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Chapter 6

Limitations and perspectives about scaling ozone impacts in trees

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Abstract

We review the need for scaling effects of ozone (O_3) from juvenile to mature forest trees, identify the knowledge presently available, and discuss limitations in scaling efforts. Recent findings on O_3/soil nutrient and O_3/CO_2 interactions from controlled experiments suggest consistent scaling patterns for physiological responses of individual leaves to whole-plant growth, carbon allocation, and water use efficiency of juvenile trees. These findings on juvenile trees are used to develop hypotheses that are relevant to scaling O_3 effects to mature trees, and these hypotheses are examined with respect to existing research on differences in response to O_3 between juvenile and mature trees. Scaling patterns of leaf-level physiological response to O_3 have not been consistent in previous comparisons between juvenile and mature trees. We review and synthesize current understanding of factors that may cause such inconsistent scaling patterns, including tree-size related changes in environment, stomatal conductance, O_3 uptake and exposure, carbon allocation to defense, repair, and compensation mechanisms, and leaf production phenology. These factors should be considered in efforts to scale O_3 responses during tree ontogeny. Free-air O_3 fumigation experiments of forest canopies allow direct assessments of O_3 impacts on physiological processes of mature trees, and provide the opportunity to test current hypotheses about ontogenetic variation in O_3 sensitivity by comparing O_3 responses across tree-internal scales and ontogeny.

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1. Introduction

Tropospheric ozone (O_3) is a likely contributing factor to tree decline in some North American and European forests (Taylor et al., 1994; Sandermann et al., 1997; Chappelka and Samuelson, 1998; Skärby et al., 1998; Matyssek and Innes, 1999; McLaughlin and Percy, 1999). For logistical reasons, most data on tree response to O_3 is from controlled exposures of juvenile trees in either indoor or outdoor chambers often using potted plants that do not experience the actual rigors of natural site conditions. Thus, there is growing concern about whether O_3 response data from juvenile trees can be extrapolated to mature trees (e.g., Samuelson and Edwards, 1993; Grulke and Miller, 1994; Samuelson and Kelly, 1996; Fredericksen et al., 1996b; Kolb et al., 1997; Matyssek and Innes, 1999; Baumgarten et al., 2000; Wieser, 2002). Although O_3 response data for mature forest trees are becoming available from free-air O_3 exposure experiments (Tjoelker et al., 1995; Matyssek and Innes, 1999; Karnosky et al., 2001), such experiments can concentrate only on a limited number of tree species. Therefore, information on changes in O_3 impacts during tree ontogeny is still needed.

In this paper, we address two aspects of scaling O_3 impacts from juvenile to mature trees. First, we examine results from juvenile trees for consistency in O_3 responses within the individual plant. Based on these results, we formulate hypotheses that may provide insight on differences in O_3 response between juvenile and mature forest trees. Second, we address studies that have compared O_3 response between juvenile and mature forest trees to highlight factors that may lead to changes in O_3 sensitivity during forest maturation. Throughout the paper, we offer perspectives about existing gaps in knowledge that currently limit scaling of O_3 responses from juvenile to old trees.

1.1. Consistency patterns of O_3 impacts within trees

Studies conducted on young trees under phytotron or chamber conditions have been the prevailing means to provide insights into physiological mechanisms of O_3 impact (Matyssek et al., 1995b; Matyssek et al., 1997). However, such studies have included a broad spectrum of plant responses at the biochemical and molecular levels (e.g., Kangasjärvi et al., 1994; Sandermann, 1996; Langebartels et al., 1997; Sandermann et al., 1997). Such highly resolved response mechanisms may not apply directly to larger trees or forest stands because of temporal variability, tree ontogeny, and multi-factorial environmental influences that characterize forest sites (Baldocchi, 1993). Therefore, incorporation of such complexity into quantitative scaling concepts that reach the stand level is problematic (Jarvis, 1993). Nevertheless, knowledge about underlying mechanisms is indispensably valuable for understanding ecophysiological tree responses to stresses such as O_3 (Waring, 1993). Thus, ecophysiological processes and responses may be regarded as ‘scaling units’ that integrate tree performance across functional levels and ontogenetic stages (Reynolds et al., 1993; Matyssek et al., 1995b).

The action of O_3 must be viewed in the context of other environmental impacts that may influence sensitivity to stress (Mooney et al., 1991; Ellenberg, 1996). From the many factors that can affect O_3 impact to trees highlighted in recent reviews (e.g., Kolb et al., 1997; Skärby et al., 1998; Matyssek and Innes, 1999), we use mineral nutrition and carbon dioxide (CO_2) as examples of how resource availability can modify O_3 sensitivity in trees (Polle et al., 2000). We address controlled experiments with young *Betula pendula* and *Fagus sylvatica* as examples of the current state of knowledge of consistency patterns in O_3 response within young trees. These species were chosen because they represent a contrast in shoot growth phenology (indeterminate versus determinate), and both are sensitive to O_3. The functional basis of scaling from leaf-level to whole-tree responses is demonstrated by ecophysiological relationships which are examined for plant-internal consistency and relevance to mature trees.

1.2. Nutrition as a modifier of O_3 impact

1.2.1. Metabolic and leaf responses

In an outdoor chamber experiment, young *Betula pendula* cuttings were grown throughout the growing season either under O_3 free-air (control) or chronic day/night O_3 exposure of 90/40 $\mathrm{nl\,l^{-1}}$. Both exposure regimes were supplied with low or high nutrition by irrigation with a balanced fertilizer. Both O_3 exposure and high nutrition increased the $\delta^{13}C$ content in tree cellulose (Fig. 1(A); Matyssek et al., 1992; Saurer et al., 1995). The decrease in discrimination against ^{13}C during photosynthesis that occurred in response to high fertilization was associated with a lower concentration of CO_2 in the mesophyll intercellular space (C_i), as predicted by Farquhar et al. (1989a), and lower stomatal conductance (G_W), indicating increased photosynthetic water-use efficiency (WUE; Schulze and Hall, 1982).

O_3 exposure also increased $\delta^{13}C$, but in contrast to the effect of nutrition, C_i either increased or did not change in response to O_3. This result was surprising as an increase in $\delta^{13}C$ is often associated with a decrease in C_i (Farquhar et al., 1989a). As an explanation, the CO_2-binding activity of the PEP-carboxylase enzyme (PEPC) increased in response to O_3 exposure (Luethy-Krause et al., 1990; Saurer et al., 1995; Gerant et al., 1996; Landolt et al., 1997), and RUBISCO activity was inhibited by O_3. PEPC can increase tissue $\delta^{13}C$ as its ^{13}C discrimination is negligible relative to that of the RUBISCO enzyme (Farquhar et al., 1989b). PEPC is part of an anaplerotic pathway that

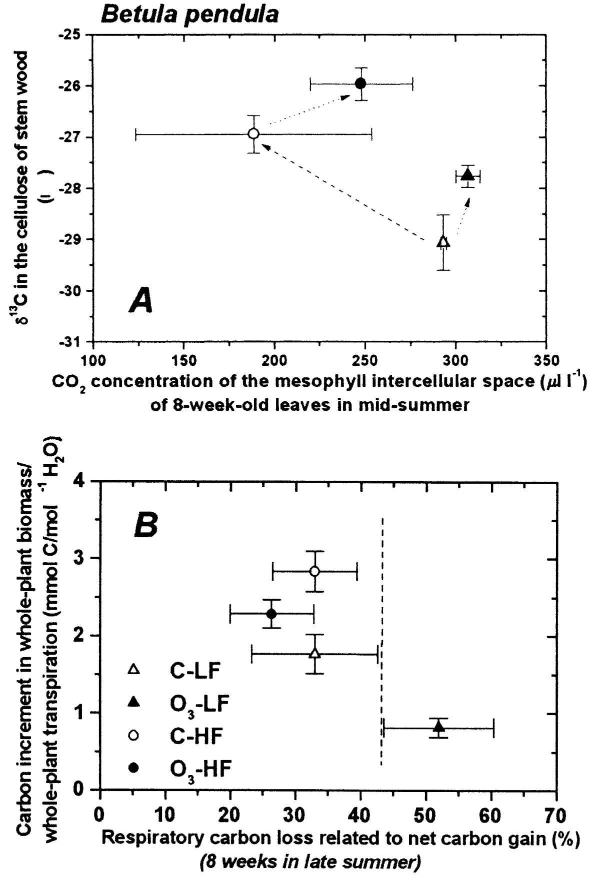

Figure 1. (A) Relationship between the $^{13}C/^{12}C$ isotope ratio in the cellulose of stem wood and the CO_2 concentration of the mesophyll intercellular space of 8-week-old leaves of young birch (*Betula pendula*) plants grown under four combinations of O_3 exposure and nutrient supply (data adapted from Saurer et al., 1995). (B) Relationship between carbon incorporated into whole-plant biomass and transpiration, and the proportion of respiration in net carbon gain of whole-plant foliage for a period of 8 weeks in late summer (data adapted from Maurer and Matyssek, 1997). Abbreviations: C-LF = O_3-free air/low-fertilized; O_3-LF = O_3-exposed/low-fertilized; C-HF = O_3-free air/high-fertilized; O_3-HF = O_3-exposed/high-fertilized (data as means ± SD).

