[Forest Ecology and Management 316 \(2014\) 3–8](http://dx.doi.org/10.1016/j.foreco.2013.07.054)

Contents lists available at [ScienceDirect](http://www.sciencedirect.com/science/journal/03781127)

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Review

Large-scale biogeochemical research with particular reference to forest ecosystems, an overview

iments. Both sources are essential.

ABSTRACT

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article info

Article history: Received 15 March 2013 Received in revised form 25 July 2013 Accepted 28 July 2013 Available online 6 October 2013

Keywords: Ecosystems Processes Methodology

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1. Introduction

Earth observation and global modeling have become increasingly important activities for analyzing anthropogenic impacts and future climate change [\(Peters et al., 2012; LeQuéré et al.,](#page--1-0) [2012\)](#page--1-0). However, models can only be predictive if they are based on understanding of the process at least at one level lower in resolution than the desired level prediction because robust scaling over time and space is only possible when conditions are not constrained within the range of available empirical relationships at the lower scale. In addition, global models should simplify reality in order to remain transparent. However, such simplifications should be based on a mechanistic understanding of the processes at lower scales or tied to earth observations. For example, if the carbon cycle of a region is reduced to a single number such as average carbon turnover in global models, it is important that this single number is based on knowledge about the underlying assumptions and processes at a refined scale ([Rödenbeck et al., 2009](#page--1-0)). The same restriction holds also for smaller scales. For example, the relationship between foliar N and net photosynthesis can be used to predict leaf-level photosynthesis if foliar N observations are available. However, the predictive value of such an empirical relation is limited if plants store nitrogen as nitrate, and not in photosynthetic protein. In this case the prediction of photosynthesis would fail ([Koch et al., 1988](#page--1-0)). Thus, most empirical relations are valid only within a limited range, and these limitations must be known to be of predictive value. This contribution summarizes experimental

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The following overview summarizes observational and experimental approaches to study plant and ecosystem processes, starting from physiological mechanisms up to continental carbon balances mainly based on Eurosiberian data. It is shown that different observational scales are needed to interpret and predict phenomena at various resolutions and that observational studies cannot replace controlled exper-

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and observational approaches of investigating plant and ecosystem processes and discusses their predictive value and limitations at various scales.

In addition to the scaling problem the verification of predictions presents an additional challenge. It has become common practice to use knowledge from 1 to 2 levels downward and upward for assessments at the scale of interest. For example, to produce data-derived estimates of biomass, inventory data of tree height, diameter, age and species are combined with remote sensing data and statistical methods (e.g. neural networks, [Papale and Valentini,](#page--1-0) [2003\)](#page--1-0) to produce spatial maps of biomass [\(Turner et al., 2007\)](#page--1-0). It is debatable, whether it would be statistically better not to use all available data for the assessment of a single parameter, but to split the information and make two or more estimates based on independent information (e.g. ground-based data versus satellite-based data). Even if a product results from multi-variant sources, it should be cross-checked by independent measurements. Thus, an additional focus of this article is to demonstrate how to reduce the uncertainty of predictions based on investigations in Europe ([Schulze et al., 2009](#page--1-0)), Siberia [\(Dolman et al., 2012](#page--1-0)) and Africa [\(Val](#page--1-0)[entini et al., 2013\)](#page--1-0).

2. Approaches of studying biogeochemical processes

2.1. Process studies of physiological mechanisms

Modeling the regulation of life becomes increasingly difficult at the molecular level, because there is more than one response; the regulative mechanisms may be stable, unstable or transient ([Begon](#page--1-0) [et al., 1990](#page--1-0)). Overyielding may be taken as one example for transient responses in successional communities [\(Roscher et al.,](#page--1-0) [2007\)](#page--1-0). This is a wide topic and in the present article I will not be able to discuss the molecular level (for details see [Schulze et al,](#page--1-0) [2005\)](#page--1-0).

