

Faculty of Bioscience Engineering

## Modeling Oak and Beech Regeneration in Mixed and Uneven-Aged Forests

A Process-Based Approach for Changing Environments

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*No one trusts a model  
except the person who wrote it  
Everyone trusts an observation  
except the person who made it*

Harlow Shapley



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# 1 Introduction

Forests are complex systems continuously in interaction with the other surrounding systems. The climate system is regulated by the forests through the carbon and water cycles. The carbon cycle is closely linked to the forests thanks to the carbon sequestration in the biomass and the soil (Pan *et al.* 2011). The water cycle is influenced by the forests with the evapotranspiration (de Wergifosse *et al.* *in review*). The forest ecosystems also give many ecological services to the society. Ecological services can be defined as the positive externalities of a forest on the environment. Some of them are purely anthropogenic such as timber or leisure activities but a lot of them are more indirect such as water and air filtration, biodiversity. All these complex interactions make difficult the prediction of forest responses to global changes. These changes are numerous such as climate change, biodiversity loss due to ecosystem destruction and fragmentation, invasive species importation or native species proliferation. Climate change is caused by the increase of carbon dioxide. It will probably lead to an increase of mean temperatures, the modifications of the rains and weather events such as drought, heavy rain, hurricanes. These events are likely to increase in frequency, duration and intensity with the climate change. The knowledge acquired about these impacts is based on long-term analysis (Ningre *et al.* 2019; Pretzsch 2006; Swaim *et al.* 2016) and controlled experiments (Coll, Balandier, and Picon - Cochard 2004; Turcsán *et al.* 2016). But due to the long lifespan of the forest stands, the experiments covering all these lifespans are unusual (Pretzsch 2006).

An approach that is promising to connect the different knowledge is modeling. It is a process that aims to make a representation of a system in order to have a better understanding of this system. As the forest ecosystem is very complex, modeling allows to divide it into different subsystems that are easier to deal with (e.g. tree growth, nutrient cycle, water cycle, radiation transfer, etc.) and choices can be made for the scale (temporal and spatial) the model work with. Those choices involve different hypotheses that affect the model abilities. Once a model is effective, it can be able to make predictions by changing the environmental conditions, the human interventions and the other disturbances. Of course these predictions will never be totally accurate but it allows to explore many scenarios to identify the most promising in order to test them in field experiments. This approach needs to invest the time in the model development but then it makes it possible to earn time and money by reducing the need in field experiment that is only necessary to validate the modeling predictions.

Forest modeling is not a new field of research. Some tools were already used to predict the yields of a stand with the characteristics of the site (climate, soil fertility, slope, etc.). An example of tool developed is yield tables which are calibrated on reference stands (Miina *et al.* 2006) and can be used to have an estimation of the yields of a specific specie on a stand with a specific site index. That kind of tool is

simple to use and accurate to have an estimation of the production but their validity domain is limited to species, site index and other conditions they were calibrated for. Another modeling approach developed was distribution models. These models use stochastic relations to simulate the evolution of a stand from an initial distribution of trees characterized by their dimensions. The updated distribution is then obtained. Individual tree models simulate the tree growth for each individual (Pretzsch *et al.* 2006). It allows to handle spatialization in the stand in distance dependent models (in opposition to distance independent models). The stand characteristics can be extracted easily from these models and the trees interaction can be modeled (e.g. crown, water, and light competition). With the changes in the forest management practices, new modeling methods were developed to handle age and species heterogeneity. The climate change also involves that the conditions are changing with the time which is another constrain on the use of models. All those considerations lead to the conclusion that empirical models are not suitable for long-term prediction in a changing environment.

A better approach that can answer those questions is process-based models. Those models are indeed more flexible in their use. Instead of calibrating the model on specific environmental conditions, the environmental conditions are an input of the model and the processes are using those conditions to calculate the outputs. This approach has many advantages and can help in our understanding of the forest ecosystem. They bring a possibility to understand the key processes behind the changes observed or simulated and identify the environmental constraints of a forest ecosystem (Mok *et al.* 2012). Unfortunately, no model is perfect and the calibration and validation of the process-based models are still restricted to a few sites and they should be used with parsimony when they are pulled outside of their validation range. The accuracy of those models for the conditions they are calibrated for is also smaller than the empirical models but it is expected that this accuracy decreases sparsely outside of the calibration range compared to empirical models.

HETEROFOR is a process-based model that tries to answer the questions raised before. (Jonard *et al. in review*). Its approach is to focus on scenario analysis at a stand scale with individualized and spatialized trees. That approach is developed within the CAPSIS modeling platform (Dufour-Kowalski *et al.* 2012). Different processes have been implemented in HETEROFOR: radiation absorption and transfer, phenological periods, water balance, photosynthesis, nutrient cycling and mortality. With those processes included in the model, the range of scenarios that are possible to explore is already interesting. The final user can start running simulations with the possibility to compare different scenarios of thinning (which is the main possible human intervention on a stand with planting). The impact of thinning on the tree growth in the neighborhood of a cut tree can be measured. The model can for instance show differences in the basal area increment under variable  $CO_2$  concentrations (Jonard *et al. in review*).

As seen before, there is a need to handle the global changes impacts on the

forest ecosystems. A known solution is to increase the resilience of them. Resilience is the ability of a system to adapt to disturbances in order to avoid a collapse. These disturbances are not only linked to climate as weather events but can be anthropogenic like timber harvesting, atmospheric and water pollution or biological such as invasive species or native species proliferation. Those species can disturb the forest ecosystem by competing with regeneration for light or soil resources. Other species can put pressure on the regeneration (browsing pressure) or on adult trees (parasites). The research should focus on the impacts of these disturbances to bring some keys to support the ecosystems in their adaptation to the fast changing conditions due to climate change. As it is known for every ecosystem, an increased biodiversity is essential to make the forest ecosystems more resilient. It means that the forest management practices have to change into mixed stands. The uneven aged stands are also important to avoid the clear cut which is a huge disturbance on the forest ecosystem. The negative effects of clear-cutting are numerous: soil mass movement, stream siltation, wind throw, and biodiversity loss (Ligot 2014). But how to choose which species have to be mixed to keep a good productivity of the forests while enhancing the resilience? That question is very complex and a good knowledge of the ecology of the different species and the between-species interactions is needed. For example beech is known to be very sensitive to climate change hazards such as drought (Coll, Balandier, and Picon - Cochard 2004) which is limiting its recruitment (Fruleux *et al.* 2016) and affects adult trees. This sensibility is visible in the beech geographical range but its drought resistance and growth rate can be improved in mixed stands (Condés and del Río 2015). In opposition, oak has a better resistance to drought but has some difficulties to regenerate because of its shading sensitivity. The main reason that explains these difficulties is the competition with beech seedlings and other shade-tolerant species. Oak seedlings need enough light through canopy opening to successfully establish whereas beech seedlings can establish before any opening (Ligot 2014). Moreover, seed predation by wild boars and browsing by ungulates is selective against acorn and oak seedlings (Kuiters and Slim 2002; Zeman *et al.* 2016).

To ensure a greater resilience, forest management methods are nowadays evolving from even-aged pure stands managed with clear-cutting to more close-to-nature practices. The objectives of the new practices are to minimize the impact of timber harvesting in order to enhance the ecological services while keeping an economic value at a similar level and reducing the negative impacts on the forest ecosystem. These practices are mixed and uneven-aged stands.

In mixed and uneven-aged stands, the objective is to maintain every tree age classes for the species of interest. It means that the regeneration is continuous to renew the tree stock. When the periods of time exceed 30 years, the distribution of species is susceptible to change. These changes could influence the results of long time simulation in models. Therefore, the evolution of mixed stand with the environmental changes cannot be predicted without taking regeneration into account.

Due to the sensitivity of the seedlings to their environment, the impact of climate change on regeneration is probably a greater factor of changes in forests composition than the impact on adult trees (Gómez-Arparicio *et al.* 2008; Mok *et al.* 2012). Moreover, mixed forests naturally evolve to pure stands with shade-tolerant species like beech. An intervention is thus necessary to keep a forest mixed. Regeneration is a continuous process in uneven-aged forest that must be taken into account because of the impacts it can have on adult trees and especially for long-term simulations.

Forest modeling focus mainly on tree growth which is the indicator of the economic value of forest management choices. Therefore, processes that are not closely linked to growth such as mortality or regeneration have been neglected. Gap models are an exception because of their objectives. They were developed to answer ecological questions, including the long-term behavior of the forest ecosystems (Bugmann 2001). Modeling the forest regeneration in the other types of models is necessary to handle long period simulations of forest growth. The attempts to model this process are often small modules based on observations that will lack of accuracy for changing environments. As for growing models, the process-based approach is able to handle the changing environments. Therefore, there is a need to reproduce a process-based forest regeneration is models.

The objective of this Master's thesis is to develop a regeneration module for HETEROFOR, a process-based and spatially explicit model. To handle the number of individuals in regeneration, the seedlings are put together into cohorts, and the cohorts are distributed in size classes. The model handles the growing process of seedlings from juvenile stage (0.2 meters) to the recruitment (12 meters) which includes the new trees in HETEROFOR. The key processes used in the module are the light availability for the seedlings height growth and the carbon resources production for the mortality process. To evaluate the model, self-thinning line were reproduced with different growing scenarios.

## 2 State of the Art

### 2.1 Definitions

**Definition 1** *Regeneration*: Replacement of mature individuals by individuals of the same species (Kroschel *et al.* 2016). This process involves different stages: seed production, dispersal and survival, germination, establishment and growth until recruitment. Regeneration is also used to talk about the whole seedlings in the understory (Miina *et al.* 2006) and can be both natural and artificial (planting).

**Definition 2** *Understory*: All the vegetation under the canopy of a forest. It may include regeneration cohorts and herbaceous layer of vegetation.

**Definition 3** *Recruitment*: is the introduction of new individuals into a population or community (Ribbens *et al.* 1994). This term is used to design seedlings newly established (seedling recruitment, Ribbens *et al.* 1994 or tree that can be considered as an adult tree. The minimal dimension to consider a tree as an adult is variable from an author to another (1.3 m high for Fulton 1991, 6 cm diameter at 1 m for Canham 1990).

**Definition 4** *Competing vegetation*: Vegetation growing in the understory of a forest except the regeneration. That vegetation can compete with regeneration for resources such as water, nutrients and light (Balandier *et al.* 2006).

**Definition 5** *Establishment*: Process in the early stage of the seedling development (Price *et al.* 2001). It starts at the germination and ends when the seedling gain enough vigor to be resistant to small disturbance in the resources availability and physical disturbances such as animal hit or grazing (Löf 2000).

**Definition 6** *Model*: Abstraction of the reality into a simpler representation of that reality (Rogers and Johnson 1998). The models are used to explore situation where no data is available (extrapolation), to interpolate the data, in order to have a better understanding of the system with a conceptual or biometric description of them (Pretzsch 2006).

**Definition 7** *process-based model*: Model based on physical, chemical and biological laws in order to analyze the behavior of a system (Makela *et al.* 2000).

**Definition 8** *Self-Thinning*: Natural mortality process which makes the stem density decrease with the seedlings growth. In this process the seedlings are only subject to competition-induced mortality (Ningre *et al.* 2019).

## 2.2 Regeneration Processes

Regeneration is a succession of a lot of different processes that goes from the flowering of an adult tree to the recruitment of a new young tree. An overview of those processes and some modeling approaches for them can be found in the literature. Despite the processes are well known and sometimes modeled, no model was found with all of them included into.

### 2.2.1 Fruit Production

It is the first step of regeneration. It includes the processes from the flowering to the seed production. For the flowering prediction, date of budburst is modeled with a main driver which is the temperature (Chuine *et al.* 1999) or heat sums (Price *et al.* 2001). Maak and von Storch (1997) also showed a strong correlation between the air temperature in January, February and March and the anomalies in the flowering date. The models are using the forcing temperature and can take the chilling temperature into account. In temperate regions, the flowering occurs in a range of time for a given specie. The photoperiod (Fitter *et al.* 1995) can also be used to predict flowering whether it is absolute or relative (along with temperature).

Seed production can be related to species, age, size and vigor of the parent tree (Price *et al.* 2001). The tree species can be grouped between heavier-seeded species which produce fewer and larger seeds and light-seeded species which produce a lot of small seeds (Kroschel *et al.* 2016). The seeds production variability is also different between heavy seed production which can have a high between-years variability such as oak with the masting process and light-seeded trees which have a more constant between-years production. An important phenomenon is the oak's fruiting dynamics called masting (Schermer *et al.* 2019; Touzot *et al.* 2018). It has been observed that oaks produce seeds sporadically between the years and the oaks in a same environment are synchronized for their seed production. Schermer *et al.* (2019) developed a resource budget model (RBM) to highlight the drivers of masting. They concluded that the resource availability and the pollen dynamics are involved in the masting process. Caignard *et al.* (2017) showed that the seed production of oak is increasing with the temperature rise in the past decades and the seed production of oak also decrease with aging.

### 2.2.2 Seed Dispersal

This process depends on the dispersal vectors, the phenology, the seed type and the fecundity of the adult tree (Kroschel *et al.* 2016). The seed dispersal can lead to species *migration* along environmental gradient (Price *et al.* 2001). Dispersibility decrease with the seed weight (Streng *et al.* 1989)

Jensen (1985) has shown the dispersal distance of *F. silvatica* and *Q. robur* seeds by rodents. That distance is between 0.5 m and 10 m from the original position (4

m on average). The seeds dispersed were found in caches in the mineral soil, the litter or the vegetation. The dispersal of beech nuts by blue jays was measured by Johnson and Adkisson (1985). The range of dispersion can be up to 4 km following wooded hedge (to escape predators). The ecological relation between oak and jay has been largely studied. The jays collect acorn from an oak and travel a variable distance (from hundred meters to several kilometers) to hide them in separate sites (Bossema 1979).

In models, seed dispersal can be simulated using deterministic seed-rain curves as a function of distance from the parent trees (Price *et al.* 2001). The dispersal agents generate a *seed shadow*, an area heterogeneously covered with seeds (Janzen 1971).

### 2.2.3 Seed Survival

Seed survival is the time between the seed dispersal and the germination. The seeds need precise conditions to germinate and the viable seed number decrease with time because of predation or aging. Two different types of seeds storing strategies can be found in the tree species: seeds stored in cones and release when some environmental conditions are met and seeds spread directly by the parent tree and stored in the soil seed bank (Price *et al.* 2001). Masting is a kind of survival strategy: the trees produce a lot of seeds on year to reach a predator satiation and no seed the rest of the time to make the predators starve (Bogdziewicz *et al.* 2018; Janzen 1971). Zeman *et al.* (2016) has measured that despite the high acorn consumption by the wild boar, the impact on oak regeneration is limited and there is enough acorn production to feed them and have a remaining stock for regeneration but Gómez *et al.* (2003) showed that acorns were quickly consumed by predators and only 4% of acorn has produced seedlings. Hille Ris Lambers *et al.* (2005) in an analysis of the forest seed banks has not found oak seeds stored despite high seed production and germination.

### 2.2.4 Germination

Germination is highly dependent to the climate conditions such as soil moisture, soil temperature, air temperature, available light but also on seed viability (Kroschel *et al.* 2016). Some seeds require winter chilling (vernalization) to germinate (Price *et al.* 2001). In general, heat sums are used to simulate the start of germination process but moisture is also essential for germination and can be used as a variable for its prediction (Mok *et al.* 2012).

### 2.2.5 Establishment

Establishment is the growth and survival process for seedlings during the early stages. Kroschel *et al.* (2016) consider that the establishment process is finished when the seedlings are older than 3 years. After germination seedlings are very

sensitive to their environment (Gómez-Arparicio *et al.* 2008; Mok *et al.* 2012) and their survival is variable with the available resources and the competition among other plants. Mok *et al.* (2012) suggest an approach based on an establishment probability in a regeneration niche calculated with environmental variables such as frost and drought events. The different factors that will affect establishment can be divided in abiotic factors, interspecies competition and browsing pressure.

### ***Abiotic Factors***

Seedling survival can be related to some abiotic factors in which light can be considered as the main driver (Balandier *et al.* 2006; Gómez-Arparicio *et al.* 2008). Soil water content can also be considered as an important driver whether it is limiting or excessive (Gómez-Arparicio *et al.* 2008). Nutrient availability can be used to a lesser extent in order to predict establishment but it is also in interaction with other factors such as high water content, which contributes to improve the nutrient mobility in the soil.

### ***Interspecies Competition***

Establishment is also subject to inter-specie competition. Balandier *et al.* (2006) use the concept of best competitor to compare the different species and predict which one will survive. The best competitor is the specie which is better adapted to the resources availability. With high resources availability, fast-growing species will be the best competitors. In opposition, in low resources availability environments, the best competitors will be plants able to reduce the losses. The competition can occur for soil resources (nutrients and water) or for light. Each resource needs specific strategies to improve the uptake or to reduce the losses.

For nutrients, the strategies to reduce losses are a long tissue lifespan and low concentration in death tissues. If the nutrient availability is low and in the places where the water is highly available, the best competitors are fast-growing species with high water loss. In forests, nutrients are usually concentrated in the top soil and water content increase with depth. The ability to adapt the root system to improve nutrient and water uptake will also determine the capacity to compete the surrounding vegetation.

The competition for light is crucial in forest environment. In bright environment, the morphology and physiology of plants are important traits to compete with neighboring vegetation thanks to a fast expansion. In low light environments, positive carbon budget maintenance, light capture optimization, low respiration rates are traits that will have the successful competitors (Balandier *et al.* 2006).

