

# Tipping Points for Forests, Using the Data Assimilation Linked Ecosystem Carbon Model, DALEC

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## Abstract

Due to changes in our climate and environment, partly caused by human behaviour, it is becoming increasingly important to understand the processes involved in Earth systems, such as the carbon cycle. There are many models that attempt to describe the dynamical behaviour of carbon stocks and stores, but, despite their complexity in attempting to describe all crucial processes, significant uncertainties remain. Our aim is to look at the qualitative behaviour of one of the simplest carbon cycle models, the Data Assimilation Linked Ecosystem Carbon (DALEC) model, and consider in detail the processes involved. DALEC is a simple vegetation model of processes involved in the carbon cycle of forests. Our analysis shows that the dynamics of both evergreen and deciduous forests in DALEC are dependent on a few key parameters and it is possible to find a tipping point at which stable sustainable behaviour of a forest gives way to widespread mortality.

## 1 Introduction

Since the Industrial Revolution the amount of carbon dioxide in the atmosphere has risen exponentially as a result of human activities, such as the burning of fossil fuels and deforestation [1]. Carbon dioxide is a greenhouse gas which absorbs and emits infrared radiation and traps the heat in the atmosphere. It affects the Earth's climate and the functioning of its ecosystems, such as the terrestrial ecosystem. In return, ecosystems can also affect the climate through biophysical and biochemical processes. It is known that a considerable amount of atmospheric CO<sub>2</sub> is taken up by vegetation. However, with increasing CO<sub>2</sub> levels and the consequent global warming, terrestrial vegetation, which formerly acted as a carbon sink, may not be able to absorb as much CO<sub>2</sub> as before or may even contribute to more atmospheric CO<sub>2</sub> by dying [2]. This is a strong motivation to understand in depth the Earth's systems, such as the carbon cycle: the exchange of carbon between the biosphere, pedosphere, geosphere, hydrosphere and the atmosphere.

Dynamic Global Vegetation Models (DGVMs) are models which simulate the key physiological processes of the terrestrial carbon cycle through both empirical and process based methods, based on

climate data and are typically quite complex. DGVMs are used not only for determining carbon stocks and stores, but also to simulate the effects of future climate change on natural vegetation.

Nowadays there exist many quite complex DGVMs, such as TRIFFID [3], LPJ-DGVM [4], SEIB-DGVM [5] and ED2 [6]. These models have detailed processes and can often distinguish between a large number of plant types. For example, LPJ-DGVM allows for ten different plant types, whereas TRIFFID uses five, and SEIB even simulates the local interaction among individual trees. Photosynthesis, evapotranspiration and soil water dynamics are modelled, using monthly, daily, hourly or half-hourly meteorological data and considering different layers of soil. Although many models are able to run independently, they can also be incorporated within global climate models (GCMs), which are used extensively for weather forecasting, understanding the global climate and climate change. For example, TRIFFID has been coupled to HADCM3 [3] and in a study by Schaphoff *et al.* [7], LPJ-DGVM was coupled to five different GCMs to compare land biosphere carbon storage projections among climate change projections from one emission scenario.

Uncertainties in observations and parameters can influence the outcome of a simulation of a complex system, such as a GCM, as a consequence of changes in the dynamics of the core model. Furthermore it is expected that future estimates of complex climate processes will produce more uncertainty in their predictions rather than less, due to the many factors that play a role, such as expected accumulation of greenhouse gases, the weighting of global climate models and uncertainty in projected regional changes [8]. Better understanding of the behaviour of different models could help to reduce some of the uncertainty. In order to begin studying the issues that arise in more complex systems we first study a relatively simple process model which is typical of that which underpins many GCMs. This is a strategy not dissimilar to that found in other areas of environmental prediction, for example the Lorenz 1963 equations [9], which were used to study thermal convection in a very simple setting and which brought to light fundamental properties of dynamical systems.

The aim of this paper is to try to understand the qualitative dynamical behaviour of the Data Assimilation Linked Ecosystem model (DALEC) [10]. DALEC is a dynamic vegetation model which simulates the carbon cycle of forests. It was especially created for data assimilation and specifically designed for calibration and testing against eddy flux data. DALEC is a simple box model of carbon pools connected via fluxes running at a daily time-step, driven by daily climate data such as temperature, irradiance and atmospheric carbon. There are many similarities between DALEC and other models but also some differences. One similarity is that DALEC uses the Farquhar photosynthesis model, which is used by other DGVMs, such as Hybrid 3.0 [11], ED2 and DOLY [12]. The main difference between DALEC and many other DGVMs is that it is an extremely simplified model, yet it aims to capture the essential dynamics of the carbon cycle.

Different versions of DALEC have been used on several occasions, for example to show how data

assimilation techniques can improve estimations of carbon fluxes and provide insights into ecosystem carbon exchange [10] and to analyse magnitude and contribution of parameter and driver uncertainty to confidence intervals on estimates of carbon fluxes [13]. DALEC is also used in the ABACUS project, which is a linked programme of plant and soil process studies, isotope analyses, flux measurements, micro-meteorology, process modelling, and aircraft and satellite observations designed to improve predictions of the response of the arctic terrestrial biosphere to global change.

We formulate the process model for DALEC as a dynamical system, iterative in time, and we study the model using dynamical systems methods, employing both analytical and numerical approaches.

The work done for this paper was motivated by a masters thesis by Ilett [14], but there are some differences in approach. Ilett focused on two aspects of the model; firstly, the dynamics of the model for a three year period, considering how the model predictions varied with different initial conditions and different parameter values; and secondly, considering how the model behaved if all time dependence in the drivers, such as the temperature and the irradiance, was removed. Our analysis sets Ilett's work in a broader context, explaining why different initial conditions lead to different behaviour.

Section 2 discusses the DALEC evergreen (DALEC EV) model in detail. In Section 3 the behaviour of the model is discussed and it is shown that although DALEC EV contains many parameters there are only a few key parameters which determine the survival or death of a forest. It is also shown that the results indicate that in DALEC it is not necessary to use daily driver data, which are highly variable, but that it is possible, whilst taking great care, to smooth the data to give drivers that depend on only a few parameters. We apply similar methods to DALEC deciduous (DALEC DE) and obtain qualitatively similar results. In Section 4 an interpretation and consequences of the results are presented.

## 2 Model Description and Methods

### 2.1 Model Description

DALEC EV [10] describes the time evolution of five carbon pools, namely foliage ( $C_f$ ), woody stems and coarse roots ( $C_w$ ), fine roots ( $C_r$ ), fresh leaf and fine root litter ( $C_{lit}$ ) and soil organic matter and coarse woody debris ( $C_{som}$ ) and one pseudo pool, Gross Primary Production (GPP). Fig. 1 shows the carbon cycle of an evergreen forest according to DALEC. The pools are connected by arrows, which represent allocation and production fluxes. Sunlight, water and  $\text{CO}_2$  are needed for photosynthesis which takes place in the needles. The photosynthate is stored in the GPP, which distributes the available carbon to the  $C_f$ ,  $C_w$  and  $C_r$  pools. During photosynthesis carbon is also respired into the atmosphere by the tree, which is called autotrophic respiration ( $R_a$ ). Decomposition of litter in and

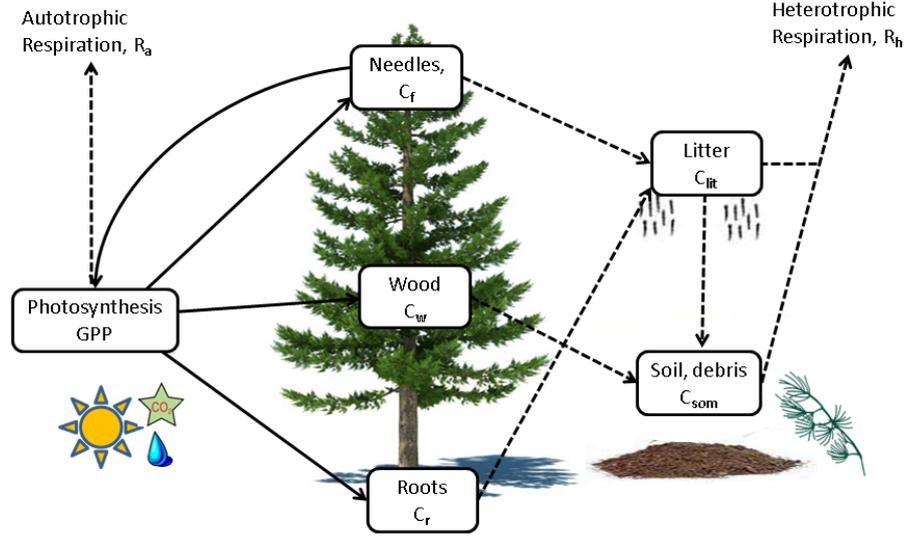


Figure 1: A schematic overview of the carbon cycle of an evergreen needle forest according to DALEC EV.

on the soil results in heterotrophic respiration ( $R_h$ ).

