

Chapter 14

The need for spatially and functionally integrated models of ozone deposition to Sierra Nevada forests

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Abstract

Ozone deposition models are needed for the Sierra Nevada to address growing ozone pollution and forest health problems in the region. Models can be used to estimate the stomatal fraction of total ozone deposition. Modeling stomatal ozone deposition, or plant ozone uptake, is critical for estimating the damaging component of plant ozone exposure. Models are an important tool for scaling from direct measurements to the landscape, for capturing the complex dynamics of ozone deposition across heterogeneous and mountainous landscapes, and for estimating temporal dynamics in ozone deposition. In this chapter, we first review the biotic and abiotic controls on ozone deposition in the Sierra Nevada. We review approaches to modeling ozone deposition from the leaf to the regional scale. We discuss in detail algorithms for estimating stomatal conductance, since ozone uptake is controlled by stomatal conductance and conductance drops progressively over the prolonged summer drought, typical of the Sierra Nevada, in response to progressively decreasing soil moisture and atmospheric humidity. We highlight examples of ozone deposition and stomatal conductance modeling efforts that provide potential approaches to modeling in the Sierra Nevada. We end with a discussion of the needs for future modeling in the Sierra Nevada and the key questions about ozone deposition facing the Sierra Nevada that can currently best be answered with models.

1. Identifying the need for models

The key feature of the Sierra Nevada ecosystem in relation to ozone uptake is the prolonged summer drought that causes progressive stomatal closure from June to October in forest ecosystems. After a burst of growth in the late spring and early summer, trees become physiologically dormant until precipitation

begins again in the fall. In general, ozone must enter foliage through stomatal pores to cause damage. Therefore, any factors that influence stomatal conductance also affect ozone uptake and must be explicitly included in models of ozone deposition. The critical role of stomatal conductance in ozone deposition is being documented in flux studies throughout the United States and Europe (Bauer et al., 2000; Emberson et al., 2000a; Finkelstein et al., 2000; Mikkelsen et al., 2000; Tuovinen, 2000; Zeller and Nikolov, 2000). The need to use different approaches in different climates and eco-regions to accurately model stomatal conductance is being recognized (Musselman and Massman, 1999; Emberson et al., 2000a; Massman et al., 2000). Of the several climatic factors that influence stomatal conductance, soil water availability and atmospheric humidity have the dominant influence on stomatal aperture in the Sierra Nevada (Bauer et al., 2000; Panek et al., 2002) because water, not light, is the limiting factor during the summer growing season. This strong relationship between moisture and conductance is not captured in many recent models of gaseous deposition developed for more mesic climates.

Ozone deposition models are needed for the Sierra Nevada to address growing ozone pollution and forest health problems. Concentration-based ozone exposure metrics used throughout the US and Europe do not characterize the ozone "seen" by forests in the Sierra Nevada. This situation calls for the development of new approaches based on models to determine ozone uptake. Ozone damage has never been compared to ozone uptake in the Sierra Nevada; thus, cause-effect relationships have yet to be developed for this region. Current direct methods of measuring ozone uptake are difficult to implement in the complex canopies and terrain of these montane ecosystems.

There is a need for models to aid in setting new regulatory standards for ozone exposure of crops and forests. In general, the ozone exposure indices used (e.g., SUM0, SUM06, SUM08, W126, and AOT40) are based on atmospheric ozone concentrations. In mesic climates and irrigated systems, where stomatal conductance is not limited by water availability, these metrics may be adequate because the concentration of ozone in the air is well-correlated to the amount of ozone entering the leaves. In seasonally drought-stressed systems such as the Sierra Nevada (Bauer et al., 2000), and even in mesic systems which are subject to periodic droughts, concentration-based metrics overestimate ozone uptake (Panek et al., 2002) because stomata close under drought stress making the relationship between concentration and uptake non-linear. Furthermore, as changes in climate cause variations in soil moisture from year to year, ozone uptake in many systems may become increasingly decoupled from ozone concentration (Panek and Goldstein, 2001) and existing metrics may not be useful for assessing potential damage. Models can provide the means to estimate ozone uptake across climate regimes and a range of spatial and temporal scales.

There is also a need for models of ozone uptake to understand mechanistic relationships between ozone uptake and forest response. Forests have a complex array of responses to ozone stress, including increased antioxidant production (Fincher et al., 1989; Madamanchi et al., 1991; Bytnerowicz, 1996; Miller et al., 1998), reallocation of carbon (Andersen and Rygielwicz, 1995; Grulke et al., 1998, 2001), changes in rates of photosynthesis and conductance (Baillon et al., 1988; Benner et al., 1988; Patterson and Rundel, 1990; Weber et al., 1993; Bytnerowicz, 1996; Grulke, 1999), changes in phenology (Duriscoe and Stolte, 1989; Grulke and Balduman, 1999) and growth (Miller et al., 1963; Miller et al., 1998), and increased crown and foliar damage (Miller et al., 1998; Arbaugh et al., 1998; Grulke, 1999). While substantial evidence of ozone damage has been observed in the Sierra Nevada, the details of its relation to ozone has been obscured by a lack of ozone uptake data. All correlations between damage and exposure have been made with ozone concentration data. Increasing the certainty of our estimates of ozone deposition to forests will allow us to better separate the cause-effect relationships in ozone-stressed forested ecosystems.

Models may be our only hope of capturing the complex dynamics of ozone deposition across heterogeneous and mountainous landscapes and for scaling from direct measurements to the landscape. Furthermore, comparison of models to measurements reveals gaps in our knowledge and provides a basis for directing measurements in the field to fill these gaps. Direct measurements of ozone uptake are difficult, time-consuming, and expensive. Currently, the best methods of directly measuring ozone uptake include gas exchange cuvettes at the leaf level and eddy covariance techniques at the canopy level (Goldstein et al., Chapter 4, this volume). However, these methods are limited to areas with easy access. Eddy covariance estimates are further limited by the nature of the terrain, which must be fairly homogeneous and flat, and may be limited by access to, or generation of, adequate electrical power to run the instrumentation (Sellers et al., 1997). Models, however, are constrained by limitations in our conceptual framework. Feedbacks between efforts to model ozone deposition and measurements in the field are critical to developing an understanding of the complex interactions between the atmosphere and forest ecosystems.

The challenges to modeling ozone deposition in the Sierra Nevada are numerous, but not insurmountable. They include the difficulties of characterizing deposition in complex mountainous terrain and complex forest structure, modeling of nighttime deposition to stomatal and non-stomatal surfaces under very stable atmospheric conditions, and adequate model descriptions of surface properties such as the presence of snow, vegetation type and condition, leaf area and distribution, and whether surfaces are wet or dry. Models must include the unique condition of periodic extreme soil moisture stress and the adaptive physiological response of forest ecosystems to moisture stress, espe-

cially in relation to stomata. Models must account for the heterogeneous distribution of water, vegetation types, and canopy density (leaf area index) in the Sierra, both temporally and spatially. Models must include interactions with other pollutant species, especially nitrogen. Scaling from local to regional flux estimates presents a significant challenge, which must involve comparisons between model results and direct measurements at a range of scales.

In this chapter, we will discuss the biotic and abiotic controls on ozone deposition that must be included in models of ozone uptake in a California montane forest. We will review approaches to modeling that have been used with success in the US and Europe, with specific attention to algorithms used to estimate stomatal conductance. We will highlight insights from case studies applicable to the Sierra Nevada. We will end with a discussion of the needs for future modeling in the Sierra Nevada, and the key questions about ozone deposition facing the Sierra Nevada that can be answered only with models.