Two species can develop at the same place without competing if there is spatial and/or a temporal segregation. For example, adult trees will grow deeper roots if there are competitors in the neighborhood. The phenology (seasonal variation) can also reduce the impact of competition for trees (Balandier *et al.* 2006).

Fruleux *et al.* (2016) has shown that beech growth suffer from conspecific competition which is due to belowground competition. In contrast, oak seedlings do not affect the growth of beech seedlings in regard to the resources competition. They also highlighted a positive interaction between oak and beech seedlings under water stress. The authors suggest that these results could be explained by the below-ground niches occupied by oak and beech seedlings which may be slightly different. Coll, Balandier, Picon - Cochard, *et al.* (2003) found similar results in a study on beech establishment and growth in old meadows. The objective was to understand the beech seedlings growth requirements. A recently abandoned meadow colonized by grass was used to study the water requirements. An old meadow colonized by 25-year-old Scot pines was used to study the light requirements. Half of the first plot was weeded periodically a part of the second has been thinned. These operations' aim is to compare the situations of high resource availability with low resources availability. The unweeded part of the plot was unsuitable for beech because of the water competition. The unthinned adult Scot pines stand (PAR 9.9%) reduces the beech growth because of the light competition. Unlike grass, the understory vegetation was not limiting beech growth with water competition. A more controlled experiment (Coll, Balandier, and Picon - Cochard 2004) has shown similar results with a growth strongly limited by grass competition due to lack of water available for beech that also have an impact on nitrogen uptake. The authors highlight that in field conditions, the beech seedlings can root deeper than grass so this competition is only effective during the first steps of establishment. In low-light conditions, the competition by grass is less intense so beech can develop. The biggest height growth rates have been observed for beech in full light condition without grass competition. In opposition to beech and birch, oak survival is less affected by desiccation (McKay *et al.* 1999).

The biomass allocation is influenced by the resources competition. The shoot/root ratio is for example modified with more resources allocated is the shoot in case of light competition and in the roots in case of water or nutrient competition (Gaudio, Balandier, Philipe, *et al.* 2011).

The better adaptation of oak to water stress could come from its ability to grow deeper roots than beech (Löf 2000) which improve the water uptake (as water content increases with depth). The impact of the competing vegetation can be related to a below-ground competition for water which leads to a reduction of the water potential. The author concludes in his paper that oak can establish more easily than beech during the first steps of its development thanks to its adaptations to water stress which result in a higher growth rate when it is subjected to below ground competition. In summary, oak has a lower tolerance to shade and a higher tolerance to drought than beech (van Hees 1997).

## *Browsing Pressure*

Herbivores can have a huge impact on a forest tree composition by selective browsing (Mitchell and Kirby 1990). Kuiters and Slim (2002) analyzed the evolution of a mixed stand after a reduction of ungulates species and concluded that the browsing pressure has a great impact mainly on oak regeneration but also on beech seedlings. This impact is not linear with the herbivore density: there is a threshold under which the regeneration is feasible. This threshold must allow a spatial and temporal variability in the browsing pressure which allows some periods of successful regeneration alternated with long periods without regeneration. With a modeling approach, Jorritsma *et al.* (1999) shown that even low ungulates densities can have a significant impact on the forest regeneration.

### **2.2.6 Mortality**

Bigler and Bugmann (2003) summaries the different approaches to model tree mortality into stand-scaled approaches and individual-based approaches. At the stand scale, the common approaches use mortality rates function of the tree age or other tree characteristics such as tree dimensions and growth rates (Holzwarth *et al.* 2013; Yang *et al.* 2003). At the tree scale, mortality can be modeled with size-related variables, growth-related variables, crown-related variables (e.g., leaf area index or crown defoliation), ratios of crown-related and growth-related variables and other variables such as age, competition, or social position. As the seedlings are mostly modeled at a stand scale, the focus will be put on this approach.

Holzwarth *et al.* (2013) describe the U-shaped curve of mortality function of size. The tree seedlings are located in the left part of the curve which means that they have a high mortality rate that is decreasing to a minimum at recruitment. The juvenile trees die mainly standing or crushed until they are 50 years. The causes of a standing dead are mostly due to a stress and can be predicted by a reduced growth which shows a struggle to maintain a positive carbon balance.

Some of the mortality description in the literature are based on the self-thinning process introduced by Reineke (1933): for a given mean dimension of trees, the density cannot exceed a threshold. It is generally described as self-thinning lines or maximum size-density lines (Charru *et al.* 2012; Ningre *et al.* 2016; Pretzsch 2006; Yoda 1963). All the self-thinning equations that can be found are calculated on the base of pure undisturbed stand.

Based on 120 years of observations, Pretzsch (2006) confirms the self-thinning lines described by Yoda (1963) for beech, oak, Scots pine and spruce. These self-tinning line follows the equation 2.1 with  $\bar{w}$  the mean tree biomass ( $kg\ tree^{-1}$ ),  $N$  the stem number and  $k'$  is equal to 15, 16, 17 as a reference.

$$\ln \bar{w} = k' - 3/2 \ln N \quad (2.1)$$

Ningre *et al.* (2016, 2019) also developed self-thinning lines that are called maximum size-density lines. The variable used to model the self-thinning is the girth at breast height ( $C_g$ ) with the equation 2.2. The value of the parameter  $a$  is equal to 13.733 for both species and the value of  $b$  is respectively equal to -1.652 and -1.512 for oak and beech.

$$\ln(N_{max}) = a + b \ln(C_g) \quad (2.2)$$

All the mortality equation seen before are empirical and a process-based mortality is essential to take the environmental changes into account (Keane *et al.* 2001; Makela *et al.* 2000). The photosynthesis and respiration processes are well known but the connection with carbon allocation and growth under stress is still necessary to understand in order to model a environment dependent mortality.

Some attempts to model mortality are focused on specific disturbances such as drought (Meir and Mencuccini 2015) but these processes are still poorly understood and difficult to predict. Wang *et al.* (2012) listed two drought-induced tree mortality processes: carbon balance based mortality (respiration demand > GPP + Stored non-structural carbohydrates) and xylem cavitation induced mortality.

### 2.2.7 Growth & Morphology

It is the survival process after a successful establishment. The young trees become more and more resistant to disturbances. Two main drivers are being studied in order to predict the seedlings growth: light and water availability.

Light is often used to predict the height growth (Ligot *et al.* 2013) but can also have an effect on biomass partitioning such as SLA or height:diameter ratio (Sevillano *et al.* 2016). Giertych *et al.* (2015) highlighted a trade-off process in shade-tolerant specie seedlings. Under shade conditions, these species allocate more carbon to storage. The dimensions and the growth rates decrease strongly with light reduction for beech seedlings (Ammer 2003). This strategy empower beech seedlings to keep a positive carbon balance. Thus the beech survival rates under low light levels are greater than oak.

Ligot *et al.* (2013) analyzed the height increment of beech and oak seedlings on a two-years period and made a prediction model for height increment estimated from the transmittance. For oak, the social status also has an effect on height increment prediction.

Water is also an important driver of seedlings growth (Löf 2000). Water stress can affect the leaf development by reducing the biomass allocation to leaves in order to increase fine roots development (van Hees 1997) which result in a reduced growth. However, Turcsán *et al.* (2016) has found height increment increase after an early summer drought event for *Quercus petraea*. This result highlight that the effect of drought on regeneration is complex and need more research to be well understood.

Some morphological traits can be correlated to the tree age such as the root to shoot ratio (Genet *et al.* 2010). Pajtík *et al.* (2011) analyzed the Biomass

Conversion and Expansion Factors (BCEF) of beech, oak and pine seedlings which is also correlated to seedling age. They show that the BCEF change rapidly at the seedling development stage but conclude to a reasonable accuracy to estimate the young forests biomass.

Allometric equations are mathematical relations that predict morphological traits from other characteristics (e.g. height or diameter). Montagnoli *et al.* (2016) analyzed the morphology of very young seedlings of oak and beech (up to 15 cm) and fitted an equation to predict the total biomass [g] from the height [cm] (equations 2.3 and 2.4). However, that relation was not significant for spruce and Scots pine.

$$Biomass_{total} = 0.0066h^{1.4681} \quad Fagus sylvatica \quad (2.3)$$

$$Biomass_{total} = 0.0071h^{1.9477} \quad Quercus ilex \quad (2.4)$$

## 2.3 Regeneration Modeling Approaches

### 2.3.1 Existing Regeneration Models

**JABOWA** is a gap model developed for individual trees on small forest plots simulation (Botkin 1993). The regeneration process consists of three decisions: the model determined if the regeneration can occur, then the number of saplings added and the height of the saplings are calculated. The variables taken into account are the soil quality, the light availability and the specie characteristics (e.g. shade tolerance).

**TACA-GEM** is a model that simulates germination and establishment of eucalyptus seedlings in Australia in response to climate change (Mok *et al.* 2012). It uses a process-based approach to determine if germination occurs and afterwards if establishment occurs. For germination, dormancy is managed with chilling day accumulation and heat sums and the germination is started if the temperature and moisture conditions are met. Once the germination happened, drought and frost days can make establishment fail. The predictions of the model are focused on the suitability for regeneration to occurs. The aim of the model is to analyze ecosystem evolution without the information about the forest productivity.

**Pukkala (1987)** developed a regeneration model for *Pinus sylvestris*, *Picea abies*, *Betula pendula* and *Betula pubescens*. It is divided into birth process including seed production, maturation and germination based on heat sums, seed predation based on a proportion of uneaten seeds, growth which depend on the specie, the height and the forest site type and mortality which depends on the seedling age and the basal area. The different processes are modeled stochastically and the model give in the end some general information about the regeneration (e.g. seedling density, covered area, survival rates to 1.3 m, etc.).

**ACORn** is a model developed by Dey (1991) that simulate even-aged oak stands in Missouri. It is a statistical model developed from measurements before and after clear cuts to simulate the two sources of oak reproduction: sprout and fruit reproduction (Rogers and Johnson 1998). The model simulates the future stand composition and structure from a preharvest inventory. The aim of the model is to help forest managers to harvest with the conditions that are likely to have a good natural regeneration.

**SIMSEED** is a stochastic recruitment model (Rogers and Johnson 1993). It is divided in two processes: the recruitment and the survival rate. The recruitment consist in a random process following an exponential distribution influenced by the existing population of seedlings and a user defined recruitment constant. The seedling survival rate is a constant that allows to calculate the fraction of the seedlings that survive from a year to another.

**SORTIE** is an empirical model based on large set of observation (Ménard *et al.* 2002). All the individuals are simulated by considering the light competition between each other. The module for regeneration is a recruitment model function of the distance from the parent tree. Ribbens *et al.* (1994) developed equations to predict the recruitment patterns in the SORTIE model. The recruitment is divided in two components: the number of seedlings recruited and the seedling density at a given distance from the parent tree.

**Schweiger and Sterba (1997)** based their recruitment model on logistic and Weibull distributions. It describes the spruce natural regeneration in Austria. The equations predict the probability that regeneration will occur with the logistic distribution and then the height and the stem number with the Weibull distribution.

**Zavala and Bravo de la Parra (2005)** developed a size-structured individual-based process-based model that combines a tree growth and mortality model with a resource dynamic model. The model includes regeneration thanks to a recruitment rate proportional to the basal area of the trees of the same specie.

### 2.3.2 Regeneration Modeling

As regeneration is a complex process, there are a lot of different method to model it. Most of the models having a regeneration module use an empirical equation (Dey 1991; Ménard *et al.* 2002) or stochastic distribution (Rogers and Johnson 1993; Schweiger and Sterba 1997) to simulate the occurrence of regeneration and directly add newly recruited trees to the growing model (recruitment models).

Some models use biological processes (e.g. flowering, germination) to predict the regeneration. These processes are controlled by the physical environment (e.g. with heat sums). For regeneration, the processes that have to be described are the

quantity and quality of seed, the seed dispersal, germination, survival and growth of seedlings (Miina *et al.* 2006). No model with all of these processes was found but some of the processes has been modeled separately with process-based approaches. Flowering can be modeled on the basis of heat sums (Chuine *et al.* 1999; Price *et al.* 2001), some attempts to model masting can also be found (Vacchiano *et al.* 2018). The seed dispersal is modeled as a function from parent trees (Ribbens *et al.* 1994) but this approach could be combined with the impact of natural dispersers (e.g. rodents, birds, and wind). The seed survival is a mainly stochastic process (Dey 1991). The density of predators could be used to influence the survival rate but no model was found with that. Germination can be managed with a process-based model with the impact of temperature and moisture (Mok *et al.* 2012). Seedlings growth can be modeled as a function of the light and the competition (Ligot *et al.* 2013; Rogers and Johnson 1993). Resources sharing models (Zavala and Bravo de la Parra 2005) along with understory dynamics models (Landuyt *et al.* 2018) seems to be the best way to model a process-based seedling mortality.

## 3 Materials and Methods

### 3.1 Heteroform

HETEROFOR is an individual-based and spatially-explicit model (Jonard *et al. in review*) hosted in the modeling platform CAPSIS.

#### 3.1.1 Capsis Modeling Platform

CAPSIS is a framework developed for forest modeling (Dufour-Kowalski *et al.* 2012). This is a software infrastructure that provides a development environment, libraries and data structures, generic components for mathematics and data visualization, execution system for the models, a user interface to set the parameters and run the simulations, documentation and a test system.

The main simulation paradigm in CAPSIS is based on scenario analysis. The final user can create a project with an inventory file and initial parameters. It results in a creation of a forest that can be grown with yearly time step with or without silvicultural treatment (e.g. tinning). The different scenarios can be compared and analyzed.

On that framework modelers can develop their own model with their own assumptions and paradigms. An assistance is brought by the CAPSIS team for the implementation to improve the efficiency (e.g. computing time, bug solving, etc.) of the model. The structure of the code is thereby clean and understandable for any other modeler despite the complexity of the models. The user interface promotes model distribution to a final user. And a script interface makes advanced analysis easier.

#### 3.1.2 General Description of Heteroform

HETEROFOR aims to integrate as precisely as possible the different processes involved in the forest ecosystem functioning to predict the tree growth. Those processes are coded in different modules interacting together. Here is a brief description of the initialization, the spatial organization and the different modules in order to understand the way the regeneration module is inserted in HETEROFOR.

**Spatial organization.** The scale of the model is a stand scale (mean surface of about one hectare). The stand is divided in square cells (the cell width is chosen by the user, the default value is 10 meters) that are used by the radiation transfer module (SAMSARALIGHT) and the regeneration module (Fig. 1). A 3-dimensional coordinate system is used to spatialize the adult trees. There are three different scales to implement the processes: the stand scale ( $\sim 1$  ha), the cell scale ( $\sim 100$  m<sup>2</sup>) and the tree scale. The different modules can be implemented at different spatial scales to meet the needs of the process: the soil horizons for the water balance and the nutrients' cycle are implemented at the stand scale, the light module and

the regeneration module are using the cell scale and the phenology, some water balance processes, the light interception by trees and the photosynthesis modules are implemented to the tree scale.

**The radiation transfer** module uses the SAMSARALIGHT library (see CAPSIS documentation: [http://capsis.cirad.fr/capsis/help\\_en/samsaralight](http://capsis.cirad.fr/capsis/help_en/samsaralight)) which calculate the radiation absorbed by trees and transmitted to the understory with a ray tracing approach (Courbaud *et al.* 2003). The model calculates the energy absorbed by the trees from ray beams that are sent to the center of each cell with a changing angle following the sun path during the day and the year. For each ray, the neighbor cells are selected to ensure that all the cells containing a tree that intercept the ray are handled. To deal with side effects, the grid is bent into a torus (the left side is connected to the right side and the top side is connected to the bottom side). For a given ray beam, the intercepting trees are sorted. The radiation extinction is calculated for each of them following the Beer-Lambert law. The variables used in the Beer-Lambert law are the path length of the ray beam within the crown, the leaf area density and an extinction coefficient. The path length is calculated with the tree geometry based on the crown form, the leaves are assumed to be randomly distributed in the crown with a spherical distribution for the leaf orientation. The regeneration module uses the remaining energy in the ray beam that reach the cell.

**Phenological** module simulates the leaves lifetime for deciduous species from budburst to falling at a daily time step. The foliage status of a tree has a great influence on the water and carbon fluxes. The interception of rainfall and the photosynthesis are influenced by the leaves development stage. The leaves development follows this path: first the chilling period starts to calculate the accumulation of coldness that breaks the bud dormancy at the forcing date. The forcing date is the start of the forcing period, an accumulation of heat that leads to the budburst. After the budburst, the leaf development can start until it is completed. At the end of the vegetation period, it will start aging. This happens during a phase of coldness accumulation which leads to the yellowing period. During the yellowing period, the leaf starts losing the photosynthetic activity until its death. After the leaves are dead, it will start falling from the tree with the influence of wind speed and frost events.

**Water balance** module handles processes linked to water in HETEROFOR. The water is stocked in the soil horizons, on the tree leaves and in the bark. The stocks and the fluxes are updated every hour. The fluxes are rainfall (divided into interception, throughfall and stemflow), water movements between soil horizons and drainage, water uptake, transpiration and evaporation from leaves, bark and soil surface. There is no surface runoff and groundwater level rise yet.

