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A simple $CO₂$ exchange model simulates the seasonal leaf area development of peatland sedges

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a r t i c l e i n f o

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A B S T R A C T

Sedges (Cyperaceae) are dominant plants in many northern wetlands and contribute to the carbon cycling in several ways. In order to more accurately estimate the carbon balance of a wetland it is essential to be able to simulate the temporal changes of the leaf area of the sedges. Our aim was to test the ability of a simple carbon dioxide $(CO₂)$ exchange model to predict the seasonal development of sedge leaf area index (LAI). The model simulates the development of sedge LAI that depends on carbon gain/loss in net photosynthesis, utilization of stored carbon in spring, and LAI decline due to senescence in late summer. The net photosynthesis model is driven by LAI, air temperature, water table depth and photosynthetically active radiation.We parameterized and validated the model with two years of observational LAI data from two boreal pristine peatland sites and included data points from both pristine and manipulated (drainage and warming) treatment plots. Model parameter values other than the timing of the start of senescence, LAI decline rate in senescence and size of carbon storage were independent of observational data. The model successfully simulated the seasonal course of LAI development and is thus an easy and adjustable tool for producing estimates of sedge LAI for other peatland sites. It can be adjusted to different sites although it cannot predict the exact LAI level of a site that is controlled by site characteristics. Its ability to simulate the interannual variation in this two-year dataset was inadequate so there is a need to test the model against longer time series of measured LAIs in order to validate models' capability to predict the interannual variability of LAI.

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1. Introduction

The leaf area of a plant canopy is often expressed as the ratio of leaf surface area to the ground area, leaf area index (LAI; m² m^{−2}). LAI drives canopy primary productivity [\(Bolstad](#page--1-0) et [al.,](#page--1-0) [2001;](#page--1-0) [Lindroth](#page--1-0) et [al.,](#page--1-0) [2008;](#page--1-0) [Street](#page--1-0) et [al.,](#page--1-0) [2007\)](#page--1-0) and transpiration rates ([Bucci](#page--1-0) et [al.,](#page--1-0) [2008\)](#page--1-0) and thus is an essential variable in various ecosystem models, including the large-scale biosphere models ([Euskirchen](#page--1-0) et [al.,](#page--1-0) [2009;](#page--1-0) [Reick](#page--1-0) et [al.,](#page--1-0) [2013;](#page--1-0) [Sitch](#page--1-0) et [al.,](#page--1-0) [2003\).](#page--1-0) [Ewert](#page--1-0)

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[\(2004\)](#page--1-0) argued that LAI is such an important factor in plant productivity models that it is impossible to make accurate predictions in regard to the effect of increasing atmospheric carbon dioxide $(CO₂)$ concentrations without improved LAI modeling. LAI also is a practical measure of biomass abundance because it can be determined using non-destructive methods, even using digital photography [\(Migliavacca](#page--1-0) et [al.,](#page--1-0) [2011;](#page--1-0) [Peichl](#page--1-0) et [al.,](#page--1-0) [2014\).](#page--1-0)

Sedges (Cyperaceae) play a key role in the greenhouse-gas balance of many northern wetlands, particularly in minerotrophic fens. Species from genera Carex and Eriophorum produce high levels of biomass especially in the aapa mire region of Europe and North-America. As a consequence of their deep rooting systems, which may extend over 2 meters in depth ([Saarinen,](#page--1-0) [1996\),](#page--1-0) sedges provide organic matter directly to the deeper anoxic peat layers where decomposition proceeds slowly and carbon thus accumulates as peat. [Laiho](#page--1-0) et [al.](#page--1-0) [\(2003\)](#page--1-0) estimated that 80% of the belowground litter in a boreal fen was from sedges so the root and rhizome mass of sedges are an important peat forming component in this ecosystem. Peat deposits in fens are dominated by sedge remnants while in the later bog phase of peatland development the peat is mainly composed of Sphagnum (e.g. [Kivinen](#page--1-0) [and](#page--1-0) [Pakarinen,](#page--1-0) [1981;](#page--1-0) [Mäkilä,](#page--1-0) [2008\).](#page--1-0) However, sedge litter has been found to decompose faster than Sphagnum litter ([Scheffer](#page--1-0) et [al.,](#page--1-0) [2001\)](#page--1-0) so its abundance directly affects the rate of heterotrophic respiration in a peatland. The presence of sedges has also been found to enhance methane (CH_4) production in peatlands as methanogenic microbes readily utilize sedge root exudates and other labile carbon substrates ([Joabsson](#page--1-0) [and](#page--1-0) [Christensen,](#page--1-0) [2001;](#page--1-0) [Waddington](#page--1-0) et [al.,](#page--1-0) [1996\)](#page--1-0) and sedges act as conduits transporting CH_4 into the atmosphere [\(Noyce](#page--1-0) et [al.,](#page--1-0) [2014;](#page--1-0) [Whiting](#page--1-0) [and](#page--1-0) [Chanton,](#page--1-0) [1992\).](#page--1-0)