feeds the oxalacetate pool of the citric acid cycle under conditions of high demand for substrate and energy (Wiskich and Dry, 1985). Such a demand is created by O_3 in leaves because of increased respiratory costs of detoxification and repair processes (Rennenberg et al., 1996; Maurer et al., 1997; Polle et al., 2000). Low WUE and reduced stomatal limitation of CO_2 uptake (Farquhar et al., 1989b) in plants exposed to O_3 resulted from distinct declines in carboxylation efficiency associated with extensive collapse of mesophyll cells (Matyssek et al., 1991; Gunthardt-Goerg et al., 1997). Exposure to O_3 decreased G_W only at low fertilization, but did not prevent a decline in WUE (Maurer et al., 1997). O_3 uptake by leaves was similar between levels of fertilization, as O_3 caused G_W of low-fertilized plants to decrease towards levels at high fertilization.

1.2.2. Whole-plant response

Betula pendula displays indeterminate shoot growth, thus formation of new leaves can continue throughout most of the growing season as long as resource availability is high. Given this feature, new leaf production may compensate for the premature loss of older, injured leaves. On the other hand, low nutrient availability may restrict new leaf production, which increases the need for maintaining injured, older leaves (Laurence et al., 1994; Fredericksen et al., 1995). This contrasting growth pattern characterized the experimental plants of *Betula pendula*, as the proportion of O_3-injured leaves was high at low fertilization (Maurer and Matyssek, 1997). Respiratory costs of foliage as a proportion of whole-plant carbon balance were higher in low-fertilized plants because of the high number of O_3-injured leaves (Fig. 1(B)), as these plants relied on the photosynthesis of injured foliage that had been formed early in the season. However, O_3 inhibited branch formation and leaf size at high fertilization (Matyssek et al., 1992). Because stomata responded to chronic O_3 exposure by partial closure only at low fertilization (Maurer et al., 1997), daily and seasonal canopy transpiration per unit of foliage area decreased only in low-fertilized plants. It appears that the 'opportunity costs' (Stitt and Schulze, 1994) were more favorable for high-fertilized plants to form new leaves rather than maintain older injured leaves as nitrogen is often reallocated from O_3-injured leaves to new leaves which stimulates their photosynthetic performance (Beyers et al., 1992; Greitner et al., 1994; Pell et al., 1994; Temple and Riechers, 1995).

The impact of O_3 on carbon allocation between root and shoot of *Betula* depended on fertilization level. O_3 decreased the root/shoot biomass ratio (R/S) more at low fertilization than at high fertilization (Maurer and Matyssek, 1997). Moreover, O_3 did not affect specific root length or carbon allocation among root diameter classes, but increased the leaf mass per area ratio (LMA), regardless of fertilization level. The dramatic decrease in root growth caused by O_3 at low fertilization was related to a high carbon demand for maintaining foliage (Polle et al., 2000) and to disruption of assimilate translocation from injured foliage (Spence et al., 1990; Matyssek et al., 1992; Gunthardt-Goerg et al., 1993). In fact, respiratory costs were high in low-fertilized plants under O_3 exposure, contributing to the low WUE of whole-plant production

(Fig. 1(B)). The effect of O_3 on WUE of single leaves (Fig. 1(A)) was consistent with the effect on the whole plant (Fig. 1(B)).

1.2.3. Synopsis

The processes linked together in Fig. 2 form a mechanistic basis for scaling O_3 effects through the tree, and may represent an ecologically meaningful scheme because they reflect the low nutritional status present in many forests. After entering the leaf through stomata, O_3 increases respiration (defense, repair) and stimulates PEPC activity which increases tissue ^{13}C content. Leaf growth decreases, LMA and stomatal density increase, and transpiration decreases because of partial stomatal closure. In parallel, P_N decreases through biochemical signals arising from the primary impact of O_3 on the mesophyll apoplast that damage chloroplasts (Sandermann et al., 1997). Tissue collapse also decreases P_N and WUE, disrupts both translocation within the leaves and phloem structure and function, and decreases carbon allocation to stem and root growth (Friend and Tomlinson, 1992; Kelly et al., 1993; Smeulders et al., 1995). Even though R/S stays low, plant growth decreases because of decreased leaf size, P_N, and branching, and the occurrence of premature leaf loss. Plants grown

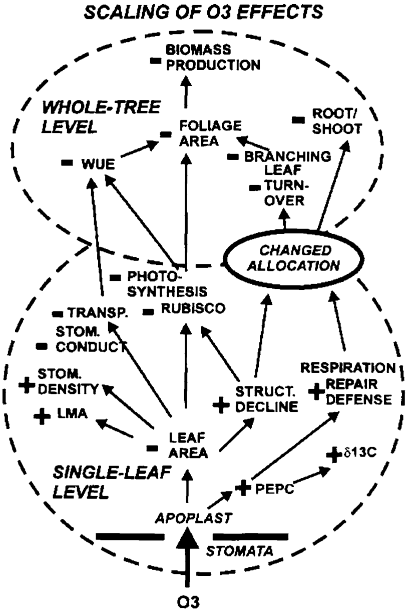

Figure 2. Scaling scheme of ozone effects on plant internal processes in young birch (*Betula pendula*) plants.

at high nutrient availability may respond to O_3 exposure at the whole-plant level by having lower respiratory costs, a smaller decline in WUE and R/S, but an increase in compensatory leaf turn-over that may partially counteract O_3 impacts on growth.

1.3. O_3 impact modified by ‘CO_2 fertilization’

In contrast to *Betula pendula*, *Fagus sylvatica* displays determinate growth, and completes foliage production during a few weeks in spring. Under favorable circumstances, a second flush (i.e., the lammas shoot) may follow in early summer, adding new foliage to the crown (Roloff, 1985; Ceulemans and Mousseau, 1994; Gruber, 1998; Saxe et al., 1998). In another phytotron experiment, three-year-old *Fagus sylvatica* plants were exposed throughout the growing season either to a regime that mimicked the climate and ambient fluctuating O_3 levels from a rural field site, or to a regime with twice-ambient O_3 levels (Grams et al., 1999; Häberle, personal communication). Both O_3 regimes were combined with contrasting exposure to CO_2 (ambient levels up to 400 $\mu l\, l^{-1}$ versus 700 $\mu l\, l^{-1}$), a ‘pollutant’ that represents another kind of nutrient which may counteract carbon limitation in plant growth (Ceulemans et al., 1999). Mineral nutrients and water were non-limiting throughout the experiment. To prevent transitional responses to CO_2, the plants were acclimated to the CO_2 treatments during one year prior to the O_3 treatments.