2. Factors controlling ozone deposition

2.1. Phenology

Ozone uptake may be unrelated to ambient ozone concentration because the timing of ozone exposure relative to plant physiological activity is critical to the ozone dose experienced by the plant. The impact of ozone exposure has been shown to depend on the phenological stage of the vegetation (Younglove et al., 1994; Pleijel et al., 1998). This can be as important for coniferous forests as it is for deciduous forests and agricultural systems. In the Sierra Nevada, for example, low temperatures delayed budbreak in *Pinus ponderosa* for a month in 1998. The consequent delay in leaf development shifted the peak in ozone uptake by a month in relation to the previous year (Bauer et al., 2000). Coniferous trees may hold onto two or more age classes of needles, which may have differing gas exchange rates, and varying capacity to respond to stress. Atmospheric turbulence in the spring can cause incursions of stratospheric ozone down into the troposphere. The subsequent high concentrations of tropospheric ozone may occur when plants are dormant, leafless, or have low metabolic rates; thus, it remains “unseen” by the plants. For example, in northern Europe ozone concentration has a spring maximum, when deciduous trees are bare and conifers are dormant (Logan, 1985; Tuovinen and Laurila, 1993; Laurila, 1996; Rummukainen et al., 1996; Tuovinen, 2000).

2.2. Stomatal ozone uptake

Any factor that affects stomatal conductance clearly affects ozone flux into the leaf, and thus must be considered in modeling ozone uptake. Stomatal aperture

is under tight biological control and is regulated to maximize carbon uptake while minimizing water loss. Stomatal regulation requires energy and involves feedback loops (e.g., in response to high CO₂ and/or hormone levels) and feed-forward loops (e.g., in response to high transpiration rates; Jones and Sutherland, 1991). Stomatal conductance is controlled in response to environmental factors such as light (trend of relationship, +), soil moisture (+), vapor pressure deficit (−), temperature (+/−), CO₂ (−), nutrients (+), and wind (−). Climate extremes, such as intense drought or freezing temperatures, can also lead to cavitation of hydraulic pathways, which may have long-term residual effects on stomatal conductance (Zimmermann, 1978; Tyree and Ewers, 1991; Sperry and Pockman, 1993; Sperry et al., 1993). This is rarely included in models of stomatal conductance, although cavitation may occur frequently and seasonally in droughted systems (Panek, 1996). Physiological factors can also play a role, including leaf water potential (+), hormone levels (+), and photosynthesis (+). A strong relationship with photosynthesis has been observed (Wong et al., 1979) and is embedded in the Ball–Berry family of conductance models, as discussed later in this chapter. Whether conductance is mechanically dependent on photosynthesis is a subject of some discussion (Wong et al., 1979; Jarvis and Morison, 1981; Ball et al., 1987); however, there is no doubt that photosynthesis depends on stomatal conductance. Stomata may not close entirely at night, which has important implications for ozone flux. In areas where ozone concentration remains elevated at night, such as montane forests, significant ozone may be taken up at night through partially open stomata (Musselman and Minnick, 2000).

The relative importance of environmental factors controlling conductance changes with species and between climate regimes. In climates that rarely experience drought, stomatal conductance may be primarily limited by light and temperature. In drought-adapted climates, such as in Sierra Nevada forests, stomatal conductance is primarily limited by soil moisture, through its effects on plant water potential, and vapor pressure deficit (VPD). Here ozone uptake can become decoupled from ozone concentrations (Panek and Goldstein, 2001). Stomatal conductance, and thus ozone uptake, drops over the summer season in response to low soil moisture and low air humidity. From July through October, *Pinus ponderosa* show progressively limited gas exchange (Law et al., 2000a, 2000b; Panek and Goldstein, 2001). Despite high ambient ozone concentrations during those months, little ozone gets into the trees. In these systems, ozone concentration is decoupled from ozone uptake both diurnally and seasonally (Fig. 1). Drought-stressed systems respond differently to environmental stimuli than mesic systems (Karlsson et al., 2000; Pio et al., 2000). Therefore, models developed in the eastern United States, for example, will have to incorporate stomatal responses to drought before being applicable to forests in the Mediterranean climate of California and the Pacific Northwest.

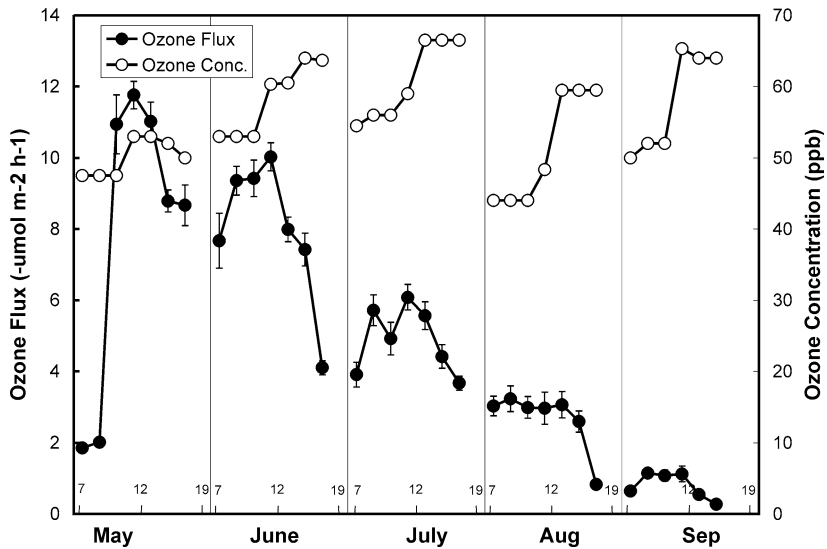


Figure 1. Stomatal ozone flux into ponderosa pine foliage, measured in the 1999 growing season at Yosemite National Park, a low-ozone-exposure site in the Sierra Nevada, California. Ozone flux is calculated from leaf-level measurement of stomatal conductance to ozone \times ozone concentration on a total leaf area basis. Each panel represents a diurnal timecourse from 700 h to 1900 h. Error bars are ± 1 SE. Ozone concentration data are from the National Park Service Air Resource Specialists.

2.3. Canopy ozone deposition

When integrating fluxes from the leaf to the canopy scale, environmental factors may not scale linearly. For example, the canopy includes both sun and shade fractions, conifer canopies may include multiple age classes of foliage, and different parts of the canopy may have varying physiological activity. Measurements of ozone flux at the canopy-scale are accomplished primarily by eddy covariance techniques (Meyers et al., 1998; Bauer et al., 2000; Finkelstein et al., 2000; Goldstein et al., Chapter 4, this volume) and by vertical and horizontal gradient measurements (Mikkelsen et al., 2000).

Ozone deposition to canopies includes deposition to stomatal and non-stomatal surfaces, i.e., biologically effective and non-effective components, respectively. Eddy covariance methods measure total deposition. Uptake by stomata can be difficult to separate from total deposition. Using a combined modeling and measurement approach, Zeller and Nikolov (2000) estimated 41% of the total ozone deposition to a subalpine coniferous forest in Wyoming was to non-stomatal surfaces, including non-transpiring plant, soil and snow surfaces. Coe et al. (1995) and Rondón et al. (1993) found that pine and spruce

canopy conductance to ozone was up to three times higher than conductance to water vapor, suggesting a significant non-stomatal sink for ozone. These researchers suggested that the leaf surface is oxidized by ozone. Jetter et al. (1996), however, found no direct oxidative transformation of epicuticular wax after exposing wax tubules to the equivalent of 1000 years of ozone at ambient concentrations (20–100 ppb). The large proportion of deposition to non-stomatal surfaces points to the importance of relating plant response to ozone assimilated by foliage, not total deposition, when assessing ozone damage to vegetation. Zeller and Nikolov (2000) proposed an index for quantifying vegetation vulnerability to ozone injury called “Physiological Ozone Uptake Per Unit Leaf Area” (POUPULA): the ratio of the time-integrated canopy ozone uptake by plant stomata to the one-sided leaf area index (LAI) of the stand.