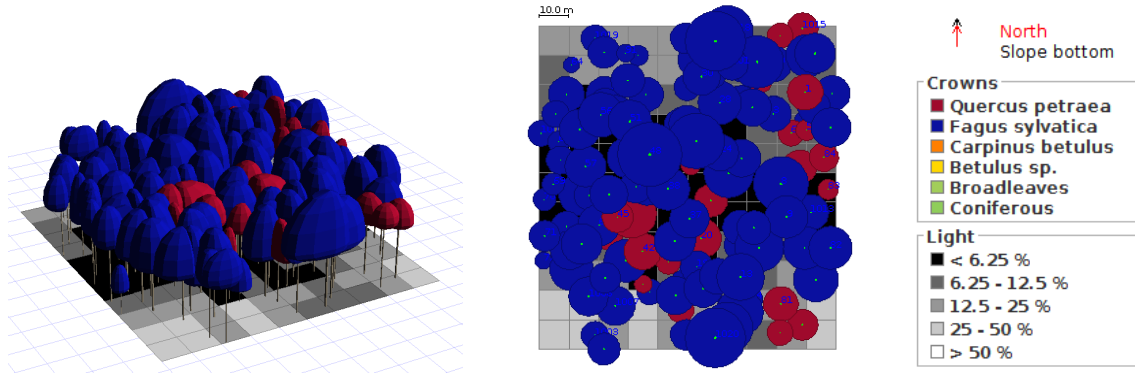


Figure 1: HETEROFOR visualization. The trees are spatialized on a 3-dimensional grid which is divided in cells (10m x 10m). Those cells have a value of the transmitted radiation expressed in proportion of the incident radiation (above the canopy) computed in the radiation transfer module (SAMSARALIGHT). That transmitted radiation is the input radiation for regeneration.

**Photosynthesis** is performed using CASTANEA library. Dufrêne *et al.* (2005) summarize the model like this:

« *The leaf photosynthesis (A) is represented using a C<sub>3</sub> plants biochemical process-based model, according to Farquhar et al. (1980). The CO<sub>2</sub> demand is determined as the minimum between Rubisco carboxylation and RuBP regeneration, while CO<sub>2</sub> supply depends on the difference in CO<sub>2</sub> concentration between the air outside the leaf and the carboxylation sites.* »

It uses a mechanist approach with the fluxes of CO<sub>2</sub>, water and the activity of Rubisco to estimate gross primary production based on Farquhar *et al.* (1980) and Ball *et al.* (1987) approaches. The assimilation rate is calculated with the carboxylation rate and the dark respiration rate. The carbon concentration in the leaves is calculated with the stomatal conductance for carbon, the carbon demand and the carbon concentration outside the leaves. The stomatal conductance for CO<sub>2</sub> can be estimate with stomatal conductance for water that is calculated from carbon demand, carbon concentration in the leaves, water stress and relative humidity with Ball *et al.* (1987) equation.

It also takes other parameters into account like temperature effect on the electron transport rate and on the carbon dioxide and oxygen concentration at the evaporative sites. Leaf nitrogen has an effect on the maximal carboxylation rate and photosynthesis is calculated separately on sunlit and shaded leaves (shaded leaves do not intercept direct radiation).

CASTANEA calculates the gross primary production (GPP) and the respiration rate with the inputs given by HETEROFOR.

The net primary production (fraction of the GPP that is not used for respiration maintenance) is translocated and allocated to the different parts of a tree. The

carbon is allocated sequentially to the different needs. First, carbon is allocated to leaves, fine roots and fruit production. Then it compensates the branch and root mortality. The remaining carbon goes to the structural growth. The structural growth is divided in the above-ground (height and diameter increment) and below-ground growth. The diameter increment is then used to calculate the crown extension.

**Nutrient cycling** module structure the soil in different horizons. The soil solution is the central nutrients compartment. It is in equilibrium with minerals and exchange complex. The model is based on the nutritional status determined based on the foliage chemistry initialized by the user. The chemical composition of the other tree compartments is then obtained from the nutritional status.

With the information of the chemical composition of the trees and their annual growth, the model calculate the nutrients demand of the trees. In parallel, the nutrient availability is calculated as the maximum of nutrients able to reach the roots. The nutrient absorption by the trees is determined by whether the nutrient demand matches the soil offer. If necessary, the nutritional status and the tree growth are adjusted.

For the moment, the module is working at an annual scale and could be improved with a monthly scale and with other flux like atmospheric deposition, mineralization and nutrient leaching.

**Initialization** The initialization is done using a set of files containing all the information for starting the model (tree inventory, soil properties, meteorological data, etc.). The user can choose which modules they need for their analysis and has to bring the files needed by each module. At this step, the model shows the initial state with the trees spatialized in the stand. Each tree is initialized with a set of characteristics that describe its position, and its dimensions. (Tab. 1). This information must be provided in the tree inventory file (e.g. with measurement campaign).

## 3.2 Regeneration Module Overview

In HETEROFOR, all the adult trees are individualized and spatialized. Another approach is chosen for the regeneration model due to the vast quantity of trees involved, to treat every single entity individually is unaffordable. This other approach was already done in the RReShar model (see CAPSIS documentation: [http://capsis.cirad.fr/capsis/help\\_en/rreshar](http://capsis.cirad.fr/capsis/help_en/rreshar)) –another model of the CAPSIS platform. The CAPSIS regeneration library made for the RReShar model has been thereby connected to HETEROFOR in order to implement the regeneration process.

The regeneration is spatially structured horizontally thanks to the cell grid. Each cell can contain regeneration which grow independently from the regeneration in the

Characteristic	Unit
Specie	/
X coordinate	m
Y coordinate	m
Z coordinate	m
H	m
DBH	cm
HCLE	m
HCB	m
C <sub>130</sub>	cm
r <sub>N,S,E,W</sub>	m

Table 1: Tree characteristics set for the initialization. HCLE is the height of the largest crown extension, HCB is the height of the crown base and  $r_x$  are the crown radius in four directions.

neighboring. The vertical structure is given by the regeneration library data structure (Tab. 2). Vertically, the regeneration is divided into seedling cohorts and layers of competing regeneration. The competing vegetation is described by its specie, height and cover. It is then grown with an empirical equation. A cohort gathers the seedlings of a same cell with the same age and specie. It is divided in different size classes (initialized by the user in the inventory file) that reflect the distribution of height in the cohort (Fig. 2).

The growth process is based on light availability. The input radiation of the regeneration module is the radiation calculated from SAMSARALIGHT which reaches the center of the cell on the ground. The value of the radiation at the top of regeneration (from 0 to 6-10 meters) is assumed to be close to the value on the ground when no vegetation intercepts it.

The distribution of the radiation is calculated following the Beer-Lambert law. The layers (competing vegetation and cohort size classes) are sorted by height (Fig. 3) and the radiation absorbed by each layer and the radiation transmitted to the next layer are calculated. The transmittance (ratio between the radiation above the layer

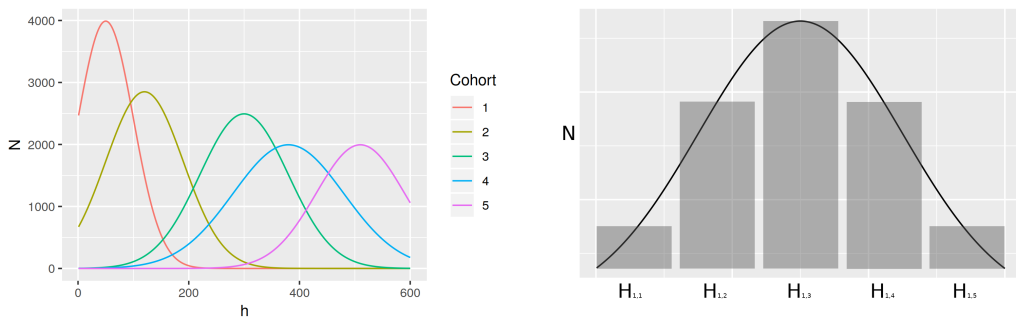


Figure 2: Organization of data structure in the regeneration module. The seedlings of a cell are distributed within different cohorts (left image) characterized by a specie and an age (e.g. cohort 1: oak, 1 year old). A cohort is divided in different size classes (right image) in order to approximate the height distribution of the seedlings inside the cohort.

Table 2: Regeneration library data structure. The competing vegetation layers are characterized by a specie, a height and a cover and the seedlings cohorts are characterized by a specie, a year of emergence. The cohorts are divided in sizes classes that have a mean height, mean diameter and a number of seedlings.

Competing vegetation layer				
X cell coord.	Y cell coord.	Specie	Height (m)	Cover (%)
Seedlings cohort				
X cell coord.	Y cell coord.	Specie	Year	Size class parameters {[H <sub>1</sub> (m), D <sub>1</sub> (cm), N <sub>1</sub> ]; [H <sub>2</sub> (m), D <sub>2</sub> (cm), N <sub>2</sub> ]}

and the radiation above the canopy) is used to calculate a height increment with an empirical equation and the radiation absorbed by a layer is used to calculate the available resources with a process-based method which allows to calculate the seedlings mortality. The competing vegetation growth is based on an empirical equation that calculated a height increment and a cover increment from the transmittance.

The recruitment is the output of the regeneration module. It is managed by spatializing the trees when a cohort reach the recruitment height which is set by the user (default at 12 meters).

### 3.2.1 Initialization of the Regeneration Module

The initialization of the regeneration module uses an inventory file (the same file that is used for the adult trees initialization) that gives all the values needed to set the regeneration cohorts and the competing vegetation layers (Tab. 2). Depending on the way the inventory file is filled, the competing vegetation and the seedlings cohorts will be implemented in different ways. The inventory file can be filled in each cell of the stand if the data is available (e.g. with a regeneration survey). The cell coordinates can be set to *-1*. In this case, the cohort is implemented on every cell of the stand. When *yearlyRegenerationCohortEmergence* is set on *true*, all the cohorts of 1 year are implemented every year in order to simulate a seedling rain.

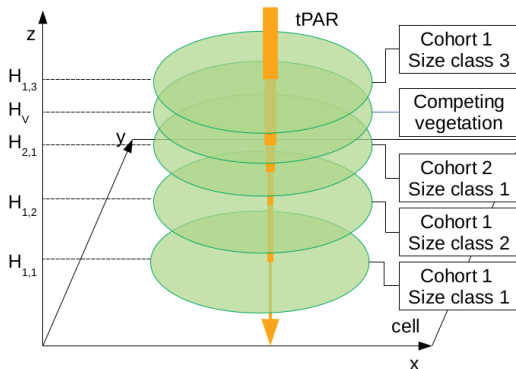


Figure 3: Height distribution of the different cohort size classes in a cell. The size classes are sorted from the highest to the lowest and the PAR is gradually decreasing while it is absorbed by the seedlings. Some competing vegetation layers which can interact with the seedlings are inserted between the size classes.

A tool has also been developed to simulate an initial regeneration from the initial state of the stand. In order to have the most realistic regeneration cohorts (with uneven age), this tool uses the initial understory light and make the regeneration grow during a few years without growing the stand. After the first tree is recruited or a given period of time, the full model can start. In the future, it is possible to implement fructification, seed dispersal and seed germination to simulate a process-based emergence of the regeneration (function of heat sums, distance from parent trees, presence of natural dispersers, etc.).

At initialization, all the characteristics needed by the model are calculated from the average height or diameter and the number of seedlings of every cohort size class with the relations described in the section 3.3. Those characteristics are derived variable (which are calculated from the height) so the only *state* variables of the model are the height, the diameter and the number of seedlings. As the diameter can be estimated from the height and the height can be estimated from the diameter, only one of them is mandatory. With all the seedling characteristics, the main processes are computed: absorption of the energy from light, gross primary production by photosynthesis, growth and mortality.

### 3.3 Seedlings Characteristics Derived from the State Variables of the Cohort Size Classes

As shown in Figure 4, the seedlings characteristics are derived from the average height and the seedling number. The objective is to predict the number of seedlings at the next step of time (one year) and the average height of the remaining seedlings (and therefore the average diameter, biomass, etc.).

#### 3.3.1 Seedling Average Properties

Average height ( $\bar{h}$ ) and diameter at 5 cm ( $\bar{d}_5$ ) are with the number of seedlings ( $N$ ) the state variables of the regeneration module. In order to make the model easier to initialize, the diameter at 5 cm can be estimated from the height (eq 3.1) and vice versa (eq 3.1')  $a$ ,  $b_0$ ,  $b_1$  and  $c$  are parameters and  $Tr$  is the transmittance defined by equation 3.10. Those relations are specie specific and some terms of the equation are not significant for every specie. In this case the associated parameter is equal to 0. The validity domain is between 0 and 6 meters for beech, hornbeam, birch and spruce and is divided for oak in two parts (between 0 and 2.5 meters and between 2.5 meters and 6 meters).

$$\bar{d}_5 = a + (b_0 + b_1 Tr) \bar{h} + c \bar{h}^2 \quad [mm] \quad (3.1)$$

$$\bar{h} = a + (b_0 + b_1 Tr) \bar{d}_5 \quad [cm] \quad (3.1')$$

With both values, the computation of the remaining characteristics needed by the model can start.

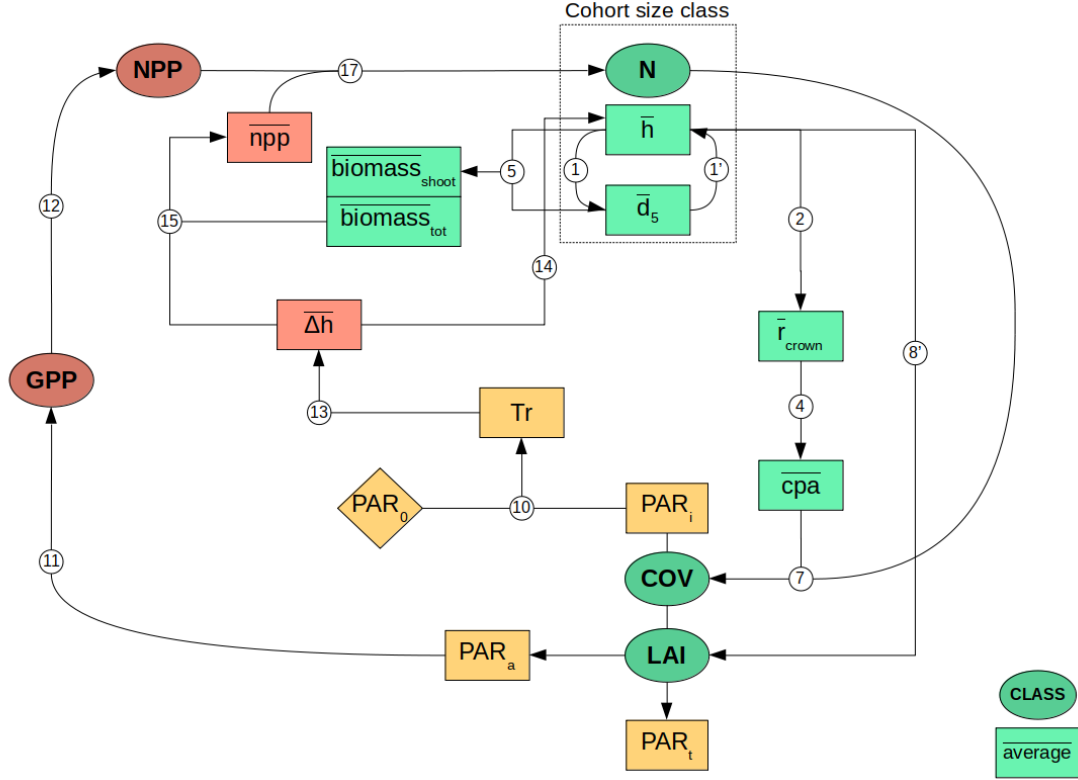


Figure 4: Flowchart of the regeneration module for one given cohort size class. In the dash rectangle are the number of seedlings  $N$ , the average height  $\bar{h}$  and  $\bar{d}_5$  the diameter at 5 cm, which are the state variables of the model. The state variables are used to calculate all the other characteristics needed to predict the yearly height increment and the mortality ( $N$  at  $t+1$ ). The first step is to calculate the cover  $COV$  (from the maximum crown radius  $\bar{r}_{crown}$  and the maximum crown projection area  $\overline{cpa}$ ) and the leaf area index  $LAI$  which are used to compute the absorbed radiation  $PAR_a$  by the size class with the Beer-Lambert's law. The transmitted radiation  $PAR_t$  is obtained by taking the difference between the incident radiation  $PAR_i$  and the absorbed radiation.  $PAR_t$  becomes  $PAR_i$  for the size class located below the size class of interest.  $PAR_a$  is used by CASTANEA to calculate the  $GPP$  and the  $NPP$  for the whole size class. On the other hand, the height increment  $\overline{\Delta h}$  is calculated from the transmittance  $Tr$  (the ratio between the incident radiation  $PAR_i$  and the initial radiation  $PAR_0$ ). It allows to estimate a biomass increment that is equal to the individual net primary production  $\overline{npp}$ . The ratio between  $NPP$  and  $\overline{npp}$  gives us the number of seedlings able to survive with the available radiation.

