Final Report

3PG-D: Modelling forest growth in a dynamic world

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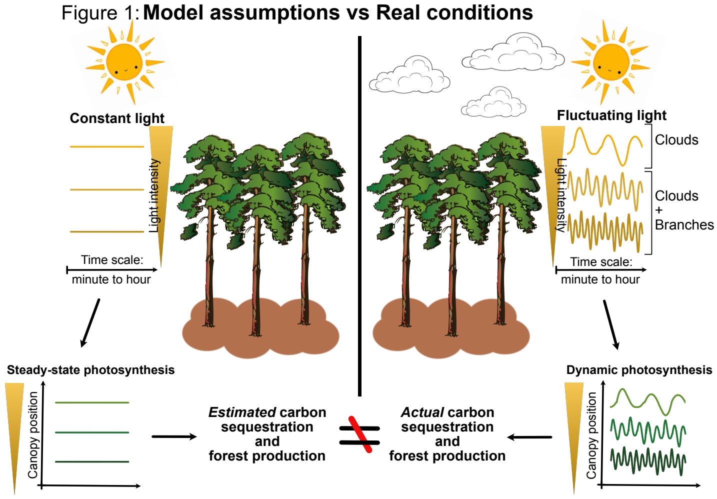
Project Summary

The aim of this project was to collect data and model the dynamic photosynthesis in Scots pine relative to canopy position and needle nitrogen content, and thereby generate relevant data for model parametrization for one of the commercially significant tree species in Sweden. Furthermore, the project aimed to create a forest growth model that accounts for the dynamic photosynthesis in forest stands under natural light fluctuations, by combining a traditional forest growth model (3PG) with the dynamic photosynthesis model. The project has led to novel findings on the dynamic photosynthesis in pine canopies, and on how it is affected by site fertility. The analysis and modelling work has revealed that a different, more comprehensive approach is needed to quantify the impact of dynamic light conditions on photosynthesis in key boreal tree species and its relevance for carbon sequestration and for modelling forest growth. This has led to a collaborative proposal for a larger, interdisciplinary project. Dr. Stangl wants to thank the Åforsk Foundation for the support through their grant for early career researchers, which led to an independent publication, and a project proposal in continuations of the current work.

Background

Figure 1: **Model assumptions vs Real conditions**



Process-based models predicting the yield of forests, such as 3PG, assume light conditions that are effectively constant on a timescale of minutes to hours [1]. Consequently, they assume steady-state photosynthesis at those light conditions. However, the natural light environment is dynamic due to cloud movements and increasingly dynamic inside the canopy where the branches and leaves constantly move and shade each-other (Fig.1). In this fluctuating light environment leaf-level photosynthesis often does not reach its maximum steady state, because it is constrained by the capacity of the underlying biochemical processes to respond fast to a sudden change in light intensity [2,3]. In order to reach steady state, a leaf needs to experience constant light from several minutes to up to half an hour, depending on the species [3]. Therefore, models based on steady state assumptions perpetually overestimate carbon assimilation, especially inside the canopy.
This inaccuracy of existing models has been widely discussed in crop sciences [2], where the need to predict yield accurately has been felt more and more acutely with the exponential growth of the human population. Dynamic photosynthesis models have been developed to describe photosynthesis inside dense crop canopies and predict carbon assimilation and yield [3]. Although it is still challenging to describe a dynamic system with complete precision, these

models have gained significance and are gradually adapted into models of crop production. Forests have produced essential raw material for human societies since centuries and are now in the focal point of our strategies towards a fossil-free society and adaptation to the changing climate. But despite its importance worldwide, the forestry industry has been slow to move away from traditional empirical models and to adopt more flexible process-base models into their management practices [4, 5]. In addition, despite the large body of research on the light conditions of forest canopies, dynamic photosynthesis models have not yet been adapted to model carbon uptake of forest stands.
Soil fertility, especially nitrogen availability, has a strong effect on photosynthesis, because it is a key element in all enzymes. Accordingly, higher nitrogen availability enhances steady state photosynthetic capacity [6], but its effect on dynamic photosynthesis in trees is unclear. An analysis of the eddy-covariance data in a fertilized vs a non-fertilized Scots pine stand has found that an increase in light-use efficiency accounted for about 70% of the increase in carbon uptake in the fertilized stand [7]. However, attempts to model this difference with a steady state photosynthesis model have failed [16], presumably because it misses to account for the dynamic components of the photosynthetic light response.
Leaves also adapt to the light conditions in which they develop. At the top of the canopy, leaves are exposed to higher light intensities, and they often have higher photosynthetic capacity, than leaves at the bottom of the canopy that typically experience lower light conditions [8]. In a recent study on beech we have shown, that leaves of this species also adapt to the typical dynamic light conditions in which they develop, so that top-canopy leaves have a higher efficiency at exploiting long periods with high light intensities, while bottom-canopy leaves are more efficient at exploiting higher frequency light fluctuations [2].