1.3.1. Leaf responses

Fagus sylvatica displayed a leaf response to high O_3 and ambient CO_2 levels commonly observed under controlled chamber conditions: P_N declined relative to the control (ambient O_3 and CO_2) treatment (Lippert et al., 1996; Zeuthen et al., 1997; Dixon et al., 1998) due to decreases in both the light and dark reactions of photosynthesis (Grams et al., 1999). In contrast, elevated CO_2 increased P_N compared with the control and ameliorated the negative effects of high O_3 on P_N (cf. Ceulemans and Mousseau, 1994; Manes et al., 1998; Volin et al., 1998). Photosynthetic parameters were not down regulated by elevated CO_2 (Mousseau et al., 1996; Heath and Kerstiens, 1997), although foliar chlorophyll and N levels decreased (Curtis and Wang, 1998). While elevated CO_2 can decrease G_W and O_3 uptake (Saxe et al., 1998), such a reduction in G_W occurred in the *Fagus* plants only during early summer, and G_W did not differ among the four treatments throughout the remainder of the growing season (Grams et al., 1999). As root density in the soil increased during midsummer under elevated CO_2, G_W was apparently not affected by constraints on root performance as reported elsewhere (Arp, 1991; Kerstiens et al., 1995; Saxe et al., 1998). As a consequence, the ameliorating effect of elevated CO_2

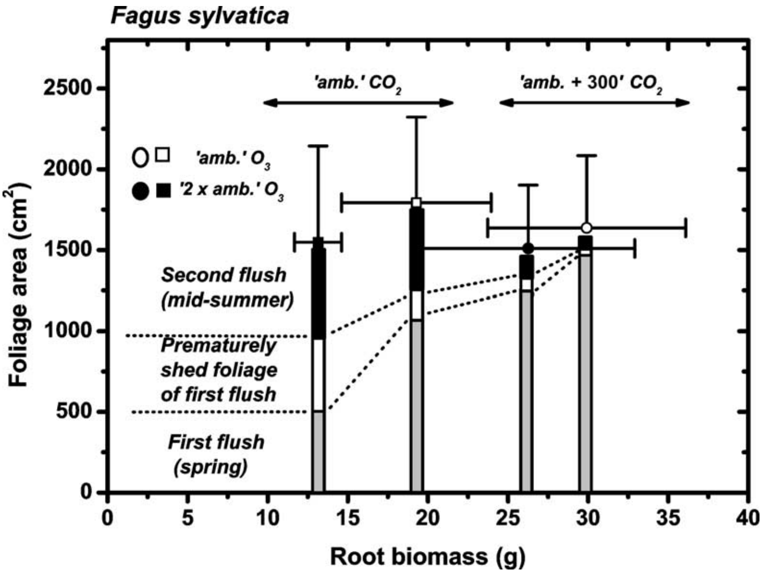

Figure 3. Relationship between root biomass and foliage area of young beech (*Fagus sylvatica*) growing under four combinations of ambient or twice-ambient ozone and CO_2 exposure (data as means ± SD). Also depicted are the proportions of first-, second-flush, and prematurely shed foliage (data from Häberle, personal communication).

on O_3 stress likely resulted from compensatory responses at the biochemical level (Anegg and Langebartels, unpublished data).

1.3.2. Whole-plant response and synopsis

Whole-plant biomass production of *Fagus* consistently reflected photosynthetic performance in each treatment: biomass was lowest at high O_3 and ambient CO_2, and highest at ambient O_3 and elevated CO_2 (El Kohen et al., 1993; Rey and Jarvis, 1997). Elevated CO_2 ameliorated the negative effects of high O_3 on biomass (Volin et al., 1998). R/S was lowest under the high O_3-ambient CO_2 regime (Matyssek and Innes, 1999).

Decreased root growth caused by high O_3 in *Fagus sylvatica* with its determinate shoot growth resulted in an R/S response similar to that of *Betula* when its indeterminate growth was restricted to the early part of the growing season by low nutrition (see above). In both cases, the need for maintaining foliage under O_3 impact apparently reduced carbon allocation to roots (Mooney and Winner, 1991). In *Fagus*, lammas shoot formation in mid-summer was a strong sink for carbon under conditions of ambient CO_2 and high O_3, and helped to compensate for the decline in P_N and loss of first-flush foliage (Häberle, personal communication; Fig. 3). Root growth was favored at high CO_2 when demand for repair, detoxification, and compensatory foliage growth was low in the absence of severe O_3 impact (Fig. 3). These studies suggest that resistance to O_3 is promoted by tree capability to create carbon sinks that facilitate compensatory responses such as high rates of leaf turnover in *Betula* or lammas shoot formation in *Fagus*. Creation of these sinks can strongly depend on nutrient availability (e.g., soil nutrition and CO_2). Long-term persistence of O_3 tolerance through elevated CO_2 (Polle et al., 2000) however, is questionable. In general, the current state of knowledge allows for scaling of ecophysiological processes and responses to O_3 across functional levels within juvenile trees.

1.4. Hypotheses for scaling air pollutant impacts to mature trees and stand conditions

Given the lack of knowledge about mature forest trees, we use findings from multi-factor experiments on juvenile trees to form hypotheses that may be relevant to scaling O_3 responses across tree ontogeny and to stand conditions (Table 1). If O_3 and low nutrition constrain shoot growth in trees of indeterminate growth habit, carbon may be allocated to maintain foliage formed early in the season. The shoot growth habit of such plants resembles that of trees with determinate growth, although the change in growth habit is caused by O_3 stress and resource limitation. Many determinate species have a high capacity to store carbohydrates that can support compensatory mechanisms leading to O_3 tolerance in older leaves (Laurence et al., 1994). Therefore, we hypothesize that trees with determinate growth, including most mature trees of indeterminate species (Kozlowski and Pallardy, 1997), respond to O_3 stress by decreasing carbon allocation to non-green organs, and to sinks associated with defense or tolerance to other stresses, more than trees with indeterminate growth because of allocation to maintain older leaves if surplus carbon is available (Hypothesis 1).

Replacement of O_3-damaged foliage leads to shifts in carbon allocation from root to shoot growth in trees with determinate growth by recurrent flushing or the formation of lammas shoots. These extra shoot flushes can be initiated by high availability of limiting resources such as mineral nutrients. However, if supply of both mineral nutrients and CO_2 are high, carbon reserves are available for allocation to O_3 detoxification and repair of damaged tissues in older leaves; under this condition, the second flush is not required, and extra internal carbon is allocated to root growth (Hypothesis 2).

O_3 often increases leaf respiration and decreases P_N, whereas high CO_2 often increases P_N with effects on respiration being unclear (Ceulemans et al., 1999; Drake et al., 1999). High respiration costs and low P_N may constrain growth of old trees more than juvenile trees provided that respiration really

Table 1. Hypotheses derived from multi-factor studies relevant to scaling O_3 impacts from juvenile to mature forest trees (see text for details)

Hypothesis 1: Carbon allocation to stem and roots and sinks associated with defense or tolerance to other stresses is reduced by chronic O_3 stress more in trees with determinate growth than trees with indeterminate growth.

Hypothesis 2: In trees with determinate growth, recurrent flushing or formation of lammas shoots will increase as a compensatory response to chronic O_3 stress if soil mineral nutrition is high; however, high atmospheric CO_2 and high mineral nutrition will increase carbon available for O_3 detoxification and tissue repair, and ameliorate O_3 damage to older leaves of the first flush, thus favoring carbon allocation to roots versus lammas shoots.

Hypothesis 3: Supply of labile carbon available for defense, compensation, and repair responses to O_3 stress will be lower in mature than juvenile trees because of higher respiratory costs for maintaining living tissues and lower photosynthetic rate of mature trees.

Hypothesis 4: Stomatal aperture limits O_3 uptake into leaves more for mature than juvenile trees because of greater resistance to water transport in larger trees.

Hypothesis 5: Scaling O_3 effects from juvenile to mature trees must consider modification of tree competitive ability as mediated through structural and functional changes in resource uptake by canopy and roots.

Hypothesis 6: Scaling O_3 impacts from juvenile to mature trees must consider influences of O_3 on mycorrhizae, and secondary effects of mycorrhizae on stress tolerance and pest resistance.

Hypothesis 7: Light limitations on photosynthesis of shaded leaves increases O_3 sensitivity because of decreased carbon available for defense and repair.

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limits growth of old trees (Waring and Schlesinger, 1985; Ryan and Waring, 1992; Ryan et al., 1997; Hunt et al., 1999). Therefore, we hypothesize that supply of labile carbon available for defense, compensation, and repair responses to O_3 stress will be lower in mature than juvenile trees (Hypothesis 3).

If water limitations constrain the growth of mature trees more than juveniles because of increasing resistance to water transport with increasing tree size (Waring and Silvester, 1993; Yoder et al., 1994; Ryan et al., 1997) or other factors (Becker et al., 2000), then reductions in G_W can limit O_3 uptake and foliar damage more for mature trees than for juveniles (Hypothesis 4; Reich, 1987; Kolb et al., 1997).

We also hypothesize that changes in carbon allocation by O_3 stress leading to decreased canopy leaf area and root growth and related changes in crown and root architecture modifies tree competitive ability (Hypothesis 5; Kuppers, 1994; Bazzaz, 1997). Further, influences of O_3 on carbon allocation to mycorrhizae (Andersen and Scagel, 1997), which have often been overlooked, and their secondary effects on stress tolerance and pest resistance in trees (Ericsson et al., 1996; Gehring et al., 1997; Langebartels et al., 1997), may play a key role for scaling O_3 effects to the stand level (Hypothesis 6).