The DALEC EV model equations [15] written as a discrete dynamical system take the form of daily maps, specifically:

$$C_f(t+1) = (1 - p_5)C_f(t) + p_3(1 - p_2)GPP(C_f(t), t), \quad (1)$$

$$C_r(t+1) = (1 - p_7)C_r(t) + p_4(1 - p_3)(1 - p_2)GPP(C_f(t), t), \quad (2)$$

$$C_w(t+1) = (1 - p_6)C_w(t) + (1 - p_4)(1 - p_3)(1 - p_2)GPP(C_f(t), t), \quad (3)$$

$$C_{lit}(t+1) = (1 - (p_8 + p_1)T(t))C_{lit}(t) + p_5C_f(t) + p_7C_r(t), \quad (4)$$

$$C_{som}(t+1) = (1 - p_9T(t))C_{som}(t) + p_6C_w(t) + p_1T(t)C_{lit}(t), \quad (5)$$

where  $t$  is time in days and  $T(t) = 0.5 \exp(p_{10}T_m(t))$  is the temperature sensitive rate parameter, which is important for decomposition.  $T_m(t)$  is the mean daily air temperature. For a description of the parameters,  $p_i$ ,  $i = 1, \dots, 10$  see Appendix A. Typically we have used the following initial conditions for the five pools:  $C_f(0) = 150 \text{ gC m}^{-2}$ ,  $C_r(0) = 160 \text{ gC m}^{-2}$ ,  $C_{lit}(0) = 60 \text{ gC m}^{-2}$ ,  $C_w(0) = 9200 \text{ gC m}^{-2}$  and  $C_{som}(0) = 11000 \text{ gC m}^{-2}$ . The values of the initial conditions for the carbon pools are based on suggestions made by the REgional FLux Estimation eXperiment (REFLEX) [15] for the forest data we used.

The GPP represents a daily accumulation of carbon produced by photosynthesis. It takes the following

form:

$$GPP(C_f(t), t) = \frac{E_0(t)I(t)g_c(t)(C_a(t) - C_i(t))}{E_0(t)I(t) + g_c(t)(C_a(t) - C_i(t))} (a_2s(t) + a_5). \quad (6)$$

The functions in the GPP are collectively called the Aggregated Canopy Model (ACM). A description of the various functions in the GPP can be found in Appendix B. The ACM is a daily step model that estimates GPP as a function of Leaf Area Index (LAI), foliar nitrogen, total daily irradiance, maximum and minimum daily temperature, day length, atmospheric CO<sub>2</sub> concentration, soil-plant water potential and total soil-plant hydraulic resistance. The LAI for evergreen forests is the projected leaf area (in  $m^2$ ) per ground area (also in  $m^2$ ). The ACM, [16] has been derived from the Soil-Plant-Atmosphere model (SPA) by Williams *et al.*, [17]. The SPA model is a process-based multi-layer (fine-scale) model simulating ecosystem photosynthesis and water balance at a 30 minute time step and for multiple canopy and soil layers. It uses the Farquhar model of leaf-level photosynthesis and the Penman-Monteith equation to predict evapotranspiration [18]. The equations for the ACM were derived from the SPA using cumulative or average values of the most sensitive driving variables. Then the ACM was calibrated so that the estimates of the GPP were similar to those of the SPA model across a wide range of the driving variables. The only parameter in the ACM which needs calibrating per site is the nitrogen use efficiency parameter,  $p_{11}$ . This parameter determines the maximum rate of carboxylation per gramme of foliar nitrogen.

In the original Fortran code for DALEC EV, provided by REFLEX [15], the LAI is set to  $\max(0.1, C_f/lma)$ , which prevents the foliar carbon from going below  $C_f/lma$ . Using  $lma = 110$ , as suggested by REFLEX, means that LAI can never go below 11. This restriction is intended to make sure that  $C_f$  never reaches zero, representing the death of the forest. However, we remove this restriction and so define  $LAI = C_f/lma$ . The implication of removing this constraint is discussed in further detail below.

In order to compute the GPP, daily drivers of maximum and minimum temperature (which produce the temperature range), atmospheric CO<sub>2</sub> concentration, solar irradiance and day of the year are needed. The other parameters in the ACM, for example soil-plant water potential and foliar nitrogen, can be set to appropriate fixed values for the evergreen vegetation in question. Latitude also plays an important role, as it influences day length and therefore the amount of photosynthate produced, but again this is another fixed parameter.

In the DALEC EV model the GPP depends on the foliar carbon,  $C_f$ , via two functions, namely  $E_0(t)$  (canopy level quantum yield) and  $C_i(t)$  (CO<sub>2</sub> concentration at site of carboxylation). This is because foliage produces the photosynthate, which none of the other carbon pools do. Therefore the foliar carbon pool is crucial in determining the amount of carbon the other pools receive and we will show that it is this pool that determines the fate of the forest.

From the model it is also possible to evaluate other quantities. These include the net ecosystem

exchange (NEE), which is the net carbon uptake or loss by the ecosystem, and net primary production (NPP), which is the net carbon flux from the atmosphere into green plants. NEE and NPP can be calculated as follows:

$$NEE(t) = GPP(C_f(t), t) - R_a(t) - R_h(t), \quad (7)$$

$$NPP(t) = GPP(C_f(t), t) - R_a(t), \quad (8)$$

where  $R_a(t) = p_2 GPP(C_f(t), t)$  and  $R_h(t) = R_{h_1} + R_{h_2} = p_8 T(t) C_{lit}(t) + p_9 T(t) C_{som}(t)$ .

In order to run the DALEC EV model, estimates of the parameters and values for the driver data are needed. We have used realistic data both for parameters and climate data from a European flux site, which was provided for the REFLEX project [15]. The purpose of this project was to compare the strengths and weaknesses of various data assimilation methods for estimating parameters and predicting carbon fluxes using DALEC, based on three years of driver data. However, in our analysis of DALEC the behaviour of the model is studied over a longer period of time, so driver data was created by averaging the three years of available data (including the atmospheric carbon,  $C_a$ ). This produces data which varies on a daily basis in a realistic manner, but is the same each year. The averaging introduces some smoothing but, as discussed in Section 4, this has little qualitative impact.

## 2.2 Methods

### 2.2.1 Fixed Point Analysis

Our goal is to understand the dynamical behaviour of the DALEC model. Previous studies have focussed on parameter fitting or measuring carbon fluxes by running the model forward in time. We commence our analysis by observing that the form of the model means that the dynamics of the foliar carbon is independent of the other pools and consequently the dynamics of all other pools are slaved to the behaviour of the foliar carbon pool. We also note that typically solutions of the DALEC model evolve to periodic solutions because of the periodicity of the drivers. These periodic states can be found either by running the DALEC EV model forward in time, as was done in order to produce Fig. 3, or by recognising that, for a periodic solution, the amount of carbon on day  $t$  in year  $n$  is the same as on day  $t$  in year  $n + 1$ :

$$C_f(t) = C_f(t + 365). \quad (9)$$

Periodic solutions can therefore be found as fixed points of an annual map, which is obtained by iterating the daily map 365 times. In this way, we find that the annual map of  $C_f$  has either one or three fixed points, depending on the parameter values. We note that  $GPP(0, t) = 0$  for all  $t$  and this implies that  $C_f(t) = 0$  is a fixed point of the daily map and therefore of the annual map for all values of the parameters. The derivative of the iteration for the annual map with respect to  $C_f(t)$ , evaluated

at  $C_f(t) = 0$  is  $(1 - p_5)^{365}$  and so, if  $p_5 < 1$ , (which is always true for physical reasons) the zero fixed point is linearly stable. There are two other fixed points for some parameter values, one of which is stable and the other is unstable. If a fixed point is stable, it acts as an attractor and so solutions close by will be drawn to this fixed point solution. If a fixed point is unstable, it acts as a repeller.

The benefits of finding the periodic states by finding fixed points of the annual map are that it is then possible to trace out the behaviour of the periodic state as a function of the parameters, by varying either one or more parameters, and that it is possible to follow both stable and unstable solutions. Although unstable solutions are not seen in simulations, they play a significant role as they allow one to map out regions of qualitatively different behaviour in parameter space.

The continuation software `CL_Matcont_for_maps` [19] was used to follow paths of fixed points of the annual map.

### 2.2.2 Smoothing the Drivers

The model is driven by highly variable drivers, see Fig. 2. In Section 3, we consider the effect that smoothing the variable drivers for temperature and irradiance has on the results. For example, we can express the maximum temperature as follows:

$$T_{max}(t) = c_0 + c_1 \cos\left(\frac{2\pi t}{365}\right) + c_2 \sin\left(\frac{2\pi t}{365}\right), \quad (10)$$

which involves only three constants. For the temperature drivers a fast Fourier transform (FFT) was used to find the constants  $c_0$ ,  $c_1$  and  $c_2$ . For the irradiation we used four dimensional variational (4DVAR) data assimilation techniques to find values of  $c_0$ ,  $c_1$  and  $c_2$  in the smooth approximation to the irradiance. Fig. 2 shows the variable and smooth drivers.