Objectives

1) Describe and model dynamic photosynthesis in Scots pine relative to needle nitrogen content (i.e. soil fertility) and canopy position
2) Integrate parameters of dynamic photosynthesis into the 3PG forest growth model, and test whether these assumptions improve the predictive capacity of the model

Method and Theory

Rosinedalsheden experimental forest site
The Rosinedalsheden experimental forest site has been established in 2005 in northern Sweden (64°10'N, 19°45'E) in a naturally regenerated, even-aged Scots pine stand, where the trees are about 100 years old currently [9]. It consists of a control site and a site with intensive nitrogen fertilisation. The site is equipped with a weather station, that records air temperature, light intensity and air humidity, and an eddy-covariance system, that records CO_2 and water vapour fluxes above the canopy. Stand growth as well as the carbon cycles of the stands have been heavily studied.

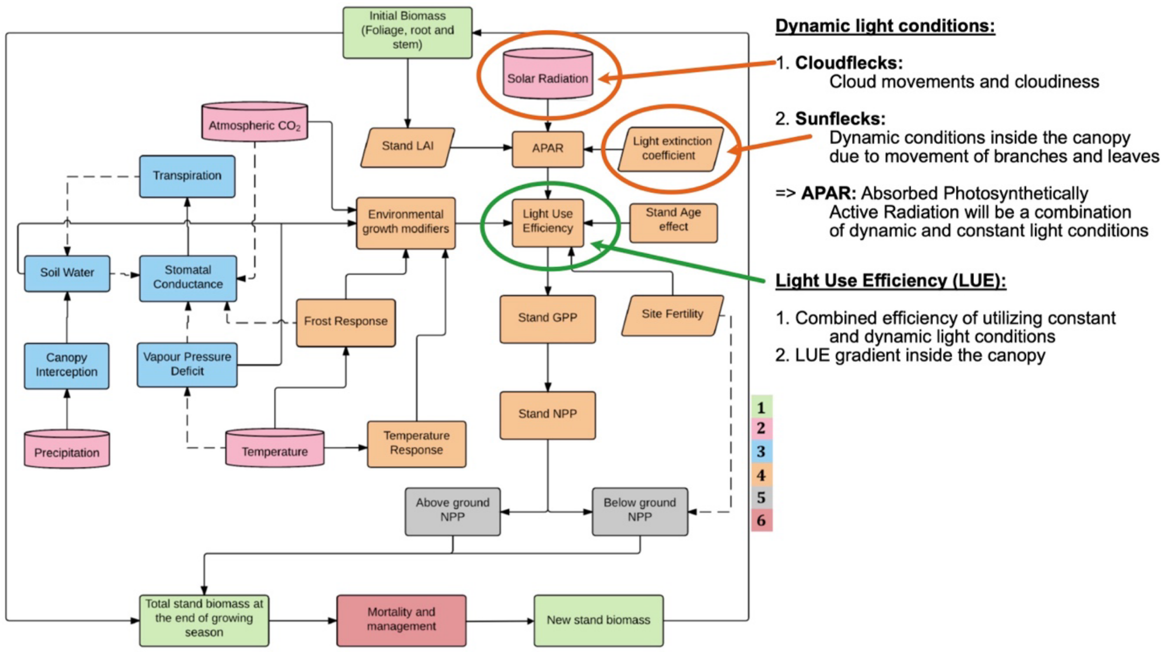
Measurements of dynamic photosynthesis in Scots pine
Shoot-level gas-exchange was measured on upper and lower canopy shoots of 6 trees per site at the Rosinedalsheden experimental forest. The measurement protocol consisted of transitions from low light (100 µmol photons m^{-2} s^{-1}) to high light (1200 µmol photons m^{-2} s^{-1}) and back to low light, to characterise both the light induction and the relaxation phase of photosynthesis in fluctuating light conditions. All measurements were done during late June and early July 2022.