Sedges are perennial plants and the maximum life span of C. rostrata shoots has been found to be as high as 6 years in northern Sweden [\(Solander,](#page--1-0) [1983\)](#page--1-0) and 2 years in a temperate site ([Bernard,](#page--1-0) [1990\).](#page--1-0) A considerable green sedge biomass may overwinter [\(Bernard,](#page--1-0) [1974;](#page--1-0) [Saarinen,](#page--1-0) [1998a\)](#page--1-0) and these living shoots commence photosynthesis and growth in spring as soon as the conditions are suitable. Stored nutrients and carbohydrates allow perennials to rapidly develop leaves in the early season ([Bernard,](#page--1-0) [1974;](#page--1-0) [Chapin](#page--1-0) et [al.,](#page--1-0) [1990;](#page--1-0) [Roseff](#page--1-0) [and](#page--1-0) [Bernard,](#page--1-0) [1979\)](#page--1-0) so that the belowground content of total non-structural carbohydrates, for example in C. lacustris, declined at the beginning of the summer but increased to a maximum by late October [\(Roseff](#page--1-0) and Bernard, [1979\).](#page--1-0) New shoots appear throughout the growing season but the highest emergence seems to occur in spring and, in some cases, again in the autumn [\(Bernard,](#page--1-0) [1974;](#page--1-0) [Saarinen,](#page--1-0) [1998a;](#page--1-0) [Solander,](#page--1-0) [1983\).](#page--1-0) [Saarinen](#page--1-0) [\(1998a\)](#page--1-0) found that the shoot mortality is highest in late autumn or winter but some mortality seems to occur throughout the growing season ([Bernard,](#page--1-0) [1974\).](#page--1-0) Despite the new growth in the autumn, leaf area generally peaks in mid-summer (late July–late August in northern hemisphere) and begins to decline thereafter ([Bernard](#page--1-0) [and](#page--1-0) [Hankinson,](#page--1-0) [1979;](#page--1-0) [Ratliff](#page--1-0) [and](#page--1-0) [Westfall,](#page--1-0) [1988;](#page--1-0) [Solander,](#page--1-0) [1983;](#page--1-0) [Wilson](#page--1-0) et [al.,](#page--1-0) [2007\).](#page--1-0) The green leaf area declines when the leaves gradually wither starting from the leaf tip; during the process the living biomass decreases although the shoots do not die.

Descriptions of sedge phenology, photosynthesis and seasonal development of leaf biomass or LAI are included in some peat-land models. [Griffis](#page--1-0) [and](#page--1-0) [Rouse](#page--1-0) (2001) presented a peatland $CO₂$ exchange model (net ecosystem exchange, NEE) that also included a model of sedge phenology and LAI development. The model has three alternative parameterizations for the phenology, the choice of which depends on the snowmelt timing and water level in early spring. The initial and the maximum LAI are predetermined for each case. The growth is controlled by photosynthesis rate, which in turn depends on irradiance and stomatal conductance, and autotrophic respiration, which is a fixed percentage of photosynthetic production, increasing with temperature. Senescence is triggered by drought stress or sub-freezing temperatures, after which the remaining leaf area decreases 1% per day. These parameterizations were based on the authors' personal observations on the studied wetland site. They concluded that the NEE modeling results are highly sensitive to the description of vegetation in the model.

