Macroecology: Exploring Forest Investment Strategies

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Declaration

I herewith declare that I have produced this work by myself with collaboration with project partners and supervisors for this thesis, and that it has not previously been presented to obtain a degree in any form.

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Abstract

In this project a novel approach to modelling allocation is proposed by using quantitative economic theory to describe allocation. Where "investment" has often been used to describe the process of allocation this framework proposes a more literal use of economic theory by the application of econometrics. Forest allocation is described in terms of capital (state), resource capture (process) and investment (allocation decision-making). The system is further bound by its focus on the photosynthetic activity in the economic framework. Photosynthetic capital is therefore defined as all apparatus directly or indirectly involved in harnessing the Sun's energy. The resource capture (photosynthesis) is then explored within the confines of the economic framework in order to see how capital drives photosynthetic uptake. Finally the investment is explored for the purpose of observing patterns and relations. A final model is then devised showing the following: (1) there is evidence to suggest that forests behave like economies holding a set capital to use for obtaining resources which are then invested within the confines of the system; (2) photosynthetic capital behaves in a productive way meaning that the subsystems of the capital contribute in varying degrees to the final outcome producing a lower result in the winter and an increase over the growing season; (3) marginal return on investment is a significant driver determining how much resource ultimately gets invested into the mechanism obtaining that resource; and finally (4) evergreen and deciduous forests show signs of different economic responses, wherein the evergreen forests are much more stable with higher capital but lower overall investment and decays and deciduous forests dedicate much bigger investment when resources available but show a decrease of capital to almost 0 during winter.

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1 Introduction

Climate change is seen as a major threat to society and the environment around the world. The many impacts predicted range from changes to species' distribution, to food production and water availability (IPCC, 2014). Therefore, one of the challenges that climate scientists now face lies in understanding how climate change will affect people, economies and the environment. The key to this challenge resides in global climate models which predict how changes in CO_2 emissions, temperature, precipitation, land use and other important factors will impact the future of the planet. They achieve this by combining knowledge of climatic, oceanic, land and anthropological feedbacks.

Originally climate models did not focus on the biosphere but on the atmosphere and oceans. Since then, this has been changed by the introduction of vegetative surfaces to models (such as Dynamic Global Vegetation Models). The development of these has been further aided by the increased use of eddy covariance techniques which measure carbon fluxes and the development of widely available databases such as FLUXNET that store this captured data from sites across the globe. Prior to the existance of FLUXNET, and other such projects, a few models were invented that analysed biosphere carbon fluxes. However, the development of FLUXNET gave biosphere modellers the flexibility of using samples from a wide range of ecosystems for the purpose of tuning and verification of model parameters on a global scale, thus boosting the development of models focusing on the biosphere (Abramowitz et al., 2008).

Dynamic Global Vegetation Models (DGVMs; e.g. LPJ (Sitch et al., 2003), TRIFFID (Cox, 2001), HYBRID (Friend et al., 1997)) are now applied to use within global climatic models to simulate feedbacks between the biosphere and the atmosphere. Though varried in the details of their build DGVMs focus on natural land processes which have significant effects on climate. Changes to land-use, surface and subsurface composition can influence the climate on local, regional as well as global scales. This is an effect of feedbacks of water, nutrients and CO_2 between the atmosphere, plants and soils. Dynamic Global Vegetation Models focus on mathematically representing these relations. One of the main focuses of these models lies in the carbon cycling between the atmosphere, vegetation and soils (Sato et al., 2015). Furthermore, they use Plant Functional Types (PFTs; such as C3 grasses, C4 grasses, evergreen broadleaf forests, etc.) to represent the differences in various vegetative surfaces and the different roles they play in the carbon cycle. Overall, the crucial part that vegetation plays in the ecosystem carbon cycle makes vegetation models a key element in modelling land surfaces (Sato et al., 2015).

However, despite the large amount of research into climate change, vegetation models are amongst the most uncertain components of earth system models (Sitch et al., 2008). These significant unknowns originate from the lack of understanding of many important and fundamental processes (Litton et al., 2007; Purves and Pacala, 2008) and an inability to parametrise at the correct scale (Dewar, 2010; Chen et al., 2013; Franklin et al., 2012).

One of the elements that causes this uncertainty is the lack of understanding of carbon allocation processes, which are a central part of vegetation models, and especially forest models (Chen et al., 2013; Dewar, 2010; Mäkelä, 2012; McMurtrie and Dewar, 2013). Since forests represent a key land carbon sink, storing 45% of carbon present on land (Bonan, 2008), they feature heavily in vegetation models. Forest models, representing several of the PFT classes, are a key element of the vegetation part of land surface models. They focus on calculating net ecosystem productivity (NEP) or the amount of carbon absorbed by the forest ecosystem. Forest models simulate carbon, water and nutrient uptake from the environment and model how these are then used in trees and the whole ecosystem for growth, maintenance reproduction and other functions. Depending on their function some models go into more detail and simulate species variance, competition and other social aspects of ecosystems (Medlyn et al., 2011). In forest models allocation is the term used to describe this process of active sequestering of carbon and other nutrients in different parts of the plant or ecosystem. The resulting growth then produces a feedback in the ecosystem determining future uptakes of carbon and nutrients. This element of feedback heavily influences forest productivity. With the importance of this process in mind, there is clearly a need for reliable allocation modelling.

However, views on how to model carbon allocation in ecosystems have long been a subject of discussion and disagreement among scientists (Ise et al., 2010). Amongst all of this discussion allocation has been branded as the Achilles heel of forest models (Le Roux et al., 2001). On a whole, it is one of the least understood processes in forest carbon modelling (Malhi, 2012). Many reasons contribute to the difficulty of modelling this phenomenon.

Firstly, allocation is not a process which can be measured directly. Current methods are based on indirect measurements of forest productivity such as biomass or carbon fluxes. Furthermore, there is an uncertainty about whether the use of surrogates (such as biomass or carbon fluxes) is a sufficient representation of allocation (Litton et al., 2007). It has already been observed that there are discrepancies between biomass gain and observed fluxes (implying that growth is not limited by carbon uptake) and most models currently focus their attention on representing fluxes (Körner, 2003, 2013). Experiments dealing with allocation have focused primarily on seedlings with a significant lack of understanding about the differences between young and mature plant allocation (Chen et al., 2013).

A second problem is that allocation occurs on different timescales. The problem of differences between allocation in young and mature plants has been touched upon in the previous point. Beyond that there is more complexity arising from reallocation and storage. Plants will often reallocate their resources upon senescence (Franklin and Ågren, 2002) leading to more complex relationships between organs. Furthermore, sometimes not all carbon is used upon uptake. Some of it is stored as non-structural carbohydrates (NSCs) to be used later when necessary (Fatichi et al., 2014). This has often been observed to occur under increased stress and is related to plants' survival strategies. However, the dynamics of NSCs are as of yet not very well understood in terms of modelling (Dietze et al., 2014). Because of this lack of understanding, storage is very rarely if at all considered in allocation schemes in major vegetation models.

Finally, further difficulty lies in unravelling how environmental and genetic factors can impose different allocation schemes to cover various survival strategies. Factors such as species or plant type are represented by PFTs which define how models tackle the differences in morphology and biogeography represented by these ecosystems (Lavorel et al., 2007). For example, simple differences such as broadleaf and needleleaf forests, or temperate and tropical climates are taken into account. However, drawbacks have been found with this approach. Purves and Pacala (2008) argue that these aggregates do not capture the dynamics of biodiversity and that climatic responses could be largely distorted because the species' feedbacks are averaged. Some believe that PFTs should be abandoned for a traits based approach which does not differentiate between types but allows variation in traits (Van Bodegom et al., 2012; van Bodegom et al., 2014). Moreover, other factors, besides tree species, such as stand age, competition and resource availability can have an effect on allocation (Litton et al., 2007).

All of these unknowns and questions factor into current models and present themselves in the form of compounding uncertainty. For example, a study done by Sitch et al. (2008) evaluating five DGVMs shows significant differences in results over a 100 year period. Questions, such as how complex the model should be, how should carbon uptake be modelled and how important are individual components do not have any one answer at this point in time and often depend on the application of the model. While some models use complex feedbacks between numerous organs and recycle nitrogen and carbon within a tree, others propose more basic approaches such as fixed proportion of carbon being allocated in the tree.

In models that are currently in-use this complexity-fuelled uncertainty presents itself in detailed mechanistic physiological modelling. Models have numerous parameters which are both difficult to measure on a global scale and, in some cases, hard to interpret (McMurtrie and Dewar, 2013). Therefore, often approximations and values selected from literature will be used (Purves and Pacala, 2008). Although the understanding of the underlying biophysics and biochemistry are well understood, because allocation is not a single process but a consequence of several processes, understanding how these come together is still a big challenge to modellers (Mäkelä, 2012). It is further amplified by the fact that most physiological models are designed to represent processes at small-scales and over short periods of time (Smith and Dukes, 2013).

All of the problems with uncertainties are further amplified by the compound effect of growth. For example, even over a 20 year period a small miscalculation of how much carbon is allocated to foliage may severely affect the under- or over-estimation of future carbon uptake. Since many models aim to predict effects of land and climate feedback over several decades all of these unknowns will add to a growing uncertainty.

Disagreement also exists about the extent to which complexity should be introduced into models. Some scientists believe that increased complexity represents a more realistic view of the ecosystem and others see it as a way of introducing error into the system. Arguments exist to support the introduction of further details, such as improved below-ground system modelling (Ostle et al., 2009), respiration (Smith and Dukes, 2013) or biodiversity (Purves and Pacala, 2008). Shortcomings of current models, especially when caused by inaccurate description of biological processes, see the rise of arguments supporting increased complexity that might improve model performance (Gonzalez-Meler et al., 2013). However, there are also many who argue against it. Looking at the natural sciences and ecology as a whole May (2004) and Lawton (1999) argue that increased complexity does not necessarily increase our understanding of the underlying process. In fact, it may do the exact opposite. Understanding the model outputs is an essential part of modelling. Drawing on Einsteins words,

A model should be as simple as possible, but not more so.

The question can therefore be raised about whether current approaches are sufficient to accurately represent allocation? Complexity, difficulties in measurement, approximations, even disagreements about the nature of allocation all lead to discrepancies between model results and force a user of the model to look carefully at assumptions to make a decision about whether the model is the right one to use (Medlyn et al., 2011).

Whilst current dynamic global vegetation models and allocation schemes are constantly being improved, moving away from current forest models and fixed allocation schemes might be the way forward in modelling forest productivity. However, while new approaches on how to model carbon allocation exist, most modellers continue to use the abovementioned complex models of photosynthesis and fixed allocation methods (Franklin et al., 2012). These new methods show promise in tackling some of the issues mentioned earlier, so prevalent in current vegetation models. Although several categorizations for vegetation models exist this project will follow the scheme devised by Franklin et al. (2012). Under this classification the following categories are identified: empirical, allometric and functional-balance techniques, evolutionary approaches and thermodynamic entropy methods. Out of these the first three are widely used in current vegetation models and represent fixed schemes (empirical) or schemes with some degree of flexibility (allometric and functional-balance) based on either individual size or resource needs. These are relatively simple approaches with functional-balance representing the most complex solution of the three. The other two approaches (evolutionary and entropy) are relatively recent and represent new thinking in the area of allocation modelling. The lack of a method for direct allocation measurement means that it may be necessary to draw theories and observations from other fields. This is something that evolutionary and entropy approaches do well and may be a significant strength in these models.

Evolutionary based approaches are amongst the most computationally expensive of methods due to their complexity. They draw on principles of ecological and evolutionary theory. They impose a top-down condition on the system that selects a so called fitness proxy: an indication of the tree's survival strategy. These models, which include optimal response, game-theoretic optimization and adaptive dynamics methods, assume that the current state of the ecosystem is a result of evolution towards a strategy optimal for tree growth and survival. They focus on finding and maximizing the fitness strategy, or in the case of the adaptive dynamics method on finding the evolution stable strategy, which can be a combination of strategies, that promote the healthiest growth for the tree. It assumes that from an evolutionary stand point the trees that have the highest survival rate are the ones that are the most fit, therefore have the biggest fitness proxy. This eliminates the need to estimate a number of allocation factors that can be both uncertain and difficult to measure (Franklin et al., 2012) but replaces it with quantification of tree fitness.