Dynamic photosynthesis model
A dynamic model [10] was fitted to the gas-exchange data to estimate the relevant parameters of dynamic photosynthesis, which are summarized in the following table:

Parameter	Description
A_{max}	Maximum rate of photosynthesis at steady state
T_{max}	Time to reach A_{max}
T_{80}	Time to reach 80% of A_{max}
SL	Maximum slope, i.e. the speed of change upon illumination

The 3-PG model

The 3-PG model (Physiological Processes Predicting Growth) was developed over twenty years ago as an intermediate between traditional mensuration-based growth and yield models, and process-based carbon balance models [1]. Since its initial publication, it has been extended to utilise satellite imaging. Briefly, 3-PG calculates the light energy absorbed by forest canopies and converts it into biomass production [5]. The efficiency of this conversion depends on the light-use efficiency of the trees, and is influenced by soil fertility, water availability, temperature and stand age. The model is based on generic principles of plant physiology, but it has to be parameterised to individual species and site. This is typically done by historical data on growth of the same species at similar sites, or at the site of interest, if data is available.



Schematic representation of the 3-PG model. Colors represent different model components:
Input data: (1) Initial stand data, (2) Climate data,
Modules: (3) Soil water balance module, (4) Biomass production module,
(5) Biomass allocation module, (6) Mortality and management module.
Solid lines represent direct relationships and dotted lines represent indirect relationships.
Figure adapted from Subramanian (2016)

Figure 2: **Schematic representation of the 3PG model** [11]. Notes on the side indicate which parts of the model are influences by dynamic light conditions and photosynthesis. This project attempted to integrate parameters of dynamic photosynthesis to influence light-use efficiency (green circle)

Results

Dynamic Photosynthesis Model of Scots pine

The goal of the gas-exchange measurements and applying the dynamic model to the gas-exchange data was to characterise photosynthesis in Scots pine under dynamic light conditions.

First, I explored how canopy position (high or low) affects the characteristics of dynamic photosynthesis. Canopy position did not affect A_{max} under non-fertilized control conditions

(Fig.3B), and photosynthetic induction was slower in the low-canopy shoots compared to the high-canopy shoots (Fig.3C and D). This is in contrast to what we found earlier [12] in the broadleaved species, beech.

Second, I explored how needle nitrogen content, related to soil fertility, affects dynamic photosynthesis, by comparing the shoots from the control site to the shoots from the fertilized site. In contrast to what I expected based on previous studies [6], A_{max} did not increase in high-canopy shoots, neither did the speed of induction change significantly in the fertilized stand. However, nitrogen fertilization strongly enhanced all measured parameters in the low-canopy shoots: A_{max} was 15% higher (Fig.3A and B), the speed of induction was 40% faster (Fig.3C and D), and A_{80} was reached more than 7 minutes earlier (Fig.3E and F) in the fertilized low-canopy shoots relative to the control.

These results indicate that pine tends to invest into enhancing the photosynthetic potential of shoots lower in the canopy if nitrogen is abundant. This is especially interesting, because it highlights the importance of dynamic photosynthesis for this species. In addition, these results suggest potentially important difference between conifer and broadleaved species.