The maximum crown radius ( $\bar{r}_{crown}$ ) is calculated from the height with a linear model (the crown diameter is calculated so it must be divided by 2 (eq. 3.2). That crown radius was fitted on free growing seedlings. An overlapping ratio ( $co_{ratio}$ ) is used to account for the crown interpenetration (eq. 3.3).

$$\bar{r}_{crown} = (a + b * h)/2 \quad [m] \quad (3.2)$$

$$corrected \bar{r}_{crown} = \frac{\bar{r}_{crown}}{co_{ratio}} \quad [m] \quad (3.3)$$

With the crown radius, the maximum crown projection area ( $\overline{cpa}$ ) can be calculated by simple geometry equation with the assumption that the crown projection is a disk (eq. 3.4).

$$\overline{cpa} = \pi * \bar{r}_{crown}^2 \quad [m^2] \quad (3.4)$$

The total biomass ( $\bar{b}_{tot}$ ) is the sum of four compartments (eq. 3.6): the shoot biomass ( $\bar{b}_{shoot}$ ), the roots biomass ( $\bar{b}_{roots}$ ), the leaves biomass ( $\bar{b}_{leaves}$ ) and the fine roots biomass ( $\bar{b}_{fineroots}$ ). First to calculate the shoot biomass, the height and the diameter are used with a parameter ( $a$ ) and is divided by 2 to express the biomass in KgC (eq. 3.5). A ratio ( $rootToShoot$ ) calculated as a function of the age (Genet *et al.* 2010) is used to know the root biomass from the shoot biomass (eq. 3.5.1). The leaf biomass ( $\bar{b}_{leaves}$ ) is calculated with an allometric equation (eq.3.5.2) from the  $\overline{dbh}$  and the crown radius ( $\bar{r}_{crown}$ ).  $\alpha$ ,  $\beta$ ,  $\gamma$  and  $leaf_{CarbonCC}$  are parameters. The fine root biomass ( $\bar{b}_{fineroots}$ ) calculated with a  $rootToFoliage$  ratio (eq. 3.5.3).

$$\bar{b}_{shoot} = a \bar{d}_5^2 \bar{h} * 0.5 \quad [KgC] \quad (3.5)$$

$$\bar{b}_{roots} = \bar{b}_{shoot} * rootToShoot \quad [KgC] \quad (3.5.1)$$

$$\bar{b}_{leaves} = \alpha * (\pi * \overline{dbh})^\beta * \left(\frac{2 * r_{crown}}{\overline{dbh}/100}\right)^\gamma * \frac{leaf_{CarbonCC}}{1000} / 1000 \quad [KgC] \quad (3.5.2)$$

$$\bar{b}_{fineroots} = \bar{b}_{leaves} * rootToFoliage \quad [KgC] \quad (3.5.3)$$

$$\bar{b}_{tot} = \bar{b}_{shoot} + \bar{b}_{roots} + \bar{b}_{leaves} + \bar{b}_{fineroots} \quad [KgC] \quad (3.6)$$

### 3.3.2 Seedling Class Properties

The cover ( $COV$ ) and the leaf area index ( $LAI$ ) are both variables that describe the whole cohort size class (class variables). The cover is the ratio between the sum of the maximum crown projection areas ( $\overline{cpa} * N$ ) and the total surface of the cell ( $A_{cell}$ ) (eq. 3.7). A specie specific crown overlapping ratio ( $co_{ratio}$ ) is used to take the crown interpenetration into account. The cover is constrained to 1 when the seedlings are filling all the surface of the cell.

$$COV = \frac{\overline{cpa} * N}{co_{ratio}^2 A_{cell}} \quad [\%] \quad (3.7)$$

The leaf area index is the sum of the leaves surface divided by the ground surface below the seedlings, the cell surface multiplied by the cover (eq. 3.8). In our case, it

is estimated directly with the average height of the seedlings based on a Michaelis-Menten equation (eq. 3.8'). This equation allows to set a horizontal asymptote which is relevant for the LAI (maximum value of LAI in an ecosystem) and this value was set to 6. The parameter  $k$  is the slope and is specie specific.

$$LAI = \frac{\bar{a}_{leaf} * N}{A_{cell} * COV} \quad [] \quad (3.8)$$

$$LAI = \frac{\bar{h} * LAI_{max}}{\bar{h} + k} \quad [] \quad (3.8')$$

### 3.3.3 Seedlings and Vegetation Layers Growth

#### *Light Interception*

As the main driver of regeneration, the light has a very important influence on the module. The input light is the light under the canopy which is calculated with SAMSARALIGHT. The layers of vegetation and seedlings size class are sorted in a descending order based on their height and the Beer-Lambert's law (eq. 3.9) is used to calculate the energy absorbed by each layer. The transmitted energy is used as the incident energy for the next layer. By this way, the light cross all the layers of competing vegetation and all the seedlings size classes from the top to the ground (Fig. 3). The cover value is also used to calculate absorbed energy only for the surface covered by vegetation or seedlings.

$$PAR_t = PAR_i(1 - COV) + COV * PAR_i * e^{-k*LAI} \quad (3.9)$$

Where:

$PAR_i$  is the energy above the layer  $[MJm^{-2}]$

$PAR_t$  is the energy below the layer  $[MJm^{-2}]$

$COV$  is the cover  $[m^2m^{-2}]$

$k$  is the extinction coefficient

$LAI$  is the Leaf Area Index  $[m^2m^{-2}]$

The radiation value used in the growth equations is the transmittance ( $Tr$ ), i.e. the ratio between the radiation above the size class ( $PAR_i$ ) and the radiation above the canopy ( $PAR_0$ ), expressed in percentage (eq. 3.10).

$$Tr = \frac{PAR_i}{PAR_0} \quad [\%] \quad (3.10)$$

#### *Photosynthesis*

The photosynthesis is done in HETEROFOR by the CASTANEA library and is therefore used for seedlings photosynthesis. In the regeneration module, the information needed by CASTANEA is prepared and the function to compute the fluxes is called (eq. 3.11). The outputs are the hourly GPP. The NPP is calculated with the equation 3.12 by multiplying the GPP and a specie specific ratio  $r$ .

$$GPP = f(aPAR, sla, \dots) \quad [KgC] \quad (3.11)$$

$$NPP = GPP * r \quad [KgC] \quad (3.12)$$

Another approach is used to calculate the *GPP* which is based on the PAR use efficiency concept. This empirical approach divides the radiation into direct and diffuse radiation and quantify the radiation intercepted by the sunlit and shaded leaves (Jonard *et al. in review*).

### **Height Growth**

The seedling height growth is based on a height increment (eq. 3.13, Ligot *et al.* 2013). This height increment ( $\overline{\Delta h}$ ) depends on the initial height ( $\overline{h}$ ), the transmittance ( $Tr$ ) above the seedlings and two parameters  $a$  and  $b$  that depend on the tree specie (Tab. 3).

$$\overline{\Delta h} = a\sqrt{\overline{h}} \frac{1}{1 + \exp(1 - \frac{Tr}{b})} \quad (3.13)$$

With the height increment, the new height is calculated (eq. 3.14) which allows to calculate the total biomass increment (eq. 3.6). The difference between biomass at  $t+1$  and  $t$  is used to calculate the individual  $\overline{np\overline{p}}$  (eq. 3.15) that is used in the mortality relation. The litter (leaves and fine roots biomass) is also added to the biomass required annually by the individuals.

$$\overline{h}_{t+1} = \overline{h}_t + \overline{\Delta h} \quad (3.14)$$

$$\overline{np\overline{p}} = \overline{b}_{tot,t+1} - \overline{b}_{tot,t} + \overline{b}_{leaves} + \overline{b}_{fineroots} \quad (3.15)$$

Table 3: Parameters values for the equation 3.13 (Ligot *et al.* 2013)

Specie	$a$	$b$
Oak	2.059	6.058
Beech	2.431	3.964

### **Vegetation Layer Growth**

The vegetation layers are managed only by the regeneration library. They are defines by their specie, height and cover, which are the state variables. The model calculate a height increment ( $H_i$ ), a cover increment ( $C_i$ ), the maximum height ( $H_{max}$ ) and the maximum cover ( $C_{max}$ ) which are the upper limit of the vegetation growth per year.

The growing process is simpler than the seedlings growth. The Table 2 shows the information needed by the model: the specie (for the moment fern, molinie and callune are implemented), the height, and the cover. From this initial state, the model makes the vegetation layer grow in height and in cover with the amount of available light (transmittance  $Tr$ ) thanks to empirical equations (eq.3.16, Gaudio, Balandier, Dumas, *et al.* 2011). The equation has the same shape for the calculation of height increment, cover increment, max height and max cover. All the parameters are given in Table 4.

$$X = a + b * Tr + c * \log(Tr^2) \quad (3.16)$$

### 3.3.4 Seedlings Mortality

The mortality process is modeled using a resource limitation method. The class  $NPP$  measure the production capacity of the cohort size class. It is the total biomass increment for the whole class. The  $\overline{np\overline{p}}$  is the individual biomass increment of the average seedling based on its annual height increment which depends on the transmittance. If the  $NPP$  is lower than the sum of the average  $\overline{np\overline{p}}$ , it means that the product of the photosynthesis is not enough to allow all the seedlings in the cohort size class to grow with such a height increment. Two solutions can handle this difference: the height increment is too high or the number of seedlings is too high. The self-thinning process can explain the difference between the two approaches. The model quantifies the number of seedlings that can survive with the ratio between  $NPP$  and  $\overline{np\overline{p}}$  (eq. 3.17).

$$N_{t+1} = \frac{NPP}{\overline{np\overline{p}}} \quad (3.17)$$

### 3.3.5 Recruitment

When a size class reach a specific height (set by the user), all the trees of the size class are recruited. It means that they are spatialized and the tree is fully characterized in HETEROFOR (Tab. 1). The variables are set in the following way:

Table 4: Parameters for the growing equations of vegetation layers by species (eq. 3.16)

	Fern			Molinie			Callune		
X	a	b	c	a	b	c	a	b	c
$H_i$	-13.31	-0.41	8.34	6.20	0.81	-0.0074	-4.36	-0.19	4.23
$C_i$	22.18	-0.21	2.83	-13.49	-0.47	9.40	-18.23	-0.35	8.01
$H_{max}$	-50.53	-1.40	28.72	25.14	1.85	-0.017	-27.29	-0.80	18.11
$C_{max}$	69.90	-0.73	7.00	-2.01	-1.25	20.50	-41.10	-1.07	20.69

The specie is the cohort specie. The coordinates X and Y in the cell are randomly chosen. The Z coordinate is the Z value of the cell. The height is the average height of the size class. An equation calculates the dbh from the diameter at 5 centimeters (eq. 3.18). The HCLE and the HCB are calculated with the height and a ratio. And the crown radius in the four directions is equal to the maximum crown radius of the size class.

$$\overline{dbh} = a + bd_5 \quad [cm] \quad (3.18)$$

The recruitment process is the output of the regeneration sub-model. After this, the trees are grown by the HETEROFOR's equations.

### 3.4 Sapling Equations

Some of the equations described before were fitted on data collected on trees below 6 meters. To have more accurate predictions above this height, the allometric equations of HETEROFOR are used (Jonard *et al. in review*). The equations that are changed are the calculation of the height, the dbh, the aerial biomass and the crown radius.

$$\bar{h} = m * (1 - e^{-\frac{\overline{dbh}-a}{b}}) \quad [m] \quad (3.19)$$

$$\overline{dbh} = -b \ln(-\bar{h}/m) + 1) + a \quad [cm] \quad (3.20)$$

$$\bar{b}_{aerial} = \alpha + \beta(\bar{h} \overline{dbh}^2)^\gamma \quad [Kg] \quad (3.21)$$

$$\bar{r}_{crown} = CrownToStemDiameterRatio * \overline{dbh}/200 \quad [m] \quad (3.22)$$

### 3.5 Module Parametrization

Some relations shown in the section 3.3 were not found in the literature. In order to estimate the seedlings characteristics needed in the model, data analysis was conducted based on two datasets employing R and JMP software.

#### 3.5.1 Data Collection

##### *Existing Datasets*

The data used to fit the relations needed in the regeneration module were given by Ligot (2014) and Baudry (2013). Both have carried a regeneration survey on beech and oak regeneration in Ardenne forests.

Ardenne is a Belgian ecoregion representative of acidophilous beech forests with mean temperature ranges between 7.4°C and 9.0°C and annual rainfall between 933 mm/year and 1357 mm/year (Ligot 2014). The sessile oak, the pendunculate oak and the beech are indigenous species that are often mixed in these forests (73% of the broadleaved forests).

Ligot (2014) selected 23 different sites with well-established regeneration that were fenced and divided in small 4 m<sup>2</sup> plots. In each plot, the seedlings height, diameter at 5 cm and DBH was measured for the 3 tallest seedlings in 2009 and in 2011. The seedlings measured in 2009 were not tagged so the seedlings measured in 2011 could have been different. The transmittance was also measured in the center of each plot.

Baudry (2013) selected 4 sites with dense oak and beech regeneration. Shading devices were placed above a part of the seedlings. The seedlings characteristics measured were the height, the diameter at 10 cm and at 130 cm, the leaves biomass and surface and the aerial biomass.

### ***Additional Measurements***

To have a relation between the height of the seedlings and the ratio between the stem diameter and the crown diameter, some measures were done on oak and beech seedlings in the Lauzelle's forest.

96 beech seedlings were measured in 3 different stands. The variables measured were the height, the diameter at 5 cm, the diameter at 130 cm and the crown diameter. The height was measured with a vertex, the diameter with a calliper and the crown diameter with a tape measure. The seedlings chosen to be measured were isolated and a target height was planned (24 seedlings 0 m high, 25 seedlings 1.6 m high, 22 seedlings 4.2 m high and 25 seedlings 6 m high).

### **3.5.2 Data Analysis**

In order to find the best relations between the seedlings characteristics, different equations were used to fit the data and compared with a statistical analysis. First to explore the data and to try some relations, *JMP* was used with the *adjustment* tool.

The final parameters were estimated with *R* which allows more flexibility especially with the package *nlme* (Lindstrom and Bates 1990). This package includes the use of non-linear models, random effects and variance function to deal with heteroskedasticity. For the 1st degree relations without heteroskedasticity, the native linear regression function *lm* was used. The Table 5 summarize which method was used for each relation.

The changing residual variance is calculated in *nlme* by a variance function called *varPower* (eq. 3.23) where  $x$  is the variable allowing to adapt the variance,  $\sigma$  is the variance and  $t$  is a parameter. On heteroskedastic data, it is essential to model the variance to have an accurate estimation of the parameters. Otherwise, the region where the data have a high variance will have a huge impact on the estimation that will affect the error in the region with smaller variance. The variance function solve the problem by giving a greater weight to the region with low variance.

$$F(\sigma) = |\sigma x|^{2t} \tag{3.23}$$

Different indicators were used to select the best relation between two seedlings characteristics: first the p-value for each parameter test whether it is significant in the model, then the  $R^2$  shows the part of the variability explained by the model,  $RMSE$  and  $AIC$  make it possible to compare the models among each other. A likelihood ratio test was also used to compare the integration of light in the height-diameter models. The likelihood ratio test (Vuong 1989) is used to compare complete model with restricted models (the complete model from which one or more parameter has been removed). For that reason it is relevant to use it for the integration of the light effect in the model. Finally, a Deming regression test (Deming 1943) was performed to check the accuracy of the model prediction compared to the observation. The 0.05 confidence intervals were used to evaluate the accuracy of the intercept and the slope of the prediction-observation regression (the intercept must be non significantly different from 0 and the slope from 1).

With all the tools described previously, the best equation was chosen. In addition to the different indicators, the equations with a small number of parameters, with good extrapolation properties and with easier generalization to other species (similar equation for the different species, sometimes with additional terms) were preferred.

**LAI** modeling from height was managed differently. The seedlings density measured by Baudry (2013) was used along with the leaf area estimation from height in order to predict the LAI from the seedlings height with a Michaelis-Menten equation. This equation allows to fix a maximum LAI and fit the slope to the data.

Table 5: Regression method for each relation. nlme is a R function for non-linear mixed models and lm is a simple linear regression function.

Relation	Method	Random effect	Variance	Dataset
$h \sim d, Tr$	nlme	Site effect	VarPower	Ligot (2014)
$d \sim h, Tr$	nlme	Site effect	VarPower	Ligot (2014)
$dbh \sim d_5$	lm	none	Constant	Ligot (2014)
$b_{shoot} \sim d^2h$	lm	none	Constant	Baudry (2013)
$a_{leaves} \sim h$	nlme	none	VarPower	Baudry (2013)
$LAI \sim h$	nlme	none	VarPower	Baudry (2013)
$SLA \sim Tr$	nlme	none	VarPower	Ligot (2014)
$r_{crown} \sim h$	lm	none	Constant	Additional measurements

## 4 Results

### 4.1 Fitting of the Basic Relations of the Regeneration Module

For each relation needed in the regeneration module, one equation was chosen with the different evaluation methods explained in the section 3.5.2. The Table 6 shows the mathematical formulation retained and the parameter estimates for each relation of each specie studied (oak, beech, and other species when the data were available). For the prediction of height from diameter and vice versa (eq. 3.1 and 3.1'), a linear model was chosen because of its simplicity and the accuracy of the predictions (Fig. 5 and 6). The implementation in HETEROFOR is also easier if the form of the equation is similar for all the species. The effect of the light is taken into account with the term  $b1Tr$  and is only significant for beech. For oak, a simple regression was not satisfying. A double regression has been chosen with a threshold at 2.5 meters as it can be seen in Figure 5b. The best relation to predict the  $\overline{dbh}$  from the  $\overline{d_5}$  (eq. 3.18) is also a linear model for all the species tested (Fig. 7). The relation chosen for the shoot biomass prediction is a linear model from the volume estimation  $d^2h$  (eq. 3.5; Fig. 8). The leaf area follows an exponential relation from the height (Fig. 9). That relation was used to fit the LAI relation from the height (eq. 3.8; Fig. 10). The crown diameter is predicted with a linear relation (eq. 3.2; Fig. 11). The relation chosen for the SLA prediction is a double exponential from the transmittance. This relation is not used in the model.