Wet surfaces vary in their ability to act as a sink for ozone. The low solubility of ozone in water suggests that wet surfaces should not be effective sinks. Wesely (1989) developed a model of deposition that reduces ozone flux to wet surfaces due to occlusion of stomatal pores by water. However, studies have shown that removal of ozone by wet vegetation ranges from small (Grantz et al., 1997) to substantial (Fuentes et al., 1992). The chemistry of the water on the surface may be a significant factor. Co-deposition of ozone and SO₂ increases the deposition of ozone because ozone oxidizes SO₂ in solution (Fuentes et al., 1994).

Nighttime ozone fluxes may be among the most difficult to characterize. Positive (away from the canopy), negative (into the canopy), and near-zero (Mikkelsen et al., 2000; Coe et al., 1995) ozone fluxes have been observed in forest systems at night. Dew often forms at night, wetting leaf surfaces and leading to ozone sink complications. It cannot be assumed that stomata close at night; therefore, separating ozone deposition into stomatal and non-stomatal components is non-trivial. Negative nighttime ozone fluxes could be attributed to either open stomata or wet surfaces. Furthermore, soil NO emissions react with and destroy ozone at night, creating yet another sink (Walton et al., 1997; Pearson et al., 1998), especially in forests with enhanced nitrogen deposition (Pilegaard et al., 1999) such as some parts of the Sierra Nevada. The observation of positive ozone fluxes at night can only be explained by advection (Zeller and Hehn, 1995). The degree to which these factors should be considered in models of ozone deposition depends on local environmental conditions.

2.4. Regional ozone deposition

On a regional scale, ozone concentration is influenced by factors that control the advection and turbulent transfer of ozone and its precursors to the area of interest (inputs) and out of the area (losses) and by deposition to the surface (losses). Controls on deposition are dependent on scale and the appropriate res-

olution of inputs and loss pathways. Inputs are controlled by climate, topography and local and upwind sources. Losses are controlled by characteristics of the surface and their interaction with environmental factors. Surface properties include abiotic factors such as surface area, soil type and characteristics, topography, aspect, surface wetness, movement of water across the landscape; and biotic factors such as vegetation type, biomass and structure (especially LAI), physiology, water stress, land use, functional groups including nitrogen fixers and C₄ vs. C₃ photosynthetic pathways (e.g., see Sellers et al., 1988; Running and Hunt, 1993; Schimel et al., 1993; Grantz et al., 1997; Mitic et al., 1997 Wesely and Hicks, 2000). Understanding the role of surface properties on controlling deposition may require some work at a smaller scale, but it is critical to modeling efforts (Schimel et al., 1993). Determining these characteristics may require a combination of ground-based measurements, geographic information systems, and remotely sensed data. Assessing techniques for stratification and extrapolation of surface ecological processes regulating gas exchange was the major thrust of the First International Satellite Land Surface Climatology Project (ISLSCP) Field Experiment (FIFE; Schimel et al., 1988; Sellers et al., 1988).

2.5. Ozone concentrations and meteorology

Because ozone deposition is a function of ozone concentration, ozone concentrations must be well characterized at the scale of interest to adequately model ozone deposition in the Sierra Nevada. Ozone concentrations are dependent on input and loss pathways: deposition to stomatal surfaces (uptake) and non-stomatal surfaces alters atmospheric concentrations, which then feed back to change deposition rates. Deposition models require meteorological input. Model needs must be matched to available data, both spatially and temporally. At the regional scale, it can be very difficult to capture the variability in meteorology across heterogeneous and mountainous terrain due to lack of input data and complex topography. Remote-sensing can provide certain meteorological parameters useful for modeling, such as incident radiation, soil and canopy temperature, albedo (Oregon Transect Ecosystem Research campaign, OTTER; Peterson and Waring, 1994), soil moisture (El Garouani et al., 2000; Huisman et al., 2001), and canopy water content (Ustin et al., 1998, 1999; Gamon et al., 1999; Serrano et al., 2000). Monitoring networks can also provide meteorological data input; however, the spatial resolution, quality and availability of such data varies. Where such data is missing, geographic information system (GIS) techniques (El Garouani et al., 2000; Coops and Waring, 2001) and models that interpolate regional climate from existing meteorological data must be used, such as the Mountain Microclimate Simulator (MT-CLIM) (Running et al., 1987; Glassy and Running, 1994).

The regional-scale modeling efforts in Europe and North America take advantage of the European Monitoring and Evaluation Program (EMEP), the Canadian Air and Precipitation Monitoring Network, and the Environmental Protection Agency's Clean Air Status and Trends Network (CASTNet). In the Sierra Nevada, meteorological stations and real-time ozone monitors are operated year-round at national park sites as a part of CASTNet and seasonally at sites for the California Air Resources Board (CARB), totaling eight sites for rural locations (Arbaugh and Bytnerowicz, Chapter 6, this volume). Other sites are monitored at various intervals as part of efforts by independent researchers. Linking these currently disparate data into a pan-Sierra meteorology/ozone database would greatly enhance ozone deposition modeling efforts. The passive ozone monitoring network of Arbaugh and Bytnerowicz (Chapter 6, this volume), which uses 80 passive samplers throughout the Sierra Nevada, is a positive step toward the kind of data that are needed to enable ozone uptake modeling. These networks measure 2-week averaged ozone concentrations.

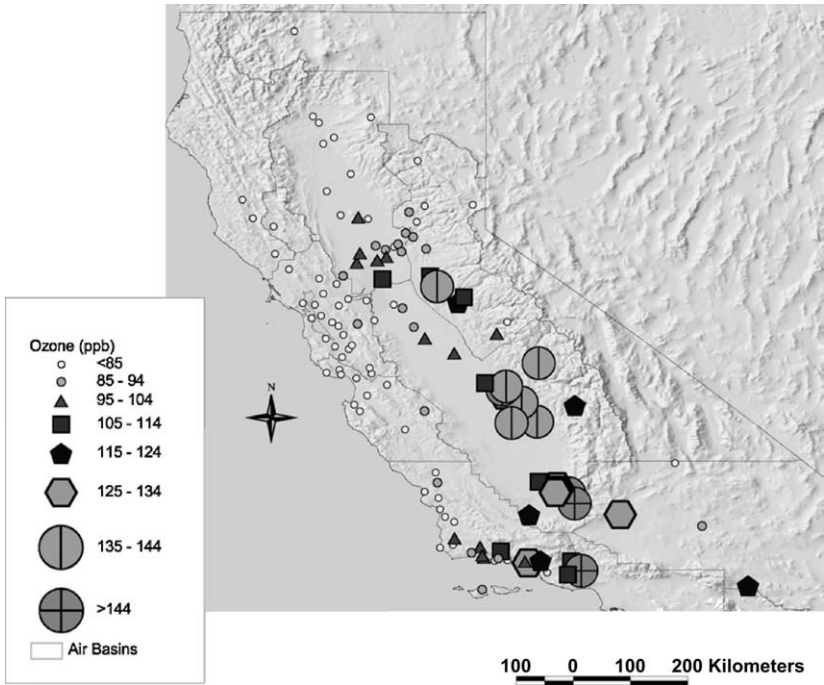


Figure 2. An example of spatial distribution of ozone concentrations during an ozone episode in the San Joaquin Valley (8/30/96). The symbols also show the locations of the routine measurement stations (Reprinted from CARB (2001) with permission).