## 3 Behaviour of the Carbon Pools

### 3.1 Behaviour of the Foliar Carbon Pool

As mentioned earlier, the foliar carbon pool is crucial in determining the amount of carbon the other pools receive. In equations (1)–(5), this is seen from the fact that the foliar carbon pool,  $C_f$ , decouples from the other carbon pools. Therefore the dynamics of the forest is driven by and depends on  $C_f$  and on the parameters in this pool, namely  $p_2$  (fraction of GPP respired),  $p_3$  (fraction of NPP allocated to foliage),  $p_5$  (daily turnover fraction of foliage) and  $p_{11}$  (nitrogen use efficiency parameter in the ACM). For the purpose of our analysis, we only consider parameters  $p_2$ ,  $p_3$  and  $p_5$ . Parameters  $p_2$  and  $p_3$  only appear in combination with each other as  $p_3(1 - p_2)$  in equation (1); we regard them in our

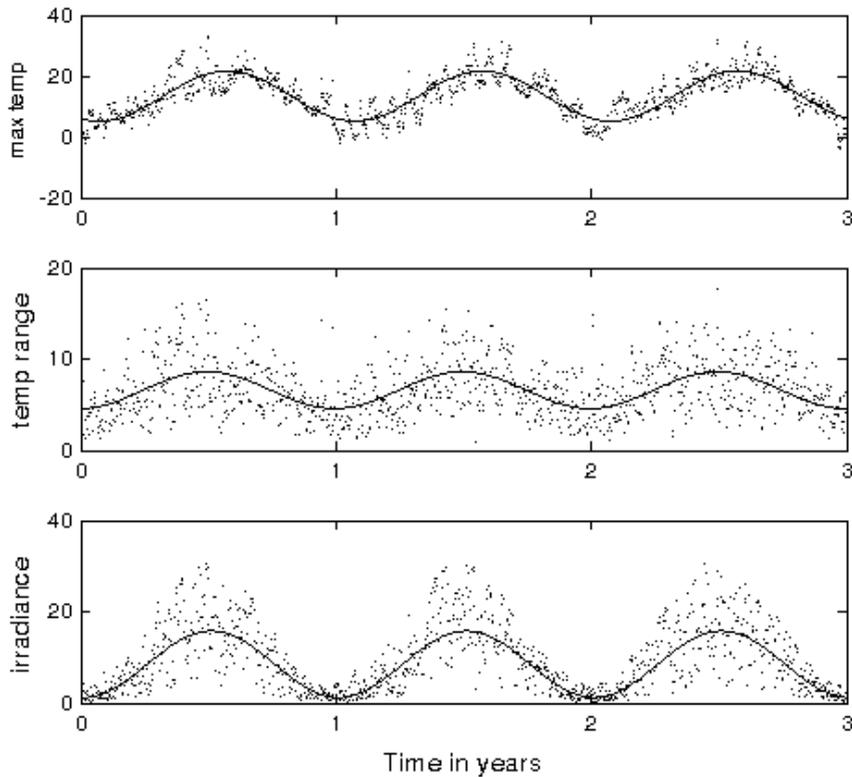


Figure 2: *Smooth and variable drivers over a three year period, data from Loobos forest in the Netherlands: (a) the maximum temperature, (b) the temperature range and (c) the irradiance. Note that the temperature rarely drops below zero.*

analysis as one parameter. Thus we define  $p_{23} = p_3(1 - p_2)$ . This parameter combination represents the fraction of GPP allocated to the foliar carbon every day. For different parameter regimes there is different behaviour of  $C_f$ .

Fig. 3 shows two graphs of  $C_f$ , resulting from running the model forward over a number of years, for two different values of  $p_5$ . The solid line ( $p_5 = 0.0024$ ) shows the foliar carbon growing to a stable periodic state with a period of one year. During this annual cycle there is more foliar carbon during the summer than during the winter, as photosynthesis is increased in the summer. In contrast, the dashed line ( $p_5 = 0.0035$ ) shows the foliar carbon steadily decreasing on average over a period of 8 to 9 years and then asymptoting to zero, which represents the forest dying. This raises the question: “How does the change in behaviour take place and for which parameter values?”

The transient behaviour of  $C_f$  that leads to a stable periodic state, as shown in Fig. 3, suggests that the DALEC EV model has a periodic solution with a period of one year for certain values of the parameters. Using `CL_Matcont_for_maps` [19] results in Fig. 4, which shows how the periodic state changes when parameter  $p_5$  is varied. It has two branches, representing two paths of fixed points, which are connected by a limit point or fold bifurcation. This limit point represents a tipping point,

where the stability of a solution is suddenly lost as  $p_5$  increases and the system makes a sudden transformation to completely different behaviour. The top branch of the curve in Fig. 4 is stable and the bottom branch is unstable. Unstable solutions are not seen in simulations, but they play a significant role in determining what kind of behaviour occurs.

For example, if a simulation is carried out with the initial value of  $C_f(0) = C_{f_0}$ , at a point anywhere on the graph between the top and bottom branch, such as at  $p_5 = 0.0024$  and  $C_{f_0} = 140$ , then  $C_f$  will be attracted to the top branch and will grow to a stable periodic state. If the initial condition is at a point below the bottom branch, for example at  $p_5 = 0.0024$  and  $C_{f_0} = 20$ , it will be repelled from the bottom branch and attracted to the fixed point  $C_f = 0$ . If  $p_5$  is chosen to the right of the limit point, for example  $p_5 = 0.0035$  then the iterates will also be attracted to  $C_f = 0$  for all initial values of  $C_f$ . For a forest this means that for an initial value of  $140 \text{ g C m}^{-2}$  of foliar carbon and a daily turnover rate of foliage,  $p_5 = 0.0024$ , it will grow and find an equilibrium, see Fig. 3, but for an initial value of  $20 \text{ g C m}^{-2}$  of foliar carbon and  $p_5 = 0.0024$ , it would die over a period of time. If  $p_5 = 0.0035$  the forest would eventually die for any initial value of the foliar carbon, see Fig. 3. Once the forest has died, it would not be possible for it to re-grow, as the line  $C_f = 0$  is an attractor.

In Fig. 4 the limit point of  $C_f$  is shown for a particular value of  $p_5$  and  $p_{23}$ . However, there are many

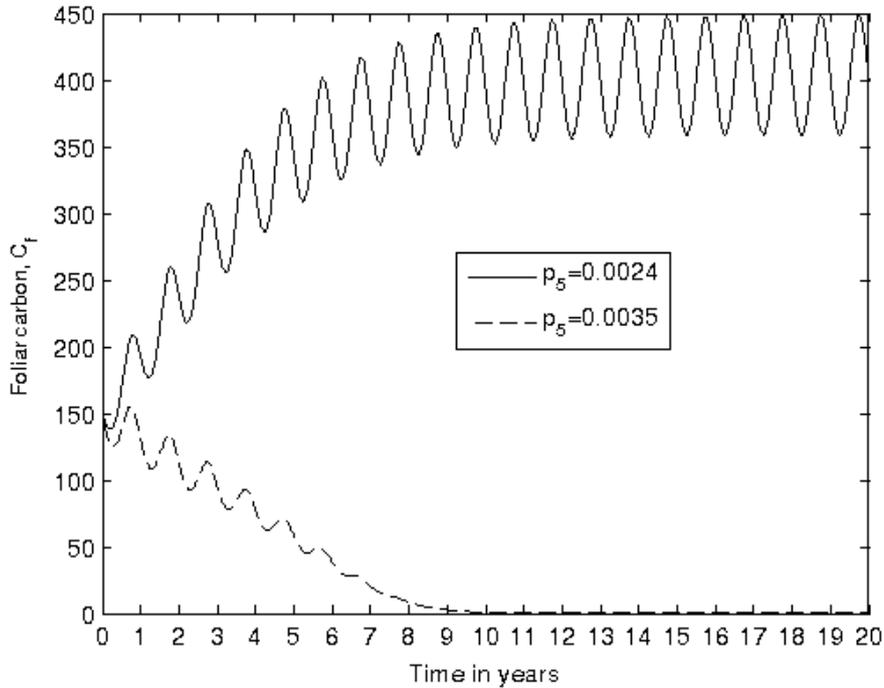


Figure 3: The top line shows that for a value of  $p_5 = 0.0024$ ,  $C_f$  stabilises on a periodic state. The bottom line shows  $C_f$  decreasing and going to zero for  $p_5 = 0.0035$ , showing several years of decline resulting in mortality. The values of the other parameters are  $p_{23} = 0.1392$  and  $p_{11} = 7.4$ . Day 1 for each year is December 21st, the shortest day of the year at a latitude of  $52^\circ$ .