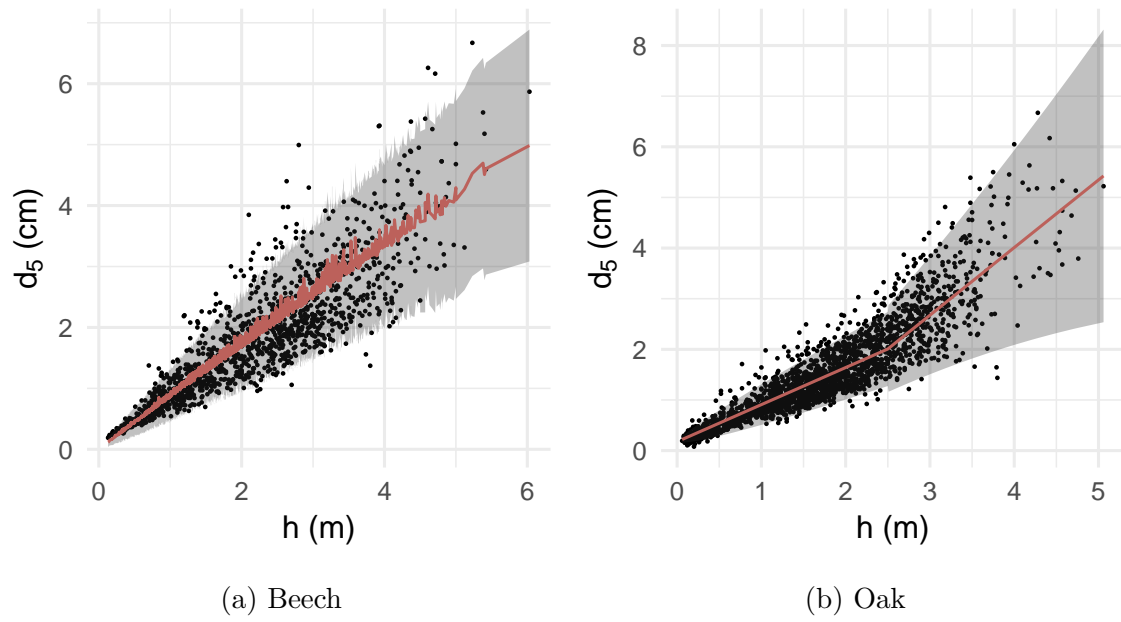


Figure 5: Regression fit for  $\bar{d}_5$  prediction from  $\bar{h}$  for beech and oak seedlings.

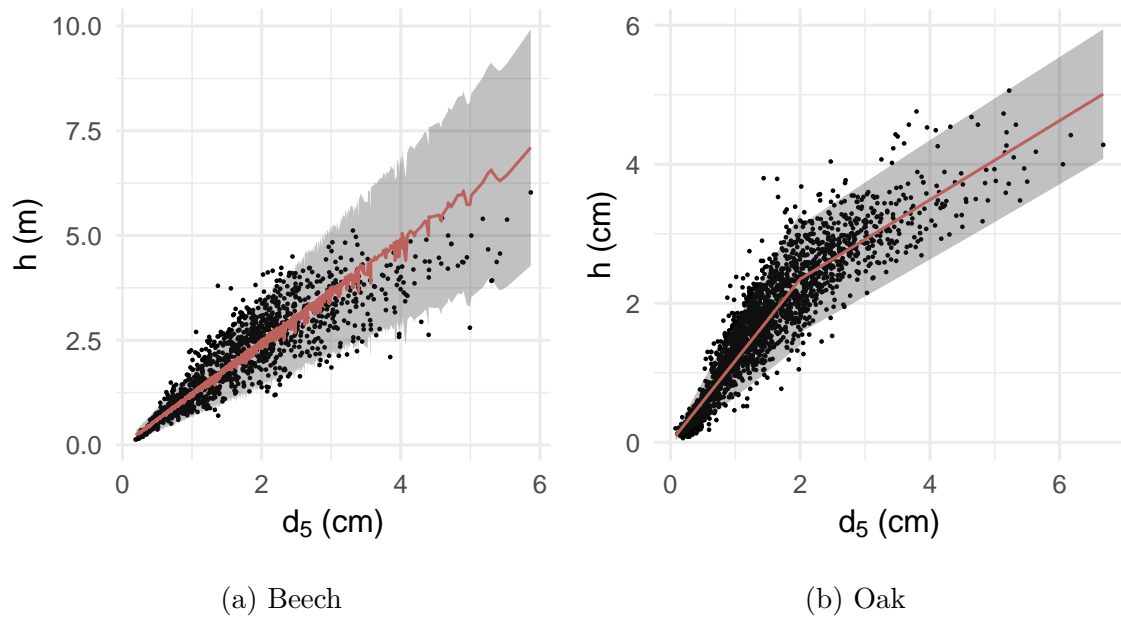


Figure 6: Regression fit for  $\bar{h}$  prediction from  $\bar{d}_5$  for beech and oak seedlings.

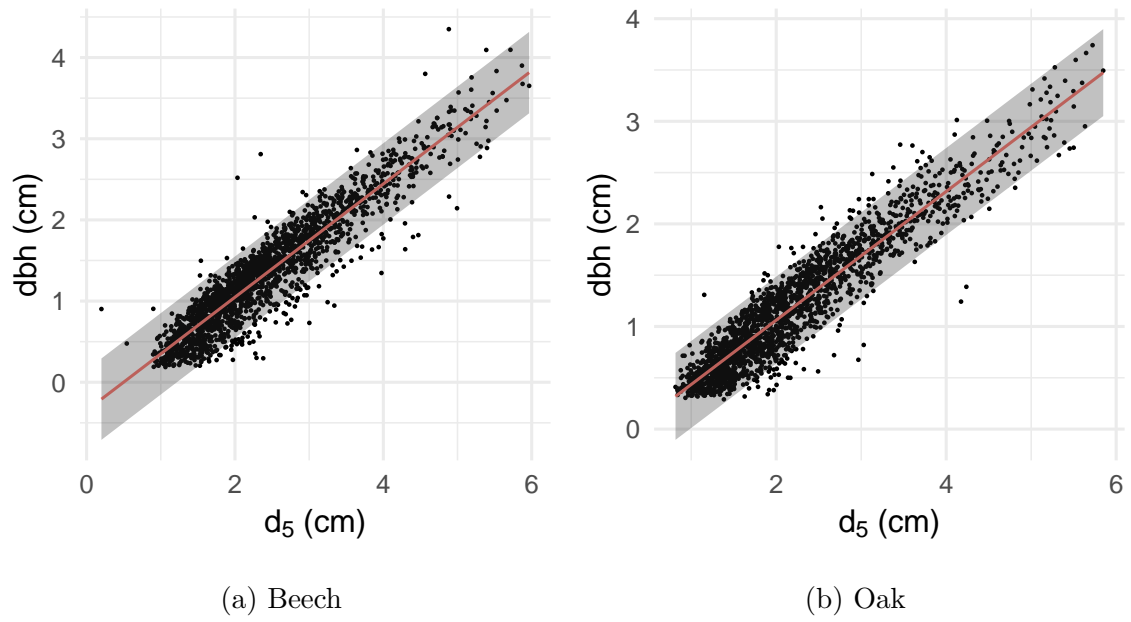


Figure 7: Regression fit for  $\overline{dbh}$  prediction from  $\overline{d_5}$  for beech and oak seedlings.

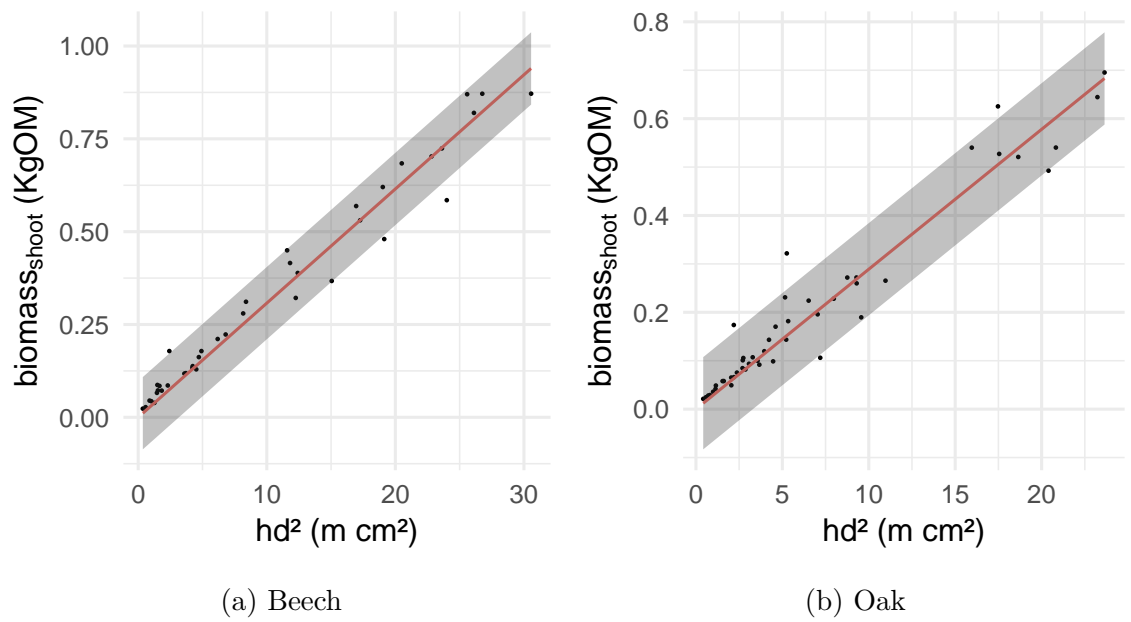


Figure 8: Regression fit for  $\overline{b_{shoot}}$  prediction from  $\overline{hd_5^2}$  for beech and oak seedlings.

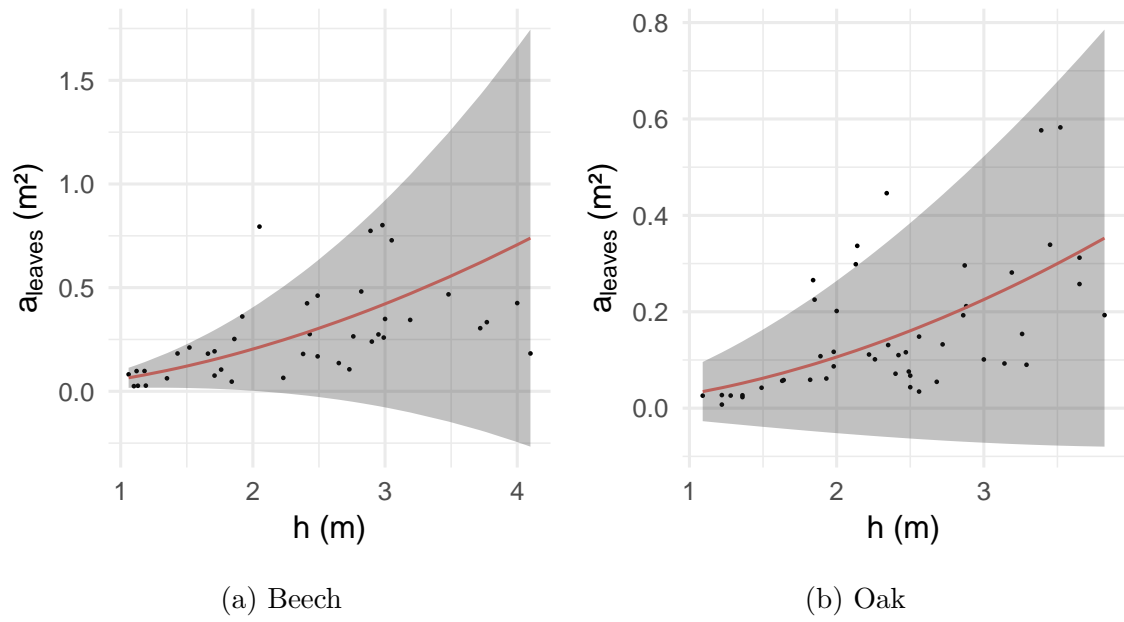


Figure 9: Regression fit for  $\bar{a}_{leaves}$  prediction from  $\bar{h}$  for beech and oak seedlings.

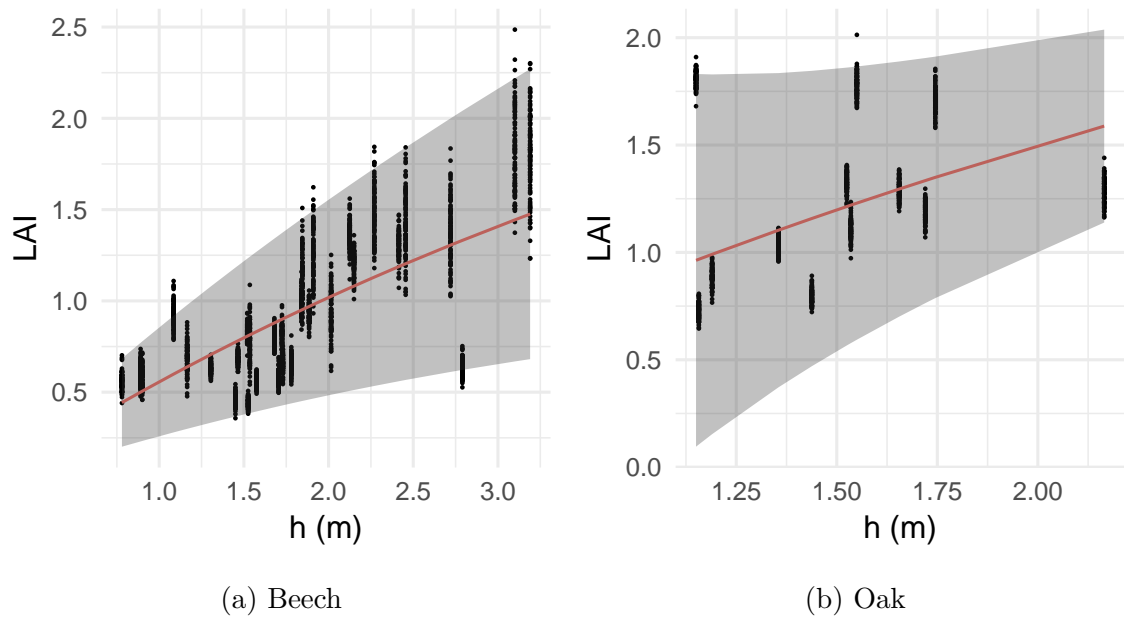


Figure 10: Regression fit for  $LAI$  prediction from  $\bar{h}$  for beech and oak seedlings.

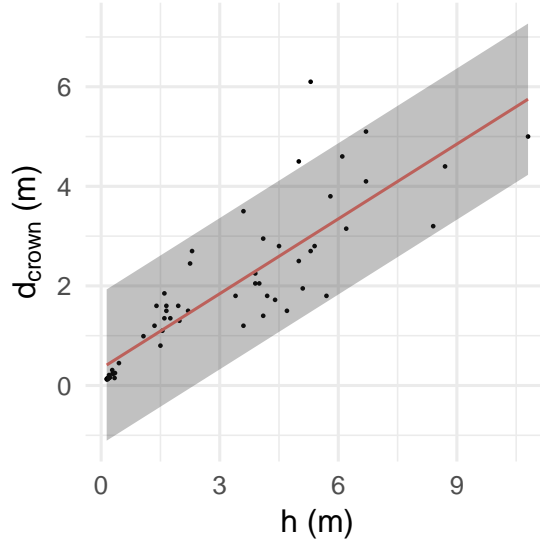


Figure 11: Regression fit for  $d_{crown}$  prediction from  $\bar{h}$  for beech seedlings.