Surface maps of ozone concentration can be produced from these data. Statistical means are used to create ozone concentration frequency histograms within that 2-week period; however, for ozone flux to be predicted accurately, *timing* of concentrations matters. When high concentrations co-occur with low conductances, little ozone may get into the foliage, as discussed earlier. Thus, passive monitors alone do not provide the kind of ozone concentration detail necessary for accurate flux estimates.

Aircraft and sonde measurements, and grid-based ozone transport modeling can provide landscape-scale ozone concentration measurements for specific periods, but these tend to be episodic. In California, a recent effort measured and modeled ozone concentrations, precursor emissions, and transport over the central portion of the state, including some sites on the western slope of the Sierra Nevada (Fig. 2, CARB, 2001). The purpose of the Central California Ozone Study (CCOS) was to collect data for testing transport models and therefore intensive instrumentation was focused on specific periods only. This type of periodic effort is well-suited for developing models of ozone surfaces, but does not provide the data needed for ozone deposition modeling over longer time scales.

3. Approaches to modeling ozone deposition

Scaling pollutant fluxes from the leaf to canopy level involves linking a leaf physio-chemical model with a canopy micrometeorological model. A physiological model is needed to predict stomatal conductance. A physio-chemical model is needed to assess leaf boundary layer resistances and gaseous uptake at the leaf surface and by water drops and films. A canopy micrometeorological model computes environmental variables which control leaf stomatal conductance. Micrometeorological models are also used to predict leaf wetness and turbulent mixing within and above the canopy. In the Sierra Nevada, however, correctly estimating the stomatal portion of canopy conductance may be one of the most important aspects of ozone deposition modeling; thus, we will describe these approaches in detail.

3.1. General leaf level considerations

The flux density of ozone to a dry leaf can be computed using a resistance-analog approach. The flux density to the leaf, F_l , is assumed to be proportional to the potential (the difference between concentrations in the atmosphere and at the leaf surface) and is inversely proportional to the sum of resistances that restrict this transfer, i.e.:

$$F_l = \frac{c(z) - c_i}{r_b + r_c} \quad (1)$$

where c is the pollutant concentration at height z , r_b is the leaf boundary layer resistance, and r_c is the surface resistance (lower-case letters are used to indicate leaf-level variables). Resistance algorithms for gaseous uptake by leaves have been used by O'Dell et al. (1977), Murphy et al. (1977), Baldocchi et al. (1987), Meyers and Paw U (1987), Baldocchi et al. (1988) and to extend computations of dry deposition to leaves to the canopy scale. The leaf surface resistance contains the parallel resistances exerted by the cuticle and the stomata. The internal concentration (c_i) and mesophyll resistance (r_m) for ozone transfer are often zero (O'Dell et al., 1977; Taylor and Tingey, 1982). Empirical relationships are usually used to specify the cuticle resistance. Stomatal resistance (and its inverse, conductance g_s) can be computed using a number of different methods.

3.2. Stomatal ozone uptake

Modeling stomatal ozone uptake is dependent on accurately characterizing stomatal conductance. A suite of models exists for computing stomatal conductance. In practice, some of these algorithms may be coupled to characterize the soil–plant–atmosphere continuum.

3.2.1. Jarvis algorithm

For the past decade, many climate and weather models (e.g., Sellers et al., 1988; Avissar and Pielke, 1991; Dickinson et al., 1991; Mascart, 1991) and gaseous deposition models (e.g., Baldocchi et al., 1987; Hicks and Matt, 1988; Wesely, 1989; Gao and Wesely, 1995; Meyers et al., 1998) have used the multiplicative and empirical model of Jarvis (1976) to calculate stomatal conductance of leaves, g_s . This stomatal conductance model has much appeal, for it considers the impact of light, temperature, humidity and soil moisture conditions on stomatal function and gaseous deposition. This model assumes that g_s is a multiplicative function of irradiance (I), temperature (T), humidity deficits (D), leaf or soil water potential stress (ψ) and carbon dioxide (C).

$$g_s = g(I)f(T)f(D)f(\psi)f(C) \cdots \quad (2)$$

One advantage of this approach is that it has the flexibility to include other factors, such as a function for stomatal response to ozone. Drawbacks include its lack of consideration of interactions among variables and problems with autocorrelation. The Jarvis algorithm has been shown to perform well in drought-stressed systems. It is the approach utilized by FOREST-BioGeoChemistry (BGC) (and related BIOME-BGC), a mechanistic model developed around stomatal response to water availability in the Mediterranean climate of the Pacific Northwest (Running, 1976, 1994; Running and Coughlan, 1988).

3.2.2. Ball–Berry algorithm

Advances in ecophysiological theory have led to an alternative approach for estimating stomatal conductance. In the late 1970s, Wong et al. (1979) reported that stomatal conductance was tightly coupled to leaf photosynthesis. They argued that stomata opened and closed to keep the ratio between intercellular and atmospheric CO₂ concentration nearly constant (about 0.7 for C₃ plants). Ball et al. (1987), Leuning (1990) and Collatz et al. (1991) drew upon those observations and their own laboratory experiments to develop a model that linked stomatal conductance to leaf net photosynthesis, relative humidity, and CO₂ concentration at the leaf surface (C_s).

$$g_s = \frac{m \cdot A \cdot rh}{C_s} + g_0 \quad (3)$$

The coefficient m is a dimensionless slope, rh is relative humidity at the leaf surface (decimal fraction), g_0 is the zero intercept, and A ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is leaf net photosynthesis. The Ball–Berry model has several appealing attributes. First, it provides an algorithm that relates stomatal conductance to ecophysiological and biochemical factors, such as leaf photosynthetic capacity and nutrition (Körner and Diemer, 1994; Schulze et al., 1994; Leuning et al., 1995) and ambient CO₂ concentration. This feature allows us to constrain the potential range of expected conductance values for a given species or plant functional type. Second, this stomatal conductance model requires fewer tuning parameters compared to the Jarvis approach. There is an accumulating body of evidence that m is a constrained parameter under ample soil moisture conditions; it centers around $10 \pm 20\%$ (Leuning, 1990; Collatz et al., 1991; Harley and Tenhunen, 1991; Reynolds et al., 1992; De Pury and Farquhar, 1997). However, under conditions of moderate to severe soil drought, m is observed to deviate significantly from a cardinal value (Sala and Tenhunen, 1996; Baldocchi, 1997). In areas such as the Sierra Nevada, where severe drought stress occurs often, modifications to the Ball–Berry algorithm could follow either the method used by Sala and Tenhunen (1996), which modifies m based on predawn water potential, or the method used by Berry et al. (1994), which modifies A based on drought-induced changes in V_{cmax} and J_{max} , the maximum rate of carboxylation ($\mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and the maximum rate of potential electron transfer ($\mu\text{mol electrons m}^{-2} \text{ s}^{-1}$), respectively. Researchers have argued that, in drought-stressed systems, stomatal conductance depends on water vapor saturation deficit and transpiration rate rather than relative humidity and transpiration (Aphalo and Jarvis, 1991; Mott and Parkhurst, 1991; Leuning, 1995; Monteith, 1995).

