoods

Forested land comprises approximately 30% of the total land area in the eastern US with 74% of it in hardwoods, and the remainder in conifers (Powell et al., 1992). Several major National Parks in the eastern US that are densely forested with eastern hardwoods are the Great Smoky Mountains National Park in Tennessee and North Carolina, Shenandoah National Park in Virginia and Acadia National Park in Maine. Ozone has been demonstrated to have an impact on several hardwood tree species found in the eastern US (Neufeld et al., 1992; Simini et al., 1992; Hildebrand et al., 1996; Chappelka et al., 1999b; Skelly et al., 1997; Chappelka and Samuelson, 1998).

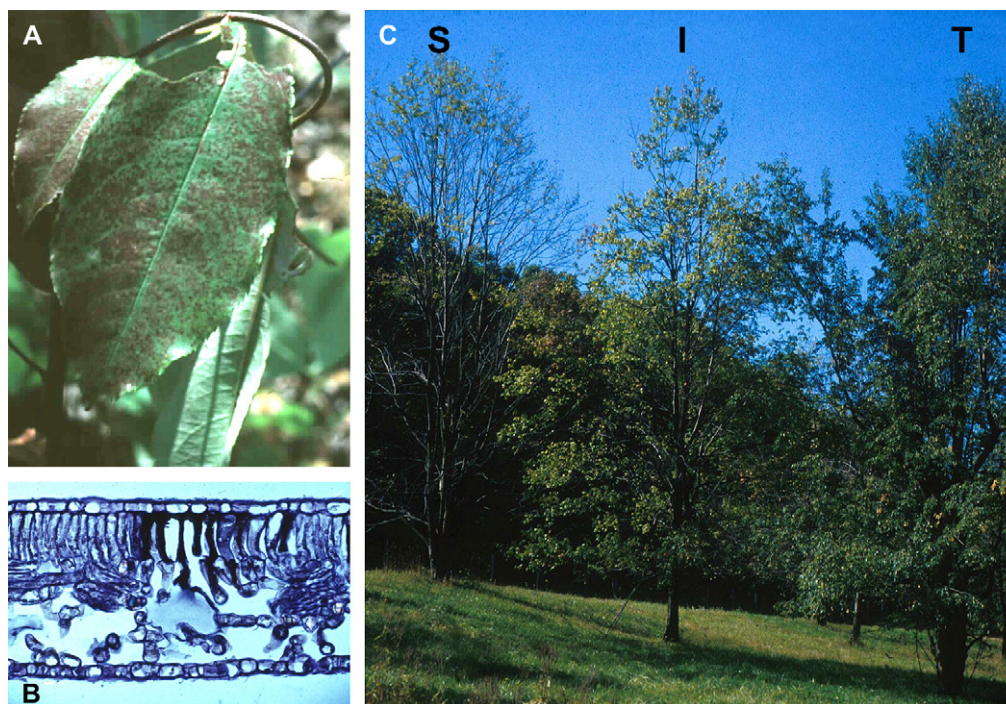


Fig. 4. Upper leaf surface stipple, red to black are the typical first symptoms of O_3 effects on many tree species including black cherry from ambient O_3 in northern Indiana (A). Individual stipple points generally involve mortality of palisade layer cells (blackened cells in cross section in (B) shown here for black cherry after artificial O_3 fumigation. (C) Genetic differences in O_3 tolerance are large in black cherry as demonstrated in this photo of three genotypes (S, sensitive; I, intermediate; and T, tolerant) differing in O_3 tolerance. (Photo credits: A,B: David Karnosky; C: John Skelly.)

3.5.1. Symptomatology

Ozone symptoms on hardwood species are generally expressed as a tan, red, brown, or purple, upper-surface stipple. Visible symptoms of O_3 have been reported on both seedlings and saplings (Duchelle et al., 1983; Neufeld et al., 1992; Simini et al., 1992), as well as mature trees (Hildebrand et al., 1996; Chappelka et al., 1999b). Results from these studies need to be interpreted with caution, since the extent and magnitude of visible injury is influenced by micro-meteorological conditions, including vapor pressure deficit, light, temperature and soil moisture (Winner et al., 1989; Showman, 1991; Hildebrand et al., 1996; Lefohn et al., 1997; Chappelka and Samuelson, 1998), elevation (Chappelka et al., 1999a) and time of year (Chappelka et al., 1997).

3.5.2. Physiological effects

Physiological sensitivity to ambient O_3 has been observed in a comparatively small number of eastern hardwood tree species. However, reports indicate exposure to O_3 has the potential to cause reductions in photosynthesis and disruptions in carbohydrate allocation patterns (Reich and Amundson, 1985; Chappelka and Chevone, 1992; Chappelka and Samuelson, 1998; Samuelson and Kelly, 2001).