Table 6: Results of the fitting of the basic relationships. Mathematical formulation retained and values of adjusted parameters.  $\sigma^2$  and  $t$  are the estimates for the variance function. When no value is given for  $t$ , the variance is assumed to be constant. R. test is the Deming regression test confidence interval for the slope (Sl.) and the intercept (In.). Significance levels: \*\*\* =  $<0.0005$ , \*\* =  $<0.005$ , \* =  $<0.05$ , † = non significant. Units:  $h$  [m];  $d$  [cm]; Biomass [ $\text{Kg}_{OM}$ ]; Tr [%]; SLA [ $\text{kg}/\text{m}^2$ ]

Model	Parameters	$\sigma^2$	$t$	$R^2$	R. test CI 95%	
Beech						
$d_5 = (b_0 + \beta + b_1Tr)h + ch^2$	$b_0$	0.8446***	0.04483	0.8475	0.5613	Sl. [0.8916 1.071]
	$b_1$	$2.858 \cdot 10^{-3}$ ***				In. [-0.2510 0.2517]
	$c$	$-1.282 \cdot 10^{-2}$ *				
	$\beta$	0.1084				
$h = (b_0 + \beta + b_1Tr)d_5$	$b_0$	1.280***	0.07218	0.9456	0.4925	Sl. [0.9563 1.148]
	$b_1$	$-0.003336$ ***				In. [-0.7805 0.2241]
	$\beta$	0.1523				
$DBH = a + bd_5$	$a$	$-0.3479$ ***	0.06545		0.8829	Sl. [0.9901 1.147]
	$b$	$0.6978$ ***				In. [-2.059 0.2024]
$d_{crown} = a + bh$	$a$	0.3409*	0.1618		0.7333	Sl. [0.6793 1.717]
	$b$	$0.5008$ ***	0.04073			In. [-1.450 0.7089]
$biomass_{shoot} = a(d^2h)$	$a$	$0.02890$ ***	0.002363		0.9860	Sl. [0.4658 1.474]
						In. [-169.1 210.1]
$a_{leaves} = h^c$	$c$	$1.427$ ***	0.9775	1.277	0.9717	Sl. [1.817 5.322]
						In. [-6549 -1104]
$LAI = \frac{\bar{h} * LAI_{max}}{h+k}$	$k$	$9.887$ ***	0.1076		0.9377	Sl. [-2.427 9.402]
						In. [-10.59 4.343]
$SLA = ae^{-bTr} + ce^{-dTr}$	$a$	$25.21$ ***	9.697	$-0.2362$	0.8098	Sl. [0.2750 1.829]
	$b$	$0.01255$ **				In. [-18.50 16.20]

Continued on next page

Model	Parameters	$\sigma^2$	t	R <sup>2</sup>	R. test CI 95%	
	<i>c</i>	131.3 <sup>†</sup>				
	<i>d</i>	0.3661 *				
<b>Oak</b>						
if $h < 250$ :	<i>a</i>	0.1760***	0.04180	0.6564	0.6853	Sl. [1.055 1.211]
$d_5 = (a + \alpha) + bh$	<i>b</i>	0.7322 ***				In. [-0.5842 -0.1844]
	$\alpha$	0.09316				
if $h > 250$ : $d_5 = 20.06 + b'h$	<i>b'</i>	1.441 ***	0.007860	1.804		
if $d < 20$ : $h = bd_5$	<i>b</i>	1.174***	0.0716	0.8564	0.7487	Sl. [ 1.114 1.277]
if $d > 20$ : $h = 234.8 + b'd_5$	<i>b'</i>	0.5699 ***	0.1234	0.1591		In. [-1.377 -0.5720]
$DBH = a + bd_5$	<i>a</i>	-0.1780***	0.04675		0.8945	Sl. [0.9820 1.139]
	<i>b</i>	0.6200***				In. [-1.778 0.2846]
$biomass_{shoot} = a(d^2h)$	<i>a</i>	0.03075***	0.002468		0.9685	Sl. [0.5129 1.460]
						In. [-101.5 123.4]
$a_{leaves} = h^c$	<i>c</i>	1.333***	0.01641	1.710	0.2158	Sl. [1.162 4.070]
						In. [-7669 -55.43]
$LAI = \frac{\bar{h} * LAI_{max}}{\bar{h} + k}$	<i>a</i>	6.251 ***	0.2013		0.9277	Sl. [0.3776 1.656]
						In. [-0.5129 0.5487]
$SLA = a + be^{-cTr}$	<i>a</i>	10.46***	45.64	-0.6389	0.5095	Sl. [0.2726 2.017]
	<i>b</i>	13.11*				In. [-16.54 11.82]
	<i>c</i>	0.04447*				
<b>Hornbeam</b>						
$d_5 = (a + \alpha) + bh$	<i>a</i>	0.1040***	0.03549	0.8912	0.5479	Sl. [0.9625 1.234]
	<i>b</i>	0.7024 ***				In. [-0.6051 0.07005]
	$\alpha$	0.02106				
$h = bd_5$	<i>b</i>	1.289***	0.1061	0.7987	0.4898	Sl. [0.9350 1.199]
						In. [-0.9851 0.3376]
$DBH = a + bd_5$	<i>a</i>	-0.2297***	0.06062		0.6582	Sl. [1.103 1.482]
	<i>b</i>	0.5363***				In. [-3.550 -0.6677]
<b>Birch</b>						
$d_5 = bh$	<i>b</i>	0.7079***	0.03758	0.4756	0.7917	Sl. [0.6355 1.584]
						In. [-1.526 0.8874]
$h = a + bd_5$	<i>a</i>	0.4053***	0.09414	0.2975	0.7857	Sl. [0.6738 1.671]
	<i>b</i>	1.128***				In. [-3.507 1.677]
$DBH = a + bd_5$	<i>a</i>	-0.3429***	0.3100		0.9326	Sl. [0.5683 1.505]
	<i>b</i>	0.7039***				In. [-5.569 4.829]
<b>Spruce</b>						
$d_5 = a + bh$	<i>a</i>	-0.03747*	0.1699	1.105	0.8626	Sl. [0.4510 1.658]
	<i>b</i>	1.808***				In. [-0.8884 0.7222]
$h = a + bd_5$	<i>a</i>	0.03239***	0.01236	1.008	0.8493	Sl. [0.4276 1.575]
	<i>b</i>	0.5240***				In. [-1.791 1.753]

## 4.2 Regeneration Module Results

To test the module, different simulations were carried on the *Baileux oak* stand. Jonard *et al.* (*in review*) describe the site:

*«The Baileux site is located in the western part of the Belgian Ardennes at 300 m elevation (50° 01' N, 4° 24' E). The average annual rainfall is slightly above 1000 mm and the mean annual temperature is 8° C. The forest (60 ha) consists of sessile oak (Quercus petraea LIEBL.) and European beech (Fagus sylvatica L.) and lies on acid brown earth soil (luvisol according to the FAO soil taxonomy) with a moder humus and an A<sub>h</sub> B<sub>w</sub>C profile. The soil has been developed on a loamy and stony solifluxion sheet in which weathering products of the bedrock (Lower Devonian: sandstone and schist) were mixed with added periglacial loess.»*

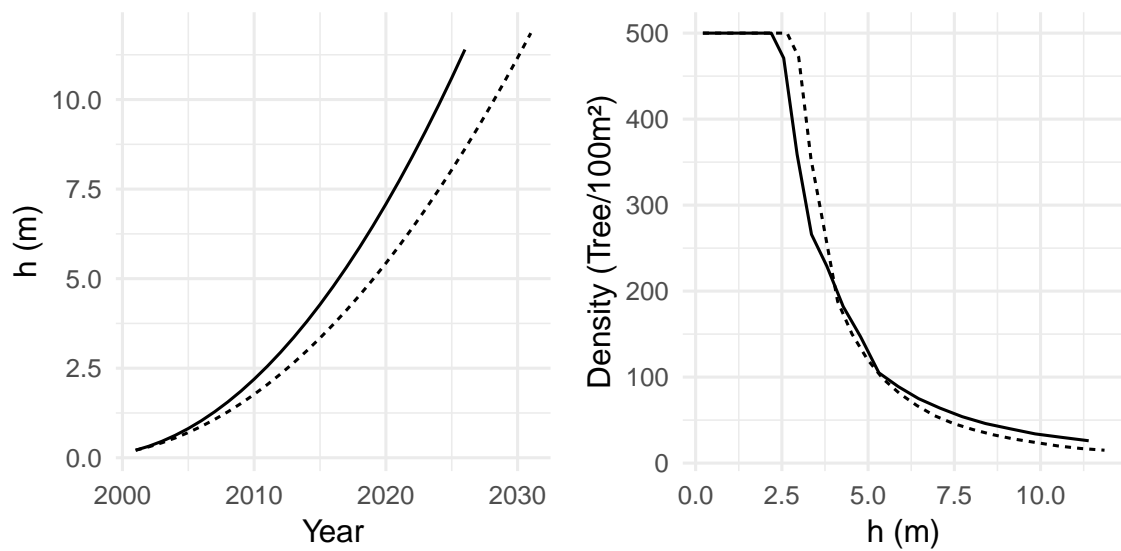
### 4.2.1 Evolution of the Cohorts Characteristics

In order to see how the seedlings characteristics are evolving, a simulation was done in full light conditions (no overstory trees). One regeneration cohort (0.2 m, 1 year old) is grown with a density of 50 000 stems/ha. The simulation time is from 2001 to the recruitment (26 years for beech and 31 years for oak).

Beech seedlings show higher height increments than oak in Figure 12a as expected from the growth equations (Ligot *et al.* 2013). The height growth depends only on the available light which is not changing in this simulation. Beech seedlings reach the recruitment height (fixed at 12 meters) after 26 years and oak after 31 years. The seedlings density is stable during the first years of simulation and after a threshold follows an exponential decrease (Figure 12b). Beech and oak seedlings handle similar density in the simulation. For the same height, oak shows higher biomass weight than beech (Fig. 12c). The gross primary production is also higher for oak than beech (Fig. 12d). The mortality is calculated from the npp (biomass increment) and the NPP (net primary production). It can explain why the densities are similar despite the expectations (a shade-tolerant specie should handle higher densities). The density at the recruitment is also very similar (around 2500 stems/ha).

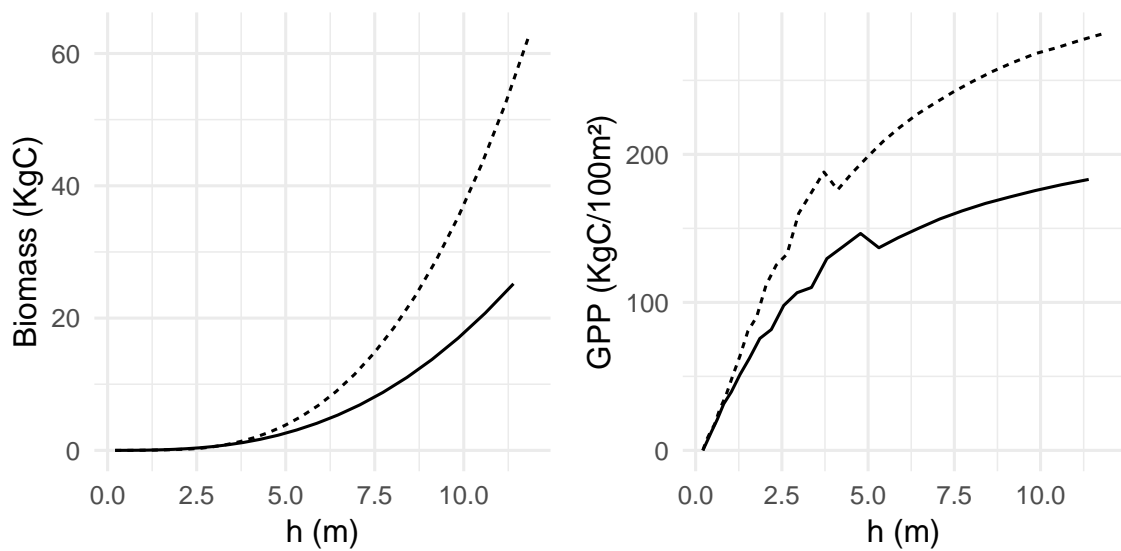
### 4.2.2 Comparison Between Photosynthesis and PAR Use Efficiency

In HETEROFOR, it is not mandatory to use CASTANEA photosynthesis in the simulations. To allow regeneration to grow in this case, the PAR use efficiency approach is used but the results are slightly different (Fig. 13a). To keep the simulation results similar with both approaches, a correction factor was added after the GPP calculation which is multiplied by 2.2 in the PAR use efficiency approach. The result of a simulation with that factor is given in the Figure 13b.



(a) Height

(b) Density



(c) Biomass

(d) GPP

Figure 12: Seedlings characteristics evolution in full light conditions for a beech cohort (—) and a oak cohort (- - -) until the recruitment at 12 meters. The seedlings start with a height of 0.2 cm and a density of 50 000 stems/ha.

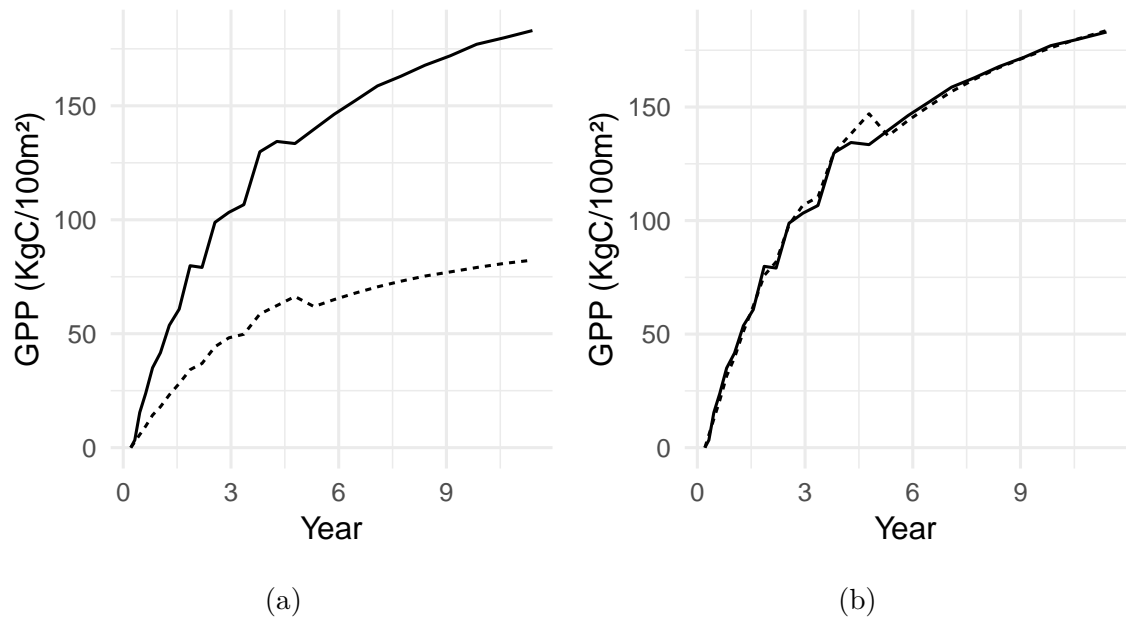


Figure 13: Comparison of the GPP evolution with time for two simulations obtained either with a GPP calculated based on the photosynthesis method of the CASTANEA library (—) or based on a PAR use efficiency approach (- - -). (a) before the correction of the PAR use efficiency approach carried out to make it similar to the photosynthesis approach (b) after the correction.

### 4.2.3 Reproduction of the Self-Thinning Process

A first scenario that can be used to evaluate the performances of the model is the self-thinning. When trees grow without any disturbance (e.g. human intervention), the density decrease with the average size of the trees. To simulate this scenario, seedlings were grown in full light conditions on the Baileux oak stand. The seedlings start with a height of 0.2 meters and a density of 50 000 stems/ha. The simulations are stopped when the seedlings reach the recruitment height (12 meters).

Different equations exist in the literature to describe this phenomenon (Charru *et al.* 2012; Ningre *et al.* 2019; Pretzsch 2006; Yoda 1963). Simulations were carried on seedlings growing without any competition to check them against theory. The Figures 14a and 14b show the results of the simulations. Yoda’s self-thinning lines (eq. 2.1) have an intercept parameter ( $k'$ ). The lines on the figures (gray) have respectively an intercept equal to 15,16, and 17. The modeled self-thinning follows the same slope than Yoda’s equation (gray lines). The simulation reproduce the self-thinning line with an intercept close to 16. The Figure 14a shows the self-thinning lines of two simulations. Both were carried with the seedlings allometric equations until a height of 6 meters. Above 6 meters, the first simulation (—) uses the sapling equations (section 3.4) and the second (- - -) uses the seedling equations until recruitment. As the self-thinning line is better reproduced with the seedling equations used until recruitment, the sapling equations are not used anymore.

The Figure 14b shows a comparison between oak and beech self-thinning. This

simulation suggest that oak handles higher densities for a given biomass but the gap between oak and beech decrease with the biomass (the slope is greater for oak). To have another point of comparison, the self-thinning based on the dbh was plotted along with the Charru *et al.* (2012) self-thinning curves for beech and oak. In the simulation, the self-thinning rate of the seedlings is higher than the theoretical curves but follow a similar shape. Moreover it does not show any differences between the two species in opposition of the empirical curves.

In another scenario, the self-thinning lines were reproduced under a canopy. The basal area was reduced to  $15 \text{ m}^2/\text{ha}$  and the beech seedlings (0.2 meters, 50 000 stems/ha) were grown during 26 years. The Figure 16a shows the difference in the mortality process between beech and oak (with the transmittance evolution in the Figure 16b). The seedlings follow a line parallel to the full light self-thinning line. With a density at constant mean biomass (12 KgC), the density is reduced from 4500 stems/ha in full light conditions to 900 stems/ha under a canopy (transmittance: 13%) for beech seedlings. Oak does not show big differences with beech regarding the self-thinning process. At low biomass, it seems to better support the shading.

#### 4.2.4 Mixed Regeneration Scenario

In the case of mixed regeneration, they are different possibilities of competition between oak and beech seedlings. If beech seedlings are taller than oak seedlings, none of the oak seedlings are expected to survive if the number of beech seedlings is enough to reduce the light resource for oak survival. A simulation with a yearly regeneration of 50 oak and 50 beech seedlings per cell ( $100 \text{ m}^2$ ) with a height of 0.2 m was done under an oak-dominated canopy. The small density of regeneration cohorts allows oak and beech seedlings to grow together during the first years. After 12 years, the seedlings are still sharing the resources and no specie has started to dominate the other. After 24 years, the beech seedlings dominate the understory (the cover reach 1) and therefore the oak seedlings die from the shading. In this scenario, only beeches are recruited.