The Ball–Berry algorithm for estimating stomatal conductance is the method of choice in a growing family of mechanistic forest models: for example, the FOREst FLUX model, FORFLUX (Nikolov et al., 1995; Zeller

and Nikolov, 2000), the CANopy OAK model, CANOAK (Baldocchi, 1997), and the Advanced Canopy–Atmosphere–Soil Algorithm (ACASA) (Pyles and Weare, 2000).

3.2.3. Constant C_i/C_a ratio

The observation that the ratio between carbon uptake and water loss in C_3 plants such as trees is constant has been used in a family of models of stomatal regulation. Wong et al. (1979) performed a set of experiments showing that C_3 plants tend to keep the ratio C_i/C_a near 0.7; for C_4 plants near 0.4. Norman (1979) has used this concept to solve a set of equations to predict stomatal conductance on the basis of a simple leaf photosynthesis model:

$$\frac{A}{C_a} = g_s \left(1 - \frac{C_i}{C_a} \right) \quad (4)$$

Baldocchi (1994) performed independent model calculations using a coupled set of equations that predict leaf photosynthesis/respiration, diffusion through the leaf boundary layer, and the Ball–Berry model for g_s . Independently, these predict that C_i/C_a is close to 0.7 for a wide range of conditions. Only when stomata close due to lack of light, does the C_i/C_a ratio become elevated (Fig. 3). Field measurements of C_i/C_a over a range of soil moisture and VPD conditions show that this ratio can deviate from 0.7 as drought stress increases over the season in the Sierra Nevada (Fig. 4).

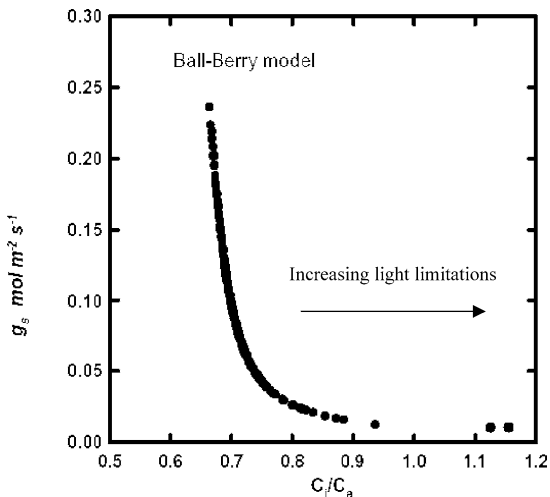


Figure 3. Computations of g_s as a function of C_i/C_a . Computations are based on a coupled stomatal conductance photosynthesis model using the Ball–Berry algorithm (Baldocchi, 1994).

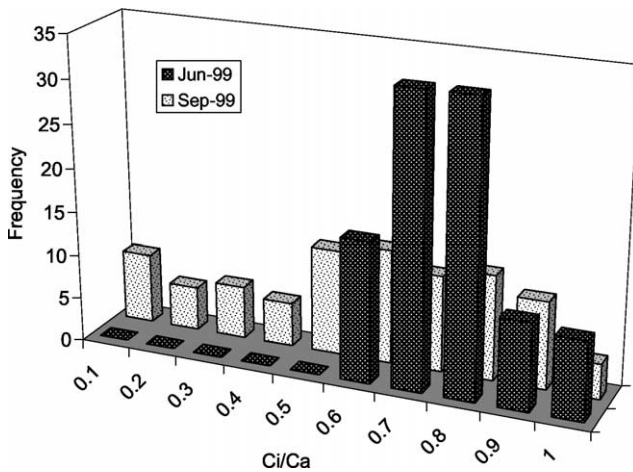


Figure 4. A frequency histogram showing the ratio C_i/C_a in the same *Pinus ponderosa* foliage measured at 2 h intervals over one day at the beginning of the summer when trees were not drought-stressed, and one day at the end of the summer when trees were drought-stressed, in Yosemite National Park, a low ozone-exposure site in the Sierra Nevada.

3.2.4. Abscisic acid

There is ample evidence that stomatal limitations on photosynthesis are associated with a hormonal signal (abscisic acid, ABA) sent from the roots (Gollan et al., 1986; Tardieu and Davies, 1993; Dreyer and Scuiller, 1996). Tardieu and Davies (1993) developed an algorithm that relates stomatal conductance to abscisic acid concentration in the xylem sap:

$$g_s = g_{s,\min} + \alpha \exp([ABA]\beta \exp(\delta\psi_l)) \quad (5)$$

The coefficient α represents the difference between $g_{s,\max}$ and $g_{s,\min}$, β and δ are fitted parameters, and ψ_l is the leaf water potential.

3.2.5. Water potential feedback loops

Several models use concepts of water flow through plants to assess the leaf water potential and use that value to constrain stomatal conductance as the soil dries (Zeller and Hehn, 1995; Williams et al., 1997). The flow of water through a plant, J_w , is modeled as a gradient in water potential between the soil and leaves and the sum of resistances along that pathway:

$$J_w = \frac{\psi_{\text{root}} - \psi_{\text{leaf}}}{R_{\text{plant}}} \quad (6)$$

With tall trees, the effect of gravitation potential on water transport is significant. In trees, one must also consider the capacitance due to water storage in the trunk. Using relations for transpiration and water flux, one can solve for stomatal conductance as a function of leaf water potential.

There are several important issues that still need to be addressed regarding the modeling of stomatal conductance under soil moisture deficits. One question relates to the impact of drought on photosynthesis. With application of the Ball–Berry equation, it is often assumed that the slope varies but that the components used to compute assimilation are unaffected by drought. But limitations on carbon assimilation accompanying soil drought can occur from non-stomatal or stomatal factors (Gollan et al., 1986; Cornic, 1994; Schulze et al., 1994; Dreyer and Scuiller, 1996). Non-stomatal limitation of photosynthesis can occur when the photochemical conversion efficiency of photosystem II decreases or when the mesophyll conductance to CO₂ diffusion decreases (Cornic and Massacci, 1996; Dickson and Tomlinson, 1996; Dreyer and Scuiller, 1996). Stomatal limitations to photosynthesis also restrict transpiration, leading to an increase in sensible heat transfer and leaf temperature. This change forces a negative feedback upon net photosynthesis because respiration rates increase exponentially in response to rising leaf temperatures (Harley and Tenhunen, 1991).

3.3. Canopy ozone deposition

The big-leaf model, adapted from evaporation studies, has been invoked to interpret deposition flux measurements (Wesely and Hicks, 1977; Fowler and Unsworth, 1979; Baldocchi et al., 1987; Hicks and Matt, 1988). The deposition velocity equals the inverse sum of the aerodynamic (R_a), quasi-laminar (R_b) and canopy resistances (R_c):

$$V_d = \frac{1}{R_a + R_b + R_c} \quad (7)$$

Most ozone deposition models utilize this resistance schema in some form. The aerodynamic resistance, R_a , is expressed as:

$$R_a = \frac{1}{\kappa u^*} \ln \frac{z-d}{z_0} - \psi_c \quad (8)$$

where $\kappa = 0.4$ is the von Kármán constant, u^* is the friction velocity, z is height, d is the zero-plane displacement, z_0 is the roughness parameter, and ψ_c is an atmospheric stability correction function. The quasi-laminar boundary layer resistance, R_b , is defined as:

$$R_b = \frac{1}{\kappa u^*} \ln \frac{z_0}{z_c} = \frac{\kappa B^{-1}}{\kappa u^*} (\text{Sc}/\text{Pr})^{2/3} \quad (9)$$