A unique example of a physiological-based process model that was capable to express a physiological process by one mathematical equation is the photosynthesis model of [Farquhar et al.](#page--1-0) [\(1980\),](#page--1-0) which is based on enzyme activities. This model has become the basis for most global estimates of photosynthesis, even though the site specific relations between photosynthesis and limiting factors of species, light, nutrition and drought still need to be determined experimentally or by observations. The photosynthesis model is also not capable to predict $CO₂$ fluxes since $CO₂$ fixation is also regulated by stomata and until now it was not possible to describe stomatal conductance by equivalent equations as in the case of photosynthesis. In this context the response of stomata to air humidity has received major attention ([Lange et al., 1971](#page--1-0)) because it links the fluxes of $CO₂$, water vapor and energy. Yet, the phenomenon is not understood on the basis of cellular water flows in the epidermis [\(Nonami et al., 1990;](#page--1-0) [Schulze and Hall, 1982; Burkhardt, 2010\)](#page--1-0). Nevertheles, a model approach to describe the stomatal response to humidity was introduced by [Ball et al. \(1987\)](#page--1-0) and [Collatz et al. \(1991\)](#page--1-0) relating conductance to relative humidity and the mole fraction of $CO₂$ at the leaf surface, following the optimization theory of [Cowan](#page--1-0) [and Farquahr \(1977\)](#page--1-0), and by [Pieruschka et al. \(2010\)](#page--1-0) relating transpiration to the available energy. It remains open if the cellular regulation follows the flux related water potential ([Slatyer,](#page--1-0) [1967\)](#page--1-0) or the relative cell hydration ([Walter, 1931](#page--1-0)), or if it is controlled by aquaporins [\(Johansson et al., 2000](#page--1-0)) regulating cellular functioning. Thus, also the [Ball et al. \(1987\)](#page--1-0)-equation remains empirical, being valid for a certain range of conditions where for instance hormonal control does not cause a functional threshold ([Heilmeier et al. 2007](#page--1-0)).

2.2. Whole plant responses

The regulation of allocation remains an open area of research ([Stitt and Schulze, 1994\)](#page--1-0). Following cell division of the cambium in a woody tree, the future cell function is determined by plant hormones, and the uncertainties of water flow [\(Schweingruber](#page--1-0) [et al., 2012\)](#page--1-0). Until now, only the CAMBIUM-model of [Drew et al.](#page--1-0) [\(2010\)](#page--1-0) is capable of constructing xylem vessels on the basis of an interaction between irregular water-flow on the surface of cell initials and the response to cytokinin. Large vessels are formed at places where more water was transported on the micro-relief in the cambium. The CAMBIUM model is capable of explaining wood formation of Eucalyptus even in a drying cycle ([Drew et al., 2009\)](#page--1-0). The observation that vessel size is determined by water flows changes the independent and dependent variables in the pipe model that predicts leaf area from sap wood area [\(Shinozaki](#page--1-0) [et al., 1964\)](#page--1-0). However, wood formation is only part of an allocation scheme, and the partitioning of carbohydrates between roots, leaves, reserves and stems remains observational. [Schulze et al.](#page--1-0) [\(1983\)](#page--1-0) used a nitrogen-fixing herbaceous plant, Vigna unguiculata, to study carbohydrate partitioning in relation to whole plant water use, avoiding interactions with nutrition. In this case, a new leaf could only be produced if there was enough water to support the existing and the additional leaf. This model was not based on any water status parameter, but purely on an optimization theorem of water versus carbon fluxes based on process understanding of plant growth.

Allocation in trees is often modeled under the assumption that the ratios between leaves, stem and roots remain constant, within certain boundaries depending on species. Tree height would be the main parameter describing the effects of site specific growing conditions. Even though allometric functions describe total biomass as a function of height and diameter over a surprising large range of conditions ([Wirth et al., 2004\)](#page--1-0), these functions do not predict tree age, which would be important for carbon turnover.

2.3. Stand growth

Moving from the single plant to the plant population means/involves not only a change from a prescribed constant set of conditions of a laboratory to the field, but also additional uncertainty caused by neighbors of the same or different species ([Schulze](#page--1-0) [et al., 2005\)](#page--1-0).

Stand level processes have been described in numerous studies ([Burkhart and Tomé, 2012](#page--1-0)). One classic example is the selfthinning model ([Reineke, 1933\)](#page--1-0), which formalizes the observation that many small plants can survive on a given area of land, but, as soon as these plants grow taller, some die due to competitive interactions, and thus make sufficient space for the survivors. The negative exponential curve of basal area with increasing density [\(Luyssaert et al., 2011\)](#page--1-0) implies that the growth rate increases with standing biomass and decreasing density as long as the stand has a closed canopy. There is no age-related decline ([Luyssaert et al., 2008\)](#page--1-0) unless the stand collapses due to external forces, such as wind, fire, or disease. Forest management uses the narrow margin close to the self-thinning line for decisions on wood extraction [\(Luyssaert et al., 2011](#page--1-0)). Even though the self thinning rule may explain some aspects of the limiting line of stand volumes in a succession, it neither explains why the majority of stands remain far below the self thinning line ([Luyssaert](#page--1-0) [et al., 2011](#page--1-0)) nor significant differences in the slope parameters ([Gadow, 1986](#page--1-0)). Further process understanding at the level of plant individuals reveals that it is the risk of accidents and fungal attack [\(Holzwarth et al., 2012\)](#page--1-0) which determines the density of forest stands. Until now the self-thinning equation has not been verified for un-even and mixed stands.

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