Another novel approach moves even further away from traditional biological observation and borrows from physics and information theory to view ecosystem growth. Entropy-based approach or maximum entropy production (MEP) fundamentally assumes a grey-box system in which the current state of the ecosystem is represented as the most likely state that the system will have reached. This likelihood is then formalized as being represented by the number of sub-states that would lead to the system being realised in that state. It defines the ecosystem in terms of probability and implies that the system state is the most probable one with several roads leading up to this realization.

Whilst very different these two approaches have several things in common. Firstly, they use biological knowledge and observations of forest systems together with other disciplines to explore ecosystems. For evolutionary approaches this is evolution theory and for entropy it is thermodynamics. In fact, Fourcaud et al. (2008) notes that the use of interdisciplinary approaches are necessary to advance research in plant growth modelling and simulation. Secondly, they both assume a top-down controlling factor whether it is the fitness function or maximum entropy production. And lastly, it has been proven that they both relate to each other and MEP can represent different plant optimization theories on different spatio-temporal scales (Dewar, 2010).

However, even these methods have their shortcomings. Evolutionary based approaches suffer from a significant issue of no consensus on which fitness function should be used. Several proxies have been suggested. However, a significant downside lies in the potential inadequacy of the fitness function (Franklin et al., 2012). Though MEP aims to bridge some of these concerns and offers a way of addressing some relations between fitness functions by offering the theory of different fitness proxies for different timescales, it is still yet to be used in mainstream vegetation models. Because allocation is so central to carbon cycling the need for understanding the drivers behind tree “decision-making” are crucial.

This projects investigates a new approach to modelling allocation, drawing from the field of economics and relating economic theory to plant growth in order to investigate this decision-making in an economic framework. Since allocation is often viewed as an investment of resources into individual plant organs it is a natural step to consider this investment in an economic framework. This idea in itself is not new. Plant systems have been compared to economic systems in the past (Bloom et al., 1985; Bloom, 1986; Givnish, 1986) but since then economic terms have been used only in their general form, with much less comparison to their economic origin.

Bloom et al. (1985) compare plants to businesses and identifies several factors that produce commonalities between them. Firstly, they identify storage as a future investment decision. When resources are available but no need for them is present storing them as NSCs is a good way of ensuring supply in periods of shortage. Furthermore, they present the case that constraints on growth are subject to theories of marginal cost and revenue in photosynthetic as well as economic processes. Finally, they show that the marginal product (the response of primary productivity to availability of carbon, nutrients and water) is also very easily represented in plant systems. Bloom et al. (1985)'s argument that economical representation provides a reasonable framework for understanding resource acquisition seems to hold true.

This metaphor is rarely returned to. Plant carbon economy, investment and trade-offs are all terms that have been used to refer to carbon balance in plants, allocation and decision-making but they rarely take into consideration the underlying economic theories. Arguments exist that say that economy and ecology can learn from each other (Shogren and Nowell, 1992). Indeed, the links between economics and ecology are resurfacing. For example, a recent vegetation model suggested by Thomas and Williams (2014) has drawn on the concept of trade-offs in the decision making process. Investment into different plant functions is then drawn from estimates of fitness during a given year. A different approach has also been to analyse payback times of leaves (Poorter et al., 2006). Here the authors try to explain the investment of trees into leaves based on how much carbon they acquire over their lifetime versus how much carbon is invested in producing them, i.e. their carbon return on investment.

However, a deeper look into "The Economic Forest" metaphor may be needed. Viewing the ecosystem from the top down may simplify the process of understanding decision-making and allocation. An opposite to current physiologically detailed approaches would be to generalise structures and sort them together by function. A model based on this process would be modular and simpler to understand, explore and expand. Therefore, this project will aim to develop a model that is based on this approach of generalisation using economic concepts to group functions and properties together. However, instead of using Bloom et al. (1985)'s idea of a business-like singular plant this model uses macroecology and macroeconomy to form the model framework.

The macroecological approach to viewing the ecosystem is not a new concept. It tackles the problem of scaling from colonies to species, from individual plants to stands. It is difficult to make generalisations in ecology because of the complexity of local systems and the desire to understand all details which for each colony of species be it animal or plant will be different and contingent on everything from inter and intra-species competition, predation to regional climatic changes and unpredictable events such as fires and floods. Macroecology therefore provides a framework for the search for major statistical patterns in types, distributions, abundance of species on both a local and regional scale and the development and testing of underlying theoretical explanations for these patterns (Lawton, 1999). Macroecology is therefore

a perfect framework for a project that wants to generalise economic patterns for plants.

Macroeconomy, the study of economy as a whole as opposed to focusing on individual markets, is a perfect tool to introduce economics into forest ecosystems through the macroecological framework. One focus of macroeconomy is growth. Though many models of growth exist the basic idea behind most is that a system's capital grows through the investment of the product of work into the system. The capital, i.e. the assets that are used in the production of goods and services or already produced goods, are then used further in production to produce more capital. A healthy economy is such that has a stable or growing capital.

In a forest framework capital can be used to represent those ecosystem elements which contribute towards the growth and acquiring of resources in the ecosystem. These forest capital assets are then used to fuel the system; some are expended by processes and some are used to sustain resource acquisition through investment into more capital, similarly as in most economic growth models. With such an understanding of the system it is easy to arrive at having three interconnected modules: forest capital, resource acquisition and forest investment. These parallel greatly with economics. The new vocabulary is also advisable to distinguish between the already numerous terms used in plant allocation modelling. Finally, a look at needleleaf and deciduous forests can give a look into how this framework behaves for two different investment strategies placed in relatively similar climates.

1.1 Aims

This project aims to develop an economics-based model of forest allocation and growth by applying macroeconomic theory to canopy-scale modelling.

It will also look at how this model connects to current concepts and theories of forest allocation and how it can use the combined knowledge and understanding from different fields and methods to view and understand carbon allocation. Observations on a yearly time scale aim to reveal within-year phenology of investment and capital as used in this model framework.

Furthermore, it can be hypothesised that evergreen and deciduous forests will show different capital and investment functions. Variations between evergreen and deciduous forests have long been highlighted in terms of leaf lifespan and adaptation (Brian F. Chabot, 1982). A comparison of these two differing system is a natural way of testing the resulting model outcomes and comparing investment strategies. Based on initial

analysis a hypothesis is made that deciduous forests show a lower overwintering capital, bigger variation of within year capital and a bigger decay. Evergreen sites due to the nature of their long-term investment into foliage are assumed to have a higher capital in non-growth periods, smaller amplitudes within a year and a lower decay than deciduous forests.

2 Model Framework

The conceptualization of the model was based on analysing plant function, focusing on resource capture and allocation, with respect to economic concepts of capital, production and investment. Resource capture, or production in economics, is the creation of goods and services that can be used to induce growth. Allocation, as used in models, can be divided into two categories: the physical composition of plants (how much carbon and other nutrients different plant organs contain) and the decision-making process that allocation represents (how much of the carbon or nutrients taken up from the environment should be put towards each organ or function). The first definition can be referred to as capital. In economics this is the part that can be used to generate more resource. The decision-making process is similar to economic investment. A tree "decides" how much of the captured resource is sequestered in the "capital" and how much of it is "consumed" for other purposes. These elements will be further analysed in sections 3, 4 and 5. Table 1 features a short comparison between the three terms described above.

Amongst the "consumed" resource is part of the respiration. Because this project is primarily focused on the "invested" resources as opposed to "consumed" resources, Gross Primary Product (GPP) data is used in this project as opposed to Net Primary Production (NPP). FLUXNET data already accounts for the division of NPP into those two fluxes (through the use of an algorithm developed by Reichstein et al. (2005)).

The terms resource capture, investment and capital are used as the basis for the economic framework in this project and will be continued to be used to describe the processes in Table 1. In the current state of allocation models processes are often coupled with states. For example, to a certain extent allocation in current models can represent both the allocated material and the process of deciding how much to allocate. In this project a clear distinction is made between processes (resource capture), system state (capital) and decision making (investment). With this in mind a visual description of the system can be created (Figure 1), which shows how these "economic" subsystems interact with each other and the environment.

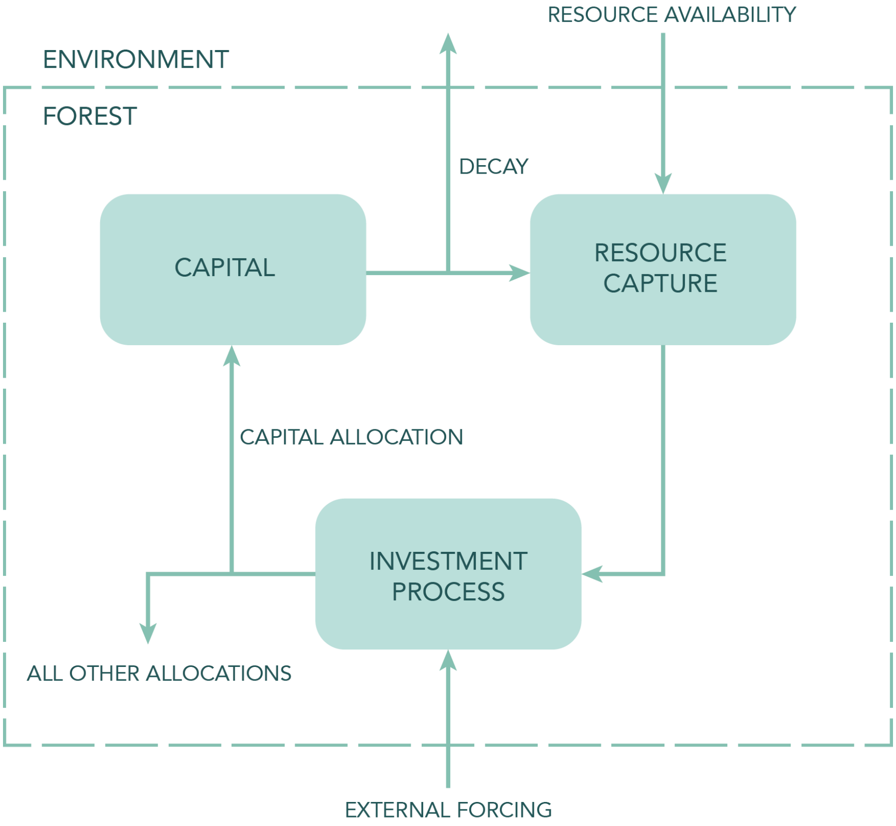


Figure 1: A simple model of forest relationships with environment in this framework. Resources are captured using the forest capital. The captured resources are then invested into producing more capital and the rest of those resources is put towards other uses (such as respiration or maintenance). The environment supplies resources and acts on the forest determining how much of the resources to allocate (this is also influenced by internal factors such as competition and baseline needs for growth). Furthermore, as capital decays it is released back into the environment.

Table 1: Economical plant comparison. A simple analysis into the differences between an economic and plant interpretation of economic terms.

Economic term	Plant Function	Economic Function
Resource acquisition (process)	Acquiring resources such as light, water and nutrients from the environment through the use of plant organs and tissues.	(also called labour function) Acquiring money and resources through the application of capital.
Investment (decision making)	The decision about how much of the acquired resources is allocated to different organs and tissues.	The decision about how much of acquired money is reinvested into back into the system.
Capital (state)	The accumulation of all the plant organs and tissues that are responsible for the upkeep of the plant through resource acquisition.	The accumulation of all the labour, equipment and other assets necessary to upkeep a company through acquiring more resources.

The decoupling of the system is a benefit to the modelling process as it allows the modeller to analyse the sub-modules separately without consideration of other systems. This will be useful in later sections when analysing the submodules and developing in depth model behaviour.