Reich and Amundson (1985) concluded that ambient O_3 levels typically found in the eastern US likely reduced leaf net photosynthetic rates in trees. However, these effects can be confounded by various factors including tree maturity, leaf structure, leaf longevity, plant defensive mechanisms, and within species variation (Skelly et al., 1997; Samuelson

and Kelly, 1997; Chappelka and Samuelson, 1998; Samuelson and Kelly, 2001).

Ollinger et al. (1997) used a canopy-to-stand-level model to predict forest response to O_3 . Using a variety of data collected on ozone uptake (Reich, 1987), relationships between photosynthesis and O_3 levels were developed. In addition, different levels of soil moisture were introduced into the model. Initial results indicated a decrease in net primary productivity (NPP) from 3 to 16% with a mean decrease in NPP of 7%. Greatest reductions were found in the southern portions of the eastern US where O_3 concentrations and potential photosynthesis were the greatest. Reductions were greatest on sites with greater water holding capacity, supporting the findings of Lefohn et al. (1997). Patterson et al. (2000) reported that O_3 uptake by several mature tree species was reduced by low soil moisture. However, recent research indicates that the effects of O_3 on water use and growth may be exacerbated by low soil moisture in certain tree species (McLaughlin et al., 2002) suggesting the Ollinger et al. (1997) model may not effectively predict O_3 responses for some situations. Recent modeling efforts by Hanson et al. (2005) that incorporate results from a diverse set of O_3 , CO_2 , temperature, and precipitation experiments have underscored the need for long-term field experiments to evaluate eastern hardwood forest ecosystems response to complex environmental scenarios.

3.5.3. Genetic implications

One question that remains unanswered is whether or not decreases in growth and biomass production are related to visible

foliar symptoms. The majority of the literature indicates that these phenomena are not necessarily related (Pye, 1988; Chappelka and Chevone, 1992; Chappelka and Samuelson, 1998). Karnosky and Steiner (1981) reported family and geographic differences in foliar injury response to O₃ in green (*Fraxinus pennsylvanica*) and white ash (*F. americana*) seedlings. No relationships to growth were established in this study. However, correlative studies suggest that visible injury and growth reductions may be related in some cases. Based on research where visible symptoms of O₃ injury were characterized on large, mature yellow-poplar (*Liriodendron tulipifera*) and black cherry trees in Great Smoky Mountains National Park (Chappelka et al., 1999b), Somers et al. (1998) compared radial growth differences among trees classified as sensitive or non-sensitive to O₃ based on the severity of visible foliar injury observed over a 3-year time-frame. Significantly more radial growth occurred for the non-sensitive yellow-poplar compared with the sensitive yellow-poplar trees over both a 5- and 10-year period. Since this study was not a controlled experiment and was limited in the number of trees used, there was no way to prove a cause–effect relationship between visible foliar symptoms and subsequent growth losses. However, these results indicate the possibility that O₃ is related to growth losses in some sensitive genotypes in yellow-poplar. No relationship between visible foliar injury and growth was observed with black cherry.

3.6. Southern pines

Southern pines are widely distributed in the US from Florida, north to New Jersey and west to east Texas and Oklahoma. There are 11 species of *Pinus* native to the southern US. Loblolly (*Pinus taeda*), shortleaf (*P. echinata*) and slash pine (*P. elliottii*) are the most important timber types. However, other species such as longleaf (*P. palustris*) and Virginia pine (*P. virginiana*) are very important from an ecosystem management perspective. Many studies were conducted during the late 1980s to early 1990s to establish cause–effect relationships between O₃ exposure and individual tree growth with these pines. The bulk of the studies were conducted within the framework of large multi-institutional cooperatives (Kelly et al., 1993; Fox and Mickler, 1995). Most studies were conducted in open-top chambers under adequate moisture conditions and free from competition with other plants (Skelly et al., 1997; Chappelka and Samuelson, 1998).

3.6.1. Symptomatology

In southern pines, O₃ symptoms appear as chlorotic mottling, necrotic banding or tip necrosis (Flagler and Chappelka, 1995). Chlorotic mottling is the most common symptom on sensitive genotypes at low to moderate (<60 ppb) ozone concentrations (Flagler and Chappelka, 1995). Symptoms are most common on recently expanded needles, although they can occur on older, more mature tissue. Necrotic banding and tip necrosis may become evident at higher concentrations (80–100 ppb). As with eastern white pine, premature needle senescence is also commonly induced by O₃.

3.6.2. Physiological effects

In these pines, O₃ has been shown to reduce carbon fixation, increase foliar and root respiration, alter patterns of mycorrhizal colonization and cause shifts in allocation patterns of carbon and nutrients (Qiu et al., 1992, 1993; Friend and Tomlinson, 1992; Baker et al., 1994; Sasek and Flagler, 1995). Teskey (1995) reported that photosynthesis of loblolly pine was negatively correlated with O₃ exposure after a threshold of 100 and 150 ppm h^{−1} was reached. The majority of this research, however, was conducted with young trees and results may differ as trees mature (Samuelson and Kelly, 2001). Growth responses due to O₃ remain more difficult to demonstrate with southern pines (Neufeld et al., 2000).