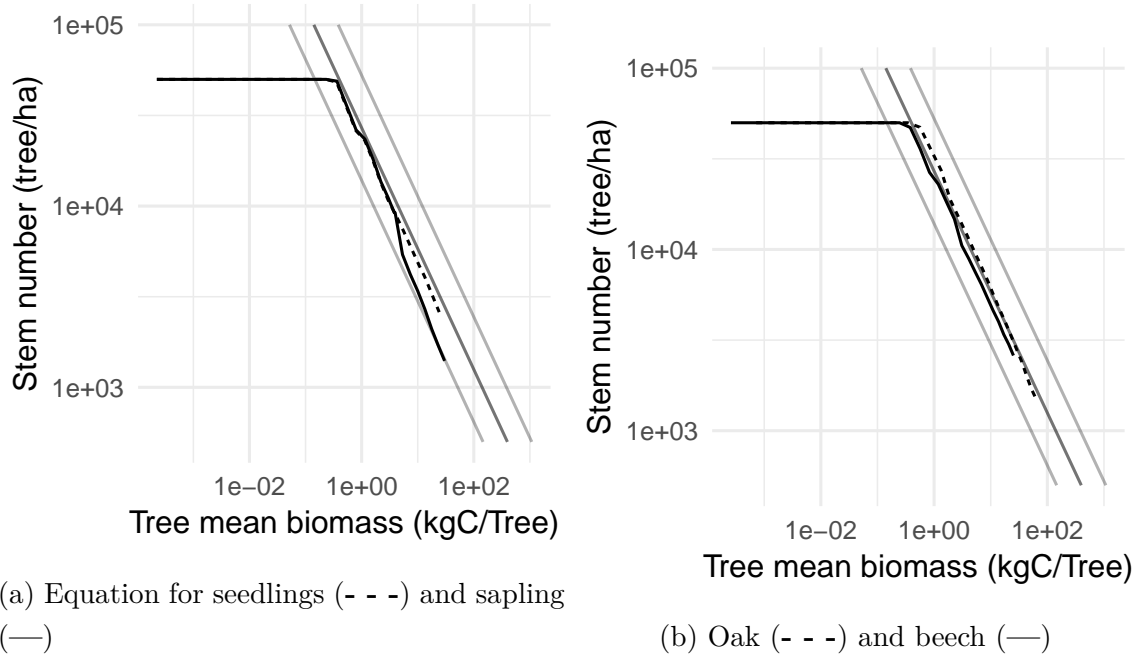
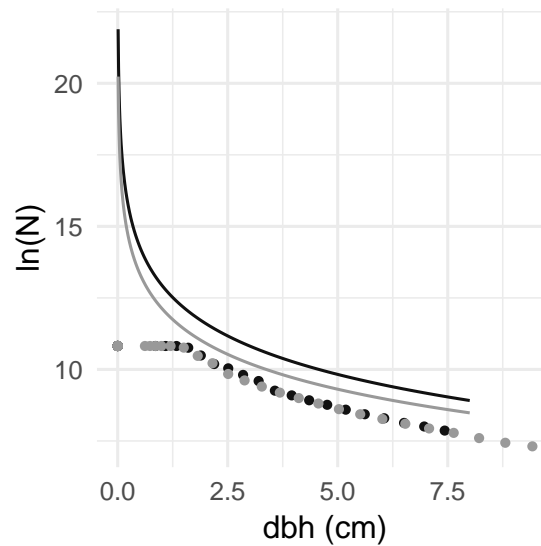


Figure 14: Self-thinning process reproduced by simulation compared with empirical equations. In gray, Yoda (1963) self-thinning lines ( $k' = 15, 16, 17$ ). (a) is a comparison between the seedlings equations combined with the saplings equations (section 3.4) above 6 meters and the seedlings equations used until the recruitment. (b) compares oak and beech self-thinning lines.



(a) Oak (gray) and beech (black)

Figure 15: Self-thinning process reproduced by simulation compared with empirical equations. The solid lines are Charru *et al.* (2012) self-thinning curves for oak (gray) and beech (black). The dots are self-thinning curves simulated for a oak (gray) and beech (black) stand.

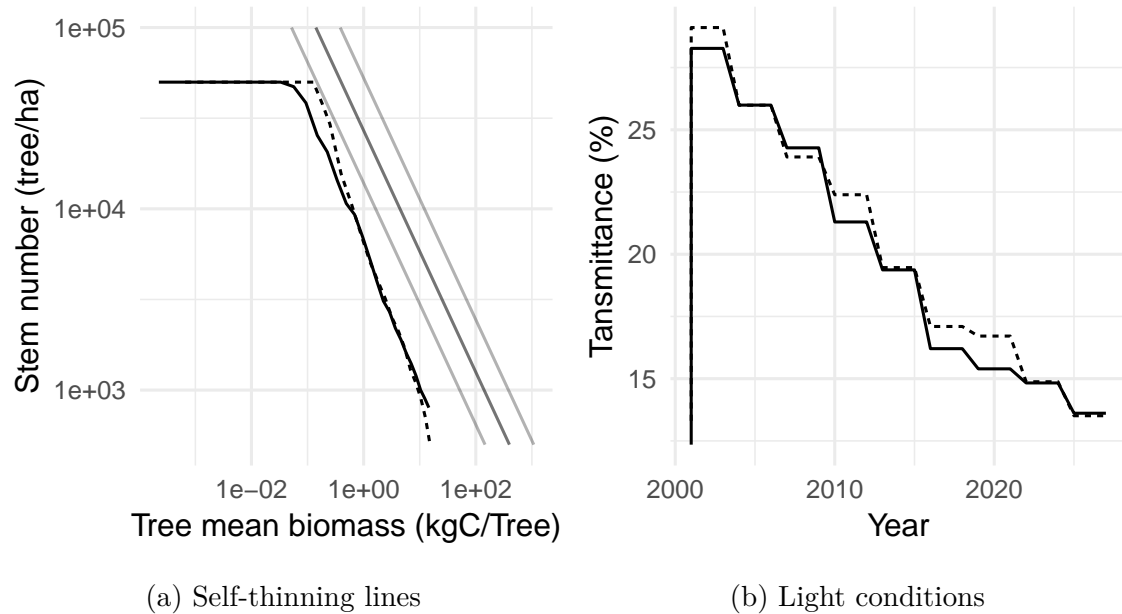


Figure 16: (a) Self-thinning process simulated under a canopy (initial basal area:  $15 \text{ m}^2/\text{ha}$ ). Comparison between beech seedlings (—) and oak seedlings (- - -). In gray, Yoda (1963) self-thinning lines ( $k' = 15, 16, 17$ ). (b) Transmittance evolution for both simulations.

## 5 Discussion

### 5.1 Seedlings Morphology

The basis of the regeneration module is the prediction of seedlings morphology. With the different evaluation indicators, the best relations for the available data were chosen. Some relations found look quite accurate (shoot biomass, dbh) but other relations could need more evaluation to ensure the accuracy of the morphology prediction. Moreover, the data used for all the fits came from Belgian Ardenne. A comparison with other conditions (climate, soil, slope, orientation, etc.) could bring more precision.

A first check that can be done is the comparison with another data set. Height and diameter at 10 cm were measured by Baudry (2013). Despite the equations are fitted to predict diameter at 5 cm, the comparison can still be meaningful. The Figure 17a compare the equations with the data for oak and beech. For oak, the double regression chosen predict accurately the diameter for the low heights (Fig. 17b). But the precision decrease with the height and the regression above 2.5 meters does not seems correct. For beech, there is a bias (predictions overestimated) but it is not changing with the height (Fig. 17c). Despite this, Pearson's  $r$  shows a good correlation between the observations and the predictions. Further analysis with other data sets in various conditions could improve this one.

Before spending time to long measurements and data hunting, a sensitivity analysis could bring a better understanding of the impact of the errors in the morphology

prediction on the regeneration module results.

## 5.2 Self-Thinning and Process-Based Mortality

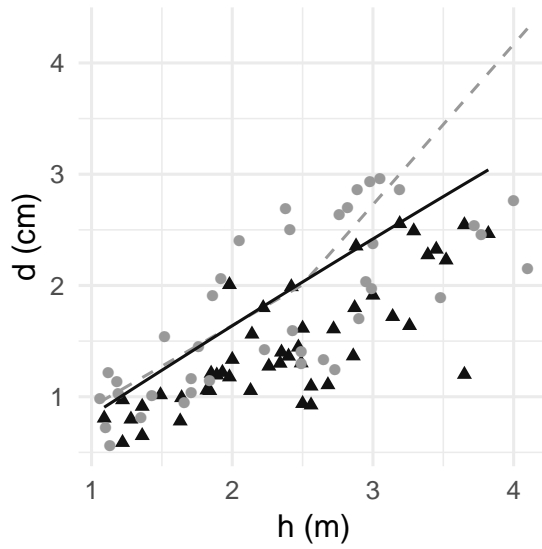
The self-thinning lines predictions suggest that the regeneration module is able to predict with accuracy the seedlings mortality process. It corresponds to the dynamic balance of an undisturbed forest. Thus it can be assumed that after a disturbance, the mortality will stop until the tree dimension reach the self-thinning for that density. Given that self-thinning concept handles a forest left without any disturbances, this evaluation is valid only in full light condition. But the comparison with the mortality of seedlings growing in a forest can be done. The figure 16a shows that for beech seedlings, the reduction of light availability affects the mortality rate but the self-thinning trajectory follows the same slope than for the full-light conditions. Oak seedlings have a more unexpected behavior. They also follow a similar trajectory with similar density than beech seedlings. The shading sensitivity of oak seedlings suggests that this result is not normal. A deeper analysis of the seedling density evolution with the transmittance may enable to find the problem and bring keys to solve it.

For example, the figures 12c and 12d show that oak biomass increase faster than beech biomass and gross primary production is also higher (in full light conditions). As these two values are responsible for the mortality calculation, differences may explain the mortality rate anomaly. The analyses of these variables with the variations of light and the different contributions of the other seedling characteristics to the GPP calculation is necessary to understand the higher oak densities.

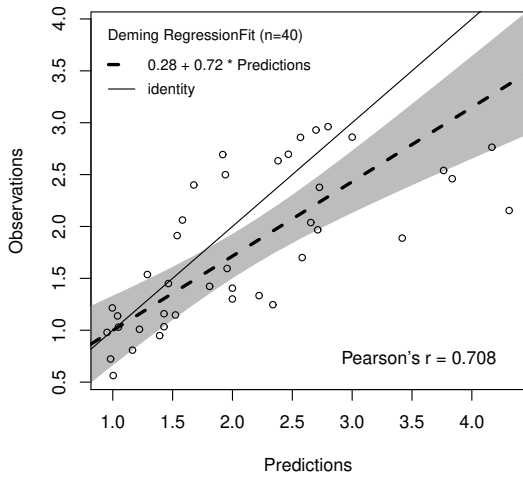
Moreover, the impact of water availability can be analyzed with the same approach. The Figure 18 shows the self-thinning lines of a simulation with modified weather input compared with the *normal* conditions. To change the weather, the rainfall have been arbitrary divided by 10 and the relative humidity reduced by 20%. The result of this simulation does not show any visible difference in the mortality. This result shows the importance of including a connection between the regeneration module and the water balance module. Without this connection, no conclusion can be taken if the water is limiting during the simulation.

## 5.3 Height Growth

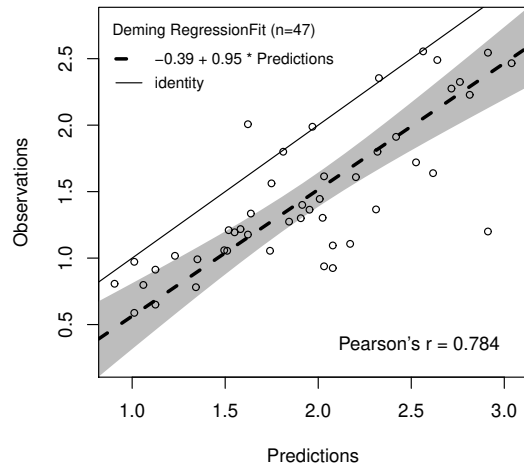
The seedlings growing rates can be compared with values found in literature. But these values are difficult to compare together because the light conditions are sometimes relative to compare different light conditions. Ammer (2003) found height increments near 1.8 cm/year for 35 cm seedlings (unknown radiation). The values at this height are close to 10 cm/year. On the other hand, Sevillano *et al.* (2016) found 42 cm/year height increment for beech and 30 cm/year for oak. The seedlings were in full light conditions with an initial height between 50 and 80 cm. For these conditions, the regeneration module calculates height increments equal to 17 cm for



(a)



(b)



(c)

Figure 17: (a) Diameter prediction from the height with equation 3.1 (lines) and measurements (Baudry 2013) (dots). Oak:  $\bullet$  &  $- - -$ . Beech:  $\blacktriangle$  &  $—$ . Observation - Prediction plot with a Deming regression fit for oak (b) and beech (c).

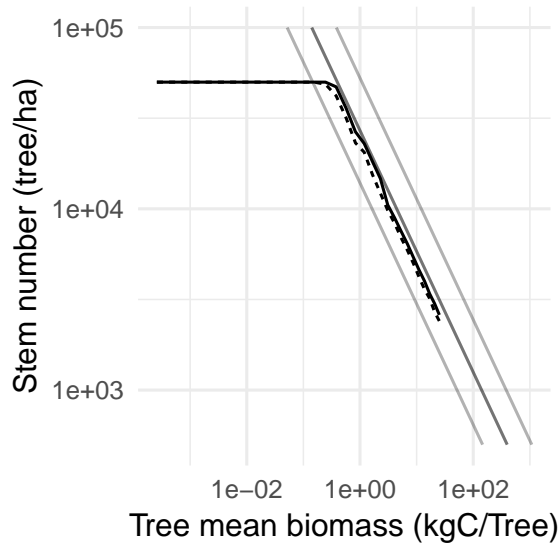


Figure 18: Self-thinning line in drought conditions. Beech seedlings grown in full light conditions with normal weather (—) and with changed weather (- - -). The changed weather is rainfall divided by 10 and relative humidity reduced by 20%

beech and 15 cm for oak. With these very different results, no conclusion can be taken on the reliability of the growing equation. Deeper literature analysis could help to evaluate it.

A different approach to evaluate height growth is to focus on the recruitment. The regeneration module can bring the information of the seedling age, height, density, and the growing light conditions. Relations between these characteristics could help to evaluate the accuracy of the growing rates. Unfortunately, this information was not found in the literature.

## 5.4 Mixed Regeneration

The mixed regeneration scenario highlights the limitations of the *seedling rain* approach. The user must define the number of seedlings that are present or that will appear annually. Thus this number is not changing and the model can not simulate the spatial and temporal variability of regeneration. This results in the survive of beech seedlings and the death of oak seedlings because of the higher growth rates for beech. If the density is decreased, the oak seedling cohort will survive until the beech cover reaches 1. Then the light is too low for the oak to survive.

It is consistent with the problematic of oak regeneration. Oak is indeed hard to regenerate in the presence of beech seedlings. But the scenario of oak replacement by beech could be improved with a more precise description of the regeneration occurrence.

## 6 Conclusion and Perspectives

To meet the objective of developing a regeneration module for HETEROFOR, the CAPSIS regeneration library was connected to the model, thus the seedlings are structured in cohort size classes. The module uses the radiation to calculate a height increment. The seedling characteristics are derived from the height or the diameter. With these, photosynthesis is computed thanks to CASTANEA library. And a mortality rate is calculated using a resource sharing method between the size class production and the individual growth needs.

The regeneration module shows promising results. Especially the self-thinning dynamic for beech seedlings. The choice to implement the mortality with a balance between the individual carbon needs for growth and the cohort production capacity appear to be valuable. To reach the objectives of the regeneration module that will make it useful for long-term simulations, some further developments are needed.

Oak mortality must be checked more deeply to account for its sensitivity to shade. As many factors are involved in the mortality process (biomass increment, LAI measure, photosynthesis process), a sensitivity analysis could be an interesting method to select the steps in the model that should be reviewed first.

The mortality linked to drought also produced poor results. The connection between the water and the regeneration modules may improve the accuracy of the mortality process. For example, the current mortality process could be kept as the *undisturbed mortality* which is the minimum mortality rate. And other mortality functions are possible to add (e.g. drought mortality, browsing mortality).

Another aspect that has not been explored is the competition with surrounding vegetation. The vegetation dynamic inherited from RReShar is usable in HETEROFOR. Some tests can be managed to evaluate the interactions between the regeneration cohorts and the competing vegetation.

As the mixed regeneration scenario shows, the seedlings can not be added uniformly in the stand to mix different species. The regeneration depends mainly on the presence of parent trees in the surrounding. Another piece of the puzzle that could be added is the seed production, dispersion and germination process. This implementation would add more heterogeneity in the stand. New perspectives of simulations such as stand colonization, disturbance-induced changes in the specie distribution.

The climate change is one of the main topics of interest in forestry. As it was the goal of this regeneration module, some long-term simulation could be handled. The analyses of the results will maybe highlight interesting and unexpected consequences.