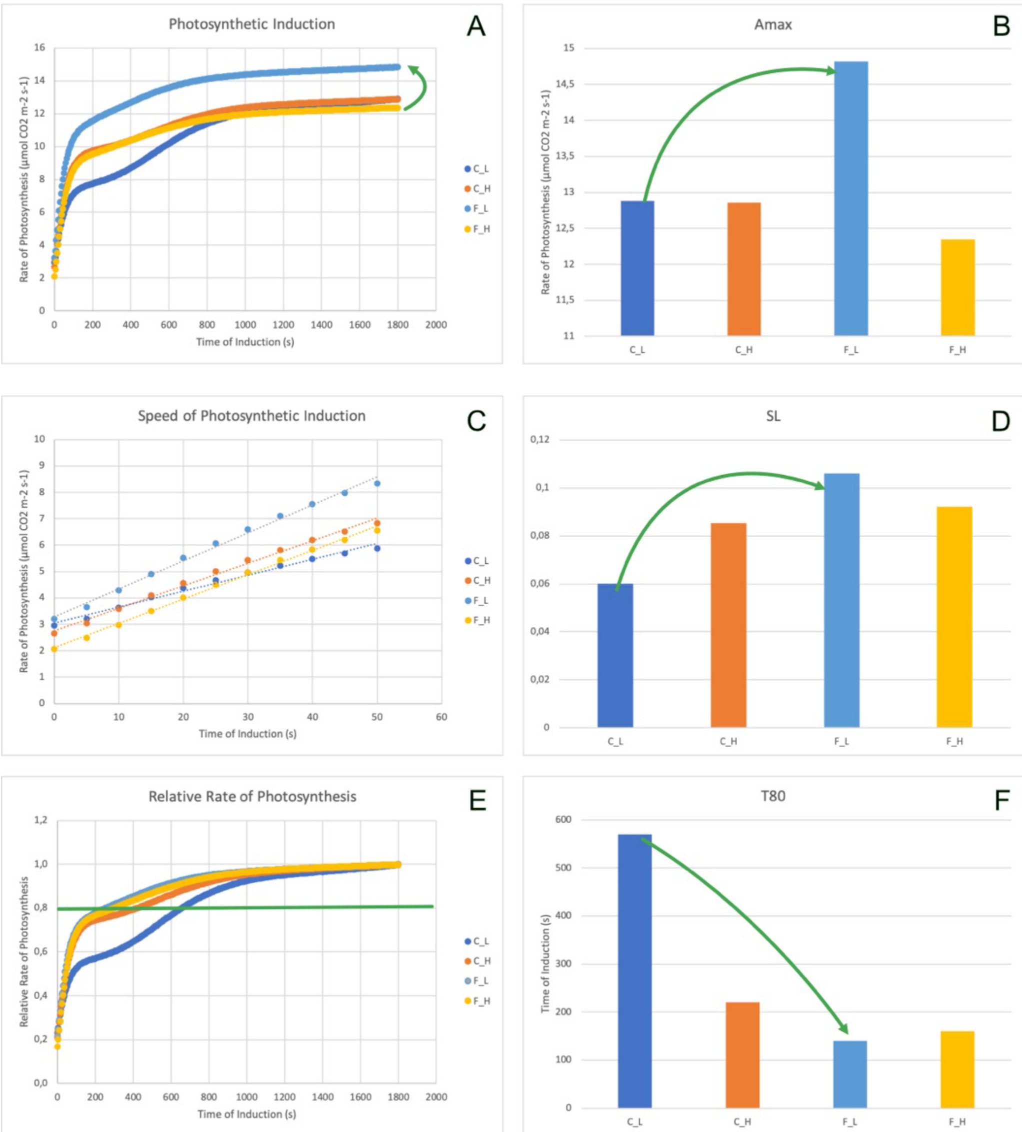


Figure 1: **Analysis of photosynthetic induction in Scots pine**. Panel A shows the induction of photosynthesis over 30 min., upon a transition from low to high light. Panel B shows the maximum rate of photosynthesis (A_{max}) under high light. Panel C shows the initial 50 s of induction upon transition from low to high light. Panel D shows the speed of induction calculated (SL). Panel E shows the relative rate of photosynthesis during induction (A/A_{max}). Panel F shows the time (s) at which 80% of A_{max} is reached (T80). C_L is non-fertilized, low-canopy shoot; C_H is non-fertilized high-canopy shoot; F_L is fertilized low-canopy shoot; F_H is fertilized high-canopy shoot.

Integrating dynamic photosynthesis into 3PG
The next step was to integrate dynamic photosynthesis into the forest growth model 3PG. The analysis led to the conclusion, that the only feasible solution in case of 3PG is to add an arbitrary correction factor to light-use efficiency, that is related to site fertility (Fig.2). However, this would not allow for a rigorous test of the contribution of dynamic photosynthesis to forest growth. I looked for expert advice, and made contact with Dr Eric Libby at the Dept, of Mathematics and Mathematical Statistics at Umeå University, who has expertise in modelling dynamic biological systems. Finally, we came to the conclusion that the best approach would be to build a separate dynamic model, that accounts for canopy structure and dynamic light conditions in the canopy, and compare that model to conventional steady state models of canopy photosynthesis. Our discussions have led to a proposal for a larger project, which we recently submitted to Formas.

Conclusions and Outlook

This project set out to modify the forest growth model 3PG, to include dynamic photosynthesis, and to test whether this would enhance the model's capacity to accurately model forest growth in a Scots pine stand, and characterise dynamic photosynthesis in Scots pine in the process. Measurements of dynamic photosynthesis have revealed contrasting patterns related to canopy position in Scots pine compared to earlier findings in beech [12]. Furthermore, they revealed a yet unknown and unexpected strategy in Scots pine to enhance the photosynthetic potential of the canopy by low-canopy shoots under high soil fertility. A manuscript is in preparation to publish these findings in a high-profile scientific journal, and eventual open-access fees will be covered by the final instalment of the grant.
The analysis and modelling work has revealed that a different, more comprehensive approach is needed to quantify the impact of dynamic light conditions on photosynthesis in key boreal tree species and its relevance for carbon sequestration and for modelling forest growth. This has led to a collaborative proposal for a larger, interdisciplinary project. If funded, this new project will cover the salary of Dr. Stangl and a postdoctoral researcher for several years, and will enable Dr. Stangl to further establish herself as an independent researcher.

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