2.1 Model elements

Based on the economic analysis it is possible to arrive at a model with three major elements: resource capture, investment and capital. The dependencies between these three subsystems are defined in equations (1a), (1b) **and** (1c)**:**

$$P_t = f(K_t, R_t, E_t), \tag{1a}$$

$$I_t = f(t), \tag{1b}$$

$$K_t = f(K_{t-1}, I_{t-1}, P_{t-1}), \tag{1c}$$

where t **represents the time step (discussed further in Section 2.3),** P_t **the resource capture or photosynthetic uptake at time** t, I_t **the investment at time** t **and** K_t **the photosynthetic capital available in the ecosystem at time** t. R_t **is the resources available at time** t **and** E_t **is the efficiency of photosynthesis at time** t **using these resources. These will be further defined and explored in the following sections.**

Individual model elements are analysed both from a module perspective and as part of the complete model. This is used to help develop an understanding of how each of the subsystems works and interacts with other elements. When analysing the three elements described above first the individual module is analysed in isolation and then as part of

the whole model. The analysis of individual modules can be done by using the relationships described in Figure 1 in a reversed order. The output of the module is instead used as an input for the purpose of optimising the module parameters (e.g. photosynthesis from resource capture to obtain capital, and that capital to find the investment).

2.2 Energy

For a plant the importance of photosynthesis lies in harnessing the sun's energy. The molecules produced through photosynthesis store this free energy and then change it through the process of respiration to compounds that can be used for synthesis and maintenance processes. In order to establish a reliable way of modelling this process it is important to take into account the efficiency of photosynthesis, i.e. the ratio of the captured to available energy. To do this, however, requires the adoption of energy as a common metric throughout the project. To the knowledge of the author this has yet to be implemented in any forest productivity models. Most are based on the use of carbon in the form of either biomass (Cairns et al., 1997) or carbon fluxes (Landsberg and Waring, 1997). No models have focused solely on exploring the potential of the use of energy in modelling.

Current photosynthesis models use photon fluxes. However, the conversion from energy units to photon flux is not fully correct as energy of a photon flux depends on the wavelength. Plants utilise only the visible part of the light spectrum for light capture therefore a band of wavelengths has to be accounted for (Landsberg, 1986, Chapter 2). Using the direct measurements of irradiance may, therefore, remove some error that comes from approximating photon fluxes. Furthermore, a problem with allocation is the disagreement about which organs and processes to include. This feeds into the problem of how these different processes interconnect. Unifying the relations between plant functions through considering energy flows and stores could help to better understand these relationships.

Therefore, perhaps a good way of viewing the problem of assimilation would be through energy transduction and using energy as a way of measuring evolutionary success. A direct measure of efficiency of the photosynthetic process can then be calculated through the direct relation between photosynthesis and incident radiation. In fact, this approach could make the look at photosynthetic efficiency more straightforward. This is because although there is a direct equivalence between using carbon and energy in the context of photosynthesis, using carbon implies losing the direct relationship between efficiency of photosynthesis and incident radiation. This happens because molecules can lose energy when changing form within the plant. Moreover, the decay of energy in the system is different to the decay of carbon. Where energy decay can prove to be much more linear the change of form of carbon within a plant can imply that its decay becomes much more complex at least on the time scale of a year, as used within this project.

Looking at potential bond energy can yield the energetic content of GPP. The energy absorbed in photosynthesis is therefore average potential photosynthetic bond energy.

$$6CO_2 + 6H_2O \rightarrow C_6H_{12}O_6 + 6O_2, \Delta G = 2.87MJ. \tag{2}$$

This value can then be used in the full conversion of $mols^{-1}$ into power in equation 3.

$$xCO_2molm^{-2}s^{-2} * 2.87MJmol^{-2} = yMJm^{-2}s^{-1} \tag{3}$$

2.3 Time Resolution

One notable difference between various models can be observed in the time scales adopted by them. This is further complicated by the fact that processes such as photosynthesis have to be integrated over time to obtain the daily photosynthesis (Thornley and Johnson, 1990, Chapter 10). A lower temporal time scale (for example, day to day photosynthetic response) removes some of the non-linearity and sensitivity of high resolution process analysis (for example, within day photosynthetic response) (Sands, 1995). Current models use time resolutions from an hour up to one year for projections up to a century ahead. This project analyses changes during a single year and for the purpose of this analysis two time scales were explored.

Hourly data is used on the relationship between irradiance and rate of photosynthesis in order to estimate the evolution of photosynthetic capital, K. However, when it comes to considering patterns of investment and the dynamics giving rise to the accumulation (and losss of) K daily data is exploited where the relationship between irradiance and the rate of photosynthesis is more linear (but nonlinear in photosynthetic capital).

2.4 Marginal Return

A good indicator of when investment can bring revenue can be provided by the marginal return on investment. In the economic parallel this marginal return describes the benefits obtained by changing the amount of resource used. For example, when there are resources available investing in structures to take up these resources is going to promote growth. However, in circumstances when this growth is inhibited by lower temperatures and higher maintenance costs a tree might remain dormant until such a time that conditions are good instead of expending stored resources on structures bringing little benefit. In terms of forest modelling, marginal returns, or marginal product as it is referred to by Bloom et al. (1985), is a way of quantifying the benefit

Figure 2: Distribution of sites used in the model.

obtained through the investment and is defined as $\delta P/\delta X_i$ where P is the production (or photosynthesis in the case of this project) and X_i is the resource considered. In this project no distinction is made between individual organs and tissues. Instead all of the apparatus used to perform photosynthesis is referred to as capital, K (see section 3 for more details). Therefore, the only resource (X_i) to consider is this photosynthetic capital (K). The marginal return is therefore $\delta P/\delta K$. This concept of marginal return is returned to in Section 5 with respect to investment decisions.

2.5 Data

The model will be developed using data available from the FLUXNET database for optimisation and verification. A total of 12 sites are used (Table 2, Figure 2). All sites represent established forests. Two types of PFTs, broadleaf deciduous and needleleaf evergreen forests, are used in the evaluation to determine whether species type will have a significant effect on investment strategy of individual forests. Data is averaged over a year for the available timespan of each site to obtain a single year of data for all of the used sites. Using yearly averages also accounts for disturbances and yearly fluctuations in data. This averaging is done at the smallest resolution available for the data (either half-hourly or hourly). A further averaging across each day (to obtain daily values) is also done (here temperature and irradiance are averaged and flux data is added together). An important assumption made here is that *the FLUXNET data used is assumed to be true.* Making this assumption makes it possible to not directly take respiration into account and instead focus solely on the energy uptake of photosynthesis, simplifying part of the analysis. Therefore, respiratory effects are not taken into account in this model.

Table 2: Table containing a description of sites used in the project. *Plant Functional Types. **Deciduous Broadleaf Forest. ***Evergreen Needleleaf Forest. Main site information is taken from https://fluxnet.ornl.gov/.

Name	Characteristics	Data Available	PFT*	Stand Age
US-Ha1 Harvard Forest EMS Tower	*Dominant species*: red oak (*Quercus rubra*) and red maple (*Acer rubrum*); *Climate*: Snow, fully humid warm summer; *Disturbances*: (Hurricanes) 1938, 1944, 1954, 1960, and 1991	1991-2006	DBF**	75110 years
DE-Hai Hainich	*Dominant species*: beech (*Fagus sylvatica*), mixed; *Climate*: Warm temperate fully humid with warm summer	2000-2006	DBF**	250 years
US-Bar Bartlett Experimental Forest	*Dominant species*: beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), and eastern hemlock (*Tsuga canadensis*) *Climate*: Snow, fully humid warm summer; *Disturbances*: (Hurricanes) 1938, (Ice storm) 1998	2004-2005	DBF**	120 years (uncut)
US-Wcr Willow Creek	*Dominant species*: sugar maple (*Acer saccharum*), basswood (*Tilia americana L.*); *Climate*: Warm Summer Continental: significant precipitation in all seasons	2001-2014	DBF**	80 years
US-UMB Univ. of Mich. Biological Station	*Dominant species*: large-tooth aspen (*Populus grandidentata*), red oak (*Acer rubrum*), *Climate: Snow fully humid warm summer*	2008-2014	DBF**	90 years
US-MMS Morgan Monroe State Forest	*Dominant species*: Sugar maple (*Acer saccharum*), Tulip poplar (*Liriodendron tulipifera*), Sassafras (*Sassafras albidum*), Black Oak (*Quercus velutina*), White Oak (*Quercus alba*) *Climate*: Warm temperate fully humid with hot summer	1999-2014	DBF**	60-80 years
CA-TP4 ON-Turkey Point 1939 White Pine	*Dominant species*: white pine (*Pinus strobus*); *Climate*: Warm Summer Continental: significant precipitation in all seasons	2001-2015	ENF***	Established 1939
US-Dk3 Duke Forest Loblolly Pine	*Dominant species*: Loblolly Pine; *Climate*: Warm temperate fully humid with hot summer; *Disturbances*: (Drought) 2001-2, 2005 (Ice Storm) 2002, Active FACE site	1997-2015	ENF***	Established 1983
US-MRf Marys River (Fir) site	*Dominant species*: Douglas fir (*Pseudotsuga menziesii*); *Climate*: Warm temperate with dry, warm summer	2005-2015	ENF***	Established 1976
US-Prr Poker Flat Research Range	*Dominant species*: Black spruce (*Picea mariana*); *Climate*: Subarctic: severe, dry winter, cool summer	2010-2014	ENF***	unknown (mature)
US-Ho1 Howland Forest (Main Tower)	*Dominant species*: spruce-hemlock-fir, aspen-birch, and hemlock-hardwood mixtures; *Climate*: Warm Summer Continental: significant precipitation in all seasons	2003-2009	ENF***	140 years
CA-Qfo Quebec Mature Forest	*Dominant species*: Black spruce (Picea mariana); *Climate*: Subarctic: severe winter, no dry season, cool summer	2003-2006	ENF***	95 years

3 Photosynthetic Capital

To make the exploration of econometric modelling in forests possible boundaries must be placed on the system. Therefore, this model focuses on the economic behaviour of photosynthesis and photosynthetic apparatus which is the photosynthetic capital, K. Capital K (capital used as shorthand for photosynthetic capital) is defined as all the apparatus used by the plants in the canopy to perform and support light energy capture and fixation. When referring to individual plant functions and organs this is not just the foliage but also all the organs that ultimately contribute to photosynthesis. For example, stems are used to transport nutrients and water taken up by the roots, both of which are essential prerequisites for photosynthesis. Therefore, they are also represented in the definition of capital. In the energy framework, as used in this project, capital is represented in units of energy density ($\mathrm{Jm^{-2}}$). This embodied energy is the energy derived from photosynthetic light capture fixed into metabolic products that are themselves used to capture and fix incident solar radiation. Therefore, it is now possible to arrive at a complete definition of photosynthetic capital as being *the amount of embodied energy available in the ecosystem that can be used to harness energy from incident solar radiation at a given moment in time per unit area.*

An important assumption to make here is that *the ecosystem is treated as one system.* The capital of individual trees is not considered and the entire system is homogeneous in terms of variables and parameters at any given time.

Photosynthetic capital can be directly compared to economic concepts. Capital, as used here in its macroeconomic context, is the accumulated assets and products that can be used in the production of goods or services or, as Smith and Nicholson (1887) defines it in the *Wealth of Nations* Book, *That part of a man's stock which he expects to afford him revenue.* For a single plant this revenue is nutrients, water and energy (Bloom, 1986). In this framework the focus is placed on energy with water and nutrients being implicitly considered in the definition of photosynthetic capital (above).

Capital in economics is most often associated with growth. In a capitalistic ideology the accumulation of capital is a goal in itself and increasing capital is what keeps an economy in motion. Not only that but capital accumulation has to overcome depreciation (capital wears out and loses value). Therefore, this investment of capital into capital is necessary to keep the system alive without the need for external investment. Growth can be considered a goal for ecosystems as well (though by no means the only one). Increasing the overall capital leads to an excess which helps in survival against disturbances such as droughts or fires. In fact, this has been observed in the balance of year to year NPP values being positive.