Another peatland model PCARS [\(Frolking](#page--1-0) et [al.,](#page--1-0) [2002\)](#page--1-0) simulates the carbon fluxes of peatland vegetation as a part of peatland carbon balance. The model divides the vegetation into five classes, one of which is graminoids including sedges. Photosynthesis rate is calculated per unit of leaf mass depending on light, temperature and soil moisture, and autotrophic respiration depending on photosynthesis rate and temperature. The gained carbon is stored in the root carbon pool, to be used to grow the leaves. Leaf biomass development over the growing season is simulated by assuming a linear increase as a function of accumulating heat sum in the spring and

Fig. 1. Overview ofthe LAI model. Processes and factors thatincrease (+) or decrease (−) the leaf area.

a drop from maximum to minimum leaf biomass during one day in the fall, after −25 chilling degree days have accumulated. The maximum possible leaf biomass is prescribed but it is not necessarily reached if the carbon pool in the roots is too low. Hence, the net primary production (NPP) of one year may affect the maximum biomass of the following year. LAI is used in the model as a variable when calculating the light attenuation in the canopy but not in the photosynthesis models. McGill Wetland model (MWM; [St-](#page--1-0)Hilaire et [al.,](#page--1-0) [2010\)](#page--1-0) is based on PCARS and, for instance, the model of vegetation is similar to that in PCARS, except it has a different formulation of photosynthesis.

[Leadley](#page--1-0) [and](#page--1-0) [Reynolds](#page--1-0) [\(1992\)](#page--1-0) simulated the growth response of Eriophorum vaginatum (biomass) to light, temperature, season length, nitrogen availability and $CO₂$ concentration. Their model was used to produce predictions of how the changing climate affects the annual peak biomass. The model scales a fixed maximum biomass (g m−² of surface area) growth rate with the prevailing CO2 concentration, nitrogen status and other factors. [Wilson](#page--1-0) et [al.](#page--1-0) (2007) modeled the sedge LAI using a semiempirical approach: they fitted Gaussian and log-normal curves into measured LAI data. This method has been frequently used afterwards to reconstruct the development of LAI on peatland sites (e.g. [Maanavilja](#page--1-0) et [al.,](#page--1-0) [2011;](#page--1-0) [Riutta](#page--1-0) et [al.,](#page--1-0) [2007a;](#page--1-0) [Schneider](#page--1-0) et [al.,](#page--1-0) [2012\).](#page--1-0)

We are not aware of any papers in which the focus would be to study the sedge LAI seasonality and variation using a processoriented modeling approach. However, since LAI has such a central role in controlling canopy productivity, it would be essential to simulate it as accurately as possible. The aimof our work was to obtain a robust model that would be capable of creating sedge LAI estimates, for example, for peatland $CH₄$ emission studies. The model simulates the seasonal LAI development of peatland sedges, specifically genus Carex, based on the carbon fluxes of the sedge canopy. It is driven with meteorological data—temperature, water table depth and solar irradiance—and therefore, it was tested against data from two pristine peatland sites, located in southern and northern boreal parts of Finland, on which we conducted a manipulation experiment for warming and draining. This experiment provided several sets of input data and observational LAI data for developing and testing the model.

2. Materials and methods

2.1. Model description

2.1.1. General

In the current paper, LAI ($m^2 m^{-2}$) refers generally to one-sided sedge leaf area per 1 m^2 of soil surface and the symbol A_L with units $m²$ is the leaf area as a variable in the model. The model simulates the development of sedge LAI driven by carbon gain/loss in net photosynthesis (P_n) , utilization of stored carbon in spring, and senescence in late summer (Fig. 1). We built up the model by combining existing and new formulations of the canopy $CO₂$ exchange and other carbon related processes so that the simulated A_L changes along with the carbon fluxes but, on the other hand, the rates of the processes depend on the current A_L . The parameterization was Download English Version:

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