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Comparing simple respiration models for eddy flux and dynamic chamber data

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Abstract

Selection of an appropriate model for respiration (R) is important for accurate gap-filling of CO_2 flux data, and for partitioning measurements of net ecosystem exchange (NEE) to respiration and gross ecosystem exchange (GEE). Using cross-validation methods and a version of Akaike's Information Criterion (AIC), we evaluate a wide range of simple respiration models with the objective of quantifying the implications of selecting a particular model. We fit the models to eddy covariance measurements of whole-ecosystem respiration (R_{eco}) from three different ecosystem types (a coniferous forest, a deciduous forest, and a grassland), as well as soil respiration data from one of these sites. The well-known Q_{10} model, whether driven by air or soil temperature, performed poorly compared to other models, as did the Lloyd and Taylor model when used with two of the parameters constrained to previously published values and only the scale parameter being fit. The continued use of these models is discouraged. However, a variant of the Q_{10} model, in which the temperature sensitivity of respiration varied seasonally, performed reasonably well, as did the unconstrained three-parameter Lloyd and Taylor model. Highly parameterized neural network models, using additional covariates, generally provided the best fits to the data, but appeared not to perform well when making predictions outside the domain used for parameterization, and should thus be avoided when large gaps must be filled. For each data set, the annual sum of modeled respiration (annual ΣR) was positively correlated with model goodness-of-fit, implying that poor model selection may inject a systematic bias into gap-filled estimates of annual ΣR.

Keywords: Absolute deviations regression; Akaike's information criterion (AIC); AmeriFlux; Cross-validation; Eddy covariance; Maximum likelihood; Model selection criteria; Respiration; Uncertainty

1. Introduction

Models are used in conjunction with measurements of surface-atmosphere CO_2 fluxes (F_{CO_2}) for a variety of reasons. These include: (1) filling gaps in the eddy

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covariance flux record (Falge et al., 2001); (2) estimating annual sums of the components of the net flux, such as total ecosystem respiration (R_{eco}) or gross ecosystem exchange (GEE) (Reichstein et al., 2005; Richardson and Hollinger, 2005; Hagen et al., 2006); (3) extracting physiological parameters from the flux data (Van Wijk and Bouten, 2002; Braswell et al., 2005; Hollinger and Richardson, 2005). Typically, these models are relatively simple functions of only a few independent variables and several parameters. Here we evaluate a range of simple respiration models using objective model selection criteria, and we investigate the implications of selecting a particular model.

The nocturnal flux measured above the canopy by eddy covariance is generally assumed to represent R_{eco}, and thus includes soil respiration (both heterotrophic respiration and root respiration) as well as various sources of above ground respiration (e.g., leaf, branch and stem respiration) (Davidson et al., 2006b). R_{eco} and its components have been modeled using a variety of approaches (e.g., Lloyd and Taylor, 1994; see also Morgenstern et al., 2004). In simple respiration models, the respiratory flux generally scales as a function of temperature (although the functional form of this relationship varies among models), representing the dominant role of reaction kinetics, possibly modulated by secondary environmental factors, such as soil water content. Most of these models lack a strict theoretical basis (cf. the Farquhar et al., 1980, photosynthesis model). This can be attributed to the fact that we still have a very poor mechanistic understanding of the relationships between environmental factors and R_{eco}, and between carbon allocation and substrate availability for respiration (Davidson et al., 2006a). A complicating factor is that soil and ecosystem respiration represent the aggregate respiratory flux from a diverse (and changing) array of organisms, each of which may be subject to somewhat different environmental conditions or limiting factors.

Previous studies have compared a number of respiration models using data from individual sites (Janssens et al., 2003; Del Grosso et al., 2005; Richardson and Hollinger, 2005) or even multiple sites (Falge et al., 2001), but to date no single synthesis has compared a wide range of simple models across different ecosystem types and measurement techniques, as we do here. Our objective is to determine which models give the best fit, and to assess the effects (in terms of model predictions) of choosing a particular model. Our emphasis is on model selection rather than hypothesis testing. Cross-validation and an information theoretic criterion are used for objective model selection, and models are ranked accordingly. We use the modeled annual sum of respiration ("annual ΣR") as a quantitative, but subjective, means by which to evaluate differences in model predictions (e.g., Hagen et al., 2006), since annual sums of fluxes are of particular interest to the community. We investigate whether rankings for models that simulate R_{eco} are consistent across three different ecosystems: coniferous forest, deciduous forest, and grassland, using nocturnal data from the Howland, Harvard Forest, and Lethbridge AmeriFlux sites. In addition to data from the main eddy covariance tower at Howland ("Howland-Main"), we also use data from a below-canopy eddy covariance system ("Howland-Subcanopy") and an array of automated soil respiration chambers ("Howland-Autochamber") at this site to investigate whether model rankings for R_{soil} are similar to those for R_{eco}.

2. Models, data and methods

2.1. Respiration models

The models we evaluate were selected from the literature and are listed in Table 1 (note that although the parameters are denoted $\theta_1, \theta_2, \ldots, \theta_n$ for each model, the optimal parameter values differ among models). These models are all simple, in that they contain (at most) a single static carbon pool, have no feedbacks, and are driven by bulk measurements of the overall ecosystem state. For example, soil temperature is typically used as a driving variable, although it may not accurately reflect the thermal state of various respiring components within the system (e.g., canopy temperature versus litter temperature versus O- and A-horizon temperature; Hollinger et al., 1994; Van Dijk and Dolman, 2004; Reichstein et al., 2005).

Respiration is controlled by both biological and physical factors. Work by Arrhenius and van't Hoff in the late-19th century on the temperature dependence of chemical reactions gave rise to notions of a relationship between temperature and respiration (see review by Lloyd and Taylor, 1994). Either a linear (model A in Table 1) or higher-order polynomial (model B) model would suffice as a simple, if naïve, representation of this relationship (at least over a limited range), but the Arrhenius equation (model C) more accurately describes many chemical systems. van't Hoff's Q_{10} model (model D), which gives an exponential relationship between respiration and temperature, has been widely used in many branches of biology. However, it assumes fixed temperature sensitivity, and predicts that respiration increases at a steady relative rate, and