where z_c is the scalar roughness length, Sc is the Schmidt number, Pr is the Prandtl number, and B is the sub-layer Stanton number. The product κB^{-1} is often assumed to be constant for uniform canopies (Garratt, 1992), but can be much greater over rough, incomplete canopies (Wesely and Hicks, 1977) such as exist in xeric environments of the Sierra Nevada. Massman (1999) has recently evaluated algorithms for κB^{-1} and shown that it can vary with canopy structure, leaf area, and source-sink distribution. Numerous field studies show that R_c is the major controller of ozone deposition to a plant canopy (Galbally and Roy, 1980). The canopy resistance (R_c) is a function of the canopy stomatal resistance (R_{stom}), the canopy cuticle resistance ($R_{cuticle}$), and the soil resistance (R_{soil}). In turn, these resistances are affected by leaf area, stomatal physiology, soil pH, and the presence and chemistry of liquid drops and films. The stomatal, leaf surface (cuticle) and soil resistances act in parallel, causing R_c to be formulated as:

$$\frac{1}{R_c} = \frac{1}{R_{stom}} + \frac{1}{R_{soil}} + \frac{1}{R_{cuticle}} \quad (10)$$

The most recent generation of models have modified the big-leaf framework to better incorporate changes in environment and physio-chemical processes throughout the canopy, developing a multi-layer approach. Multi-layer models are used to mechanistically scale leaf level fluxes to the canopy level (Baldocchi et al., 1988; Meyers and Baldocchi, 1988; Meyers et al., 1998; Zeller and Nikolov, 2000). This improved approach reduces errors associated with using forcing variables at some decoupled location a distance away from the site of action, rather than using those in the local environment.

3.4. Regional ozone deposition

At larger spatial and temporal scales, the long-range transport of ozone and its precursors becomes increasingly important. Modeling ozone deposition at these scales requires the linking of a resistance-based deposition model with grid-based atmospheric transport models (Sellers et al., 1988; Running and Hunt, 1993; Schimel et al., 1993; Massman et al., 1994, 1995; Pederson et al., 1995; Emberson et al., 2000a, 2000b). Depending on surface characteristics and atmospheric turbulence, R_a and R_b may dominate, but it is more common for R_c to control deposition. R_a and R_b may be characterized in various ways, depending on the availability of driving variables. Massman et al. (1994) and Padro et al. (1994) evaluated different formulations of R_a , R_b and their associated stability functions using data from the California ozone deposition experiment (Pederson et al., 1995). R_c is linked to surface characteristics and meteorological variables which drive deposition within each grid cell. In general, grid-based transport models use independent deposition velocities for

each grid cell (Marr et al., 2002), or subdivide grid-cells based on land cover and derive independent deposition velocities for each land-cover type. These are applied as land-cover-weighted net deposition rates to the entire grid cell (Simpson et al., 2001).

One key concern when scaling up ozone deposition in the Sierra Nevada is the method for compositing ozone concentration data over time. Simple arithmetic averages will not work. As discussed above, timing of ozone concentration peaks may be decoupled from peak stomatal conductance, diurnally and seasonally (Fig. 1). Diurnal patterns of ozone concentration and conductance must be preserved for accurate scaling of ozone flux.

4. Case studies of ozone deposition modeling: Potential approaches for the Sierra Nevada

We review some current ozone deposition modeling efforts with a critical eye toward those approaches that might be applicable to the Sierra Nevada. One of the most distinguishing characteristics of ozone uptake in the Sierra Nevada is the strong limitation imposed on conductance by drought during the summer months; thus, ozone uptake is moisture-limited not light-limited (Bauer et al., 2000; Panek and Goldstein, 2001; Panek et al., 2002). Therefore, perhaps the most important need for modeling ozone uptake adequately is to correctly model stomatal conductance response to soil moisture, VPD, and hydraulic pathways.

4.1. H2O-TRANS to BIOME-BGC

Although not an ozone deposition model, the evolution from the leaf-level H2O-TRANS in 1976 to the region-level BIOME-BGC includes insights into many of the difficult issues of scaling from the leaf-level to the region (Running, 1976, 1980, 1984a; Running and Coughlan, 1988; Running and Hunt, 1993). H2O-TRANS was designed to model transpiration in a single leaf, particularly the influence of drought stress on diurnal stomatal conductance in the Mediterranean climate of the Pacific Northwest, a climate with stomatal limitations very similar to the Sierra Nevada. Stomatal conductance is modeled following the method of Jarvis (Jarvis, 1976; Jarvis and Morison, 1981). In scaling up to a tree, the predictability of daily transpiration rates allowed for dropping much of the internal flow dynamics, the generalization to a daily timestep, and the development of DAYTRANS, which addresses the seasonal hydrologic balance of a tree (Running, 1984b; Running and Hunt, 1993). Questions regarding water-use efficiency and net primary production in forest ecosystems drove the development towards FOREST-BGC which scales

up to include forest stand carbon cycling, allocation, litterfall, respiration, decomposition, growth, and later the nitrogen cycle. An annual time-step was included. To scale meteorology to the landscape, FOREST-BGC was coupled with MT-CLIM, to interpolate site-specific values from existing meteorology (Running et al., 1987; Glassy and Running, 1994). Scaling from forests to biomes (BIOME-BGC) required the linking of the model to remotely-sensed drivers, especially leaf area index, canopy chemistry, net primary productivity, radiation, albedo, and temperature (Goward et al., 1985; Peterson et al., 1987; Running et al., 1989; Spanner et al., 1990; Peterson and Waring, 1994).

Model validation has required the use of remotely sensed, ground-based, and tower measurements (Running et al., 1989, 1999; Running, 1990; Running and Hunt, 1993; Peterson and Waring, 1994; Kimball et al., 1997; Cienciala et al., 1998). FOREST-BGC has been tested in a number of different ecosystems, including a steep climatic gradient in Oregon, a boreal forest in Canada (Boreal Ecosystem–Atmosphere Study, BOREAS; Sellers et al., 1997) and a boreal forest in Sweden (Northern Hemisphere Climate-Processes Land-Surface Experiment, NOPEX; Lundin and Halldin, 1994; Cienciala et al., 1998). With regard to conductance, some tuning with hydrologic variables such as predawn water potential, was required to fit the model to observed conductances in Oregon (Running, 1994). In Sweden, the scalar function relating conductance and VPD was changed and a function was added that reduced conductance when the leaf surface was wet (Cienciala et al., 1998). With modifications, modeled conductance values showed generally good agreement with measured data (Fig. 5). Model overestimates were a result of wet days with low evaporative demand.

The diurnal dynamics in stomatal conductance are critical to accurately estimating ozone uptake in the Sierra Nevada, but were lost in scaling up the timestep to mean daily gas exchange and conductance in the BGC family of models. If the BGC family of models made explicit the diurnal patterns in stomatal conductance and coupled them with measured diurnal patterns in ozone concentrations, the model would be a great tool for predicting stomatal ozone uptake.