The Solow-Swan model of economic growth provides a framework for defining the recursive capital growth rate that can also be applied to an ecosystem:

$$\dot{K}(t) = I_t \cdot P(t) - \epsilon \cdot K(t), \tag{4a}$$

$$K_{t+1} = (1 - \epsilon) \cdot K_t + I_t \cdot P_t. \tag{4b}$$

Here, equation (4b) is a discrete version of the continuous equation (4a) for a daily time step described in Section 2.3. P_t represents production, I_t is the investment share of production where all other production is consumed and ϵ is the depreciation of capital. This can be very easily translated to an ecological setting where P_t is now used to represent photosynthetic uptake, I_t is the investment into capital at time t and ϵ is the decay rate of capital.

A further assumption must be made about the decay rate of capital. Whilst this is by no means an illustration of reality ***the decay of capital is assumed to be constant throughout the year.*** In reality the number of capital subsystems undergoing decay at vastly different rates is most likely infinite. However, no way of accounting for these is predicted in this system. Furthermore, the variation in capital is expected, under this condition, to be determined mainly by the variation in investment.

4 Resource Capture

In this section a provisional resource capture function is specified and analysed. However, the preliminary aim of doing this is to use this framework to estimate and explore the seasonal dynamics of photosynthetic capital, K.

The instantaneous rate of photosynthis is invariably described by the Farquhar et al. (1980) biochemical model of photosynthetic CO_2 assimilation in leaves. Johnson and Thornley (1984) provide a simplified version of this model and it is their model framework that is exploited here. Johnson and Thornley (1984) describe the observed nonlinearity between the rate of photosynthesis and incident irradiance, R, using the rectangular hyperbola 5:

$$P_t = \frac{\alpha R_t C_{it}/r_x}{\alpha R_t + C_{it}/r_x}, \tag{5}$$

where α is the photochemical efficiency, r_x is the carboxylation resistance and C_{it} is the internal CO_2 concentration. One way of deriving this expression is as the outcome of a linear feedback system. In this system photosynthetic capital, K_t, is consumed by increasing the rate of photosynthesis

$$P_t = K_t R_t, \tag{6}$$

$$K_t = K_{max} - \beta P_t. \tag{7}$$

Here K_{max} represents the total photosynthetic capital available at any point in time, as determined by all prior investments in developing the spectrum of apparatus required to support photosynthesis. R_t is the resources available in the environment, in this case irradiance. Combining equations 6 and 7 then gives,

$$P_t = \frac{K_{max} R_t}{1 + \beta R_t}, \tag{8}$$

so by extension $P_{max} = K_{max} * R_{max}$ and $\beta = \frac{K_{max} - K_t}{P_t}$. This applies to a within day situation where it can be assumed that efficiency, β and K_{max} remain constant. What is useful about equation (8) is that it can be used to estimate the values of K_{max} and β from hourly (or half hourly) FLUXNET data of GPP and incident solar irradiance pooled over some time period where it might be assumed K_{max} is not changing significantly. This then provides a daily value of K_{max} which can be used to investigate how capital is accumulated by forest systems.

In order to obtain daily values of K_{max} and explore the capital response equation (8) was fitted using a 5 day moving window using non-linear least-squares. The results are shown in Figure 3. β is inversely proportionate to K_{max}, tending to go towards infinity when no capital is present and staying relatively constant during the growing season.

The capital pattern stays low during the winter period and increases to a plateau during the summer. This response is similar for both deciduous and evergreen forests but for evergreen sites displaying a longer growth period. The capital obtained can then be used to estimate investment changes throughout the year.

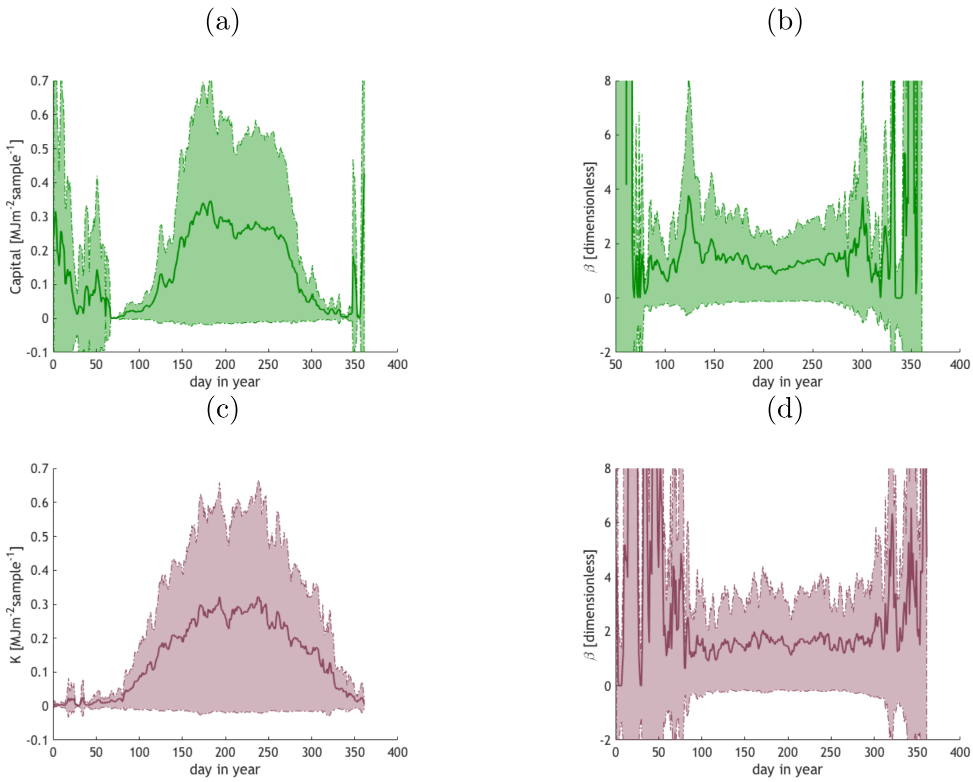


Figure 3: Capital, K, and β responses with confidence intervals from fittiing (8) for two example sites: US-Ha1 (3a and 3b and US-Ho1(3c and 3d). Both reach a very similar level of capital with evergreen forests showing activity for a longer period of time throughout the year. Some deciduous forests also show artefacts (such as seen above in a) due to very low values of GPP data causing singularity. Deciduous forests especially show a relation to leaf area index (LAI). β observes high values in the winter periods (often nearing set parameter boundary, implying infinity). Referring to the definition of capital the amount of embodied energy capable of capturing energy from incident radiation is very low in the beginning of the year (low photosynthetic capability, no leaves, lower nutrient uptake and transport capabilities) which then increases during the growing season (earlier for evergreen, later for deciduous) with higher nutrient availability and new growth, stabilises and decreases over the autumn (lowering of temperatures, decrease of nutrient availability, leaf senescence). β stayed relatively stable throughout the growing period implying it regulates photosynthetic use of capital. High values during the winter period are singularities consistent with fitting to zero or near-zero values of photosynthesis.

5 Investment

Investment, I, is the part of the energy captured that the ecosystem portions out towards its energy capture and fixation mechanism. Investment along with decay regulates forest growth. Since capital must always remain positive to maintain the light capture mechanisms, investment into capital must also account for losses in decay.

Having obtained the capital it is possible to find the investment using the capital accumulation function in equation (4b)**. This is done by reversing the relationships shown in Figure 1. For the purpose of generating an investment pattern a number of nodes were fitted using the least-squares method and the CAPTAIN interpolation function irwsm (integrated random walk function), which is a method for smoothing and interpolation (Taylor et al., 2007). The number of nodes used to determine the investment pattern was 12 as it was found to work best for the data available.**

The non-linear least-squares method was used to fit parameters to photosynthesis. Fitting to photosynthesis implies that another resource capture function had to be considered (section 2.1). Equation 9 was used as a provisional resource capture function to account for the integration of photosynthesis over a day (see section 2.3).

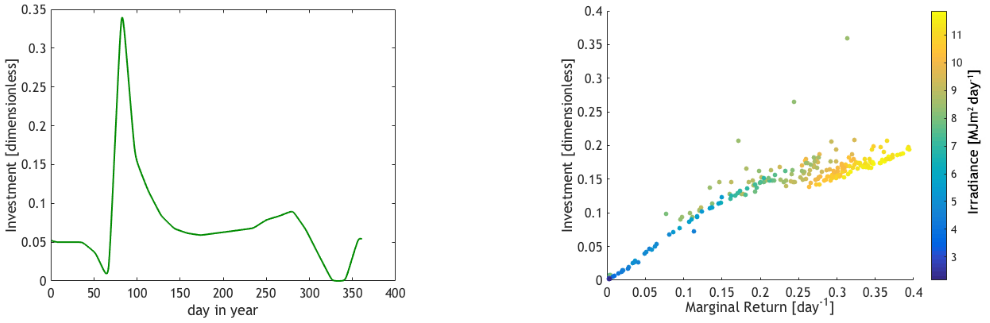
$$P_t = \epsilon_e K_t R_t, \tag{9}$$

where ϵ_e is the efficiency of photosynthesis and R_t is the available resource, in this case irradiance.

Marginal return is a measure of benefits obtained on investing in a single resource (in this framework capital). This is of course dependent on both the amount of capital as well as other external conditions. A natural assumption is that a good time to invest is during a time when returns are high. Therefore, perhaps, marginal return on capital is one of the drivers of investment. This was explored by obtaining the marginal return function through differentiating photosynthesis, P, with respect to the capital, K (equation (8)**) yielding equation 10.**

$$M_t = \frac{R_t}{1 + \beta R} \tag{10}$$

An illustration for this fitting for a sample deciduous site can be seen in Figure 4. As can be observed there is a relationship between marginal return and investment (Figure 4b). This relationship appears to be approximately linear, possibly saturating for higher values of M.



(a) (b)

Figure 4: Investment pattern during a year (a) and comparison with marginal return (b) of sample site US-MMS fitted using only a simple random walk function for investment. (a) A noticeable spike at the beginning of the year for the growing period can be observed which can be related to higher availability of nutrients which corresponds to an increase in percentage allocation into photosynthetic mechanisms (due to low capital at the time a high investment may be needed for a rapid response to better growing conditions). It might also represent a kick-starting of the system after a period of low activity. This then lowers and stabilises over the rest of the summer season and decreases into winter (due to fitting to zero the winter period itself is often shown as unconstrained). This behaviour also seems to be related to the marginal return on capital as seen in (b). Aside from the peak during the growth period (not shown in (b)) there is a saturating relationship of investment with marginal return. A similar increased investment at the beginning of the year was present in most but not all sites. The winter period is largely unconstrained (due to zero values of photosynthesis) in most sites and fitting often led to increased investment outside of the growing period.

6 Complete Model Analysis

The findings described in sections 3, 4 and 5 explore what the relationships between the model elements look like. Based on these it was tested how the model performed when all the elements were combined. Four different investment functions were tested, including the one used in section 5, another two introducing more rigid relations with marginal return (saturating and linear) and finally one with a time-varying parameter used in a relationship with marginal return ($I_t = \epsilon_5 M_t$). After evaluation of these options the last function was chosen.

The resource capture function was also changed from its form in (9). First of all, it was assumed that in a similar principle to that of Beer's law the benefit of more capital becomes smaller with increasing the capital. This can happen for several reasons among them decreased availability of resources or competition in the form of leaf self-shading or root competition.

Furthermore, it was important to take into account photosynthetic efficiency. During a yearly calculation it could no longer be assumed that efficiency remained constant. A significant process affecting the rate of photosynthesis is temperature (Linder and Troeng, 1980; Landsberg, 1986). Based on this 4 efficiency functions were tested: a constant efficiency, efficiency around the average temperature, efficiency around a parameter-fitted temperature and a linear relationship with temperature. All 4 were tested and evaluated within the full model. Fitting around the mean temperature proved to produce a matching photosynthesis for all but one site, performing best out of all the efficiency functions.