Shaded portions of the canopy occur in many mature forest trees but are typically absent in juvenile trees grown in the open or under controlled chamber conditions. Photosynthate available for repair and defense against O_3 stress may be limiting in shade leaves (Tjoelker et al., 1993; Matyssek et al., 1995a; Matyssek et al., 1995b; Tjoelker et al., 1995; Fredericksen et al., 1996a), and shade leaf morphology may promote O_3 injury (Bennett et al., 1992). Therefore, we hypothesize that light limitation increases O_3 sensitivity of leaves and this limitation must be considered in attempts to scale O_3 impacts across tree ontogeny (Hypothesis 7).

2. O_3 impacts on juvenile and mature trees

2.1. Effects of O_3 on leaf physiology of juvenile and mature trees

Effects of O_3 on some aspects of leaf chemistry and carbon relations appear to be qualitatively similar for juvenile and mature trees. For example, changes in N and carbohydrate concentrations in response to O_3 stress occurred in the same direction in leaves of seedlings exposed to O_3 in indoor or outdoor open-top chambers, and mature trees exposed with whole-tree or branch chambers for *Pseudotsuga menziesii* (Smeulders et al., 1995) and *Quercus rubra* (Samuelson et al., 1996). Similarly, levels of ascorbate, an anti-oxidant compound, did not vary among 8-, 15-, and 36-year-old trees of *Picea abies* growing in the same forest (Wieser, 2002). These few studies suggest similar metabolic responses to O_3 injury in leaves of juvenile and mature trees, and no fundamental changes in foliar defensive mechanisms against oxidant injury during tree maturation.

Another issue that is relevant to scaling leaf-level impacts of O_3 from juvenile to mature trees is the amount of O_3 exposure that causes the onset of leaf injury. A recent study of *Fagus sylvatica* (Baumgarten et al., 2000) showed that visible symptoms of O_3 damage (leaf discoloration) on seedlings exposed to O_3 in an indoor chamber started at a higher cumulative exposure (AOT40) than for mature trees exposed to ambient concentrations in the forest (Fig. 4). However, when exposure was expressed as cumulative O_3 uptake into the leaf mesophyll (calculated from ambient O_3 concentration and stomatal conductance), damage symptoms started at a similar cumulative O_3 uptake for seedlings and mature trees (Fig. 4). Similar results were reported for *Picea abies* for the relationship between cumulative O_3 uptake and reduction of P_N by O_3 exposure (Wieser, 2002). In contrast, visible foliar damage symptoms to sun leaves of *Prunus serotina* seedlings growing in an open field started at lower cumulative O_3 uptake into the leaf compared with sun leaves of mature trees in a nearby forest (Fig. 5), suggesting lower capacity for defense or repair for mature trees

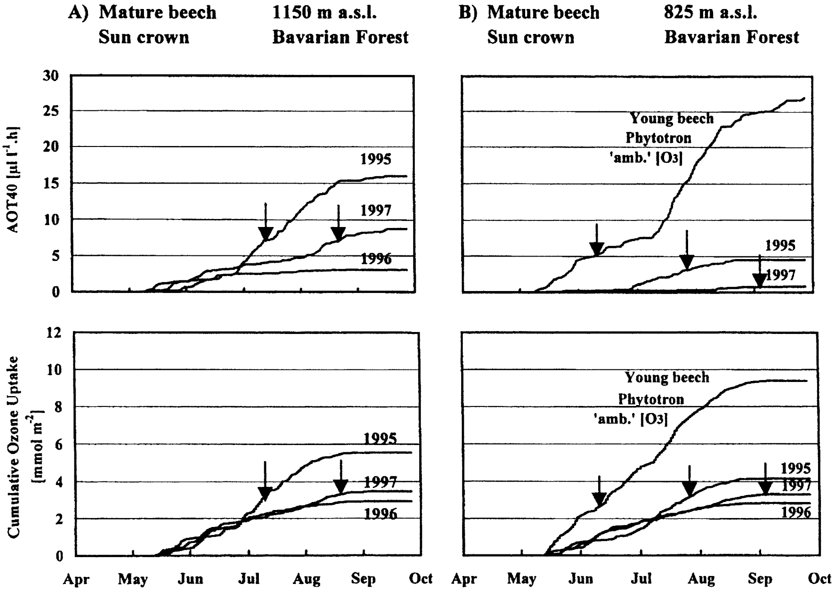

Figure 4. AOT40 (sum of external O_3 exposure > 40 nl l^{-1}; cf. Fuhrer and Achermann, 1999) and cumulative O_3 uptake into the leaf mesophyll for mature beech (*Fagus sylvatica*) trees in the Bavarian forest at two sites (1150 m a.s.l., 825 m a.s.l.) and over three years (1995, 1996, 1997), and for beech seedlings exposed to O_3 in a phytotron experiment. The arrow indicates the onset of visible leaf discoloration. O_3 uptake is based on two-sided leaf area. (After data in Baumgarten et al., 2000).

at low rates of uptake. However, damage symptoms on seedling leaves eventually exceeded symptoms on mature trees because of higher cumulative O_3 uptake resulting from greater G_W (Fredericksen et al., 1996b). These results for *Prunus serotina* are consistent with Hypothesis 3 (Table 1), whereas the results for *Fagus sylvatica* and *Picea abies* are not.

Lower capacity for defense or repair of O_3 damage for mature trees may be a consequence of a decline in P_N during tree aging (Fredericksen et al., 1996c; Ryan et al., 1997; Hubbard et al., 1999; Niinemets et al., 1999; Bond, 2000; Kolb and Stone, 2000). Sunlit leaves of old trees often have lower P_N than sunlit leaves of young trees because of reduced G_W likely caused by greater frictional resistance to water flow through xylem of large trees (Becker et al., 2000; Bond and Ryan, 2000; Mencuccini and Magnani, 2000). The tissues most responsible for frictional resistance to water flow in xylem are not understood well, but current evidence suggests that intercellular connections in the xylem (e.g., pits, perforation plates), branch junctions, and bud scars are important (Zimmermann, 1983; Tyree and Ewers, 1991; Rust and Huttl, 1999).

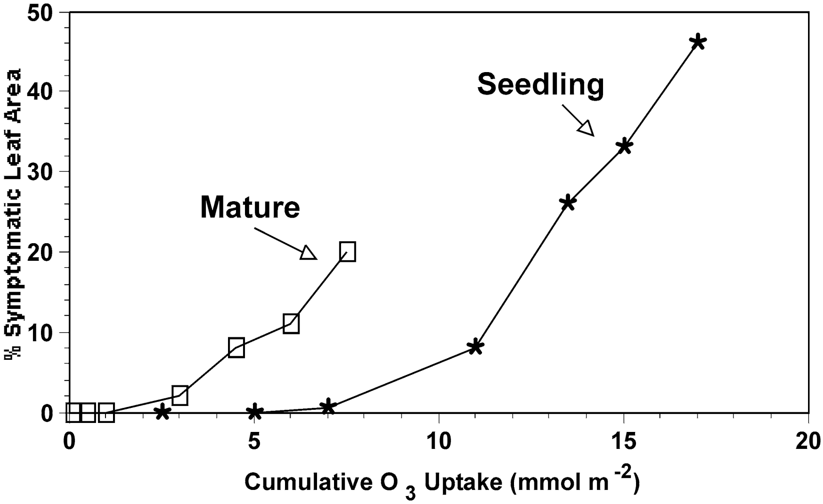

Figure 5. Average percent of leaf area with visible symptoms of O_3 injury (dark adaxial stipple) on shoots of unshaded seedlings and the upper canopy of mature forest trees of *Prunus serotina* during 1994 in central Pennsylvania versus cumulative O_3 uptake. The seedlings were growing in an open field, and the mature trees were growing in an adjacent, natural forest. Cumulative O_3 uptake was calculated as the product of stomatal conductance to O_3 and O_3 concentrations using hourly concentrations > 60 ppb. $N =$ all leaves on 3 shoots for each of 5 seedlings, and all leaves on 5 shoots for each of 4 mature trees (after data in Fredericksen et al., 1996b).

These sources of resistance should be more important in large trees because of their greater size and complexity. Also, large trees may close stomates earlier in the day than small trees because of lower leaf water potential (Kolb and Stone, 2000), greater stomatal sensitivity to vapor pressure deficit, and lower soil-to-leaf hydraulic conductance (Hubbard et al., 1999; Ryan et al., 2000). These factors suggest less O_3 uptake into the leaf mesophyll of mature versus juvenile trees, consistent with Hypothesis 4 described earlier (Table 1).

