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Short communication

A novel approach to combine response functions in ecological process modelling

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ABSTRACT

A novel approach to combining response functions, e.g., temperature and soil moisture dependency, is presented. This approach is in analogy of resistances connected in parallel and mathematically to the inverse function of the sum of reciprocal response functions. The approach presented is applicable for a wide range of response functions, and demonstrate better performance as the multiplicative approach if the limiting factor dominates the process rate more than the other factors. It was applied to a gross nitrification data set acquired from beech litter samples in the laboratory using the barometric process separation (BaPS) method. Compared with the minimum and the multiplicative approaches, the best fit was achieved with the novel approach, using the Residual Sum of Squares and r^2 values as indicators. Additionally, two examples from the literature were presented to demonstrate the potential and benefits of the approach, which is a good alternative combining two or more response functions.

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1. Introduction

Processes in ecosystems such as transformation processes or transport often depend upon more than one factor; hence to simulate processes in ecosystems by mathematical modelling, an accurate combination of the specific response function is necessary. Due to the complexity of interactions between environmental factors, primarily the influence of each factor was investigated discretely and the multiplicative approach was used to combine the response functions.

A handful of functions are available to describe the dependency of processes from temperature and soil moisture

(Rodrigo et al., 1997; Antonopoulos, 1999). Nevertheless, approaches to combine two or more response functions are scarce. Current models use the multiplicative approach (Rodrigo et al., 1997; Antonopoulos, 1999; Paul et al., 2003):

$$F = k_{\max} f(x) f(y) \quad (1)$$

where F is the transformation, k_{\max} the rate under optimal environmental conditions, and $f(x)$ and $f(y)$ are the response functions of environmental factors, normally scaled between 0 and 1. This approach does not consider any interaction between moisture and temperature effects. A way to account

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for an interaction between temperature and moisture has been considered in the minimum approach, based on the Liebig law (Liebig, 1840), in which the limiting factor dominates the process:

$$F = k_{\max} \min(f(x), f(y)) \quad (2)$$

Unfortunately, the discontinuous differentiability causes problems in the numerical solution of the differential equation and restricts possible applications.

In this paper an approach is presented which is based on the description of parallel connected resistances and also combines the idea of Liebig with the advantage of continuous differentiability. The approach is tested against three data sets, first at a gross nitrification data set from beech litter. Nitrification is an important process of the soil N-cycle, since nitrification controls the allocation between the less mobile NH_4^+ and the more mobile NO_3^- (Abbasi and Adams, 1998). Another two examples are presented: one is plant transpiration which depends upon salinity and water stress (Homaee et al., 2002) and the other is malondialdehyde content in plants, an indicator of free radical damage to cell membranes under stress conditions whereby the content depends upon temperature and soil moisture (Xu and Zhou, 2006). Water Stress and soil salinity are two important factors for reduced yield in semiarid regions. Because soil water pressure and osmotic potential are additive in reducing the free energy of soil water, it was assumed that their effect on transpiration is also additive (Meiri, 1984).

If plants are subjected to adverse conditions such as high temperature, drought, or salinity stresses, the scavenging system may lose its function, resulting in oxidative damage of cell membranes. Malondialdehyde (MDA) is a product of peroxidation of unsaturated fatty acids in phospholipids and it is a marker for cell membrane damage (Xu and Zhou, 2006).

2. Materials and methods

2.1. Measurements of gross nitrification

Litter samples were collected in October 2004 from a mature beech-tree stand at the “Dübener Heide”, located 30 km north of Leipzig, Germany. The typical soil type in this region is an Eutric Cambisol (FAO system). The beech stand has a temperate continental climate with cool winters and hot summers, an annual precipitation value of 539 mm, and a mean annual temperature of 9.3 °C.

The litter was homogenized carefully by hand and filled according to the natural bulk density in seven cylinders (100 ml each). Measurements of gross nitrification (duplicated) were carried out using the barometric process separation (BaPS) technology (UMS, Germany) (Ingwersen et al., 1999). The litter was equilibrated at each temperature (1 °C, 10 °C, 20 °C, 30 °C and 35 °C) for different moisture steps (130%, 180%, 250%, 300% 440% $\text{g H}_2\text{O g}^{-1}$ dry litter) for 36 h before measurements. Litter pH-values were measured in 0.01 M CaCl_2 (litter: CaCl_2 1:5) with a pH-Meter (Hanna Instruments Inc., USA). Litter moisture was determined gravimetrically after each moisture step and by a dried sub-sample at the end of the experiment. The samples

were dried (48 h at 65 °C) and milled before analysis of total N content (N_t) and organic carbon (C_{org}) by an element-analyser (Elementar, Germany).

2.2. Model approach

In most concepts, response functions are combined by multiplication (e.g., N-turnover in soils: Rodrigo et al., 1997). The presented approach is the inverse function of the sum of reciprocal response functions. The mathematical formula is:

$$g(x_1, \dots, x_n) = \frac{n}{\sum_{i=1}^n 1/f(x_i)} \quad (3)$$

with $g(x_1, \dots, x_n)$ is the response function; n the number of considered factors; $f(x_i)$ is the response function for one factor (e.g., temperature or moisture).

This approach can be expanded to three or more factors. For the evaluation of the applicability of the approach in ecological modeling, (1) a data set of gross nitrification at different soil temperatures and moisture conditions, (2) plant transpiration measurements under different water and salinity stress and (3) plant production of malondialdehyde by water and temperature stress were used.

2.3. Temperature and moisture response on gross nitrification

The influence of temperature on N-transformation processes has been investigated in numerous studies, and many papers and reviews disclosed the best relationship (e.g., Stark and Firestone, 1996; Kätterer et al., 1998; Dalias et al., 2001). Since the measured rate at 35 °C is lower than at 20 °C and 30 °C, the optimum function from O'Neill (Diekkruger et al., 1995) was used. This function is more suitable to characterising microbiological processes at high temperatures than the monotonically increasing Arrhenius function. The O'Neill function increases quasi-exponentially at lower temperatures and decreases at temperatures beyond the optimum:

$$f(T) = \left(\frac{T_{\max} - T}{T_{\max} - T_{\text{opt}}} \right)^a e^{a((T - T_{\text{opt}})/(T_{\max} - T_{\text{opt}}))} \quad (4)$$

with T is the soil temperature (°C); T_{\max} the maximum temperature of the O'Neill function (°C); T_{opt} the optimal temperature of the O'Neill function (°C); a is the shape parameter of the O'Neill function.

A variety of functions are presented for soil moisture as well (Paul et al., 2003). High soil water content often leads to decreasing turnover rates, due to the limitation of one or more reactants. The same interrelation was found in this study for the gross nitrification rate, which was decreasing at high moisture conditions. Therefore, an optimum function, first presented in Diekkruger et al. (1995), was used to describe the influence of soil moisture on the gross nitrification rate:

$$f(M) = \left(\frac{M}{M_{\text{opt}}} \right)^b e^{1 - (M/M_{\text{opt}})^b} \quad (5)$$

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