3.6.3. Genetic implications

The existence of a large genetic variation in O₃ responses in loblolly pine has been reported (Kress et al., 1982; Winner et al., 1987; McLaughlin et al., 1994). Similar variation has also been observed in other commercially important southern pines such as shortleaf and slash pine. Sensitivity in response to O₃ exposure ranged from very sensitive to tolerant based on visible injury and growth. In addition, growth effects were observed in some families in the absence of visible foliar injury (Shafer and Heagle, 1989). However, all of these experiments have been conducted under controlled conditions with young trees (<5 years old). It is not known if O₃ has had an effect on resistance of this species under ambient conditions. Taylor (1994), using data from the literature, examined loblolly pine growth to O₃ levels currently found in southeastern forests. He reported O₃ effects on growth would be expected to occur at a growing-season 12 h mean of 45 ppb for ≥110 days. This threshold is 15% below the mean exposures currently being experienced in the South. Sensitive cohorts experienced growth losses at a threshold of 25 ppb. These results indicate that O₃ has the potential to reduce growth of sensitive genotypes at current ambient levels. Chappelka and Samuelson (1998) and Teskey (1995) reported that these growth losses probably range from 0 to 10% depending on the genotype.

4. Exposure systems and research strategies for O₃ studies of forest trees

The exposure systems and research strategies to study the impacts of O₃ on forest trees in the US have evolved dramatically over the past 50 years (Fig. 5). Early studies utilized a number of different forms of chambers inside growth rooms, laboratories or greenhouses (Evans and Miller, 1972a,b; Davis and Wood, 1973; Houston, 1974). These simple chamber studies with primitive O₃ generation and monitoring systems were valuable in demonstrating that O₃ in relatively low concentrations could elicit visible O₃ symptoms on foliage (Berry and Ripperton, 1963; Dochinger et al., 1970; Houston, 1974; Karnosky, 1976). Later, continuously stirred tank reactors (CSTRs) were developed (Heck et al., 1978) and became commonly used indoor chambers, offering reliable and uniform O₃ delivery and uniform environmental conditions ideal for assessing foliar injury, as well as for physiological and