The final form of the model as guided by sections 3, 4 and 5 as well as the analysis described above can be seen below. Table 3 describes the final model parameters.

$$K_{t+1} = (1 - \epsilon_1)K_t + I_t P_t \tag{11a}$$

$$P_t = E_t(1 - e^{-\epsilon_2 K_t})R_t \tag{11b}$$

$$E_t = \epsilon_3 e^{\epsilon_4 T_t - \bar{T}} \tag{11c}$$

$$I_t = \epsilon_{5t} M_t \tag{11d}$$

$$M_t = \frac{\delta P}{\delta K_t} = E_t \epsilon_2 e^{-\epsilon_2 K_t} R_t \tag{11e}$$

A few final tests were performed to confirm the number of nodes used to predict the investment pattern and comparing different fitting starting points. The number of nodes was tested between 6 and 18 and the optimal number turned out to be around 12. The final evaluation suggested that a daily resolution provided the appropriate balance between retaining information and expressing the turnover of capital. Fitting starting

Table 3: Parameters used in the model.

Parameter	Unit	Description	Boundaries
K_0	MJm^{-2}	Starting capital	$0 < K_0$
ϵ_1	day^{-1}	Decay rate	$0 \geq \epsilon_1 \geq 1$
ϵ_2	$MJ^{-1}m^2$	Efficiency of capital use	$0 \geq \epsilon_2 \geq 1$
ϵ_3		Temperature efficiency parameter 1	$0 \geq \epsilon_3 \geq 1$
ϵ_4	$^{\circ}C^{-1}$	Temperature efficiency parameter 2	$0 \geq \epsilon_4 \geq 1$
ϵ_5	day	Time-varying internal investment influence control parameter	$0 \geq \epsilon_5 \geq 1$

points were originally chosen close to 0 as most parameters tended to have their minima at low values (as tested by a Monte Carlo analysis). Changing the starting day (after 75, 150, 225 and 300 days) did not significantly impact the shape of the resulting capital and investment functions but did change their magnitude.

Having confirmed the model and the fitting options the final version of the model was fitted using simulated annealing. This method was chosen because it explores the parameter space thoroughly and decreases the probability of using a sub-optimal solution because of its proximity to the chosen starting point. It does not accept the first minimum as the solution. Furthermore, it considers all the parameters as independent which guards against spurious correlations between parameters. The downside of this technique is that it took a significantly longer amount of time to run than gradient-based nonlinear least squares searches because of the thorough search, hence the decision to only use it in the final stage of model development.

In order to obtain parameter confidence intervals using simulated annealing the fitting was run 20 times and the 95% confidence interval was calculated using the formula $x_{ci} = 1.96 * \frac{\sigma_x}{\sqrt{n}}$**, where** x_{ci} **is the parameter confidence interval,** σ_x **is parameter variance and** n **the number of runs. This assumes a normal distribution of solutions. Fitting was done using the sum of the photosynthesis error (**$\Sigma(P - \hat{P})^2$**) as the function error.**

6.1 Results

The following section shows results obtained from running the final model using simulated annealing unless otherwise stated. An average is also calculated from deciduous and evergreen sites respectively and used in most of the analysis and figures. One erroneous site was observed (Mary's River fir site, US-MRf) and not used in further calculations or

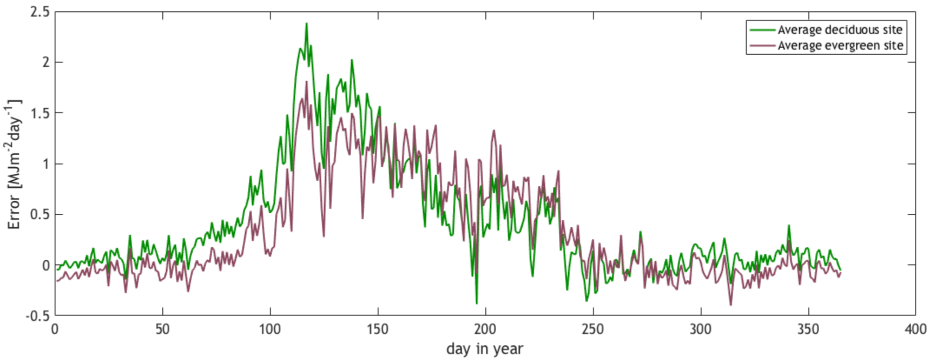


Figure 5: Errors for both evergreen and deciduous sites. Both sites show a similar error with higher uncertainty in the growing period. Furthermore, both errors show a very high autocorrelation which is not unexpected given the recursive nature of the capital accumulation function.

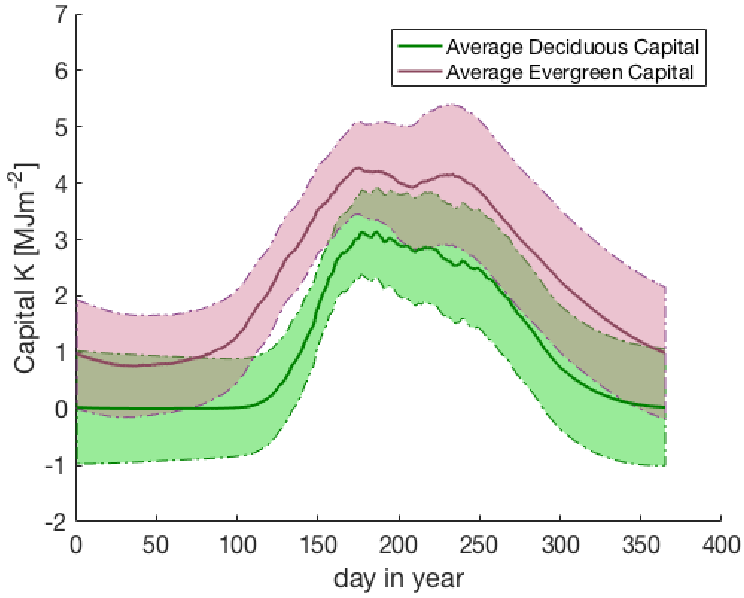
observations aside from a brief analysis into the nature of its behaviour (Figure 9 shows the individual results for this site).

The mean error for an averaged deciduous site was 21%. For evergreen sites this value was 27%. On top of this all sites showed very high autocorrelation and were normally distributed. Figure 5 displays the error for averaged deciduous and evergreen sites.

Average changes in capital are shown in Figure 6. Typically, deciduous sites had a lower minimum capital compared to evergreen. The minimum capital for an average deciduous site was 0.013 ± 0.82 MJm^{-2} and for an average evergreen site 0.74 ± 0.90 MJm^{-2}. The maximum was 3.77 ± 0.75 MJm^{-2} and 4.57 ± 0.82 MJm^{-2} for deciduous and evergreen respectively. The amplitudes between maximum and minimum values were 3.76 ± 1.57 and 3.83 ± 1.72 MJm^{-2}.

Figure 7a shows the yearly investment pattern for deciduous and evergreen site averages. The average investment for deciduous and evergreen sites varied between 2.8 ± 1.0 % and 27.9 ± 5.0 % being the minimum and maximum for the deciduous sites and 0.6 ± 0.4% and 24.6 ± 4.3% minimum and maximum for evergreen sites. Sites showed a spike of investment at the beginning of the growing season, usually around a 75-150 days into the year. After this spike the investment decreased, settling at a plateau for the rest of the growing season and decreased to near-0 outside of the growing season. Investment was also compared to the marginal return, M. Results for this are presented in Figure 7b. For all sites this relationship appeared to be linear, often, to a degree, dependent on the irradiance (not shown here) with bigger irradiance resulting in bigger investment.

(a)



(b)

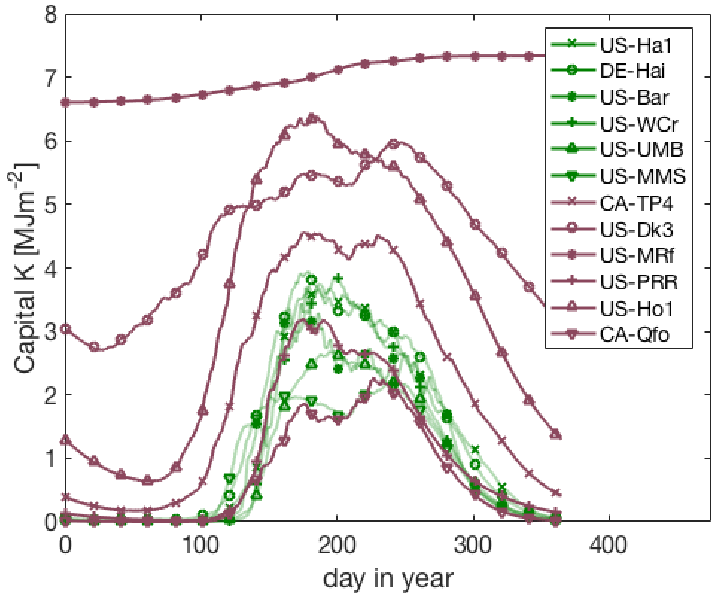


Figure 6: (a) Yearly capital change for averaged deciduous and evergreen sites. Deciduous sites had a capital which tended towards 0 outside of the growing period and was on average lower. Evergreen sites held some capital over winter months. As expected the overwintering capital is generally higher for evergreen sites, however, the degree of variation throughout the year seems to be very similar for both. (b) Combined view of all sites' capital. All deciduous forests showed a the average behaviour (in a) and two evergreen sites showed deciduous-like behaviour. Both of those were the northern-most sites used suggesting heavy snowfall and low temperatures potentially inhibiting photosynthesis. The high degree of evergreen variation could to an extent be attributed to climate but on a whole is quite surprising. All but one seem to follow the same pattern of approximately bell-shaped change throughout the year.

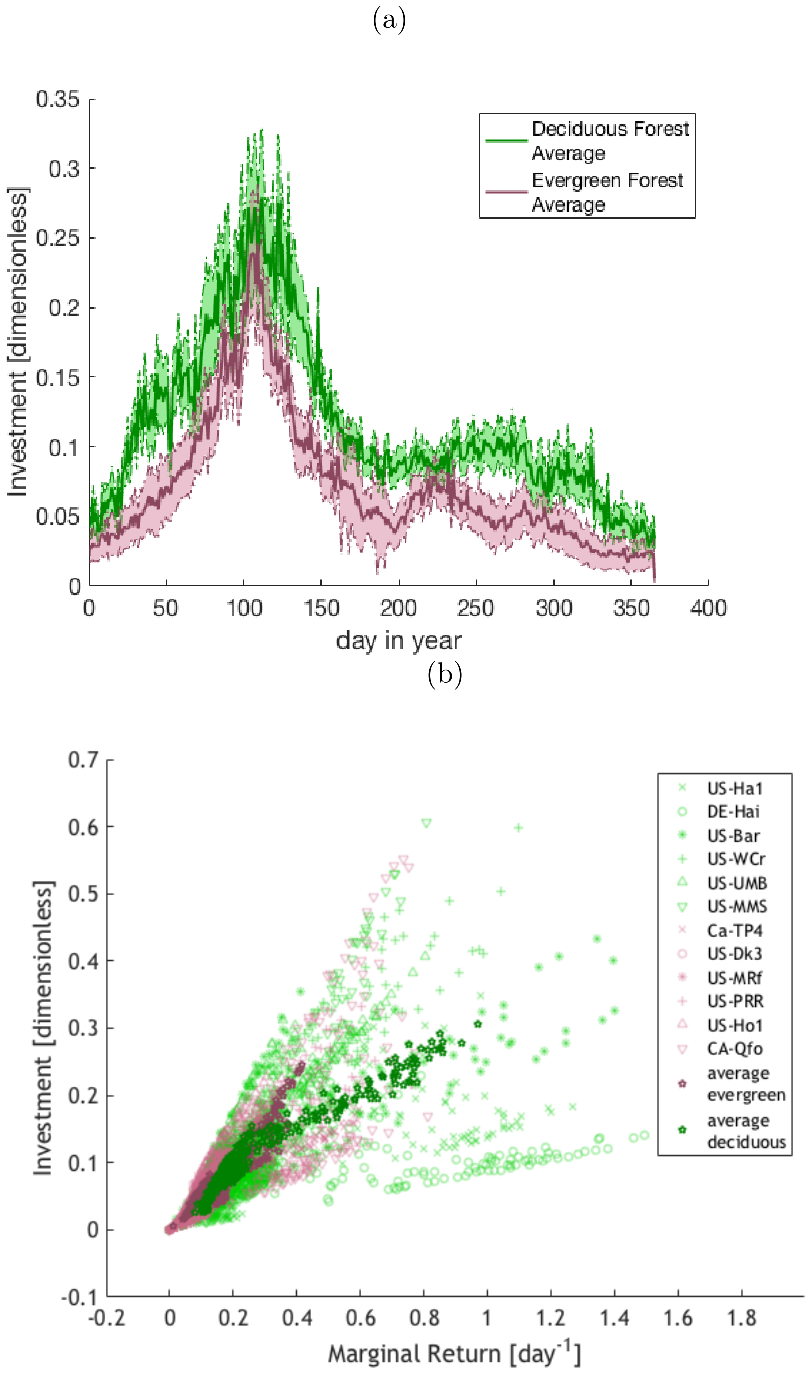


Figure 7: (a) Average investment pattern for deciduous and evergreen sites. On a whole deciduous sites showed a higher investment pattern than evergreen sites, though both peaked at around the same value. (b) Investment when compared to marginal return. Individual sites showed a very linear relationship which was also observed in the averages. Evergreen sites had a steeper incline, however the maximum marginal return was also lower suggesting deciduous sites held off investment until higher returns were obtained. More variance was also observed in deciduous sites.