Several studies have quantitatively compared effects of O_3 on leaf condition of juvenile and mature trees (Rebbeck et al., 1992; Rebbeck et al., 1993; Samuelson and Edwards, 1993; Grulke and Miller, 1994; Hanson et al., 1994; Samuelson, 1994a; Fredericksen et al., 1995; Fredericksen et al., 1996b; Samuelson and Kelly, 1996; Momen et al., 1996; Momen et al., 1997). O_3 exposure had greater negative effects on carbon balance of sun leaves of juvenile versus mature trees in all studies, except those on *Quercus rubra* (Fig. 6). For *Pinus ponderosa*, O_3 exposure decreased P_N similarly for juvenile and mature trees (Fig. 6), but stimulated foliar respiration rate more in juveniles (Momen et al., 1996), indicating greater negative impacts of O_3 on leaf carbon balance of juveniles. Effects of O_3 on leaf respiration rate of *Sequoiadendron giganteum* juvenile and mature trees (Grulke and Miller, 1994) were similar to those

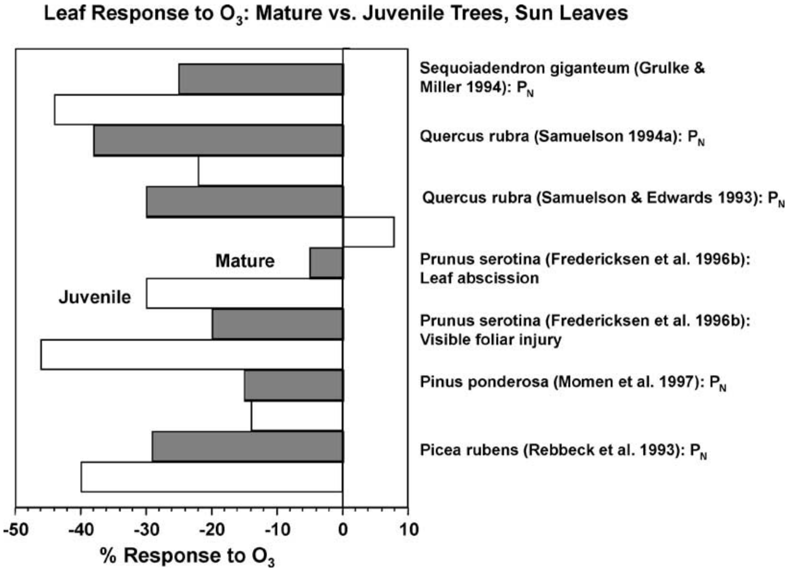

Figure 6. Percent response to O_3 for sun leaves of juvenile and mature trees of several tree species. Response variables are listed for each study (P_N = net photosynthetic rate). For studies using controlled exposures (Rebbeck et al., 1993; Grulke and Miller, 1994; Samuelson and Edwards, 1993; Samuelson, 1994a; Momen et al., 1997), the percent response was calculated for the highest level of exposure compared with the lowest level. For field studies where trees were exposed only to ambient O_3 concentrations (Fredericksen et al., 1996b), the percent response is the mean amount of leaf abscission or visible foliar O_3 injury for each tree size.

reported for *Pinus ponderosa*. Greater negative impacts of O_3 on P_N of juvenile compared with mature trees is suggested for *Prunus serotina* based on greater visual symptoms of O_3 injury in juveniles, and the strong negative relationship between these symptoms and P_N for this species (Samuelson, 1994b; Fredericksen et al., 1996b). In contrast to the findings for the other species, O_3 exposure reduced P_N of mature *Quercus rubra* trees more than for juveniles (Fig. 6). The mechanisms that underlie this result for *Quercus rubra* are not clear, but may include stimulation of G_W, and thus O_3 uptake, in mature trees by strong carbohydrate sinks such as seed development (Maier and Teskey, 1992; Luxmoore et al., 1995), a reduction of G_W and O_3 uptake in the container-grown seedling used in the study because of restrictions on root growth, and frequent watering of trees in the experiment that may have minimized differences in water relations between the juvenile and mature trees. In summary, available evidence suggests that O_3 has less effect on the carbon balance of sun leaves in mature trees than sun leaves in juveniles, with *Quercus rubra* being a notable exception to this trend. Low O_3 uptake by leaves of mature trees resulting from low G_W (Hypothesis 4, Table 1) may override

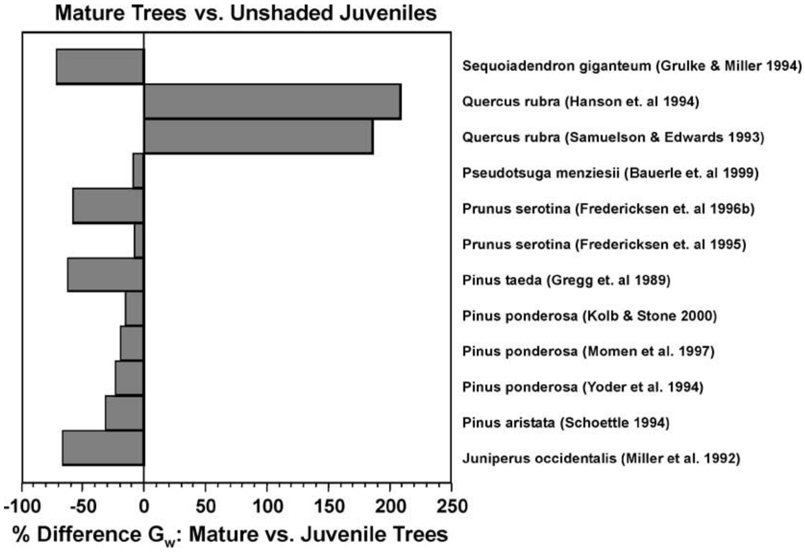

Figure 7. Percent difference in stomatal conductance (G_W) between sunlit leaves of mature trees and unshaded juveniles for several tree species. Negative values indicate lower G_W of mature trees versus juveniles, and positive values indicate greater G_W of mature trees versus juveniles. The differences were calculated based on seasonal or daily maximum values where possible; otherwise, seasonal mean values were used.

possible shortages of carbon available for defense, compensation, and repair responses (Hypothesis 3, Table 1), and thus limit leaf-level damage.

The difference in response of sun leaves to O_3 exposure between juvenile and mature trees (Fig. 6) can be partly explained by differences in G_W. Several studies have shown lower G_W, and thus lower O_3 uptake assuming the same O_3 concentration at the leaf surface, for mature trees than juveniles (Fig. 7). Again, *Quercus rubra* is an exception to this trend; G_W was much greater for mature trees than container-grown juveniles (Fig. 7). Regardless of the direction in the difference in G_W between juvenile and mature trees, the tree size with the greatest G_W (Fig. 7) also had the largest negative response to O_3 exposure (Fig. 6). Interestingly, this linkage between leaf-level physiological response to O_3 and G_W is the same as that reported for comparisons among species by Reich (1987). These findings suggest a consistent scaling pattern of O_3 impacts on the carbon balance of sun leaves during tree ontogeny.

2.2. Factors influencing differences in G_W between juvenile and mature trees

Given the linkages among leaf physiological response to O_3 and G_W, understanding of how environmental factors influence differences in G_W between

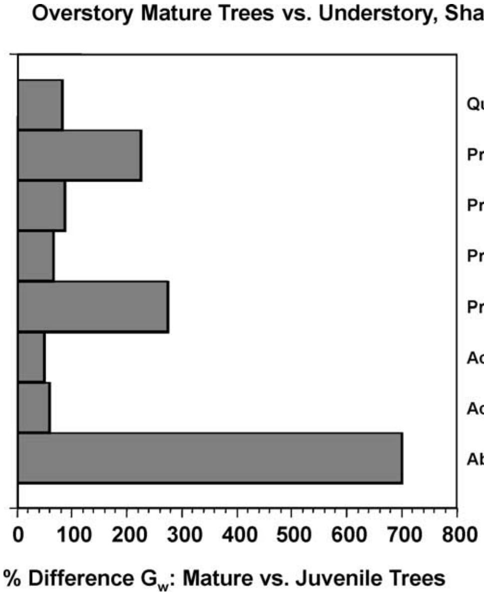

Figure 8. Percent difference in stomatal conductance (G_W) between sunlit leaves of mature trees and leaves of shaded, understory juveniles for several tree species. Positive values indicate greater G_W of mature trees versus juveniles. The differences were calculated based on seasonal or daily maximum values where possible; otherwise seasonal mean values were used.

juvenile and mature trees may be relevant towards scaling O_3 impacts to forest ecosystems. The data in Fig. 7 suggests that mature trees often have lower G_W than juveniles for sun leaves. However, because of shading within forests, this comparison applies only to the outer canopy of mature trees and small juveniles growing in openings. When G_W is compared between sun leaves of mature trees and leaves of shaded juveniles of the same species growing in the forest understory, a very different pattern emerges (Fig. 8). In this case, sun leaves of mature trees have much greater G_W than leaves of shaded juveniles. When G_W is measured at ambient light levels, heavily shaded juveniles often have lower G_W than overstory mature trees because light intensity in the understory is below photosynthetic saturation. Also, shade leaves often have lower G_W than sun leaves even when compared at photosynthetically saturating light intensity because of lower leaf N concentration per leaf area and lower LMA (Abrams and Kubiske, 1990; Ellsworth and Reich, 1993; Samuelson and Kelly, 1997). Thus, sun leaves of overstory mature trees should take up more O_3 than leaves of shaded understory juveniles based on differences in G_W.