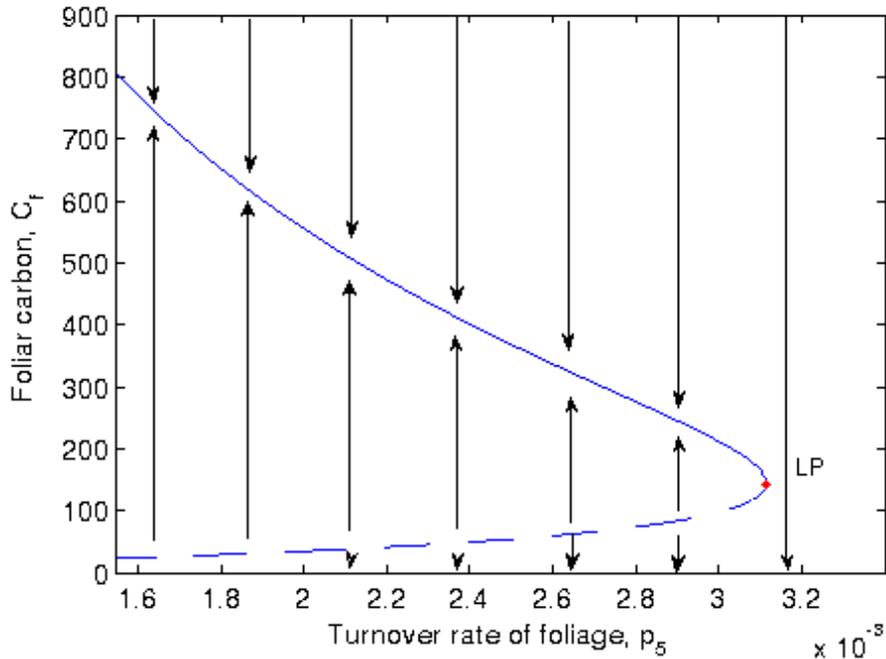


Figure 4: *Path of fixed points for the annual map for  $p_{23} = 0.1392$ . The top branch is stable, the bottom branch is unstable and there is also a stable fixed point branch at  $C_f = 0$ . On the vertical axis the value of  $C_f$  on day 1 of each year (December 21st) is shown.*

possible combinations of  $p_5$  and  $p_{23}$ , all producing a different limit point. Using `CL_Matcont_for_maps` and varying  $p_{23}$  as well as parameter  $p_5$  creates a line of new limit or tipping points, as for each value of the parameter  $p_{23}$  there is a curve, such as the one in Fig. 4. If  $p_{23}$  changes, the curve will move and the limit point will move with it. In this way one can imagine a whole series of new curves with new limit points. By finding the limit points of all the possible combinations it becomes possible to define for which values of the parameters a forest has a chance of growing to a periodic state and living, depending on the initial value of  $C_f$ , and for which values the forest is doomed to widespread mortality. Fig. 5 shows the line of tipping points along with a schematic series of curves illustrating how the line of tipping points varies. The computed surface of fixed points and the line of tipping points is shown in Fig. 6.

As  $C_f$  is central to the distribution of carbon to the different carbon pools, it is possible to conclude that for values of  $p_{23}$  and  $p_5$ , situated on the left hand side of the line of limit points, the evergreen forest either grows to a stable periodic state and lives or it will eventually die, depending on the initial condition for  $C_f$ . For values of the parameters on the right hand side of the line of limit points the conditions are such that an evergreen forest will eventually die, whatever the initial value of  $C_f$ . This answers the question on how the behaviour of the foliar carbon pool changes for different values of the parameters,  $p_2$ ,  $p_3$  and  $p_5$ . It is interesting to note that the parameter values from the REFLEX project result in a point near the tipping point line, see Fig. 5.

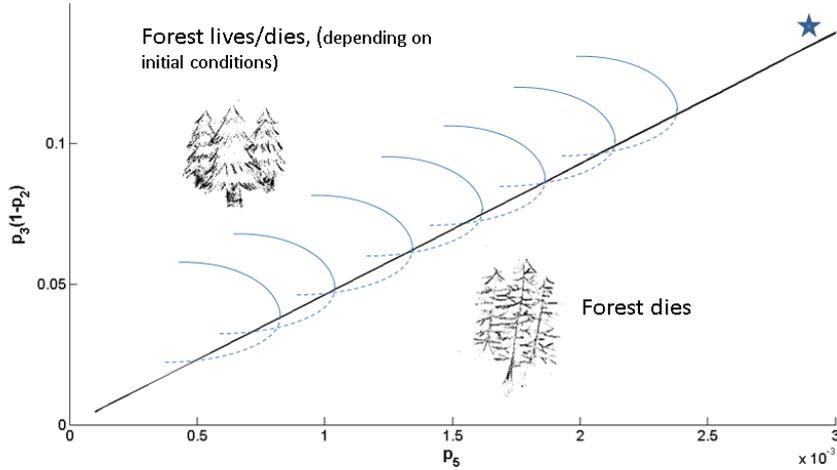


Figure 5: Schematic diagram showing how the limit points (tipping points) divide the parameter plane into two different regions. Note the star near the line of tipping points, which represents the real parameter values used in the REFLEX project.

The model is used to simulate the carbon cycle of an evergreen forest and, although in our analysis we have assumed that the drivers are periodic on an annual timescale, in reality the atmospheric carbon is increasing year by year, partly due to human activities such as the burning of fossil fuel [20]. The effect of atmospheric carbon is included in the model of photosynthesis, see equation (18) in Appendix B. Fig. 7 shows the effect that raising the atmospheric carbon,  $C_a$  has on the curve in Fig. 4. For fixed  $p_{23}$ , as  $C_a$  increases, the value of  $C_f$  at the limit point increases also. For a given value of  $p_5$ , with more  $\text{CO}_2$  used in photosynthesis, the forest grows towards a higher periodic solution and the region on the graph where a forest can live is bigger. Such a response is in agreement with McMahon *et al.* [21], who identify increased atmospheric carbon as a possible factor in increased growth of trees through carbon fertilisation. However, growth is also dependent on other resources. Research by McCarthy *et al.* [22] found that during a six year experiment at a Free Air  $\text{CO}_2$  Enrichment (FACE) site in Duke Forest, USA, pines receiving elevated  $\text{CO}_2$  had on average about 17 percent more needles than untreated pines, mainly depending on the amount of nitrogen present in the soil.

Interestingly, the increase of mean daily temperature by a constant amount of  $2.4^\circ \text{C}$  has no significant effect on the curve. Several studies suggest that this is the approximate amount the temperature will rise by the end of the 21<sup>st</sup> century even if the atmospheric carbon level is kept at its current value [23]. This lack of effect could be due to the fact that the data used is from a forest in a moderate climate. There are only 23 days in the data where the temperature during the day is slightly below zero. Also, in DALEC EV no provision is made for when the temperature goes below zero, which is

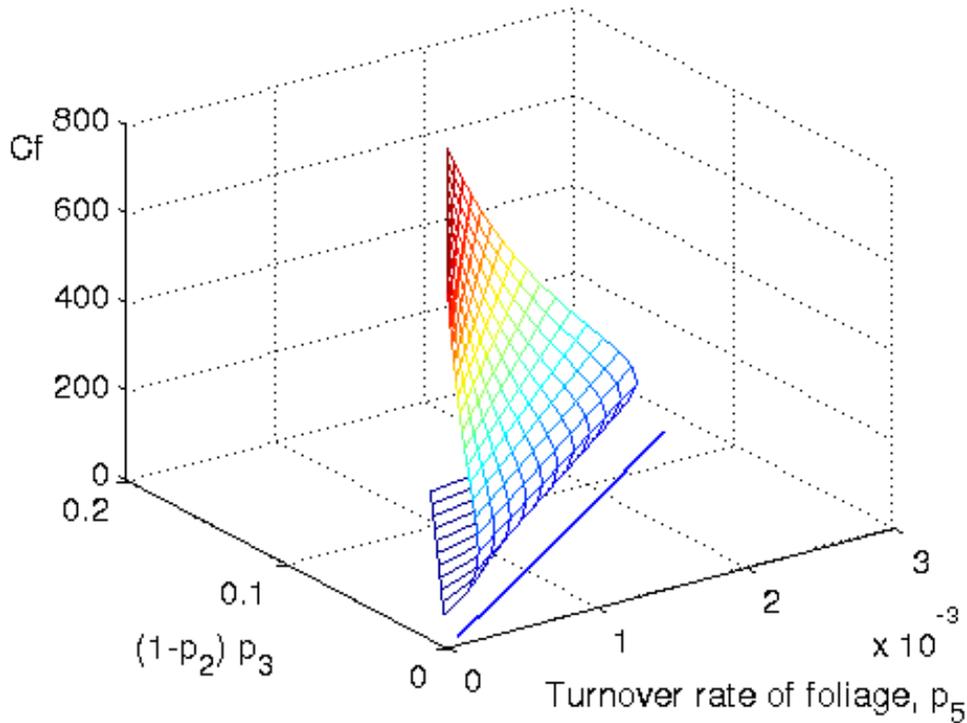


Figure 6: A plot of the surface of fixed points with the line of limit points projected onto the parameter plane.

when photosynthesis slows down or stops [24]. In DALEC EV photosynthesis takes place whatever the temperature. One might anticipate more temperature dependence for deciduous forests, as a temperature increase here could result in an increase in the length of the growing season.