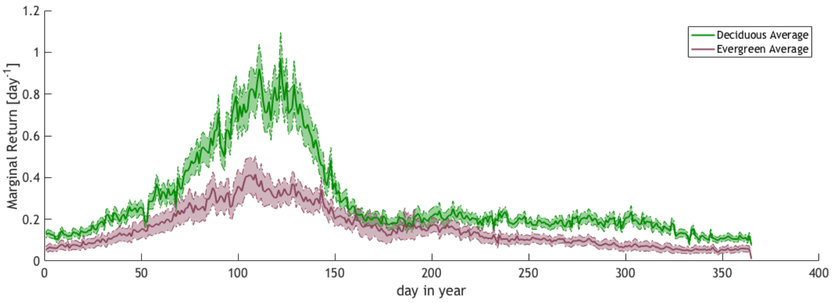


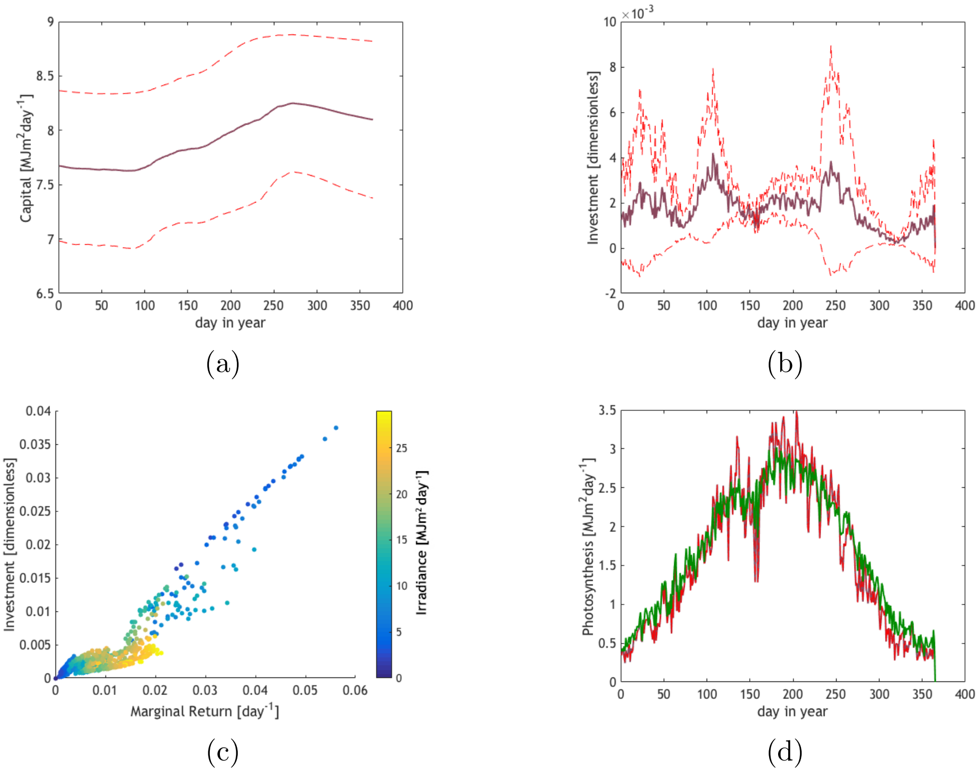
Figure 8: Yearly pattern of marginal return for average evergreen and deciduous forests. Deciduous forests displayed a much higher marginal return in the growing season than evergreen forests. However, during the rest of the year, although, deciduous forests continue to have higher marginal return the difference between the two sites is much smaller. Furthermore, the shape and pattern of the marginal return for both forests matches the investment function (Figure 7a).

6.2 Model parameters

Table 4 shows the results for the sites' parameter values. Furthermore, averages were taken for each site type. There were no significant differences between parameter values between sites. The biggest uncertainty was in the K_0 parameter which was 4.57 ± 1.22 MJm^{-2} for deciduous sites and 3.93 ± 1.26 MJm^{-2}. However, the uncertainty of the starting point was also handled by using a three-year period to allow for the necessary adjustment. It does suggest that allowing space for the model to adjust when fitting its parameters is a necessary step to consider when doing future work.

On average the decay was 0.061 ± 0.012 day^{-1} for deciduous sites and 0.027 ± 0.015 day^{-1} for evergreen sites. When looking at results for individual sites, the dispersion was between 0.011 ± 0.002 day^{-1} and 0.073 ± 0.008 day^{-1} which suggests a turnover rate of capital between 13.7 ± 1.4 and 91 ± 19.2 days. Decay is fully discussed in Section 7.2.

Parameters to do with capital-use efficiency (ϵ_2) and photosynthetic efficiency(ϵ_3 and ϵ_4) were on average 0.72 ± 0.09 MJ^{1}m^2 (deciduous) and 0.54 ± 0.10 MJ^{1}m^2 (evergreen) for ϵ_2, 0.087 ± 0.083 and 0.70 ± 0.76 for ϵ_3 and 0.042 ± 0.063 $^{\circ}C^{-1}$ and 0.032 ± 0.050 $^{\circ}C^{-1}$ for ϵ_4. In all cases evergreens had lower values than deciduous but this was considered significant enough only in ϵ_2. Since ϵ_2 is the capital-use efficiency it would make sense that deciduous forests where capital is present for shorter periods of time would be better adapted to use capital when it is available.



(a) (b)

(c) (d)

Figure 9: Results for the site Mary's River fir site (US-MRf). Despite producing a different capital response (a) to other sites as well as investment pattern (b) and (c) this site produced very little error (d). In fact, there was also very little variance between photosynthesis outcomes.

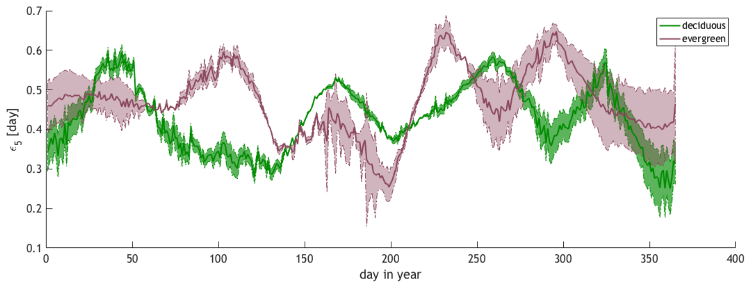


Figure 10: Time-variation of ϵ_5 for average deciduous and evergreen sites. Though some variation across the year the calculated variance for both is 0.007. This along with the near linear relation between investment and marginal return supports the claim for ϵ_5 to be constant.

Figure 10 shows the time-varying parameter ϵ_5 for average deciduous and evergreen sites. ϵ_5 was on average 0.43 ± 0.02 days for deciduous sites and 0.47 ± 0.03 days for evergreens (ϵ_5 values were obtained from equation (11d)). No noticeable patterns were observed for either the averages or the individual sites and the outcome oscillated around a mean value. The variance for both types of sites was 0.007 suggesting that there was little within-year variation. This and the observation of linearity between marginal return and investment suggests that ϵ_5 should be constant. From this observation and from the average values of ϵ_5 in conjunction with equation 11d it can be said that investment is 43% and 47% of marginal return for deciduous and evergreen averages respectively (marginal return pattern can be observed in Figure 8). It was then possible to do a linear regression fit of the average investment and marginal return to confirm whether these observations were correct. For deciduous sites the fit turned out to be lower than predicted from ϵ_5 at 0.28 days, but for the evergreen the obtained value was 0.49 days, very close to the average ϵ_5 for evergreen forests. This supports the claim that ϵ_5 should be a constant value.

6.2.1 Sensitivity Analysis

A sensitivity analysis was performed on the final results. This was done by running the model with obtained parameters but changing each of them one at a time by 10%. For the parameter ϵ_5 all nodes were increased together by 10%. The photosynthesis, capital and investment outcomes were investigated. The response was obtained by averaging $(\frac{\hat{X}}{X})^2 - 1$ across the output year, where $\hat{X}$ is the value obtained from the sensitivity analysis and X is the original result. It was also noted if function shapes changed significantly. US-MRf was also included in this analysis to see if changing the parameters can alter the response.

Table 4: Parameter results for individual sites (ϵ_5 not included).

Site	K_0	ϵ_1	ϵ_2	ϵ_3	ϵ_4
US-Ha1	0.57 ± 1.36	0.078 ± 0.016	0.728 ± 0.089	0.101 ± 0.068	0.043 ± 0.020
DE-Hai	3.73 ± 1.32	0.055 ± 0.008	0.655 ± 0.083	0.143 ± 0.016	0.008 ± 0.096
US-Bar	9.01 ± 1.52	0.073 ± 0.008	0.682 ± 0.069	0.067 ± 0.003	0.045 ± 0.003
US-WCr	0.42 ± 1.59	0.057 ± 0.009	0.754 ± 0.143	0.042 ± 0.176	0.076 ± 0.025
US-UMB	6.93 ± 1.47	0.048 ± 0.008	0.677 ± 0.108	0.083 ± 0.060	0.043 ± 0.068
US-MMS	4.31 ± 1.47	0.055 ± 0.014	0.827 ± 0.093	0.088 ± 0.084	0.037 ± 0.094
CA-TP4	5.00 ± 1.14	0.032 ± 0.055	0.607 ± 0.110	0.075 ± 0.096	0.029 ± 0.065
US-Dk3	3.629 ± 1.17	0.011 ± 0.002	0.417 ± 0.091	0.088 ± 0.003	0.017 ± 0.002
US-MRf	0.714 ± 1.49	0.000 ± 0.001	0.950 ± 0.065	0.121 ± 0.001	0.000 ± 0.000
US-PRR	5.268 ± 1.20	0.024 ± 0.003	0.624 ± 0.085	0.036 ± 0.059	0.045 ± 0.080
US-Ho1	0.173 ± 1.06	0.018 ± 0.006	0.351 ± 0.089	0.101 ± 0.057	0.028 ± 0.004
CA-Qfo	8.792 ± 1.51	0.052 ± 0.009	0.717 ± 0.129	0.049 ± 0.163	0.039 ± 0.100

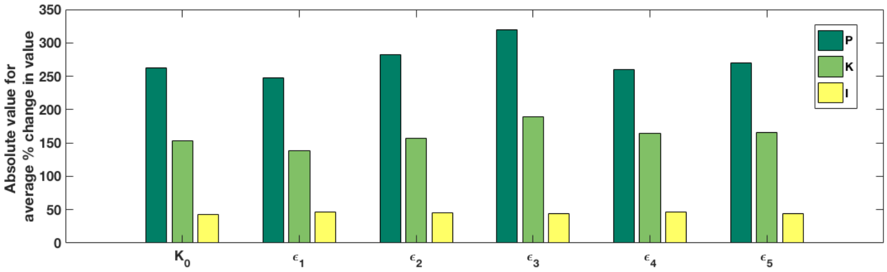


Figure 11: Sensitivity analysis of the 6 parameters used in the simple model. Each parameter obtained from the simulated annealing results was increased by 10% for each site used and the model simulated results using the changed parameters. Ratios between new and original results were averaged across the year (using squared values) and then across all sites. CA-Qfo and US-WCr were not taken into account for photosynthesis as they were too big compared to other values and would most likely have a big impact on the results. ϵ_3 has the biggest impact on resulting values. P is most affected by changing parameters, most likely because it is directly impacted by not only the efficiency of photosynthesis but also of capital use (ϵ_2).