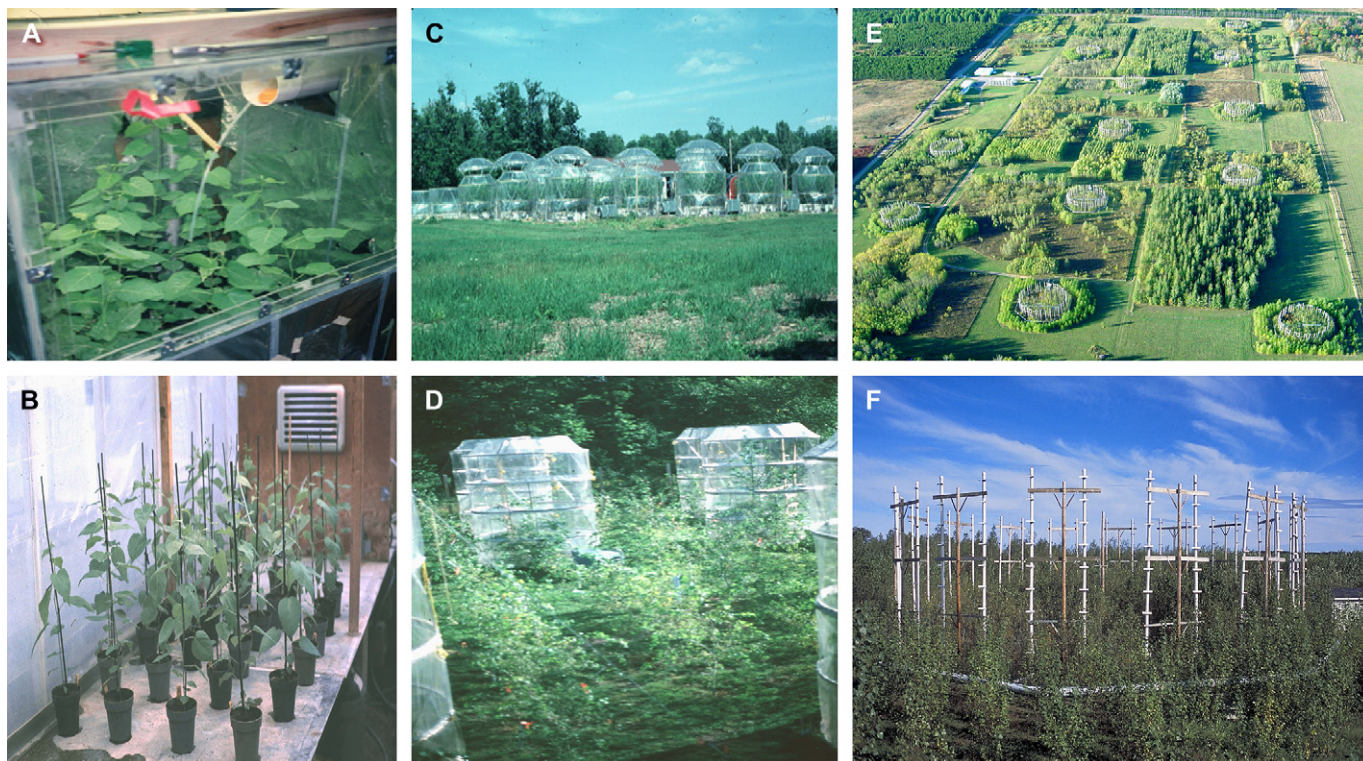


Fig. 5. Over the years systems to fumigate forest trees with O_3 have evolved from plastic chambers in the laboratory (A) to chambers in the greenhouse (B) to field open-top chambers (C,D) to open-air field exposures (E,F). (Photo credits: David Karnosky.)

biochemical studies (Davis and Skelly, 1992; Lee et al., 2002). Since these indoor chambers did not truly replicate field conditions, and since trees in them had to be grown in pots, there was a need to develop alternative field systems. Subsequently, open-top chambers, developed for crop plants by Heagle et al. (1973, 1979), began to be used for potted forest tree seedling studies or with seedlings planted in the ground. These simple but very useful open-top chambers were valuable in demonstrating that background ambient O_3 could elicit visible symptoms (Fredericksen et al., 1995) and reduce growth (Wang et al., 1986a,b; Simini et al., 1989). They were also useful in studies of the effects of ambient plus added O_3 on growth and biomass production (Shafer and Heagle, 1989; Neufeld et al., 1992, 1995; Rebbeck, 1996).

Later, these open-top chambers were modified to include larger diameters (to accommodate more seedlings), larger vertical size (by stacking them) to accommodate larger saplings, and/or covered with rain-exclusion tops to allow exclusion of rainfall for studies of $O_3 \times$ drought $\times$ rain interactions (Hogsett et al., 1985; Musselman and Hale, 1997). Open-top chambers have been extremely valuable in studies of O_3 effects on physiological processes (Tingey et al., 1976) and on growth and productivity (Chappelka et al., 1988; Kress et al., 1981; Adams et al., 1990). A compilation of a number of exposure–response studies with tree seedlings grown in open-top chambers was used to model O_3 impacts on eastern forest trees (Hogsett et al., 1997). Unfortunately, tree seedlings grown in open-top chambers were sometimes different than seedlings of the same source and age growing at the same site, but

outside the chambers (Karnosky et al., 1996). This was most likely because in some locations the chambers created a microclimate that was warmer, more humid, had less light, and less wind than outside the chambers (Hendrey et al., 1999; McLeod and Long, 1999; Karnosky et al., 2001). Therefore, it became important to develop closer to reality field exposure systems (Manning, 2005).

Several alternative systems were concurrently developed to study the effects of O_3 in the field. Branch chambers were developed to allow studies of O_3 effects on larger trees (Houpis et al., 1991; Teskey et al., 1991; Thornton et al., 1994). These were particularly useful in studies of gas exchange dynamics (Grulke et al., 1996). The chemical ethylenediurea (EDU), which acts as an O_3 protectant (Roberts and Jensen, 1985; Long and Davis, 1991), has been used to study O_3 effects in open-top chamber studies (Kuehler and Flagler, 1999) and in the field (Ainsworth et al., 1996; Long and Davis, 1991). Several authors have used dendrochronometer bands to study daily diameter growth patterns and correlate those to ambient O_3 concentrations (McLaughlin and Bräker, 1985; McLaughlin et al., 2002). Using this method, McLaughlin and Downing (1995, 1996) implicated adverse effects of O_3 on diameter growth of mature loblolly pine trees in the southeastern US.

Natural O_3 gradients also offer opportunities to examine the impacts of O_3 on forest trees although finding large O_3 gradients over relatively small areas is problematic. However, effects of ambient O_3 have been successfully examined along natural O_3 gradients in both elevational gradients (Winner et al., 1989) and regional gradients (Karnosky et al., 1999; Arbaugh et al., 2003).