The drivers for temperature and irradiance commonly used are highly variable, see Fig. 2. We now consider the effect that smoothing the drivers, as described in Section 2.2.2, has on the results as, for mathematical analysis purposes, it is more desirable to work with simple functions rather than raw data. In Fig. 8 the graph for  $C_f$  is obtained by running the model forward over three years and drawn with the original noisy drivers and the smoothed drivers. This shows that the effect of the smoothing on  $C_f$  is minimal and certainly does not change the qualitative behaviour.

The bifurcation graph and the line of limit points graph produced using the smoothed drivers also show qualitatively very similar behaviour, see Figs 9 and 10. The only difference is a small change in the path of fixed points for the foliar carbon and in the position of the limit point. The use of smoothed drivers greatly simplifies the analysis of the model as expressing data in terms of functions means it is not necessary to use separate data files. It can also simplify data collection as only three parameters are required, namely the mean, amplitude and phase.

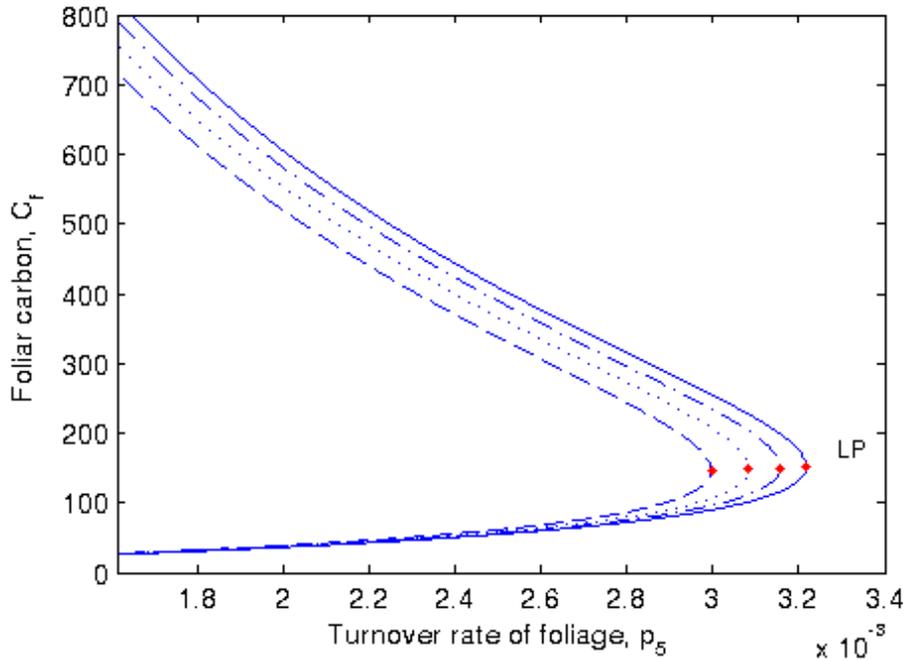


Figure 7: *Fold bifurcations for  $C_a = 380$  (dashed) ,  $C_a = 430$  (dot),  $C_a = 480$  (dash-dot) and  $C_a = 530$  (solid).*

According to Medvigy *et al.* [25], natural variability in drivers is important and ecosystems respond to it. His research shows that by taking away high-frequency variability decadal Net Ecosystem Production (NEP), GPP and total respiration is significantly enhanced. However, the ACM only takes into account daily measures of climate data and therefore the high frequency variability has already been taken out.

### 3.2 Behaviour of the Other Carbon Pools

For each of the fixed points of the annual map for the foliar carbon pool we can find corresponding fixed points for the other four carbon pools. For the fixed point  $C_f = 0$  it can be shown that all other pools also have a fixed point at zero. The roots carbon pool,  $C_r$ , and the litter carbon pool,  $C_{lit}$ , reach their fixed points relatively quickly, on the same time scale as the foliar carbon pool, see Fig. 11. However, the soil and organic matter carbon pool,  $C_{som}$ , and the woody carbon pool,  $C_w$  take a very long time (thousands of years) to reach their fixed points, due to the very small values of the parameters  $p_6$  and  $p_9$ . The wood pool,  $C_w$ , grows faster than the soil and organic matter pool, as is shown in Fig. 12. Due to the very slow growth of  $C_{som}$ , we can regard the initial value of  $C_{som}$  as a pseudo-fixed point on a decadal scale.

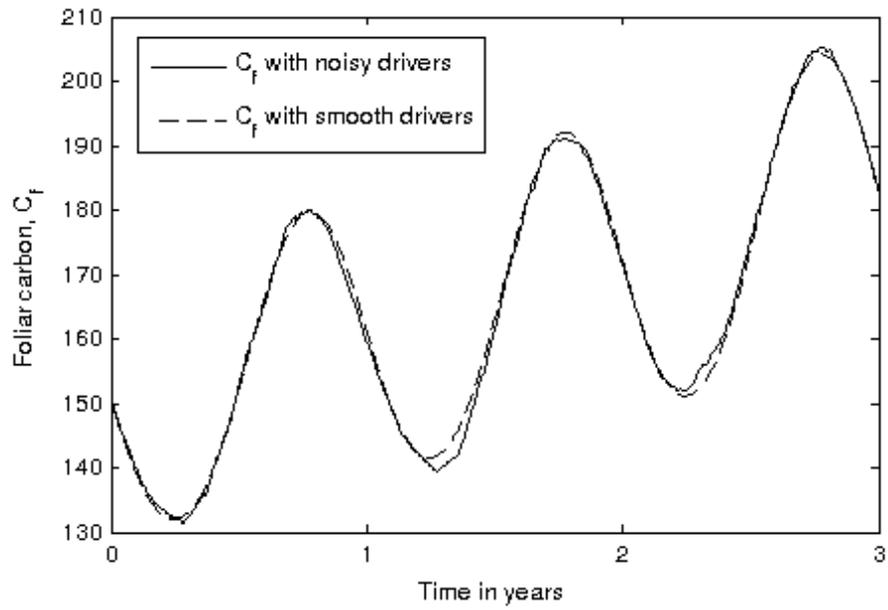


Figure 8:  $C_f$  over three years shown using noisy drivers and smoothed drivers.

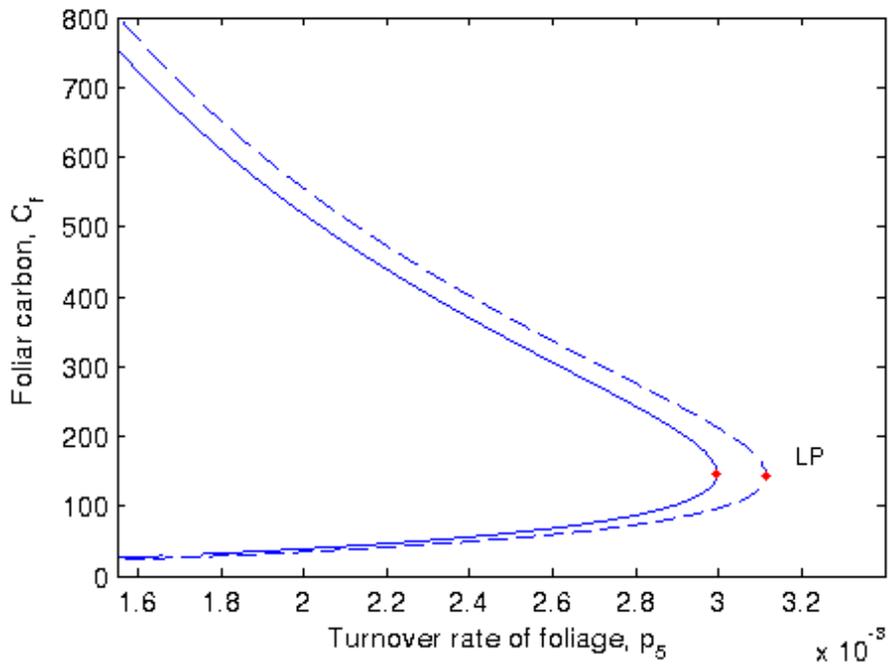


Figure 9: The solid curve is the result of using smoothed drivers, the dashed curve is the result of using noisy drivers.