Figure 11 shows an average change for all sites. Quebec (CA-Qfo) and Willow Creek (US-WCr) were two sites that showed very high sensitivity of photosynthesis compared to other sites (approximately 8- and 10-fold of other sites' outcomes) and, therefore, were removed from the average photosynthesis displayed to avoid biasing the outcome. Photosynthesis was the most sensitive to change in parameters followed by capital. Observing the shapes of the functions, significant changes have been observed for most sites with regards to photosynthesis and capital. Investment was the least affected with only CA-Qfo, US-WCr and US-PRR (Poker Flat Research Range) significantly changing their investment pattern. Out of all the parameters ϵ_3 caused the most change to the results and ϵ_1 the least.

Looking at how the changes affected individual sites, increasing ϵ_1 had the least effect on change in the photosynthesis error where changes in ϵ_3 and ϵ_4 had the greatest impact. For changes in the capital ϵ_3 imposed the biggest changes for half the sites and ϵ_1 for a quarter of sites. However, these two parameters also imposed the least amount of change where they have not been the biggest impact. Therefore, no conclusion can be drawn from individual changes in capital. Finally, investment was most impacted by ϵ_4 and least by ϵ_1.

Considering the bigger impact of efficiency related parameters (mostly, ϵ_3) it is worth in further work to test the efficiency function and examine the impact of temperature on efficiency. However, it must also be noted that the average changes did not vary significantly from parameter to parameter suggesting that the system is very sensitive to change and that there is significant coupling between parameters involved causing this high sensitivity. This is not surprising when looking at the recursive nature of equation (11a) in conjunction with the integration of most model elements into equation (11b).

6.3 Environmental Effects

In addition to marginal return affecting investment, it was investigated whether temperature can have an influence on the outcomes of the model. Average daily and yearly temperature was used to detect patterns in investment, capital and the decay rates of individual sites.

No clear relation between investment and temperature was noticed from plotting these two variables together. Correlation between investment and temperature along with P-values were computed for each site. However, while most sites produced a P-value output below 0.05, 2 sites showed no statistical significance ($P > 0.05$). The observations and P-values were not considered enough to support the existance of a clear correlation between investment and temperature.

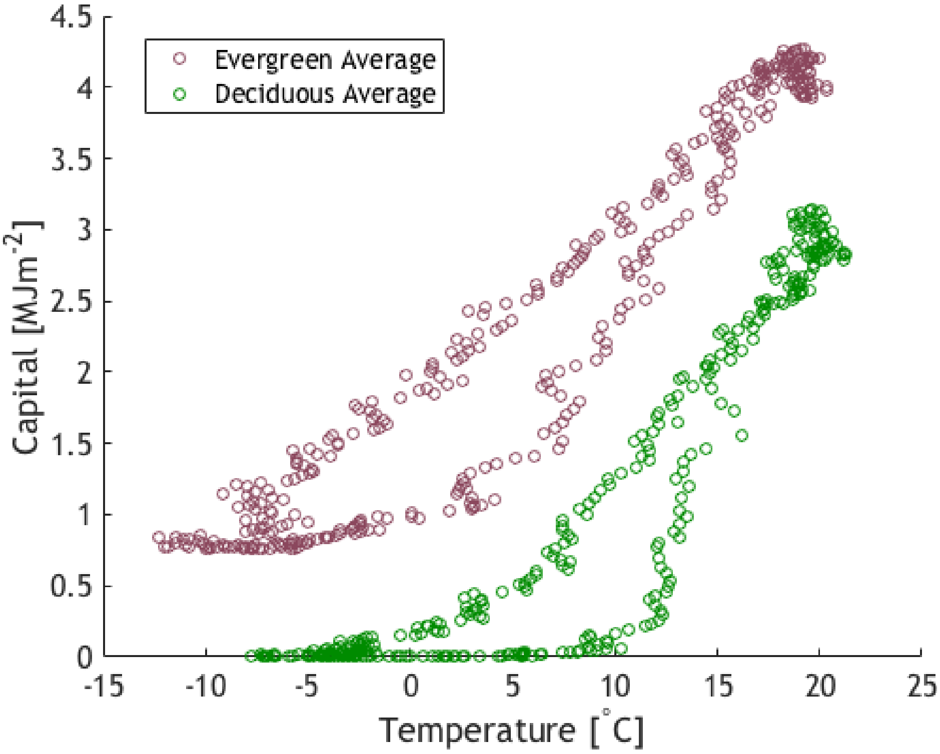


Figure 12: Relationship between capital and temperature. It can be observed that there is an approximately linear relationship between the two variables, with some hysteresis present. However there appear to be two relations one steeper, beginning with higher temperature. This one appears to be connected to the spring rise of capital. The other one, less steep, is the decline of capital at the end of the growing season and into winter.

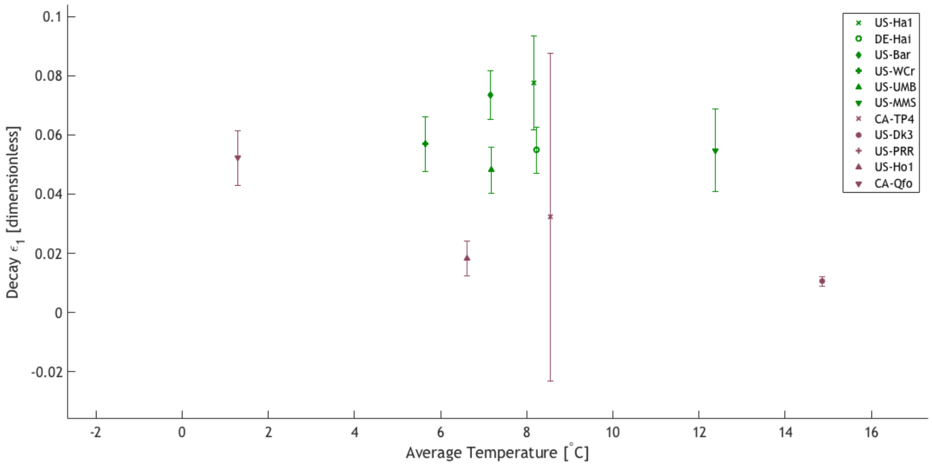


Figure 13: Relationship between decay values and average yearly temperatures for all sites. No clear relation can be observed for deciduous sites. Evergreen sites tend to have a higher decay value when experiencing lower temperatures.

Capital, on the other hand, showed a clear relation to temperature, most likely driven by the temperature-dependent efficiency of photosynthesis. Figure 13 shows the relationship between capital and temperature for average deciduous and evergreen forests. It can be clearly seen that capital increases with rising temperature.

Comparing decay values to individual sites revealed that for the evergreen forests it could be said that lower temperatures called for higher decay. On the other hand, observations of deciduous sites showed no clear correlations between temperature and decay. Overall, a bigger sample would be necessary to confirm whether patterns exist or not.

Based on these initial observations, temperature was not investigated further with respect to the outcomes of the model.

7 Discussion

In relation to the purpose of this study it can be said that indeed economic theory can be used to model plant productivity and allocation. With the exception of one site, all sites tested presented similar patterns of relation to investment and capital. On a whole all deciduous sites lost most of their capital during the winter and most evergreen needleleaf sites held positive capital during the winter period. The only evergreen site for which the capital neared zero over winter was a taiga site in Alaska (US-PRR) which could suggest that in colder conditions even evergreen sites can struggle to maintain higher active photosynthetic capital.

The change in capital seemed to proceed in yearly cycles with capital decreasing to a minimum in the wintertime and rising during the growth period to a peak or plateau over the summer. This behaviour does not necessarily follow the idea of "accumulation" when compared to traditional ideas of cumulative growth. However, if capital was "productive" as opposed to cumulative the observations could be justified. The notion behind productive capital is that different capital parts partake to a different extent in photosynthesis. Therefore, the presence of foliage creates a big boost in capital, whereas other organs such as stems contributes significantly less photosynthetic capacity and, therefore, are less represented in the final value. This change follows LAI dynamics which can be said to represent the capital on the daily time scale that this analysis follows. On a longer or shorter time scale these dynamics are likely to be different. Though the quantitative analysis of the underlying capital is not of interest in this project, the qualitative inspection gives some explanation to support this theory.

Another explanation for the small wintering capital could be that the outcome presented is of the "consumed" photosynthetic capital only. Product invested into active photosynthetic capital is only between 5 and 30 % during the growing period. Assuming an average of 50% of photosynthetic product is spent on respiration this leaves between 20% and 45% leftover for other uses (other forms of capital). Part of this could be "dormant" photosynthetic capital designated to "jump-start" the growing season next year (for example, new shoots, stored NSCs). Another part must be used to maintain the tree structure by moving nutrients and water (where this is not related to short term photosynthesis) but also importantly for reproduction (a multi-year investment, therefore, not observed in this analysis) and growth of non-photosynthetic structures. It is, therefore, likely that the other forms of capital are where the rest of the photosynthetic product is invested. In fact, both of the above theories are likely to work together to form a productive capital representing only the active photosynthetic capital without accounting for longer-term dormant effects.

Though this analysis did not cover multiple years it is likely that the maximum photosynthetic capital fluctuates over several years. Forest behaviour will likely change when analysed at different time frames. Furthermore, it is not impossible that the maximum photosynthetic capital increases over several years with a growing forest. Looking at individual years also gives an opportunity to look into factors that might affect outcomes such as water availability (where it is assumed that in an average year response this is not considered a limiting factor) or disturbances.

The investment patterns are very similar for deciduous and evergreen sites, different only in their magnitudes. The spike in investment can clearly be associated with the start of the growing season. For deciduous sites this is also when nutrients turned over from the previous year become available after thawing and when temperatures rise enough to support photosynthesis. The subsequent lowering of investment could be caused by redirecting resources to other areas (for example, reproduction or storage) but also by competition due to lower resources or the ageing of foliage and subsequent lowering of photosynthetic capacity. Lower photosynthetic capacity of leaves suggests that there might be less incentive to invest in older leaves. This phenomenon is reflected in the marginal return on investment which shows a clear positive relation to the investment.

In fact, it is possible to go as far as to say that investment is driven by marginal return values. This relationship can be approximated to a linear one in the next iteration of the model. This is another argument supporting the application of an economic framework to plant growth. Marginal return is a measure of return on an investment supporting the idea that when the returns are high it is good to invest. The marginal return pattern did not follow the capital or photosynthesis pattern but instead looked more like the investment with a peak in spring time. This is consistent with the nutrient availability and young leaf age described above. When leaves are young they are more efficient in light capture and therefore will give more energy returns than older leaves with smaller efficiency. This naturally implies a younger leaf will warrant more investment. In a similar manner higher availability of nutrients will cause more investment into nutrient catching mechanisms. Both of these are reflected in the marginal return on investment. Under this analysis forests do indeed appear to behave like economies basing their decision-making on “economic observations”.