Differences in water availability to juvenile and mature trees can cause large differences in G_W in some environments. In particular, dry soil can impose greater constraints on G_W for shallow-rooted juveniles than for deep-rooted mature trees that use deep soil or ground water that is not available to small trees (Dawson and Ehleringer, 1991; Donovan and Ehleringer, 1991; Dawson and Ehleringer, 1993; Dawson, 1996). These examples demonstrate that site-specific environment conditions can strongly influence the direction and magnitude of differences in G_W between juvenile and mature trees. Leaves of mature trees may have lower G_W and O_3 uptake than leaves of juveniles under some environmental conditions (e.g., sun leaves for both tree sizes, a large difference in tree height), but they also may have greater G_W and O_3 uptake than leaves of juveniles under other conditions (e.g., sun leaves of mature trees vs. shade leaves of juveniles; Samuelson and Kelly, 1997).

Studies of tree maturation that have compared scions from branches of juveniles with scions from mature trees after grafting onto seedling rootstocks have shown that G_W can also vary with tissue age because of tree maturation processes independent of differences in tree height, light environment, or water availability (Rebbeck et al., 1993; Greenwood, 1995). Limited evidence suggests that some changes in physiological traits during tree maturation result from changes in phytohormones and gene expression (Hutchison et al., 1990; Greenwood, 1995). Hence, tree ontogenetic stage, G_W, and O_3 uptake may be inherently linked.

2.3. Modification of O_3 impact by light environment

Light environment can influence leaf physiological response to O_3. Shade leaves can show greater foliar O_3 injury symptoms than sun leaves (e.g., *Prunus serotina* and *Acer saccharum*, Fig. 9), or vice versa (e.g., *Populus*, Fig. 9). The greater O_3 sensitivity of shade leaves may be related to their low palisade/spongy mesophyll ratio and less compact mesophyll structure that increases O_3 exposure of palisade cells compared with sun leaves (Bennett et al., 1992). Also, exposure of shade leaves to O_3 can cause uncoupling between P_N and G_W (Volin et al., 1993; Tjoelker et al., 1995; Fredericksen et al., 1995; Fredericksen et al., 1996a), which reduces WUE. After chronic exposure to ambient levels of O_3, shaded leaves of *Prunus serotina* seedlings, saplings, and mature trees had a higher ratio of O_3 uptake per P_N (Fig. 10) and greater visible foliar O_3 damage than sun leaves (Fredericksen et al., 1996a, 1996b). This result is consistent with Hypothesis 7 (Table 1).

An additional aspect of the light environment that might be important in scaling leaf-level response to O_3 in forests is the possibility of differences in O_3 uptake at night between juvenile and mature trees. Although darkness is often assumed to severely limit stomatal aperture, G_W can be surprising high at night (Tobiessen, 1982) because of low vapor-pressure deficit and perhaps other factors (Wieser and Havranek, 1993; Matyssek and Innes, 1999). G_W and

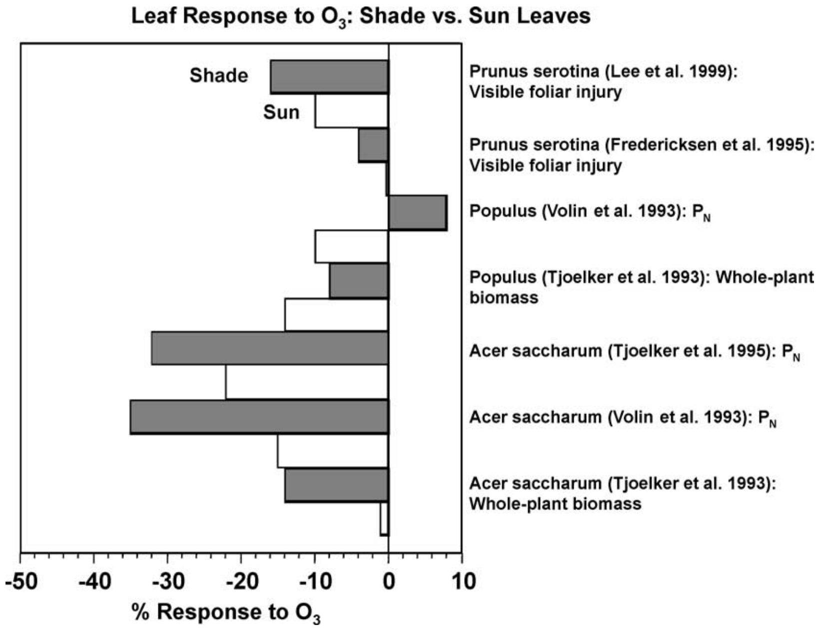

Figure 9. Percent response to O_3 exposure for sun and shade leaves of several tree species. Response variables are listed for each study (P_N = net photosynthetic rate). For studies using controlled exposures (Tjoelker et al., 1993; Volin et al., 1993; Tjoelker et al., 1995), the percent response was calculated for the highest level of exposure compared with the lowest level. For field studies where trees were exposed only to ambient O_3 concentrations (Fredericksen et al., 1996b; Lee et al., 1999), the percent response is the mean amount of visible foliar O_3 injury for each leaf type.

O_3 uptake were high at night in young, well-watered *Betula pendula* cuttings exposed to O_3 in outdoor chambers (Matyssek et al., 1995a). Further, nighttime plus daytime exposure to O_3 reduced biomass growth and altered carbon allocation patterns of these cuttings about two-fold more than daytime exposure alone (Matyssek et al., 1995a). This finding has implications regarding calculations of cumulative O_3 uptake for juvenile and mature trees if nighttime G_W varies with tree age and high concentrations of O_3 occur at night. In a study of different-sized *Prunus serotina* trees, nighttime G_W of mature trees was about 6% of maximum daytime values, whereas nighttime G_W of seedlings was about 18% of maximum daytime values, and seedlings had higher G_W than mature trees during both day and night (Fredericksen et al., 1996c). Given that O_3 concentrations in forests can be high at night under some conditions (Lefohn and Jones, 1986; Krupa and Manning, 1988; Wieser and Havranek, 1993), seedlings may take up more O_3 at night than mature trees.

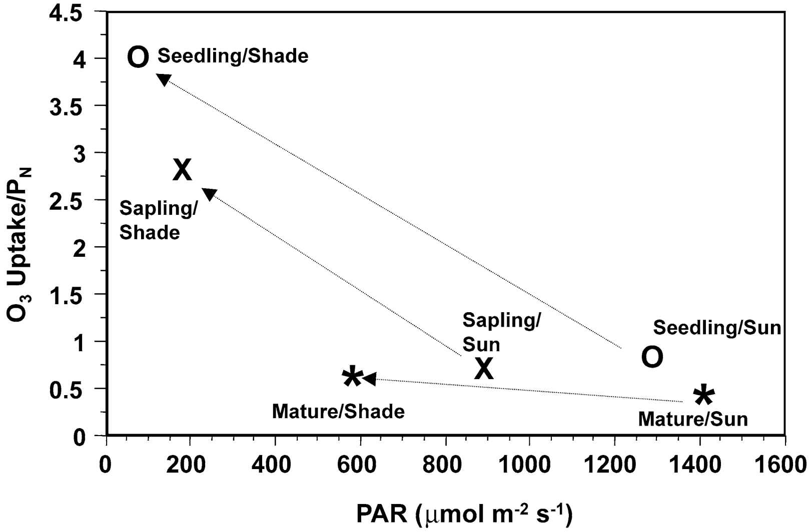

Figure 10. Mean ratio of O_3 uptake to P_N (nmol m^{-2} s^{-1} O_3 μmol m^{-2} s^{-1} CO_2) for leaves of seedling, sapling, and mature *Prunus serotina* growing in sun or shade environments in Pennsylvania, and mean daily photosynthetically active radiation (PAR) for each tree size in each environment between June and September, 1993. $N = 10$–30 leaves per tree size for each of four mature trees, five saplings, and five seedlings measured diurnally every two weeks (after data in Fredericksen et al., 1996a).