The examination of open-air systems for exposing trees to O₃ was first attempted in the UK using young conifers (McLeod, 1995). Subsequently, Hendrey et al. (1989) showed that a system similar to a free-air CO₂ enrichment (FACE) system could be used for delivering reliable concentrations of O₃ to large plot sizes. Later, such a FACE system for exposing trees to elevated CO₂ and/or O₃ was developed in northern Wisconsin (Karnosky et al., 1999; Dickson et al., 2000). This system has been used to expose aspen, aspen/birch and aspen/maple ecosystems since 1998 (Karnosky et al., 2003a, 2005; Fig. 5E,F).

5. Interacting factors

Since the early discovery that O₃ was linked to visible foliar symptoms in the 1960s for western pine and eastern white pine, it has been known that interacting factors can exacerbate or ameliorate the adverse effects of O₃ (Kress et al., 1981; Kickert and Krupa, 1990; Isebrands et al., 2000). These factors include tree age, genetic makeup, microclimate, nutrition, competition, and co-occurring stresses such as insect and disease pests, other pollutants such as gaseous SO₂ and acidic deposition of various sulfur and nitrogen compounds, and most recently, rising atmospheric CO₂. Unfortunately, most studies have been done on the effects of O₃ alone, in studies of limited genetic materials exposed at a single age in a single environment and without co-occurring stresses. Thus, scaling results from these studies to complex forests growing over wide areas and which are also being exposed to co-occurring stresses is very difficult. In this section, we will briefly examine interacting factors that can modify the impacts of O₃ on forest trees.

5.1. Tree age

Since the vast majority of O₃ impact studies on forest trees have been done on seedlings or saplings, scaling impacts of O₃ to forests composed of many age trees remains difficult (Kolb and Matyssek, 2001). Studies comparing O₃ effects on seedlings versus mature trees have shown larger amounts of visible symptoms in mature trees for the same cumulative O₃ uptake (Fredericksen et al., 1996), larger reductions in photosynthesis in mature trees than seedlings (Rebbeck et al., 1993; Grulke and Miller, 1994), and increased (Hanson et al., 1994) or decreased (Fredericksen et al., 1996) stomatal conductance in mature trees, while others have shown no difference between seedlings or mature trees in O₃ effects on respiration (Wullschlegel et al., 1996), photosynthesis (Momen et al., 1997), or diameter growth (Samuelson et al., 1996). Whether or not seedlings are reasonable surrogates for trees in regard to O₃ impacts remains an important research question that needs to be addressed with more species (Kelly et al., 1995; Kolb and Matyssek, 2001). Studies of the same genotypes will be most useful in addressing this question so that genetic differences do not confuse the differences attributable to age. Long-term O₃ studies starting with seedlings, such as the Aspen FACE project which began in 1998, are also excellent for examining O₃ responses as trees age.

5.2. Genetics

Since the earliest studies of O₃ effects on eastern white pine, scientists have been aware of the strong role in genetics in determining O₃ sensitivity (Berry and Ripperton, 1963; Dochinger and Seliskar, 1970; Houston and Stairs, 1973). The role of genetics has been further shown with seed source trials with several important tree species (Townsend and Dochinger, 1974; Steiner and Davis, 1979; Karnosky and Steiner, 1981; Kress et al., 1982; Winner et al., 1987; Horton et al., 1990; Richardson et al., 1992; Shafer et al., 1993; McLaughlin et al., 1994; Taylor, 1994). With trembling aspen, genetic differences in O₃ sensitivity have been documented in clonal trials (Karnosky, 1976; Berrang et al., 1986; Wang et al., 1986a; Yun and Laurence, 1999; Isebrands et al., 2001; Karnosky et al., 2005). Studies estimating heritability of O₃ tolerance further emphasize the strong genetic control of O₃ sensitivity (Houston and Stairs, 1973; Karnosky, 1977; Lee et al., 2002). Furthermore, Staszak et al. (2004) have shown genetic differences between O₃ sensitive and tolerant ponderosa pine trees via differences in allele frequencies using isozyme analyses.

There are a number of important implications of the genetic differences in O₃ sensitivity or tolerance in a given species. First, O₃ can reduce the competitive fitness of sensitive genotypes leading to stage 1 of natural selection, which is the elimination of sensitive genotypes (Karnosky, 1980; Berrang et al., 1986, 1989, 1991; McDonald et al., 2002; Karnosky et al., 2003b). Second, studies comparing O₃ impacts of multiple species or examining interactions of O₃ responses of any given tree species with other factors should be done with multiple genotypes or families so that genetic variation in responses can be evaluated.

5.3. Microclimate

Environmental factors contributing to microclimate changes in the forest can have important effects on O₃ impacts. For example, temperature (Davis and Wood, 1973; Chappelka et al., 1990), light intensity (Volin et al., 1993; Tjoelker et al., 1993, 1995; Fredericksen et al., 1996), and soil moisture (Greitner et al., 1994; McLaughlin and Downing, 1996; Panek et al., 2002; Panek, 2004) can all affect O₃ impacts on forest trees. Alternatively, O₃ can also alter forest tree responses to microclimate, as was demonstrated by the decreased frost hardening of loblolly pine seedlings (Chappelka et al., 1990). These complex interactions of O₃ and microclimate make it very difficult to separate out O₃ effects in large trees growing in natural forest conditions (McLaughlin and Downing, 1995, 1996; McLaughlin et al., 2002).