When comparing investment patterns to current allocation schemes some parallels in GPP partitioning can be found. Looking at allocation patterns for a number of sites Litton et al. (2007) found that the partitioning to foliage (foliage NPP and respiration) of GPP amounts to 0.26 ± 0.03 and remains relatively constant. The results for maximum investment for average deciduous and evergreen sites fall within this range. However, it must be emphasised that photosynthetic capital does not incorporate only foliage but other structures as well. Furthermore, foliage serves other purposes besides photosynthesis (such as storage), therefore, it is not necessarily the case that the allocation to foliage will be a constant minimum for investment (as can be observed by the subsequent drop in investment after the peak). However, it is not improbable that during the beginning of the growing season most of this investment is directed towards new foliage as matched by the maximum investment outcomes and Litton et al. (2007) data. The subsequent lowering of investment can indicate foliage use for other non-photosynthetic purposes and investment into other structures.

The Mary's River Fir Site (US-MRf; Figure 9) was the only site that showed little agreement with other results. When comparing to results from other sites and averages it is clearly visible that this site behaves differently. The capital does not decline significantly into the winter period and the investment remains relatively constant and low throughout the year (as opposed to high capital). However, it does produce a photosynthetic pattern that matches the input data. No major disturbances were found. When compared to other evergreen forests it had the smallest temperature amplitude of all sites and it was one of 2 evergreen sites whose GPP did not reach zero over winter. US-MRf had also the highest maximum GPP of all evergreen sites.

It was possible to observe two sites other than US-MRf showing signs of capital patterns that did not align with the average capital results. This was done by unravelling each of the individual results of the Monte Carlo simulation of simulated annealing results for each sites. Because the final result obtained was an average of these runs these discrepancies were not significant enough to affect the final result. However, when individual results from the Monte Carlo simulation were displayed the two sites (Ontario Turkey Point, CA-TP4, and Willow Creek, US-WCr) both showed 4 and 5 individual capital patterns respectively that did not match the average capital pattern. Furthermore, these were also revealed to be the two most sensitive sites in the sensitivity analysis. However, even the different patterns observed in individual sample responses were different to the one observed in US-MRf suggesting that sensitivity is not the reason for observing a different outcome (US-MRf did not have a very high sensitivity result in the sensitivity analysis).

Finally, climate could be a factor influencing this change in behaviour. US-MRf is part of the Pacific Temperate Rainforest along the western coast of North America. The increased rainfall might be contributing to this very different response. The effect of climatic differences has not been considered in depth in this analysis but should be further investigated, perhaps as part of further study. The mild climate could be contributing to a whole-year high activity, however, it does not explain why other southern needleleaf forests (such as Duke's Forest US-Dk3) do not show the same relationship. An investigation into other year-round producing systems such as tropical forests could help understand whether this site is an outlier or climatic conditions are changing the capital response acutely from other sites. An increased number of sites used can also contribute to increasing the understanding behind these behaviours. For the purpose of this study though, no definitive reason for this different relationship can be established.

7.1 Parameters

In order to fully understand the model it is also necessary to understand the model parameters. The decay, or depreciation as it is known in economics, ϵ_1, will be further discussed in Section 7.2.

The shape of the photosynthesis response (equation 11b) suggests, that the photosynthesis, P, is saturating with respect to capital, K. This is similar to the law of self-shading implying that holding more capital does not necessarily mean it can be used as efficiently due to internal light or resource competition. This is further inhibited by ϵ_2, which determines the efficiency with which the capital can be used in photosynthesis. Evaluating ϵ_2, it appears to be higher for sites under more limiting conditions (eg. time limitation such as for deciduous sites which can only perform photosynthesis for a limited time in the year or climate limitation for northernmost evergreen sites where average temperatures are around 0°C and therefore photosynthesis might not be possible for part of the year due to temperature limitations). It can be seen (Table 4) that deciduous sites are more efficient in their capital use than evergreen (photosynthesis is inhibited for part of the year) but so are northernmost evergreen sites which experience temperature forcing. In both cases, photosynthesis is ceased or limited for part of the year leading to an increase in the efficiency of capital use, ie. ϵ_2, to account for this limitation.

The parameters ϵ_3 and ϵ_4 are both efficiency parameters used to help determine how temperature impacts photosynthetic efficiency. Though an exponential function has been used it is clear from the low values for ϵ_4 in Table 4 that the response is near linear relationship between temperature and efficiency suggesting that perhaps in the next iteration of this model equation (11c) should be a linear equation. The values of efficiency (equation (11c)) vary between approximately 1 and 18%. When comparing this to photosynthetic efficiency values calculated by Bolton and Hall (1991), the upper boundary of this is slightly higher than the proposed 13%. This mismatch in value together with the near-linearity of photosynthetic efficiency with temperature suggests that perhaps some revision might be necessary of the efficiency relationship.

The final parameter is the time-varying parameter ϵ_5 which is responsible for the decision-making process in investment. It was discussed before in Section 6.2. From initial analysis it appears to be approximately constant throughout the year, indicating that the main driver for photosynthetic investment is, in fact, marginal return. However, once again, this observation might indicate a need to adjust, or rather simplify, the part of the model responsible for the investment function.

7.2 Decay

The turnover rates for the forests vary between 13 and 91 days with all deciduous sites below 20 days and most evergreen sites, with the

Table 5: Leaf Longevity based on literature. Due to the nature of the leaves deciduous sites are all considered to have an average of 5 months despite likely variability between sites and climates. Site US-Ho1 is not included because it is a mixed forest.

Species	Leaf Longevity	Site presence	Reference
Black Spruce (*Picea mariana*)	15-20 years	US-PRR, CA-Qfo	(Hom and Oechel, 1983)
Douglas Fir (*Pseudotsuga menziesii*)	8-10 years	US-MRf	(Ishii et al., 2002)
White Pine (*Pinus strobus*)	36 months	CA-TP4	(Gower et al., 1993)
Loblolly Pine (*Pinus taeda*)	18 months	US-Dk3	(Radoglou and Teskey, 1997)
Deciduous (all)	5 months	all deciduous sites	(Gower et al., 1993)

exception of one evergreen forest, above this threshold.

Capital decay occurs for several reasons such as leaf senescence, fine root turnover, environmental weathering or pests. Root turnover rates can be affected by herbivore pressure, internal competition for resources, seasonality (Majdi et al., 2005) and soil microsite conditions (Gill and Jackson, 2000). Belowground productivity (BNPP) can account for 30-50% of the total NPP of a forest (Vogt, 1991) as caused by both respiration and root decay, which can be observed in some of the capital decay in this model framework. A study by Gill and Jackson (2000) found that tree systems tended to have a fine root turnover rate of around 10% yearly. All decay results obtained (Table 4) were lower than the root turnover rate. Of course, the root system is considered only a part of the capital that partakes in photosynthesis. Therefore, there is another process extending the decay of photosynthetic capital. Most likely a big part in this is played by the decay of foliage.

From the perspective of capital the decay of leaves is a more complicated process than root turnover. No reallocation occurs at the end of life of fine roots. However, leaves serve not only as carbon absorbing organs but also as storage for plant's nutrients which get reallocated at leaf senescence (Brian F. Chabot, 1982). Because of this it cannot be said that all foliage allocation is considered to be photosynthetic capital but also not all photosynthetic capital decay can be expressed by the lifetimes of leaves. Nevertheless, leaf longevity should present some guidelines for decay values between sites (Table 5).

It is possible to suggest that photosynthetic decay rate should be dependent on the dominant species, being smaller for sites with spruce forests (leaf lifespan of several years) and larger for pine forest and deciduous forests which have a much shorter leaf longevity. However, for most sites the opposite is observed. Black Spruce Forest (CA-Qfo) displays the greatest decay rate of all evergreen forests, and a Loblolly Pine site shows the lowest decay rate of all the sites.

Therefore, the calculated decay rates are significantly different to the leaf longevity values. None of the decay values are big enough to account for the several months of leaf longevity in deciduous plants and even less so for the years of leaf longevity in evergreen plants. However, the decay rate is not only dependent on leaf longevity but also on various other processes present in the plant. All decay values are below the 10% root turnover rate. General climatic conditions also seems to have little impact on the decay of evergreen trees with two northernmost sites having vastly different decay rates. However, it can be observed that two sites (US-Ha1 and US-Bar), which are situated in neighbouring states, have very similar parameter responses (including decay) despite having vastly different starting capital, suggesting that microclimates may have a much stronger effect than other factors on the magnitude of decay.

Finally, the payback time of various capital subparts must also be considered. Here only leaf payback time is considered. For deciduous broadleaves this appears to be 15 days and for evergreen needleleaves it can be as long as 50-80 days (Saeki and Nomoto, 1958). The photosynthetic capital decay of deciduous forests appeared to be lower than this payback time whereas the evergreen site performance was much better and falling within the boundary.

Probably the most important factor impacting the values of decay is the time-variability of decay. Because of the difficulty of predicting the varying decay of capital subsystems, decay was assumed to be an average of these, constant throughout the year. However, this was an entirely pragmatic decision. Under variable climatic conditions this turnover rate is likely to vary in time. Therefore, in future work it is worth investigating how the decay might change with time and with environmental factors.

8 Conclusions and Future Work

Through the use of econometric methods, computational analysis and fitting the potential of using economic theory in plant productivity modelling was explored. The analysis suggests that economic principles govern decision-making in forests. Where previous studies used economic language none have previously attempted to use quantifiable methods

to explain this connection, giving justification for the language used. This project serves also to stimulate change in the way allocation can be viewed, with allocation modelling in mind. Several points can be made from this analysis:

1. Economic modelling in plant sciences has great potential. The resulting investment, capital and other model parameters were sufficient to support the claim that plants can behave like economies (quantitatively) and the topic is open to further exploration. Concepts of investment, capital and marginal returns, which are purely based on economic theory, have their place within a forest ecosystem and can be related to the process of photosynthesis and allocation.
2. Productive capital explains the observed capital pattern. Furthermore, the photosynthetic capital may be assumed to only contain active capital, ignoring any dormant investment. The remaining captured resource is directed towards respiration, maintenance, storage, reproduction and other functions not analysed further in this work.
3. Marginal return serves as a driver and control for investment with plants behaving very much like businesses and investing when their returns are high and not when they do not look to gain much from their investment. This relationship between investment and marginal return was observed to be near linear. It shows great potential as the main driver of investment decisions.
4. There was a distinct difference between evergreen and deciduous forest responses. Evergreen forests had a lower decay of capital and none except one of the sites reached near-zero capital over the wintering period. On the other hand, deciduous forests had a clearly lower minimum capital and a much higher turnover rate. Climate also seemed to be a significant factor impacting different outcomes (northernmost evergreen sites showing patterns similar to deciduous sites) suggesting that, not surprisingly, environmental stresses may have a significant effect on the investment strategies of forests. This was only revealed in a direct relationship between temperature and capital but suggests another avenue to explore.

Despite answering the most important question of this work about the potential of using econometrics in forest modelling, there is much that can be expanded upon in future work. From a purely mechanical perspective these can be adjustments to model functions such as adjusting the investment function to include the linear marginal return relationship and further evaluation of the efficiency function.

Beyond the mechanisms of the model several important biological factors have not been taken into account or would be worth exploring:

1. Nitrogen content. Nitrogen has been proven to be a limiting element in plant growth. Many models include nitrogen and it would be interesting to see how nitrogen uptake combined with photosynthesis would perform

within this economic framework and behave in terms of energy, capital and investment.

2. Water content. Water content is an important element affecting the rate of photosynthesis through stomatal conductance. Seeing whether water content can impact the efficiency of photosynthesis or how water limitation could impact capital behaviour in this framework would be another interesting topic to explore.

3. Further work into comparing different plant types. It has already been observed how climate and species type can affect the decay of ecosystems in this framework. Further work which focuses more on selecting sites in close proximity to each other and with a selection of different dominating plant species traits or climate characteristics could reveal more about mechanism driving forest economy. Finally, exploring tropical forests may give a clue to behaviour of evergreen sites in this analysis.

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