2.4. *Influence of leaf production phenology on O_3 response*

Indeterminate growth is a trait of certain tree species and occurs more often for seedlings than for older trees (Kozlowski and Pallardy, 1997). As noted earlier for *Betula pendula*, leaf production phenology of juvenile trees is a plastic trait that can be modified by resource availability (Maurer and Matyssek, 1997) and may be linked to O_3 effects on carbon allocation (Hypothesis 1, Table 1). Differences in phenology of leaf production between juvenile and mature forest trees have been shown to influence cumulative leaf exposure to O_3. Seedlings of *Prunus serotina* grown in an open field had indeterminate growth and produced leaves continuously between May and August whereas mature trees in an adjacent forest had determinate growth and finished leaf production in June (Fig. 11). Despite greater instantaneous rates of O_3 uptake for seedlings because of greater G_W (Fig. 12(A)), many seedling leaves were exposed to O_3 for only part of the growing season, resulting in lower cumulative uptake per average leaf for seedlings than mature trees (Fig. 12(B)). This finding suggests that Hypothesis 4 (Table 1)—stomatal aperture limits O_3 uptake into leaves more for mature than juvenile trees—must also consider the influence of leaf production phenology and leaf longevity on cumulative O_3 uptake.

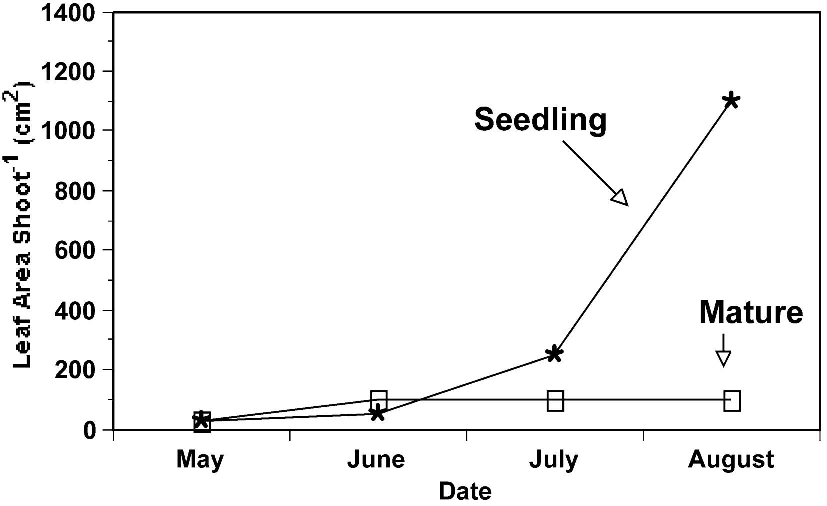

Figure 11. Average leaf area per terminal shoot for seedlings and mature trees of *Prunus serotina* averaged over upper and lower crown positions during 1993 in Pennsylvania. The seedlings were growing in an open field, and the mature trees were growing in an adjacent, natural forest. $N = 20$ shoots per tree for each of 4 mature trees and 12 seedlings. The bars show one standard error of the mean (after data in Fredericksen et al., 1995).

2.5. Changes in O_3 exposure during tree maturation

Spatial variation in O_3 concentration within forests, or variation between forests and areas where test seedlings are grown, could result in differences in O_3 exposure between mature trees and seedlings. Vertical gradients in O_3 concentration in forests may be caused by dense vegetation that is an O_3 sink, resulting in a decrease in O_3 concentration from atmosphere to the forest floor (Kozlowski and Constantinidou, 1986; Fuentes et al., 1992; Taylor and Hanson, 1992; Coe et al., 1995; Skelly et al., 1996; Samuelson and Kelly, 1997; Baumgarten et al., 2000). In addition, nitric oxide (NO) produced by soil microorganisms, which converts O_3 to oxygen, may reduce O_3 concentration near the soil surface (Baumbach and Baumann, 1989). On the other hand, volatile hydrocarbons produced by trees might stimulate the formation of O_3 in the forest because such hydrocarbons are precursors to O_3 formation (Enders et al., 1989; Stockwell et al., 1997).

The interplay among factors that influence local O_3 concentration could result in important spatial variations in O_3 concentration within forests that would need to be considered when comparing responses of juvenile and mature trees. For example, average O_3 concentration was about 33% lower near the forest floor compared with in the upper canopy in a *Fagus sylvatica* forest

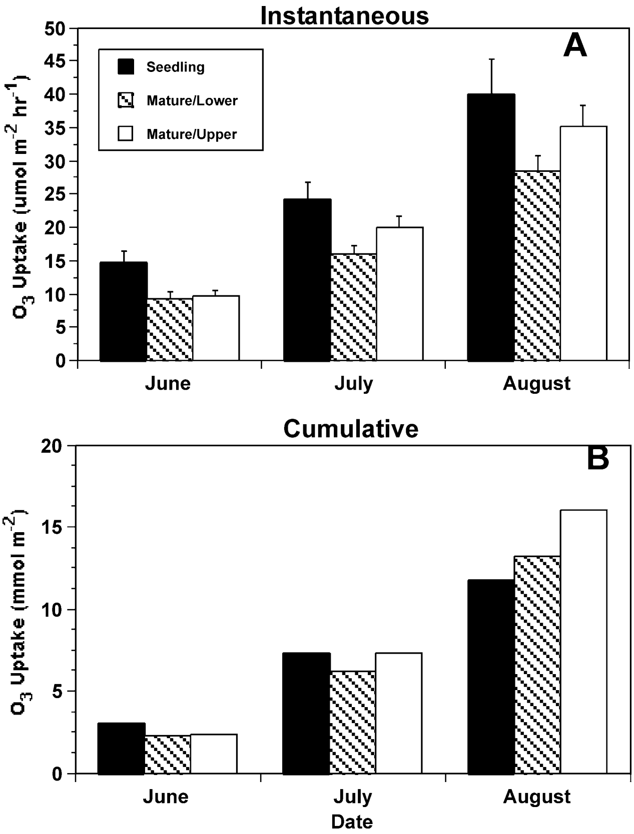

Figure 12. Instantaneous O_3 uptake rate (A) and cumulative O_3 uptake (B) for unshaded seedlings and lower and upper canopy positions of mature forest trees of *Prunus serotina* during June–August 1993 in Pennsylvania. The seedlings were growing in an open field, and the mature trees were growing in an adjacent, natural forest. Instantaneous O_3 uptake rate was calculated from monthly averages of diurnal measurements of O_3 concentration in the canopy and stomatal conductance for each tree size. Cumulative uptake was calculated by summing instantaneous rates of uptake during the study. Because of indeterminate growth of seedlings, cumulative uptake was weighted for this tree age by the proportion of leaf area (monthly mean leaf area/total end-of-season leaf area) exposed to O_3 each month. $N = 30$ to 60 leaves per date for each of 5 seedlings and 4 mature trees. The bars in (A) estimate one standard error of the mean based on pooled variances for O_3 concentration and stomatal conductance (after data in Fredericksen et al., 1995).

in Germany (Fig. 13). Samuelson and Kelly (1997) reported similar vertical gradients in O_3 concentration in a dense hardwood forest in Tennessee. In contrast, only small differences in O_3 concentration occurred for *Prunus serotina* in Pennsylvania among the canopies of mature forest trees, saplings growing in

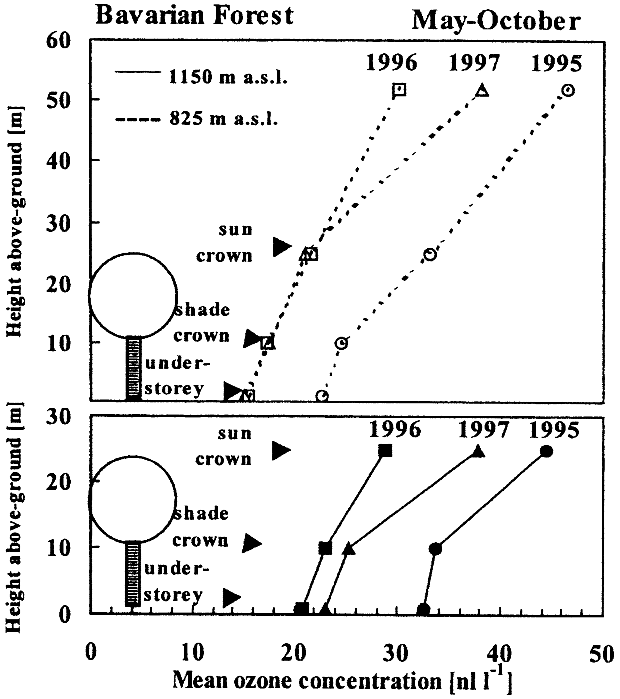

Figure 13. Variation in mean O_3ozone concentration (May–October 1995–1997) within and above a mature forest of *Fagus sylvatica* at altitudes of 1150 m and 825 m in the Bavarian forest (after data in Baumgarten et al., 2000).

a forest opening, and seedlings growing in a field adjacent to the forest during the day when G_W and O_3 uptake were highest (Fig. 14). Obviously, canopy architecture, roughness, and leaf area index may influence spatial patterns of O_3 exposure within stands.