4.2. The Pan-European approach

Emberson et al. (2000a, 2000b), Simpson et al. (2001) and Tuovinen et al. (2001) developed an approach to estimate regional-scale ozone uptake across Europe that explicitly incorporates the stomatal component of ozone flux. Their approach makes use of three existing pan-European datasets: European Monitoring and Evaluation Program (EMEP) grid-based model estimates of boundary layer ozone concentrations at a 50×50 km spatial resolution (Jonson et al., 1999), Norwegian Meteorological Institute climate data, and land

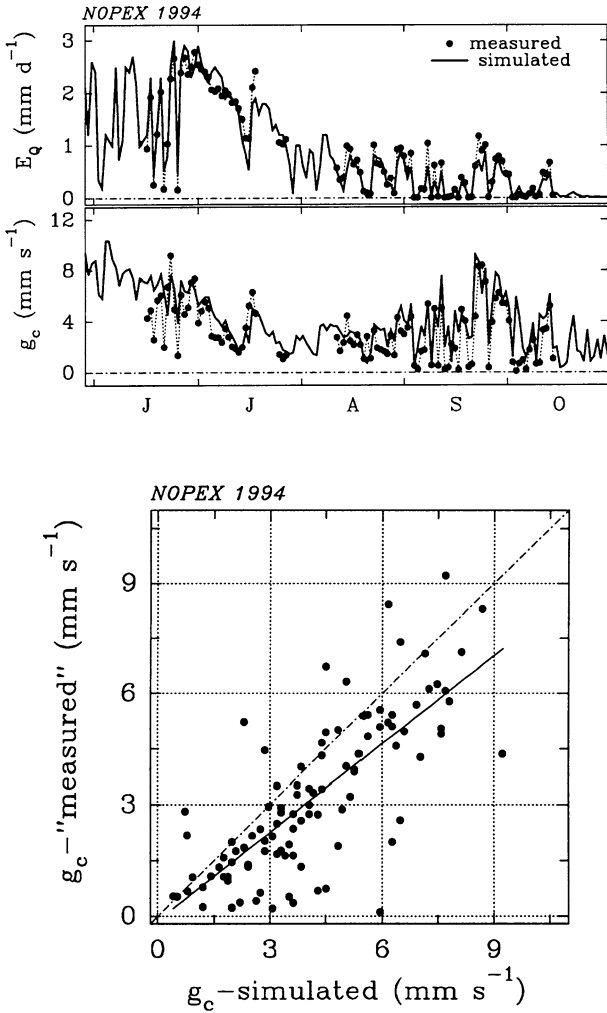


Figure 5. Comparison of measured NOPEX data and FOREST-BGC modeled canopy conductance (g_c) and canopy transpiration (E_q) values (Cienciala et al., 1998). Top: Temporal dynamics over the 1994 growing season. Bottom: The dashed line shows the 1 : 1 relationship, and the solid line is the regression. $R^2 = 0.59$, slope of regression = 0.79, $P < 0.001$. Reprinted with permission from the publisher.

cover and soil type maps assembled at the Stockholm Environmental Institute (SEI). Their deposition model successfully estimates ozone uptake across steep climatic gradients, including the Mediterranean region most similar to California (Figs. 6, 7).

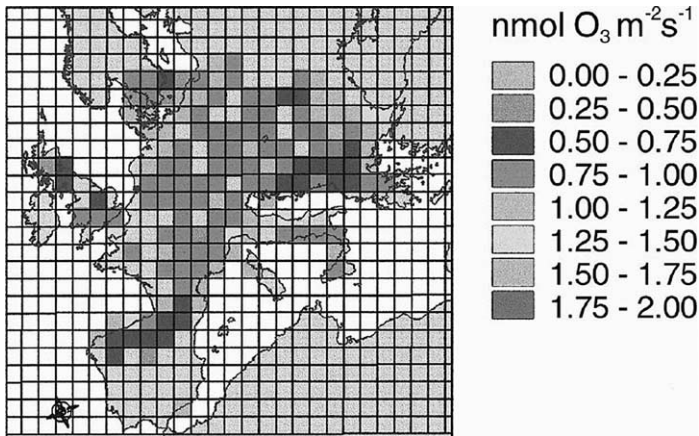


Figure 6. Mean monthly stomatal ozone flux ($\text{nmol m}^{-2} \text{s}^{-1}$) to *Fagus sylvatica* in Europe in June 1994 (Emberson et al., 2000a; reprinted with permission from the publisher).

The model evaluates R_a and R_b using the standard resistance formulations. R_c is calculated as a function of LAI-weighted stomatal resistance, area-weighted surface resistance (cuticular and other plant surfaces), the in-canopy resistance, and the ground-surface resistance. The approach differs from other existing methods by using a detailed stomatal uptake model. A multiplicative Jarvis-type algorithm is used to modify g_{\max} based on literature-derived parameters describing species-specific phenology and response to light, temperature, VPD, and soil moisture. This conductance value is incorporated into a big-leaf resistance model. Using this scheme allows the distinction between stomatal and non-stomatal components of deposition (Emberson et al., 2001). Their deposition model subdivides grid-cells based on land cover and derives independent deposition velocities for each land-cover type. These are applied as land-cover-weighted net deposition rates to the entire grid cell (Simpson et al., 2001). The land-cover-specific stomatal component of ozone flux is parameterized for 14 different classes of land cover by identifying species with similar aerodynamic and stomatal conductance characteristics (Emberson et al., 2001).

They found that the factors most important in limiting ozone uptake were VPD, soil moisture deficits (especially in the Mediterranean region), and phenology (Emberson et al., 2000a). Their approach might be used in the Sierra Nevada, as empirical relationships between stomatal conductance and environmental parameters exist for a range of species here (Helms, 1972; Patterson and Rundel, 1990; Grulke, 1999; Panek and Goldstein, 2001).

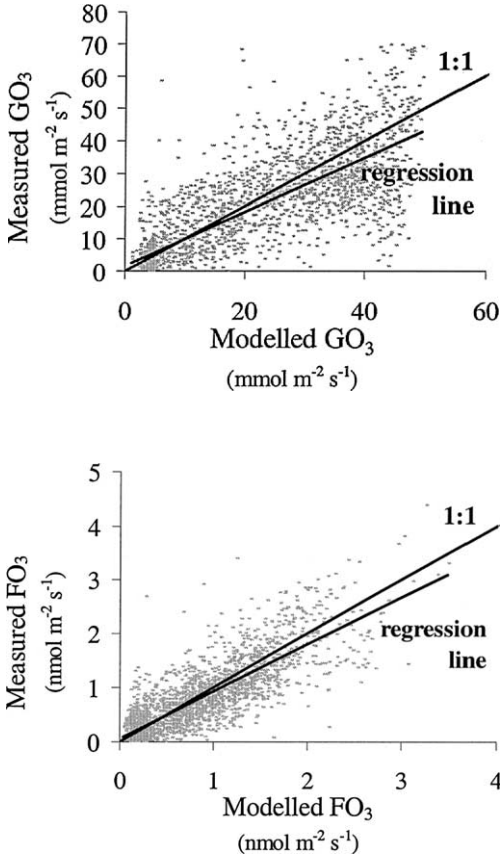


Figure 7. Comparison between measured and modeled stomatal conductance to ozone (GO₃, mmol m⁻² s⁻¹) and stomatal ozone flux (FO₃, nmol m⁻² s⁻¹) for 1989 and 1990. Measured GO₃ = 0.8319 × Modeled GO₃ + 1.5882, R² = 0.66; Measured FO₃ = 0.8929 × Modeled FO₃ + 0.0269, R² = 0.72 (Emberson et al., 2000b; reprinted with permission from the publisher).