5.4. Nutrition

Forest trees generally grow in soil environments with less than optimal nutrients. However, it is well known that anthropogenic N deposition has increased N levels in large areas of

the southwestern (Fenn et al., 1995; Bytnerowicz, 2002) and northeastern US (Galloway, 1998; Galloway et al., 2002). Ozone can exacerbate nutrient deficiencies by causing reduced foliar nutrition via accelerated senescence (Greitner et al., 1994) or reduced N acquisition and retranslocation (Samuelson et al., 1996; Grulke and Balduman, 1999). The interactions with soil nutrition and O₃ impacts appear to be rather complex as O₃ effects have been shown to be exacerbated by both low (Karnosky et al., 1992) and high nutrients status (Tjoelker and Luxmoore, 1991), whereas other studies have shown no impact of soil nutrition on O₃ effects (Greitner et al., 1994). Nutrition is also closely linked to water relations (Temple and Riechers, 1995) leading to complex O₃/water/nutrition interactions which have not been characterized for most tree species.

5.5. Competition

Given that availability of light, water and nutrients are all affected by competition, and that O₃ effects interact with all three of these factors, it is not surprising that competition between trees can have a dramatic effect on how trees respond to O₃ (McDonald et al., 2002). Since the vast majority of O₃ studies have been done with little or no competition (i.e. with a small number of trees in chambers), it is difficult to scale results from O₃ effects in open-grown tree experiments to the forest situation where strong competitive interactions affect environmental conditions, carbon allocation patterns, and pest susceptibility. Competition from understory vegetation can also impact community responses to O₃ (Barbo et al., 1998).

5.6. Insect and disease pests

Interactions between O₃ and insect and disease pests are complex and highly variable (Hain, 1987; Manning and Tiedemann, 1995). The first reported O₃/pest interaction of forest trees was predisposition of western pines by O₃ to attack by bark beetles in southern California (Stark et al., 1968). This bark beetle/O₃ interaction was later found to be a very complex one including drought and N deposition (Jones et al., 2004). In feeding preference studies, gypsy moth larvae have shown a preference to feed on O₃-exposed oak seedlings (Jeffords and Endress, 1984) and beetles have preferred O₃-exposed eastern cottonwood foliage (Jones and Coleman, 1988). These interactions with insects likely result from O₃-induced changes in foliar chemistry (Kopper and Lindroth, 2003) or from O₃ impacts on parasitoid populations (Percy et al., 2002; Kopper and Lindroth, 2003; Holton et al., 2003).

Altered performance of forest tree pathogens can also be induced by elevated O₃. Increased susceptibility of hybrid poplar to *Septoria* canker was demonstrated by Woodbury et al. (1994). Similarly, increased susceptibility to *Melampsora* leaf rust has been shown in trembling aspen trees exposed to elevated O₃ (Karnosky et al., 2002; Percy et al., 2002).

5.7. Other pollutants

It was apparent in the early O₃ research that the effects of co-occurring pollutants such as SO₂ could increase visible symptoms caused by O₃ (Dochinger et al., 1970; Costonis, 1970; Houston, 1974). Later, more complex studies showed that interacting pollutants could increase, decrease, or not affect growth responses for trees exposed to elevated O₃ (Jensen, 1981; Kress et al., 1982; Yang et al., 1983).

The influx of air pollution research related to the National Atmospheric Deposition Program (NAPAP) resulted in a large number of papers published in the decade from 1985 to 1995. However, the most realistic of these studies dealt with interacting O₃ and acidic deposition at high altitudes, or where fog co-occurred with elevated O₃. In these situations the effects of O₃ may be difficult to distinguish from those of acidic deposition. For example, the pine forests in the southern Sierra Nevada Mountains of California are now known to have long been exposed to both elevated O₃ and acidic deposition (Fenn et al., 1995; Grulke and Balduman, 1999; Bytnerowicz, 2002). Similarly, high elevation spruce-fir forests of the Northeast are frequently exposed to elevated O₃ and acidic precipitation which may be affecting cold tolerance of these forests (Thornton et al., 1994).

5.8. Rising atmospheric CO₂

Since pre-industrial times, the concentrations of atmospheric CO₂ and O₃ have increased by over 30% (IPCC, 2001). These two co-occurring pollutants are quite interesting as they act in diametrically different directions with regard to forest tree growth and productivity. While O₃ generally adversely affects forest trees, elevated CO₂ generally enhances growth and productivity, albeit these relationships vary by species (Karnosky et al., 2003a, 2005), soil nutrition (Oren et al., 2001) and age of the forest.