3. Conclusions

Even though short-term effects of O_3 on juvenile trees in controlled experiments may be ameliorated through high supply of CO_2 or mineral nutrients, prevention of chronic injury under forest conditions is questionable because of changes in internal carbon allocation that may compromise resource capture, competitive ability, and defense or tolerance against other stresses (Herms and Mattson, 1992; Bazzaz, 1997). Such controlled experiments on juvenile trees have been valuable in elucidating physiological responses at scales ranging

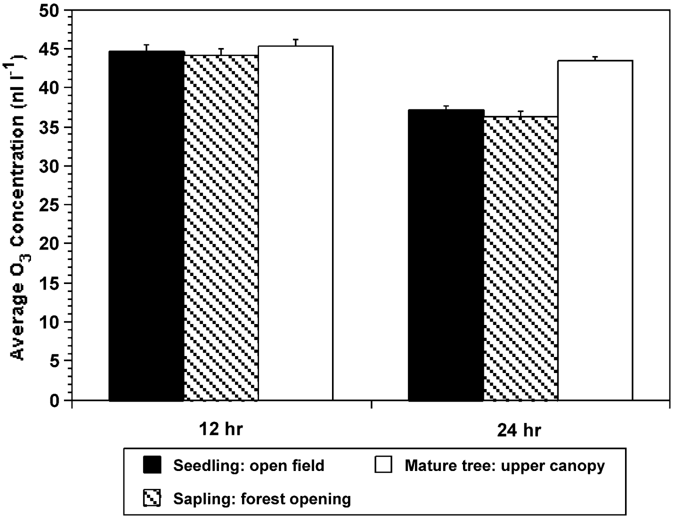

Figure 14. Monthly ambient O_3 concentration (May–August 1994) based on 12 and 24 hour means within the canopies of seedlings, saplings, and mature trees of *Prunus serotina* in a local forest area in Pennsylvania. The seedlings grew in an open field adjacent to the forest containing the mature trees, and the saplings grew in a small forest clearing (after data in Fredericksen et al., 1996b).

from the biochemical level to whole-plant growth. The general similarity between individual leaf and whole-plant responses for water and carbon relations in these experiments have led to scaling diagrams (Fig. 2) that outline probable linkages among molecular, biochemical, tissue, organ, and whole-plant responses. Such linkages form the conceptual basis for scaling units that may be valuable for understanding impacts of O_3 across functional levels of individual trees and during tree ontogeny.

Our analysis of multi-factor studies on plant-internal scaling relationships led to the formulation of seven hypotheses that may be relevant to scaling O_3 responses within forest ecosystems (Table 1). Only three of these hypotheses could be directly evaluated with results from comparisons between juvenile and mature trees, namely Hypotheses 3, 4, and 7. We found inconsistent support in studies with three species for Hypothesis 3—supply of labile carbon available for defense, compensation, and repair responses to O_3 stress will be lower in mature than juvenile trees because of higher respiratory costs for maintaining living tissues and lower photosynthetic rate of mature trees. Obviously, Hypothesis 3 needs to be tested more thoroughly with more species and over a wider range of environmental conditions. We found general support for Hypothesis 4—reduced G_W limits O_3 uptake and mesophyll damage more for mature trees than for juvenile trees—but only for sun leaves. However, this hypothesis does not explain the greater negative impacts of O_3 on the carbon balance of shade leaves (low G_W) compared with sun leaves (high G_W) reported for several species. In this case, high O_3 sensitivity of shade leaves can be conceptually understood to result from an imbalance between O_3 exposure of mesophyll cells and photosynthate available for repair or defense, providing support for Hypothesis 7.

The other four hypotheses (1, 2, 5, 6; Table 1) were difficult to evaluate directly with existing O_3 response data from mature trees, but they should be considered for evaluation in future studies that address quantitative scaling of O_3 effects in forests. Because several of these hypotheses include effects of chemicals that are influenced by human industrial activities (e.g., N compounds, CO_2), they may have particular relevance to understanding impacts of simultaneous changes in levels of O_3 and other air pollutants.

Leaves of juvenile and mature trees show similar qualitative responses in carbon relations and chemical composition to O_3 injury, but quantitative leaf-level responses of juvenile trees to O_3 exposure (e.g., percent reduction in P_N) cannot be assumed to accurately reflect leaf-level responses of mature trees. Factors such as light intensity, vertical profile of soil water availability, rooting depth, spatial variation in light intensity, canopy proportions of sun and shade leaves, and competition from other trees can influence differences in G_W and O_3 uptake between juvenile and mature trees (Kolb, 2002), suggesting problems in generalizing results from leaf-level O_3 responses beyond study site conditions. However, we are encouraged that some of these factors are the subject of current research efforts. These research efforts are especially critical given that leaf-level responses of juvenile trees to O_3 are being used increasingly in process models to predict O_3 impacts on mature forests (e.g., Reich et al., 1990; Taylor et al., 1994; Constable and Retzlaff, 1997; Constable and Taylor, 1997; Ollinger et al., 1997; Retzlaff et al., 1997; Weinstein et al., 1998). The reliability of quantitative predictions of O_3 impact on mature forest trees from process models should increase in the future if such models are refined to include changes in physiological characteristics during tree maturation as highlighted in our review. Certainly, predictions of O_3 impact from such process models are preferable to predictions of impact based on current threshold concepts of damaging O_3 levels (e.g., "Critical Levels for Ozone", formulated by UN-ECE as AOT40, i.e., accumulated O_3 exposure over a threshold of 40 $\mathrm{nl\,l^{-1}}$; Skärby et al., 1998; Fuhrer and Achermann, 1999), as the validity of such threshold concepts to mature trees is questionable due to the lack of appropriate databases and conceptual weaknesses in definitions (Matyssek and Innes, 1999). Assessments of O_3 uptake rather than exposure (as adopted by the AOT40 concept) will also improve understanding of O_3 effects on forests.

Tree sensitivity to O_3 is not only determined by O_3 uptake and leaf physiological responses, but also by plant-internal resource allocation to support repair, defense, and compensation mechanisms of coping with O_3 damage. Little is known about controls over internal resource allocation, especially for mature trees, and this is presently a crucial challenge in plant ecophysiological research (Bazzaz, 1997; Lerdau and Gershenzon, 1997). Ontogenetic changes in resource allocation patterns are clearly relevant to understanding differences in O_3 sensitivity between juvenile and old trees, and these patterns likely change during tree ontogeny because of physical (e.g., tree size), environmental (e.g., resource availability, competition), or genetic (e.g., changes in gene expression) factors.

Factorial scenarios that arise from interactions among environment (e.g., light regime, mineral nutrition, atmospheric CO_2), tree genotype, and tree ontogeny likely interact in complex ways to determine tree sensitivity to O_3, thus complicating attempts to scale O_3 impacts to forest trees from responses of juveniles. Free-air O_3 fumigation experiments of forest canopies (Musselman and Hale, 1997; Häberle et al., 1999; Karnosky et al., 2001) alleviate some of these problems, and provide the opportunity to analyze O_3 responses across tree-internal scales and ontogeny. Free-air fumigation experiments in combination with improved assessments of O_3 influx into leaves are likely to resolve some of the remaining uncertainties in understanding O_3 impacts on mature forest trees, and will provide information needed for more credible risk assessments of chronic O_3 stress in forests. Such risk assessments are clearly relevant to concerns about global change, as tropospheric O_3 concentrations will likely stay high in the future (Fowler et al., 1999) and may mitigate the carbon sink strength of forests (Saxe et al., 1998; Ceulemans et al., 1999).

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