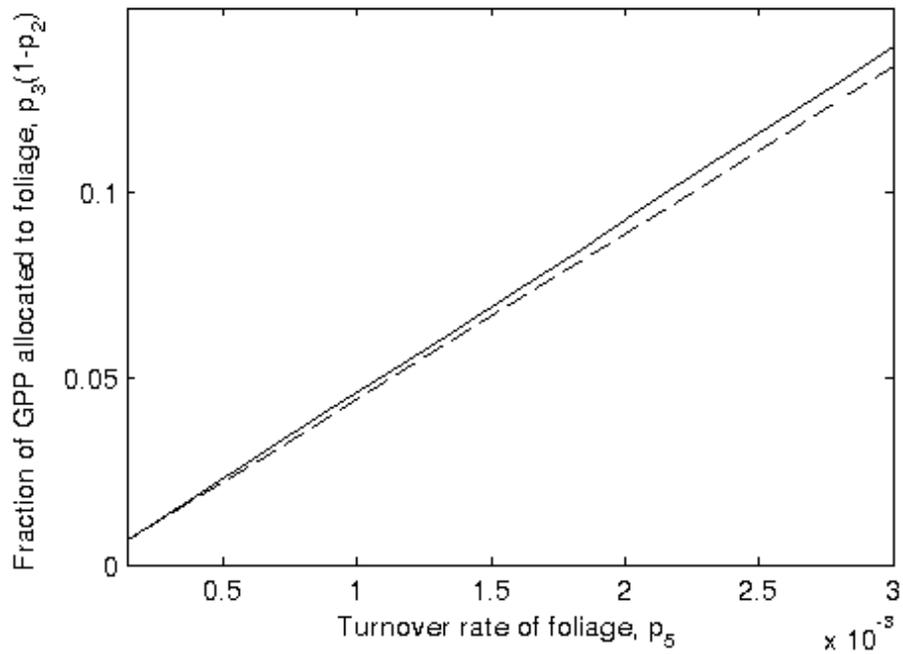


Figure 10: *The continuous line of limit points is the result of using smoothed drivers, the dashed line is the result of using noisy drivers.*

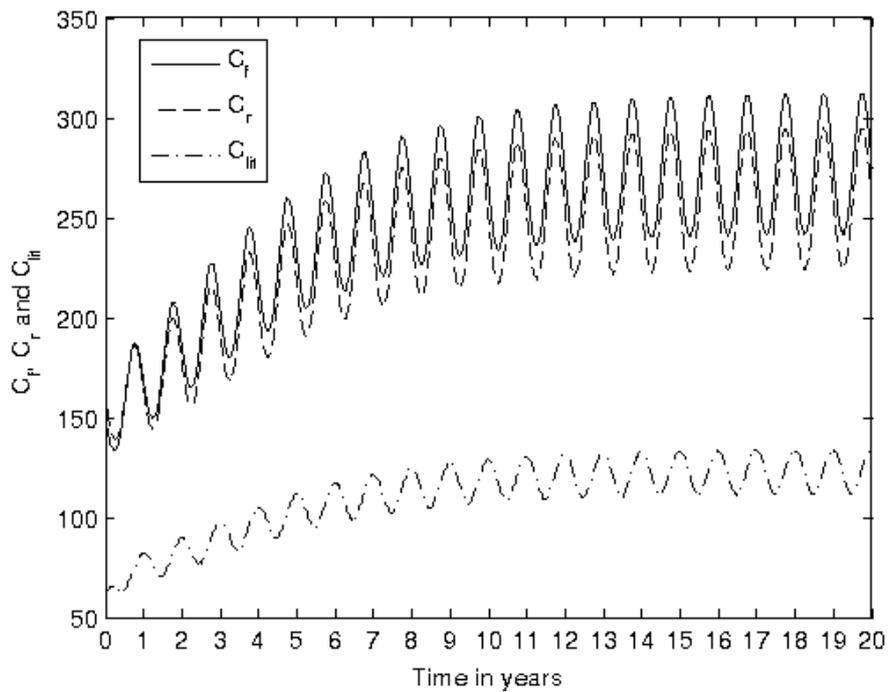


Figure 11: *Behaviour of  $C_f$ ,  $C_r$  and  $C_{lit}$  over 20 years; all three of these carbon pools reach a periodic state within this time.*

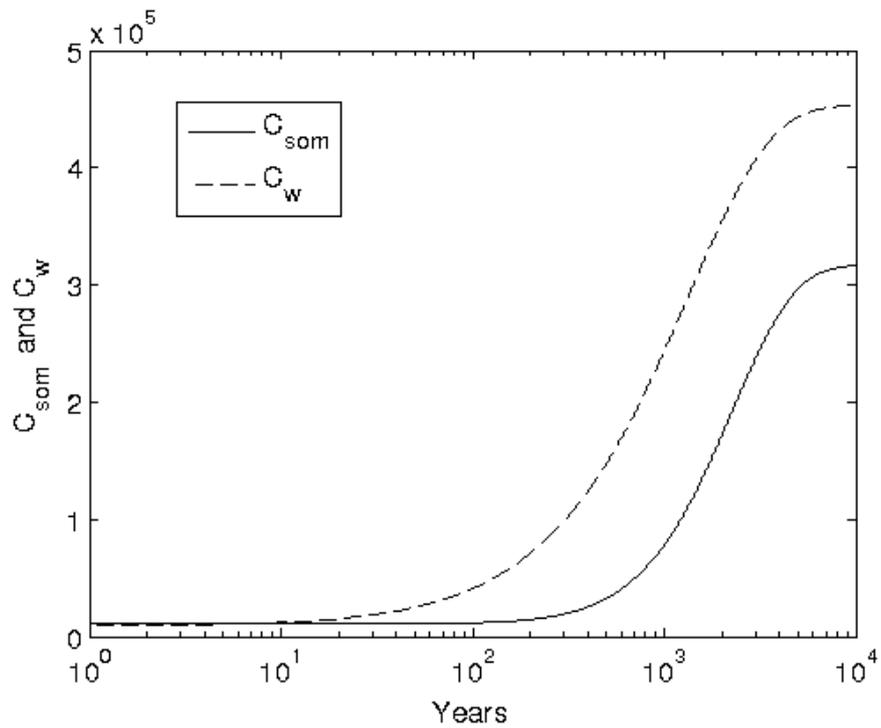


Figure 12: Only one point per year plotted, removing the periodic behaviour:  $C_{som}$  and  $C_w$  do not reach their fixed points until after 10,000 years (note the log scale).

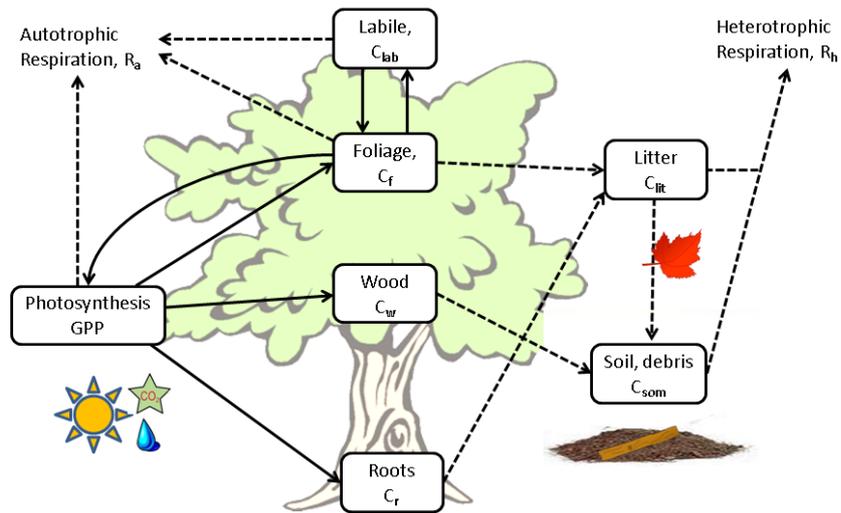


Figure 13: A schematic overview of the carbon cycle of a deciduous forest according to DALEC DE.

### 3.3 Preliminary Results for DALEC Deciduous

DALEC Deciduous, DALEC DE, is another version of the DALEC model, see Fig. 13. In this section we find that the model structure of DALEC DE is similar to that of DALEC EV.

As for DALEC EV the DALEC DE model equations [15] take the form of daily maps, specifically:

$$C_f(t+1) = ((-p_5(p_{14} + (1 - p_{14})T(t)))m_{tf} + 1)C_f(t) + (\min(p_{17} - C_f(t), p_3(1 - p_2)GPP(t)) + p_{15}(1 - p_{16})C_{lab}(t)T(t))m_{tl}, \quad (11)$$

$$C_{lab}(t+1) = (-p_{15}T(t)m_{tl} + 1)C_{lab}(t) + p_5(1 - p_{14})(1 - p_{16})C_f(t)T(t)m_{tf}, \quad (12)$$

$$C_r(t+1) = (1 - p_7)C_r(t) + p_4((1 - p_2)GPP(t) - m_{tl}(\min(p_{17} - C_f(t), p_3(1 - p_2)GPP(t)))), \quad (13)$$

$$C_w(t+1) = (1 - p_6)C_w(t) + (1 - p_2)(1 - p_4)GPP(t), \quad (14)$$

$$C_{lit}(t+1) = (1 - (p_1 + p_8)T(t))C_{lit}(t) + p_7C_r(t) + p_5p_{14}m_{tf}C_f(t), \quad (15)$$

$$C_{som}(t+1) = (1 - p_9T(t))C_{som}(t) + p_1T(t)C_{lit}(t) + p_6C_w(t), \quad (16)$$

where  $t$  is time in days and  $T(t) = 0.5 \exp(p_{10}T_m(t))$  is the temperature sensitive rate parameter.  $T_m(t)$  is the mean daily air temperature. There are 17 parameters in DALEC DE; for a description see Appendix A. The variable  $m_{tf}$  switches the turnover of foliar carbon on or off and  $m_{tl}$  switches the turnover of labile carbon on or off, depending on the time of year. Typically we have used the following initial conditions for the five pools:  $C_f(0) = 80g C m^{-2}$ ,  $C_{lab}(0) = 80g C m^{-2}$ ,  $C_r(0) = 80g C m^{-2}$ ,  $C_{lit}(0) = 60g C m^{-2}$ ,  $C_w(0) = 8800g C m^{-2}$  and  $C_{som}(0) = 7100g C m^{-2}$ . The GPP is the same as for the DALEC EV model, as given in equation (6). Also, as for DALEC EV, the values of the initial conditions for the carbon pools are based on suggestions made by REFLEX [15].