## References

- Ammer, C. (2003). Growth and biomass partitioning of *fagus sylvatica* l. and *quercus robur* l. seedlings in response to shading and small changes in the r/fr-ratio of radiation. *Ann. For. Sci.* 60, 163–171.
- Balandier, P., Collet, C., Miller, J., Reynolds, P., & Zedaker, S. (2006). Designing forest vegetation management strategies based on the mechanisms and dynamics of crop tree competition by neighbouring vegetation. *Forestry*, 79.
- Ball, J. T., Woodrow, I. E., & Berry, J. A. (1987). *A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions*. Biggins J.
- Baudry, O. (2013). *Réponse de la régénération naturelle de chêne et de hêtre au stade fourré à la refermeture du couvert* (Doctoral dissertation, UCLouvain).
- Bigler, C. & Bugmann, H. (2003). Growth-dependent tree mortality models based on tree rings. *Can. J. Forest Res.* 33(2), 210–221.
- Bogdziewicz, M., Espelta, J. M., Muñoz, A., Aparicio, J. M., & Bonal, R. (2018). Effectiveness of predator satiation in masting oaks is negatively affected by conspecific density. *Oecologia*, 186, 983–993.
- Bossema, I. (1979). *Jays and oaks: An eco-ethological study of a symbiosis* (Doctoral dissertation, University of Groningen).
- Botkin, D. B. (1993). *Forest dynamics: An ecological model*. Oxford University Press.
- Bugmann, H. (2001). A review of forest gap models. *Clim. Change*, 51, 259–305.
- Caignard, T., Kremer, A., Firmat, C., & et al. (2017). Increasing spring temperatures favor oak seed production in temperate areas. *Sci. Rep.* 7(8555).
- Canham, C. D. (1990). Suppression and release during canopy recruitment in *Fagus grandifolia*. *Bulletin of the Torrey Botanical Club*, 117, 1–7.
- Charru, Seynave, Morneau, Rivoire, & Bontemps, J.-D. (2012). Significant differences and curvilinearity in the self-thinning relationships of 11 temperate tree species assessed from forest inventory data. *Ann. For. Sci.* 69(2), 195–205.
- Chuine, I., Cour, P., & Rousseau, D. D. (1999). Selecting models to predict the timing of flowering of temperate trees: Implications for tree phenology modelling. *Plant Cell Environ.* 22, 1–13.
- Coll, L., Balandier, P., & Picon - Cochard, C. (2004). Morphological and physiological responses of beech (*Fagus sylvatica*) seedlings to grass-induced belowground competition. *Tree Physiol.* 24, 45–54.
- Coll, L., Balandier, P., Picon - Cochard, C., Prévosto, B., & Thomas, C. (2003). Competition for water between beech seedlings and surrounding vegetation differing in light availability and vegetation composition. *Ann. For. Sci.* 60, 1–8.
- Condés, S. & del Río, M. (2015). Climate modifies tree interactions in terms of basal area growth and mortality in monospecific and mixed *fagus sylvatica* and *pinus sylvestris* forests. *Eur. J. For. Res.* 134(6), 1095–1108.
- Courbaud, B., de Coligny, F., & Cordonnier, T. (2003). Simulating radiation distribution in a heterogeneous norway spruce forest on a slope. *Agric. For. Meteorol.* 116, 1–18.
- de Wergifosse, L., André, F., Beudez, N., de Coligny, F., Goosse, H., Jonard, F., Ponette, Q., Titeux, H., Vincke, C., & Jonard, M. (*in review*). HeteroFor 1.0: A spatially explicit model for exploring the response of structurally complex forests to uncertain future conditions. ii. phenology and water cycle.
- Deming, W. E. (1943). *Statistical adjustment of data*. Dover Publications edition.
- Dey, D. (1991). *A comprehensive ozark regenerator* (Doctoral dissertation, Univ. of Missouri, Columbia).
- Dufour-Kowalski, S., Courbaud, B., Meredieu, C., & de Coligny, F. (2012). Copsis: An open software framework and community for forest growth modelling. *Ann. For. Sci.* 69, 221–233.

- Dufrêne, E., Davi, H., François, C., le Maire, V., G. le Dantec, & Granier, A. (2005). Modelling carbon and water cycles in a beech forest part i: Model description and uncertainty analysis on modelled net. *Ecol. Model.* *185*, 407–436.
- Farquhar, G., von Caemmerer, S., & Berry, J. (1980). A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species. *Planta*, *149*, 78–90.
- Fitter, A., Fitter, R., Harris, I., & Williamson, M. (1995). Relationship between first flowering date and temperature in the flora of a locality in central England. *Funct. Ecol.* *9*(1), 55–60.
- Fruleux, A., Bonal, D., & Bogeat-Triboulot, M.-B. (2016). Interactive effects of competition and water availability on above- and below-ground growth and functional traits of European beech at juvenile level. *For. Ecol. Manag.* *382*, 21–30.
- Fulton, M. R. (1991). Adult recruitment as a function of juvenile growth rate in size-structured plant populations. *Oikos*, *62*, 102–105.
- Gaudio, N., Balandier, P., Dumas, Y., & Ginisty, C. (2011). Growth and morphology of three forest understorey species (*Calluna vulgaris*, *Molinia caerulea* and *Pteridium aquilinum*) according to light availability. *For. Ecol. Manag.* *261*, 489–498.
- Gaudio, N., Balandier, P., Philipe, G., Dumas, Y., Jean, F., & Ginisty, C. (2011). Light-mediated influence of three understorey species (*Calluna vulgaris*, *Pteridium aquilinum*, *Molinia caerulea*) on the growth of *Pinus sylvestris* seedlings. *Eur. J. Forest. Res.* *130*, 77–89.
- Genet, H., Bréda, N., & Dufrêne, E. (2010). Age-related variation in carbon allocation at tree and stand scales in beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) using a chronosequence approach. *Tree Physiol.* *30*, 177–192.
- Giertych, M., Karolewski, P., & Oleksyn, J. (2015). Carbon allocation in seedlings of deciduous tree species depends on their shade tolerance. *Acta Physiol. Plant.* *37*, 216.
- Gómez-Arparicio, L., Pérez-Ramos, M., Mendoza, I., Matías, L., Quero, J., Castro, J., Zamora, R., & T., M. (2008). Oak seedling survival and growth along resource gradients in Mediterranean forests: Implications for regeneration in current and future environmental scenarios. *Oikos*, *117*, 1683–1699.
- Gómez, J. M., Garcia, D., & Zamora, R. (2003). Impact of vertebrate acorn- and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. *For. Ecol. Manag.* *180*(1), 125–134.
- Hille Ris Lambers, J., Clark, J. S., & Lavine, M. (2005). Implications of seed banking for recruitment of southern Appalachian woody species. *Ecology*, *86*, 85–95.
- Holzwarth, F., Kahl, A., Bauhus, J., & Wirth, C. (2013). Many ways to die – partitioning tree mortality dynamics in a near-natural mixed deciduous forest. *J. Ecol.* *101*, 220–230.
- Janzen, D. H. (1971). Seed predation by animals. *Annu. Rev. Ecol. Syst.* *2*, 465–492.
- Jensen, T. (1985). Seed-seed predator interactions of European beech, *Fagus sylvatica* and forest rodents, *Clethrionomys glareolus* and *Apodemus flavicollis*. *Oikos*, *44*, 149–156.
- Johnson, W. C. & Adkisson, C. S. (1985). Dispersal of beech nuts by blue jays in fragmented landscapes. *Am. Midl. Nat.* *113*, 319–324.
- Jonard, M., André, F., de Coligny, F., de Wergifosse, L., Beudez, N., Davi, H., Gauthier, L., Ponette, Q., & Vincke, C. (*in review*). HeteroFor 1.0: A spatially explicit model for exploring the response of structurally complex forests to uncertain future conditions. i. carbon fluxes and tree dimensional growth.
- Jorritsma, I., van Hees, A., & Mohren, G. (1999). Forest development in relation to ungulate grazing: A modeling approach. *For. Ecol. Manag.* *120*(1), 23–34.
- Keane, R., Austin, M., Field, C., Huth, A., Lexer, M. J., Peters, D., Solomon, A., & Wyckoff, P. (2001). *Clim. Change*, *51*, 509–540.
- Kroschel, H. A., King, S. L., & Keim, R. F. (2016). Tree regeneration by seed in bottomland hardwood forests: A review. *Southeast. Nat.* *15*, 42–60.
- Kuiters, A. & Slim, P. (2002). Regeneration of mixed deciduous forest in a Dutch forest-heathland, following a reduction of ungulate densities. *Biol. Cons.* *105*, 65–74.

- Landuyt, D., Perring, M., Seidl, R., Taubert, F., Verbeeck, H., & Verheyen, K. (2018). Modelling understorey dynamics in temperate forests under global change-challenges and perspectives. *PPEES*, 31, 44–54.
- Ligot, G. (2014). *Managing understory light to maintain the coexistence of forest tree species with different shade tolerances* (Doctoral dissertation, Universite de Liege - Gembloux Agro-Bio Tech).
- Ligot, G., Balandier, P., Fayolle, A., Philippe, L., & Claessens, H. (2013). Height competition between quercus petraea and fagus sylvatica natural regeneration in mixed and uneven-aged stands. *For. Ecol. Manag.* 304, 391–398.
- Lindstrom, M. & Bates, D. (1990). Nonlinear mixed effects models for repeated measures data. *Biometrics*, 46, 673–687.
- Löf, M. (2000). Establishment and growth in seedlings of fagus sylvatica and quercus robur: Influence of interference from herbaceous vegetation. *Can. J. For. Res.* 30, 855–864.
- Maak, K. & von Storch, H. (1997). Statistical downscaling of monthly air temperature to the beginning of flowering of *Galanthus nivalis* l. in northern germany. *Int. J. Biometeorol.* 41, 5–12.
- Makela, A., Landsberg, J., Ek, A. R., Burk, T. E., Ter-Mikaelian, M., Agren, G. I., Oliver, C., & Puttonen, P. (2000). Process-based models for forest ecosystem management: Current state of the art and challenges for practical implementation. *Tree Physiol.* 20(5-6), 289–298.
- McKay, H. M., Jinks, R. L., & McEvoy, C. (1999). The effect of desiccation and rough-handling on the survival and early growth of ash, beech, birch and oak seedlings. *Ann. For. Sci.* 56, 391–402.
- Meir, P. & Mencuccini, R. C., M.and Dewar. (2015). Drought-related tree mortality: Addressing the gaps in understanding and prediction. *New Phytol.* 207(1), 28–33.
- Ménard, A., Dubé, P., Bouchard, A., Canham, C., & Marceau, D. (2002). Evaluating the potential of the sortie forest succession model for spatio-temporal analysis of small-scale disturbances. *Ecol. Model.* 153(1), 81–96.
- Miina, J., Eerikäinen, K., & Hasenauer, H. (2006). Modeling forest regeneration. In H. Hasenauer (Ed.), *Sustainable forest management: Growth models for europe* (pp. 93–109). Berlin, Heidelberg: Springer Berlin Heidelberg.
- Mitchell, F. J. G. & Kirby, K. J. (1990). The impact of large herbivores on the conservation of semi-natural woods in the british uplands. *Forestry*, 63(4), 333–353.
- Mok, H.-F., Arndt, S., & Nitschke, C. (2012). Modelling the potential impact of climate variability and change on species regeneration potential in the temperate forests of south-eastern australia. *Glob. Change Biol.* 18, 1053–1072.
- Montagnoli, A., Terzaghi, M., Fulguro, N., Stoew, B., Wipenmyr, J., Ilver, D., Rusu, C., Scippa, G., & Chiatante, D. (2016). Non-destructive phenotypic analysis of early stage tree seedling growth using an automated stereovision imaging method. *Front. Plant Sci.* 7(1644).
- Ningre, F., Ottorini, J.-M., & Le Goff, N. (2016). Modeling size-density trajectories for even-aged beech (*Fagus sylvatica* l.) stands in france. *Ann. For. Sci.* 73, 765–776.
- Ningre, F., Ottorini, J.-M., & Le Goff, N. (2019). Size-density trajectories for even-aged sessile oak (*Quercus petraea* (matt.) Liebl.) and common beech (*Fagus sylvatica* l.) stands revealing similarities and differences in the mortality process. *Ann. For. Sci.*
- Pajtk, J., Konôpka, B., & Lukac, M. (2011). Individual biomass factors for beech, oak and pine in slovakia: A comparative study in young naturally regenerated stands. *Trees*, 25, 277–288.
- Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S., & Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science*, 333(6045), 988–993.

- Pretzsch, H. (2006). Species-specific allometric scaling under self-thinning: Evidence from long-term plots in forest stands. *Oecol.* *146*, 572–583.
- Pretzsch, H., Biber, P., Dursky, J., Gadow, K., Hasenauer, H., Kändler, G., Kenk, G., Kublin, E., Nagel, J., Pukkala, T., Skovsgaard, J. P., Sodtke, R., & Sterba, H. (2006). Standardizing and categorizing tree growth models. In H. Hasenauer (Ed.), *Sustainable forest management: Growth models for europe* (pp. 93–109). Berlin, Heidelberg: Springer Berlin Heidelberg.
- Price, D. T., Zimmermann, N. E., Van der Meer, P. J., & et al. (2001). Regeneration in gap models: Priority issues for studying forest responses to climate change. *Clim. Change*, *51*, 475–508.
- Pukkala, T. (1987). Simulation model for natural regeneration of *Pinus sylvestris*, *Picea abies*, *Betula pendula* and *Betula pubescens*. *Silva Fenn.* *21*(1), 37–53.
- Reineke, L. (1933). Perfecting a stand-density index for even-aged forests. *J. Agric. Res.* *46*, 627–638.
- Ribbens, E., Silander Jr., J. A., & Pacala, S. W. (1994). Seedling recruitment in forests: Calibrating models to predict patterns of tree seedling dispersion. *Ecology*, *75*(6), 1794–1806.
- Rogers, R. & Johnson, P. (1993). Describing population dynamics of northern red oak. In *Symposium on environmental constraints and oaks: Ecological and physiological aspects* (p. 95). Nancy, France: Centre National de Formation Forestiere.
- Rogers, R. & Johnson, P. (1998). Approaches to modeling natural regeneration in oak-dominated forests. *For. Ecol. Manag.* *106*, 45–54.
- Schermer, E., Bel-Venner, M.-C., Fouchet, D., & et al. (2019). Pollen limitation as a main driver of fruiting dynamics in oak populations. *Ecol. Lett.* *22*, 98–107.
- Schweiger, J. & Sterba, H. (1997). A model describing natural regeneration recruitment of norway spruce (*picea abies* (l.) karst.) in austria. *For. Ecol. Manag.* *97*(2), 107–118.
- Sevillano, I., Short, I., Grant, J., & O'Reilly, C. (2016). Effects of light availability on morphology, growth and biomass allocation of *fagus sylvatica* and *quercus robur* seedlings. *For. Ecol. Manag.* *374*, 11–19.
- Streng, D. R., Glitzenstein, J. S., & Harcombe, P. A. (1989). Woody seedling dynamics in an east texas floodplain forest. *Ecol. Monograph.* *59*(2), 177–204.
- Swaim, J. T., Dey, D. C., Saunders, M. R., Weigel, D. R., Thornton, C. D., Kabrick, J. M., & Jenkins, M. A. (2016). Predicting the height growth of oak species (*quercus*) reproduction over a 23-year period following clearcutting. *For. Ecol. Manag.* *364*, 101–112.
- Touzot, L., Bel-Venner, M.-C., & Gamelon, M. (2018). The ground plot counting method: A valid and reliable assessment tool for quantifying seed production in temperate forests? *For. Ecol. Manag.* *430*, 143–149.
- Turcsán, A., Steppe, K., Sárközi, E., Erdélyi, É., Missoorten, M., Mees, G., & Mijnsbrugge, K. V. (2016). Early summer drought stress during the first growing year stimulates extra shoot growth in oak seedlings (*quercus petraea*). *Front. Plant Sci.* *7*, 193.
- Vacchiano, G., Ascoli, D., Berzaghi, F., Lucas-Borja, M. E., Caignard, T., Collalti, A., Mairota, P., Palaghianu, C., Reyer, C. P., Sanders, T. G., Schermer, E., Wohlgemuth, T., & Hackett-Pain, A. (2018). Reproducing reproduction: How to simulate mast seeding in forest models. *Ecol. Model.* *376*, 40–53.
- van Hees, A. (1997). Growth and morphology of pedunculate oak (*quercus robur* l) and beech (*fagus sylvatica* l) seedlings in relation to shading and drought. *Ann. For. Sci.* *54*, 9–18.
- Vuong, Q. H. (1989). Likelihood ratio tests for model selection and non-nested hypotheses. *Econometrica*, *57*(2), 307–333.
- Wang, W., Peng, C., Kneeshaw, D. D., Larocque, G. R., & Luo, Z. (2012). Drought-induced tree mortality: Ecological consequences, causes, and modeling. *Environ. Rev.* *20*(2), 109–121.
- Yang, Y., Titus, S. J., & Huang, S. (2003). Modeling individual tree mortality for white spruce in alberta. *Ecol. Model.* *163*(3), 209–222.

- Yoda, K. (1963). Self-thinning in overcrowded pure stands under cultivated and natural conditions. *J. Inst. Polytech. Osaka City Univ.* 14, 107–129.
- Zavala, M. & Bravo de la Parra, R. (2005). A mechanistic model of tree competition and facilitation for mediterranean forests: Scaling from leaf physiology to stand dynamics. *Ecol. Model.* 188, 76–92.
- Zeman, J., Hrbek, J., Drimaj, J., Plhal, R., Kamler, J., Adamec, Z., & Heroldová, M. (2016). Wild boar impact to the natural regeneration of oak and acorn importance in its diet. *Acta Univers. Agric. Silvic.* 64(2), 579–585.



# Modeling Oak and Beech Regeneration in Mixed and Uneven-Aged Forests

A Process-Based Approach for Changing Environments

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## ABSTRACT

Climate change and human impacts on the forest ecosystems forced to review forest management practices. The forests need to be more resilient to face these disturbances. The solution found for this is mixed and uneven-aged forests which bring a lot of positive externalities in addition to the increased resilience. But the complexity of the forest systems is therefore increased. Process-based and spatially explicit models can bring the tools to integrate this complexity and predict the behavior of the ecosystem along with the changes associated with climate change. This is the aim of HETEROFOR, a process-based model. But the uneven-aged stands need to take regeneration into account to make long-term predictions. This Master's thesis focus on the development of the regeneration module in HETEROFOR. The seedling morphology, growing process, and mortality process are described for oak and beech. The module uses the radiation to calculate a height increment. The seedling characteristics are derived from the height or the diameter. With these, photosynthesis is computed thanks to CASTANEA library. And a mortality rate is calculated using a resource sharing method between the size class net primary production and the individual growth needs. The validation of the module is carried by reproducing the self-thinning lines with different scenarios. The self-thinning lines were well reproduced in full light conditions. Other simulations were carried to analyze the behavior of seedlings in mixed regeneration, under a canopy, and with water stress.

**Keywords:** Regeneration; Process-based; Model; Seedlings; Beech; Oak; Self-thinning

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