While several authors report that elevated atmospheric CO₂ generally ameliorates the effects of O₃ on photosynthesis and growth (Dickson et al., 1998; Volin et al., 1998; Loats and Rebbeck, 1999; Rebbeck and Scherzer, 2002), negative interactions of these two pollutants have also been reported (Kull et al., 1996; McDonald et al., 2002; Olszyk et al., 2002). One likely outcome of the future is that increasing levels of ambient O₃ will likely diminish the potential of forest trees to sequester additional CO₂ under rising atmospheric CO₂ (Karnosky et al., 2003a; Beedlow et al., 2004).

6. Research needs

After 50 years of research on the effects of O₃ on forest trees, there remain a large number of important research questions to be addressed in order to truly understand impacts of O₃ and to predict the influence of O₃ air pollution in a changing global environment (Karnosky et al., 2003c).

6.1. Numbers of forest and native plants showing ozone-induced symptoms

There is a continuing need to determine exposure/response relationships under ambient O₃ exposures for more forest tree species. In comparison to the myriad species which comprise our natural plant communities and forests, only a relative handful of higher plant species have been studied. In addition, for most investigated species, we have simply determined sensitivity by use of O₃-induced foliar symptoms (Skelly, 2000). Since foliar injury is likely indicative of more serious and adverse physiological changes that have taken place, the more species that are identified as being O₃-sensitive, the more it becomes important to reduce the primary precursor air pollutants that contribute to the photochemical process leading to O₃ formation. The list of O₃-sensitive plants continues to grow through investigations by Skelly et al. (1999), VanderHeyden et al. (2000), Innes et al. (2001), Orendovici et al. (2003), and Davis et al. (2005).

6.2. Ozone impacts on forest productivity

The majority of experiments to determine the impacts of O₃ on forest productivity have been done on young seedlings in chambers. Unfortunately, these studies are of limited value in predicting the impacts of O₃ on forest productivity as they represent only a brief glimpse of the entire life history of a forest stand, the physiology of seedlings and mature trees may be very different, and the lack of competition in chamber studies could affect responses to O₃ (McDonald et al., 2002).

In order to make better predictions of impacts of O₃ on long-term forest productivity, long-term studies are needed of O₃ exposure in realistic forest stands such as: (1) the FACE experiments that have been used to study impacts of global change (Miglietta et al., 2001; Karnosky et al., 2003a, 2005; Körner et al., 2005); and (2) dendrochronology bands (McLaughlin and Downing, 1995; McLaughlin et al., 2002). Natural O₃ gradients around and downwind of metropolitan areas may also be useful for documenting O₃ effects on forest productivity (Simini et al., 1992; Gregg et al., 2003; Karnosky et al., 2003b). However, co-occurring pollutants can confound such studies. Finally, comparing multiple studies of different types with common sets of genetic materials can be useful in adding to the predictive power, if results are similar. For example, a common set of genetic materials (aspen clones) has been used in growth and productivity studies in 3-year studies within open-top chambers (Karnosky et al., 1996), open-air (FACE) exposure systems (Isebrands et al., 2001; Percy et al., 2002; Karnosky et al., 2003a, 2005) and a natural O₃ gradient (Karnosky et al., 1999, 2003b). These plant materials have behaved similarly in terms of visible foliar symptom development, growth depression and fitness under relatively long-term O₃ exposures in varied environments and soil conditions. This helps us begin to develop a clear picture of the impacts of O₃ on aspen productivity, under both current and projected exposures to ambient O₃.

6.3. O₃ impacts on forest ecosystems

The impacts of O₃ on forest ecosystem processes such as nutrient and water cycling, trophic interactions, community development, and fitness are largely unknown (Heck et al., 1998; Laurence and Andersen, 2003; Karnosky et al., 2003c; Percy et al., 2003). Undoubtedly, the most studied forest ecosystem impacts are those from the mountains of southern California (Miller and Millecan, 1971; Miller et al., 1996; Bytnerowicz et al., 2003). In these southern California studies, O₃ impacts on long-term changes in forest community structure and composition (Miller, 1973) and complex long-term interaction with bark beetles (Stark et al., 1968) have been documented. More recently, the complex nature of the O₃ and N deposition interaction has been discovered (Bytnerowicz, 2002).

The Aspen FACE project, which is examining the long-term impacts of O₃ on a northern Wisconsin forest ecosystem dominated by aspen, is also beginning to yield valuable insights into the impacts of O₃ on forest ecosystems. In the FACE project, O₃-induced impacts have been studied on trophic interactions (Karnosky et al., 2002; Percy et al., 2002; Kopper and Lindroth, 2003; Mondor et al., 2004), litter decomposition (Parsons et al., 2004), soil carbon accumulation (Loya et al., 2003), mineral weathering (Holmes et al., 2003; Karberg et al., 2005), soil microbial communities (Phillips et al., 2002; Larson et al., 2002), soil invertebrate diversity (Loranger et al., 2004), and competitive indices (McDonald et al., 2002).