The main difference between the two models is that DALEC DE has an extra labile pool,  $C_{lab}$ . Fig. 14 shows graphs for both the foliar pool,  $C_f$  and the labile pool,  $C_{lab}$ . The shape of both graphs are caused by the switching on and off of foliar turnover and labile turnover. In the autumn, around day 200, foliar turnover is switched on and labile turnover is switched off. The trees drop their leaves and photosynthesis comes to a halt. The foliar carbon pool is depleted and carbon is stored in the labile pool until spring (approximately between day 100 and 150), when the foliar turnover is switched off and the labile turnover is switched on to kick start the growth of leaves and replenish the foliar pool. In the summer, both the labile pool and the foliar pool remain unchanged for some time (approximately between day 170 and 200), which is when both the foliar turnover and the labile turnover are switched off.

We see that in this model, the foliar and labile pools are coupled but decouple from the other four equations. Even though the dynamics of the forest now depends on two carbon pools, we found a bifurcation structure which is similar to that of DALEC EV, see Fig. 15. Additionally, Fig. 16 shows

a similar path of limit points for both versions. We used the same climate data as for DALEC EV and the same values of the common parameters to provide an appropriate comparison between the two versions.

## 4 Discussion and Conclusion

We have analysed the qualitative dynamical behaviour of DALEC EV and DALEC DE, which are simple process-based vegetation models for carbon stocks and stores of evergreen and deciduous forests that have been used to study model uncertainty, parameter estimation and carbon fluxes. We have shown that the dynamics of an evergreen forest, according to the DALEC EV model, fundamentally depends on the behaviour of the foliar carbon pool and the parameters involved in this pool,  $p_3(1-p_2)$  (fraction of GPP allocated to foliage) and  $p_5$  (daily turnover rate of foliage). The dynamics of the foliar carbon pool show a tipping point, which is dependent on the value of these parameters and explains how, for certain values of the parameters, according to the model, a forest is expected to die out, without any chance of coming back to life. Likewise, for other values and depending on the initial conditions of the foliar pool, a forest grows to an annual cycle and lives. For example, Fig. 4 shows the tipping point for the daily turnover rate of foliage,  $p_5$ , with a value of approximately 0.00315. Beyond this value and for a fixed value of  $p_{23}$ , the trees lose too much carbon through the loss of their needles to survive. Since leaves produce photosynthate, this means that the trees cannot feed themselves and they will die eventually. The three parameters are dependent on each other and there needs to be a balance between them for the forest to thrive. Suppose, in Fig. 5, that the forest is at a point in the graph where  $p_{23} = 0.04$  and  $p_5 = 0.0002$ . This is a point in the area of the graph where a forest is expected to show widespread mortality. The reason for this is that the fraction of GPP allocated to foliage is not in balance with the daily turnover rate of the foliage. For a value of  $p_{23} = 0.04$ , the daily foliar turnover rate,  $p_5$ , would need to be smaller than 0.001 for a forest to have a chance to stabilise and live, depending on the initial conditions of the foliar carbon. We could look at it from yet a different perspective: if  $p_3(1-p_2)$  is very small then this will almost always result in the forest dying, since very little of the GPP is then allocated to the foliage. Clearly, these conditions should be avoided in order for the forest to live. It is interesting to note that, using data for a real forest, the parameter values are near the tipping point.

This research can help users of the model to set and find sensible values for the parameters. Also, although the model does not have a hydrological component, the photosynthesis term,  $C_i$ , contains a hydrological variable, which is set to a constant. Varying the constant could allow for experimentation with drought shocks, which could change the location of the tipping point and affect the fate of the forest. Additionally we have shown that it may not be necessary in DALEC, for a forest that is living in a steady climate, to use daily driver data, but that it is sufficient to represent the drivers

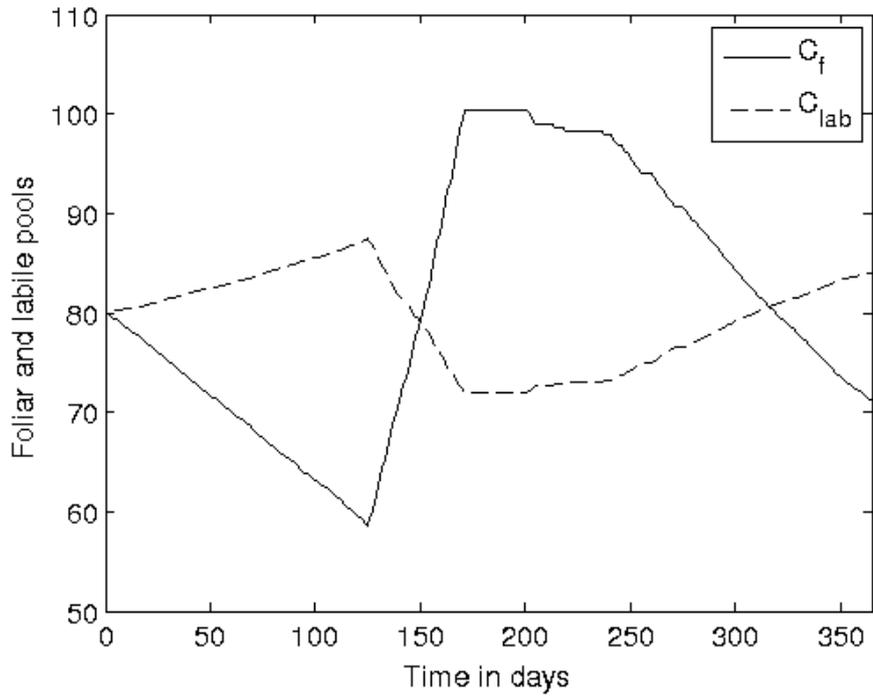


Figure 14: *The foliar and labile pools plotted over one year.*

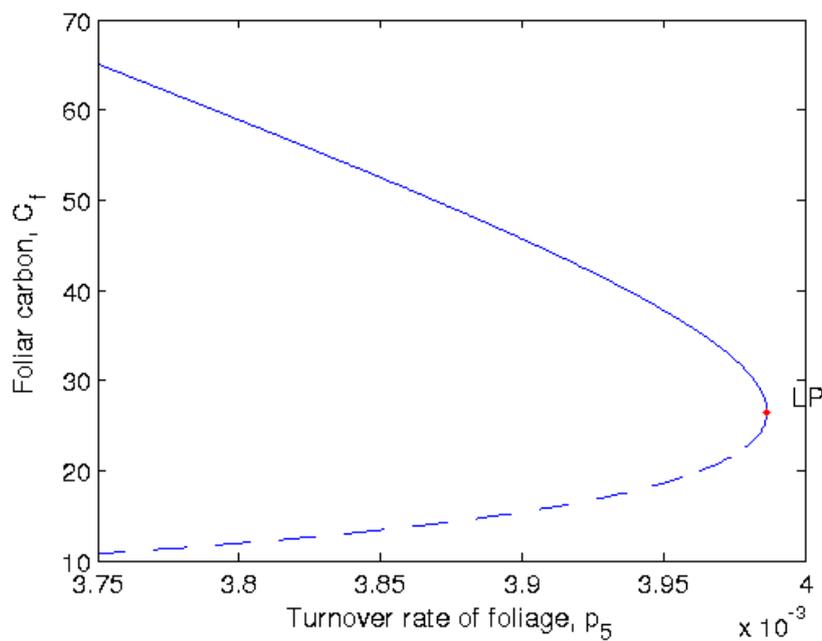


Figure 15: *Limit point for parameter  $p_5$  on a path of fixed points of the annual map for  $C_f$  for DALEC DE. The top branch is stable, the bottom branch is unstable and there is also a fixed point branch at  $C_f = 0$ . The fixed points are sampled on day 1 of each year, which is December 21st.*