4.3. FORFLUX

FORFLUX is a multi-layer biogeochemical model that couples a leaf-level physiology module (LEAFC3, Nikolov et al., 1995), a canopy flux module, a detailed soil process module, and a snow-pack module (Nikolov, 1997a, 1997b; Zeller and Nikolov, 2000). FORFLUX is novel in that both hormonal and hydraulic root signaling are incorporated into the calculation of stomatal conductance. The model links the Ball–Berry algorithm for stomatal conductance with an algorithm based on equations by Tardieu and Davies (1993) to

compute a root signal as a function of root water potential and ABA concentration. This signal, expressed as a multiplier between 0 and 1, is then used to reduce the parameter m in the Ball–Berry stomatal model. This is a means by which the Ball–Berry approach to estimating conductance can be made more responsive to soil moisture stress. Soil moisture dynamics are explicitly simulated by the soil module, which follows heat and water flow with a physically based stochastic algorithm.

The model runs on an hourly timestep, and thus captures the diurnal dynamics of stomatal conductance in relation to ozone concentration. This feature, as well as the detailed treatment of soil moisture, and the sensitivity of stomatal conductance to moisture, make the model well-equipped to characterize ozone fluxes in drought-stressed systems like the Sierra Nevada. Ozone deposition is explicitly simulated to both stomatal and non-stomatal surfaces, which makes it a good tool for interpreting eddy covariance flux measurements.

LEAFC3 was tested in *Picea engelmannii*. Modeled leaf-level stomatal conductance was compared against leaf-level cuvette measurements, with a resulting R^2 of 0.56 and slope of 1 (Nikolov et al., 1995). FORFLUX was tested in a subalpine ecosystem dominated by *Picea engelmannii* and *Abies lasiocarpa* in southern Wyoming. Modeled canopy-scale ozone flux

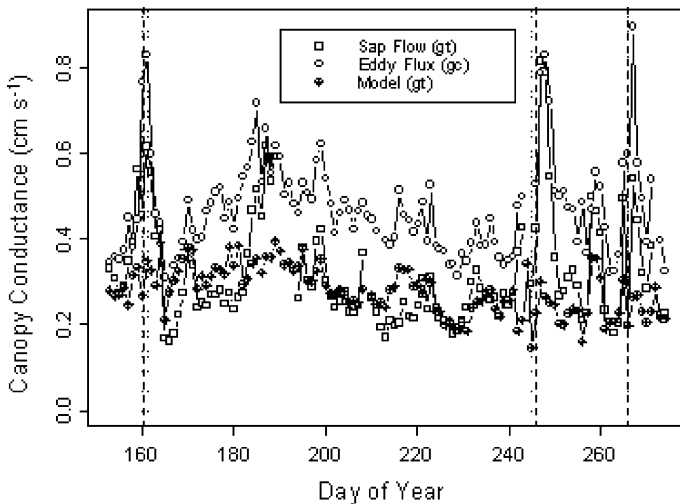


Figure 8. Daytime mean canopy conductance (cm s^{-1}) in a Sierra Nevada *Pinus ponderosa* stand, measured by sap flow and eddy flux, compared to output from FORFLUX (note: model and sap flow include only stomatal deposition elements). Rain events are indicated by vertical dashed lines (Kurpius, 2001, reprinted with permission from the author).

was compared to flux measured by eddy correlation over a 9-day period in early August 1996 (Zeller and Nikolov, 2000). The model successfully tracked diurnal ozone flux cycles; however, occasional positive fluxes demonstrated the need to account for advection of ozone in measured fluxes. The regression between measured and modeled ozone flux resulted in an $R^2 = 0.54$ and a slope of 0.64. The model underestimated peak excursions of ozone flux. The model has been used in the Sierra Nevada. It was applied in a *Pinus ponderosa* plantation at 1300 m elevation to estimate stomatal conductance to ozone over a 120-day period. Although the magnitude of the modeled conductance was similar to conductance derived from sapflow measurements, peak excursions were underestimated (Fig. 8; Kurpius, 2001).

5. Future directions for modeling in the Sierra Nevada

Models, alone and in combination with eddy covariance measurements and remote-sensing techniques, offer the most promising approach for estimating ozone uptake across large landscapes such as the Sierra Nevada. There exist significant challenges to accomplishing this; however, models will become more accurate with time as these challenges are addressed. Several important questions facing the Sierra Nevada can be addressed only through models. Thus, the development of modeling approaches is critical.

There is significant evidence of ozone injury in *Pinus ponderosa* forests across the Sierra Nevada. To date, most of this injury has been attributed to ambient ozone concentrations, with scant data on whether ozone is getting into the vegetation (Miller et al., 1998; Arbaugh et al., 1998). Only recently has ozone uptake been measured in the Sierra Nevada (Bauer et al., 2000; Panek and Goldstein, 2001) with an eye toward revisiting relationships between ozone and forest injury. There is evidence that the ozone injury varies spatially in the Sierra Nevada. It is not known whether the spatial variation in environmental factors and their potential to influence stomatal conductance and ozone uptake are responsible. For example, groundwater is distributed heterogeneously across the landscape in the Sierra Nevada. Rainfall varies with elevation, latitude, and topography. All of these affect soil moisture, which controls stomatal conductance and thus ozone uptake. Models are the only way to move beyond concentration-based vegetation exposure indices to estimates of ozone exposure based on ozone uptake. Significant progress is being made in Europe towards replacing or modifying AOT40 with modeled uptake estimates in a regulatory framework (Emberson et al., 2000a, 2000b, 2001; Simpson et al., 2001; Sofiev and Tuovinen, 2001; Tuovinen et al., 2001). Separating ozone

deposition into stomatal and non-stomatal fractions at the regional scale can only be done with models and is essential to estimating ozone impact on vegetation.

Models can be used to move beyond site-based assessments of ozone deposition to characterize the spatial patterns of ozone uptake at the regional scale and over time. One application with great promise is the linkage of spatially-explicit, modeled ozone uptake data with remotely-sensed spectral reflectance data showing chlorotic mottle or other biochemical signatures related to ozone damage at the landscape scale (Kraft et al., 1996). Maps of ozone uptake would provide insight into the extent of ozone exposure in different parts of the landscape, identify potentially vulnerable forest populations, and point to areas where damage at the scale of the individual trees or changes in growth and population dynamics would be expected. Areas with high ozone uptake rates may be susceptible to other stresses such as pathogens or fire. These areas may become hot-spots, acting as conduits of stress to otherwise healthy forest regions.

Once modeling tools exist that allow the analysis of landscape-scale patterns, changes over time can be monitored. This is especially significant given climate change scenarios for the Sierra Nevada. Most climate predictions for California and the Pacific Northwest indicate that both temperature and precipitation will increase (Field et al., 1999; Leung and Ghan, 1999; Mote et al., 2004); however, models differ in the seasonal timing and magnitude of these changes (Mote et al., 2004). In general, increases in precipitation are forecast to occur in the winter and spring months, when soils are already near or at saturation. Increased temperatures are predicted to diminish the snowpack, and despite the increased precipitation, this may lead to drier summers because the snowpack currently stores water and releases it throughout the early summer. A reduced snowpack will lead to reduced runoff and lower soil moisture. If summers become drier, then forests will remain dormant longer and ozone uptake will decrease. Forests may be protected from ozone stress by drought, but carbon limitation may occur during the summer. However, if summers become wetter, as predicted by some climate models (Mote et al., 2004), then uptake will increase, leading to increased ozone exposure, but greater carbon assimilation as well. Finally, warmer temperatures may increase wintertime ozone uptake due to increased stomatal conductance of non-deciduous vegetation during this season. High uncertainty accompanies these predictions, however. Because it is unclear which scenarios are likely to occur, it is all the more important to investigate these changes over time. Currently, models are the best available means of monitoring climate changes and assessing the impact on ozone production and deposition at the regional level.

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