6.4. Risk analysis and the adequacy of O₃ standards to protect forest ecosystems

In 1997, the US EPA replaced the former 1979 primary O₃ National Ambient Air Quality Standard (NAAQS) with a new primary O₃ NAAQS set at 0.08 ppm (80 ppb) calculated as the 3-year average of the annual fourth highest daily maximum 8-h O₃ concentrations measured at each monitor within an area (Federal Register, 1997). However, the success of this standard in protecting forest trees and forest ecosystems is far from certain (Percy et al., 2003; Percy et al., in press a,b).

Studies are needed to compare forest productivity and forest health to various O₃ metrics. A long-lasting and ongoing debate is the relative importance of short-term O₃ peaks versus long-term seasonal accumulation of O₃ in determining the extent of O₃-induced impacts on plants (Musselman et al., 1983). Clearly, the current standard does not protect sensitive individuals of many tree species from visible symptom development in rural areas, as evidenced by the common occurrence of these symptoms even in areas in compliance with the current standard (Hildebrand et al., 1996; Chappelka et al., 1999b).

6.5. Remote area monitoring of O₃

The current network of O₃ monitoring for compliance with O₃ standards is inadequate to quantify O₃ exposures in most remote forest areas in North America (Laurence and

Andersen, 2003). While more extensive monitoring with mechanical O₃ monitors is clearly needed, ambient O₃ monitoring can be supplemented with surveys using O₃-induced symptoms on forest trees (Smith et al., 2003) and with the use of passive samplers (Manning et al., 1996; Yuska et al., 2003). A current survey system is providing valuable insights into O₃ exposure in remote forest areas (Smith et al., 2003). Passive samplers can be particularly useful to supplement mechanical monitors in remote areas as they are less expensive to establish and maintain than active monitors, thus allowing more complete coverage of O₃ monitoring over the landscape.

6.6. Interacting factors

Ozone deposition to forest trees does not occur in the absence of other interacting factors. Additional studies are needed to help understand the complex interactions of O₃ with the changing atmospheric conditions, including global warming, elevated CO₂, and N deposition (Kickert and Krupa, 1990; Ollinger et al., 2002; Karnosky et al., 2003c). In addition, the interaction of O₃ and forest tree insects and/or diseases have only been examined for a few tree species.

6.7. O₃ effects at the landscape and global levels

Additional work is needed to scale results from stand and community level O₃ responses up to the landscape or global level. Clearly, more research is needed in modeling the future extent and concentrations of O₃ over the earth surface (Fowler et al., 1999). While some attempts have been made to scale O₃ responses to the landscape level (Felzer et al., 2004), better dose–response functions, as in Percy et al. (in press b), are needed to develop accurate landscape-level predictions of O₃-induced responses to forests and native vegetation (Karnosky et al., 2005).

7. Concluding remarks

Ozone is a natural constituent of the atmosphere in which US forests grow. While peak O₃ concentrations have been declining, background levels in many forested areas have, in fact, been increasing (Vingarzan, 2004). Recent ecosystem modeling work indicates the large negative impact (up to 13%) that historical O₃ levels may have had on US terrestrial net ecosystem production (NEP) (Felzer et al., 2004). Ozone at ambient levels in a number of forest regions is known to induce visible foliar symptoms in ecologically and commercially important tree species. Sensitive genotypes of key species have already been impacted. Adverse impacts at cellular, leaf, organ and tree levels are known to occur in diverse systems that are geographically widely dispersed. Productivity of some species is likely being reduced, whereas others may be more disposed to other biotic and abiotic stresses. Whereas the underlying processes controlling O₃ formation and deposition are well understood, cause–effect linkage in the field for O₃ effects on ecosystem structure and function with few exceptions remains problematic. Given the predominant role of

meteorology in controlling O₃ entry into the plant and the variability inherent in forest ecosystems, it is not surprising that factors controlling O₃ flux remain as important research questions. Scaling O₃ effects to landscape and region remain as pressing research needs to facilitate more accurate and reliable O₃ risk analysis across the US.

Acknowledgements

This review was partially supported by the US Department of Energy's Office of Biological and Environmental Research, Grant No. DE-FG02-95ER62125, USDA Forest Service Northern Global Change Program, the USDA Forest Service Central Research Station, Michigan Technological University, the Praxair Foundation, the McIntire-Stennis Program, and the Canadian Forest Service. The authors acknowledge the valuable suggestions for the manuscript from Dr Donald D. Davis and Dr Howard Neufeld.

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