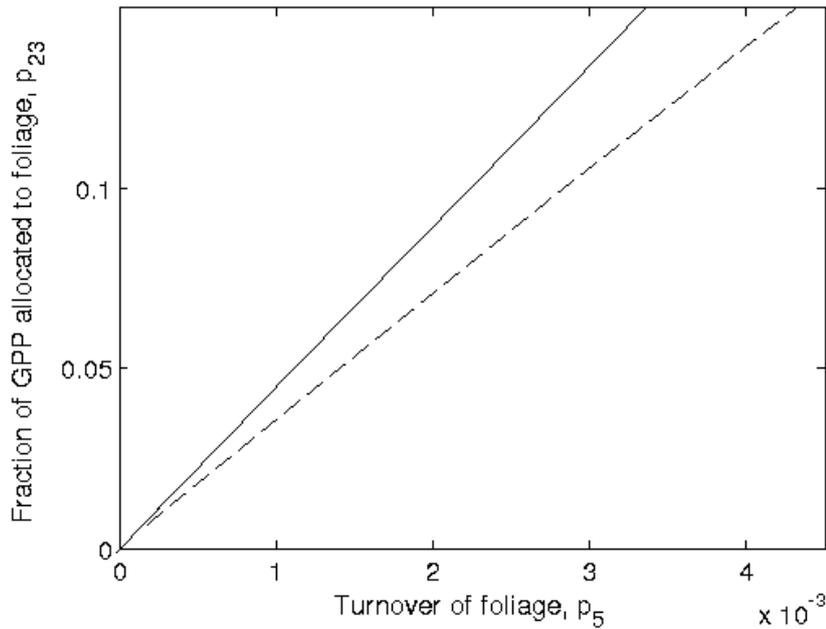


Figure 16: *The continuous line shows the path of limit points of  $C_f$  for parameters  $p_{23}$  and  $p_5$  for DALEC EV, the dashed line is the path of limit points of  $C_f$  for parameters  $p_{23}$  and  $p_5$  for DALEC DE.*

by a smooth cosine wave, where all that is needed is to measure the amplitude, mean and phase of the annual cycle. However, we do acknowledge that smoothing the drivers takes away the natural variability, to which ecosystems respond. According to Medvigy *et al.* [25], removal of high-frequency variability significantly enhances decadal Net Ecosystem Production, NEP (measurement of the net gain or loss of carbon in a system over a period of time), GPP and total respiration. Interestingly, according to his research, solar radiation has a strong effect, whereas temperature variability only has a minor impact by comparison. During our smoothing exercise, we found that the model seems to be more sensitive to solar radiation, which is why we had to resort to data assimilation methods to make the function fit, than to the temperature data. In DALEC, using the smoothed drivers did not make much difference to the results, perhaps as the high frequency variability was already taken out, the data being daily averages rather than hourly observations.

There are of course other limitations to the model. In reality a forest as a whole is not dependent on the foliar carbon alone. For example, when a forest dies because a tipping point has been reached, there will be stocks in the soil, such as seeds, which could make a forest come back to life if circumstances change. The model does not allow for this in its current form. For simplicity, the model also does not allow for any changes in soil moisture, which affects the survival of a forest in reality. For the forest data considered here, from three non-drought stressed years, it is reasonable to neglect the effect of water. However for other regions, this may not be true and other versions that include hydrological modelling are needed, such as DALEC Water [13].

The DALEC EV model does seem to catch the qualitative behaviour of describing carbon stocks and stores: “*We have attempted to strike the correct balance between sufficient model complexity to capture the essential dynamics of the system while maintaining simplicity*” [26] and in future research it would be interesting to compare this simple model to more complex models to see if they have the same qualitative dynamics.

We have already shown that DALEC deciduous, which is an example of a slightly more complex model due to leaf loss in the autumn and the requirement of an extra carbon pool, exhibits a similar structure. From Fig. 16, which shows a comparison between DALEC EV and DALEC DE, one could suggest that DALEC DE seems to be more robust than DALEC EV, as there is a larger range of parameter values for which a forest can survive.

It would be interesting to investigate the effect of adding a hydrological module to DALEC and to examine the grassland version, which we expect to show similar behaviour. As mentioned in the introduction, many other DGVMs use a similar photosynthesis model based on the Farquhar model, and so it is expected that they will exhibit similar behaviour as well. Photosynthesis sits at the heart of all process-based models and it is the nonlinearity of the photosynthesis model that underlies the structure that is seen in DALEC EV and DALEC DE. Although many models are more complex than the DALEC models, one should also expect a similar bifurcation structure to occur.

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## Appendix A

This appendix contains the parameters.

### Parameters to be calibrated:

	Description	Value in our analysis
$p_1$	Daily decomposition rate	0.0000044100
$p_2$	Fraction of GPP respired	0.52
$p_3$	Fraction of NPP allocated to foliage	0.29
$p_4$	Fraction of NPP allocated to roots	0.41
$p_5$	Daily turnover rate of foliage	0.0028
$p_6$	Daily turnover rate of wood	0.00000206
$p_7$	Daily turnover rate of roots	0.003
$p_8$	Daily mineralisation rate of litter	0.02
$p_9$	Daily mineralisation rate of soil and organic matter	0.00000265
$p_{10}$	Parameter in exponential term of temperature dependent parameter	0.0693
$p_{11}$	Nitrogen use efficiency parameter in ACM	7.4
<b>Only used in DALEC DE</b>		
$p_{12}$	GDD value causing leaf out (GDD is the growing degree day factor)	300
$p_{13}$	Minimum daily temperature causing leaf fall	12
$p_{14}$	Fraction of leaf loss transferred to litter	0.5
$p_{15}$	Daily turnover rate of labile carbon	0.0028
$p_{16}$	Fraction of labile transfers respired	0.2
$p_{17}$	Maximum $C_f$ value ( $\text{g C m}^{-2}$ )	100

### Parameters viewed as constants, all in ACM:

	Optimised Value
$a_2$	0.0156
$a_3$	4.22273
$a_4$	208.868
$a_5$	0.0453
$a_6$	0.3783
$a_7$	7.1929
$a_8$	0.0111
$a_9$	2.1001
noisy $a_{10}$	0.7897

## Appendix B

This appendix contains the functions in the GPP.

### Canopy Conductance, $g_c(t)$

$$g_c(t) = \frac{|\psi|^{a_{10}}}{0.5T_{range}(t) + a_6R_{tot}}, \quad (17)$$

where:

$$\begin{aligned} \psi &= 2 \text{ (constant),} \\ R_{tot} &= 1 \text{ (constant).} \end{aligned}$$

### CO<sub>2</sub> Concentration at Site of Carboxylation, $C_i(t)$

$$C_i(t) = \frac{1}{2} \left[ C_a + q - p(t) + \sqrt{(C_a + q - p(t))^2 - 4(C_a q - p(t)a_3)} \right], \quad (18)$$

where:

$$\begin{aligned} C_a &= 380 \text{ (constant averaged over three years);} \\ q &= a_3 - a_4 = -204.64527 \end{aligned}$$

### Photosynthate, $p(t)$

$$p(t) = \frac{p_{11}NL(t)}{g_c(t)} \exp(a_8T_{max}(t)), \quad (19)$$

where:

$$\begin{aligned} N &= 4 \text{ (EV) and } 1 \text{ (DE) (constant),} \\ L(t) &= C_f(t)/lma, \\ lma &= 110 \text{ (EV), } 22 \text{ (DE) (constant).} \end{aligned}$$

### Canopy Level Quantum Yield, $E_0(t)$

$$E_0(t) = \frac{a_7L(t)^2}{L(t)^2 + a_9}, \quad (20)$$

where:

$$L(t) = C_f(t)/lma,$$

## Solar Declination

$$\delta(t) = -23.4 \cos(2\pi t/365)(\pi/180) = -0.408 \cos(2\pi t/365). \quad (21)$$

## Day Length

$$s(t) = 24 \cos^{-1}(-\tan(\text{lat}) \tan(\delta(t)))/\pi,$$

where:

$$\text{lat} = 52^\circ \text{ (constant)}$$

## Appendix C

This appendix contains a list of symbols.

<b>Symbol</b>	<b>Description</b>
$\psi_d$	Max soil-leaf water potential difference (MPa)
$T_r$	Daily temperature range ( $^{\circ}\text{C}$ )
$R_{tot}$	Total plant-soil hydraulic resistance ( $\text{MPa m}^2\text{s mmol}^{-1}$ )
$N$	Foliar nitrogen ( $\text{g N m}^{-2}$ leaf area)
$lma$	Leaf mass per area ( $\text{g C m}^{-2}$ leaf area)
$L$	Leaf area index ( $\text{m}^2 \text{m}^{-2}$ ) (LAI)
$T_{max}$	Maximum daily temperature ( $^{\circ}\text{C}$ )
$T_m$	Mean daily air temperature ( $^{\circ}\text{C}$ )
$C_a$	Atmospheric $\text{CO}_2$ concentration ( $\mu\text{mol mol}^{-1}$ )
$\delta$	Solar declination (radians)
$D$	Day of the year
$lat$	Site latitude ( $^{\circ}$ )
$I$	Irradiance ( $\text{MJ}^{-1} \text{m}^{-2} \text{day}^{-1}$ )
$R_a$	Autotrophic respiration
$R_h$	Heterotrophic respiration, $R_{h_1} + R_{h_2}$ ( $\text{g C m}^{-2}$ ) $R_{h_1}: p_8 C_{lit} T(t)$ $R_{h_2}: p_9 C_{som} T(t)$